

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

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

**Trophic Interactions within South African Intertidal
Mussel Beds**

by

Craig Stewart Stobie

Thesis presented for the degree of Master of Science

In the Department of Zoology

Faculty of Science

UNIVERSITY OF CAPE TOWN

Supervised by:

Prof. George Branch and Prof. John Field

November 2002

Declaration

I hereby declare that this thesis is my own unaided work apart from the guidance from my supervisors and have received no assistance except as acknowledged. No part of this thesis has been submitted previously for a degree at the University of Cape Town or any other university.

Signed by candidate

Craig S. Stobie

29.11.2002

Acknowledgements

Thanks goes to the many people involved in the completion of the round the coast predator caging experiment, including: Sean Bailey and Dr. Louis Cilliers (Oceanographic Research Institute, Durban); Prof. Arthur Dye (University of Transkei); Prof. Chris McQuaid (Rhodes University); Jenny Griffin (University of Cape Town); and Dr. Jean Harris and Cherise Ackers (Ezemvelo KwaZulu-Natal Wildlife). Much gratitude is due to my supervisors: Prof. George Branch and Prof. John Field (Marine Biology Research Institute, University of Cape Town) for advice and vision in the project and special thanks to my parents for their encouragement and financing my long residence at UCT. Financial support for the caging experiment was received from the South African Network for Coastal and Oceanic Research (SANCOR) and personal financial support from a grantholder bursary held by my supervisors, from the National Research Foundation. Funding was also received from the Mellon Foundation in the form of a grant to Prof. George Branch.

Abstract

Community structure of intertidal rocky shore mussel beds has been previously shown to be strongly influenced by trophic interactions, particularly interactions between predators of mussels and their prey. This investigation involved, firstly, construction of models to simulate trophic interactions in the mussel beds of the west coast of South Africa under different conditions of wave exposure and shore height and, secondly, field-caging experiments to investigate predation on mussels around the entire coast of South Africa. These two studies allowed for a comparison between predator interactions in the model and in the field.

Mussel-bed models were constructed using the modelling software, Ecopath 4 (Christensen and Pauly 1992, Christensen *et al.* 2000). This required existing quantitative input data on the trophic relationships of the 19 living groups used in the model, which included 99.7% of the biomass of sessile flora and fauna as well as many of the mobile predator groups. The models were easily mass-balanced due to the large levels of non-predatory mortality. Network flow analysis of the mussel community in the zone where it is most dominant (wave-exposed lower balanoid shores with 3.24 kg Ash Free Dry Mass. m^{-2}) revealed that predators consume 10% of the production of mussels. Algae and limpets experience the greatest predatory mortality (30 – 95%). Anemones are the largest consumers of mussels, passively consuming 0.55 kg AFDM $\text{m}^{-2} \cdot \text{yr}^{-1}$, although *Nucella* spp. are the most important active predators, consuming 0.19 kg AFDM $\text{m}^{-2} \cdot \text{yr}^{-1}$. Imports of 55 kg AFDM $\text{m}^{-2} \cdot \text{yr}^{-1}$ are required to support the system; over 90% of this is in the form of detritus suspended in the water column and 7 kg AFDM $\text{m}^{-2} \cdot \text{yr}^{-1}$ of unconsumed production is dislodged and washed from the rock. Mussel predation decreases with shore height and increases with wave exposure. Total flows, imports and exports in the mussel bed generally follow changes in the total biomass per unit area, which generally decreases with shore height and increases with wave exposure. Primary production is slightly larger on semi-exposed shores although in total contributes minimally to mass flows compared to flows associated with filter feeders. Increased simulated levels of bird predation (20x) and predation by drilling whelks (10x) showed a greater impact by the whelks, although these did not imbalance the flows in the mussel community.

The field caging experiment was undertaken at five sites around the coast of South Africa, and was designed to exclude separately large vertebrate predators and smaller invertebrate predators as well as to test the effects of intensified predation of drilling whelks (*Nucella* spp.) within intertidal mussel beds. Treatments on the east and west coasts of South Africa did not show significant effects due to predation except one treatment with intensified whelk predation on a west coast site. Heavy mussel recruitment occurred at another west coast site, which may have switched the predation by drilling whelks onto the smaller recruits and swamped the effects of predation. On the east coast, heavy wave action removed mussels from the control plots at one site and heavy sand inundation occurred at two of the sites, and these effects dominated the survivorship of the experimental mussels rather than predation. The lack of predator effects on mussels in the field on the west coast correlates well with the results from the trophic model.

Within the existing mussel beds of South African shores, the community-structure seems to be little influenced by the effects of predation. The trophic modeling suggests that west coast mussel beds are characterised by very inefficient flows between the trophic levels in a community that is supported mostly by subtidal imports.

Contents

	Page
Chapter 1: General Introduction and Aims	1
Chapter 2: Construction of the Trophic Models	5
2.1 Introduction	5
2.2. Methods	7
2.2.1. Study area	7
2.2.2. Definitions	7
2.2.3. Information sources	9
2.2.4. Boundaries of the ecosystem	9
2.2.5. Wave exposure	9
2.2.6. Shore height	10
2.2.7. Derivation of the input parameters for the groups	11
2.2.7.1. Biomass	11
2.2.7.2. Dietary composition	12
2.2.7.3. Production	12
2.2.7.4. Consumption	12
2.2.7.5. Assimilation Efficiency	13
2.2.8. Exports	13
2.2.9. Imports	13
2.2.10. Detritus compartments and detritus fate	14
2.2.11. Balancing of the Ecopath models	15
2.2.12. Analysis of the Ecopath models	15
2.3. Summary of the Trophic Links in the Modelled Mussel Bed	16
Chapter 3: Input Data for the Mussel Bed Models	18
3.1. Heterotrophs	18
3.1.1. Group 1: <i>Haematopus moquini</i> (African Black Oystercatcher)	18
3.1.2. Group 2: <i>Larus dominicanus</i> (Kelp Gull)	19
3.1.3. Group 3: resident intertidal fish	21
3.1.4. Group 4: <i>Mytilus galloprovincialis</i>	22

3.1.5.	Group 5: <i>Aulacomya ater</i>	25
3.1.6.	Group 6: Anemones	28
3.1.7.	Group 7: <i>Gunnarea capensis</i>	30
3.1.8.	Group 8: Barnacles	31
3.1.9.	Group 9: <i>Scutellastra granularis</i>	32
3.1.10.	Group 10: <i>Scutellastra argenvillei</i>	34
3.1.11.	Group 11: Other Limpets	37
3.1.12.	Group 12: Nereids	40
3.1.13.	Group 13: <i>Nucella</i> spp.	42
3.2.	Autotrophs	43
3.2.1.	Group 14: Thin Tubular and Sheetlike Algae	43
3.2.2.	Group 15: Delicately Branched Algae	44
3.2.3.	Group 16: Coarsely Branched Algae	45
3.2.4.	Group 17: Kelps Algae	46
3.2.5.	Group 18: Coralline Algae	47
3.2.6.	Group 19: Epilithic Algae	48
Chapter 4: The Mussel Bed Models		49
4.1.	Results	49
4.1.1.	Balancing the models	49
4.1.2.	General model of the mussel bed	50
4.1.2.1.	Dietary composition matrix	52
4.1.2.2.	Basic input and output parameters	53
4.1.2.3.	Summary statistics and major flows	59
4.1.2.4.	Required primary production	60
4.1.2.5.	Mixed trophic impact assessment	61
4.1.2.6.	Sensitivity analysis	63
4.1.3.	Trophic aggregation of the general model of the mussel bed	65
4.1.3.1.	Basic input and output parameters	65
4.1.3.2.	Trophic flows between groups	67
4.1.4.	Trophic flows specific to the <i>Mytilus galloprovincialis</i> group	69
4.1.4.1.	Ecotrophic efficiencies	69

4.1.4.2.	Food intake by <i>Mytilus galloprovincialis</i> predators	70
4.1.5.	Comparison of wave exposures and shore heights	71
4.1.5.1.	Total flows	71
4.1.5.2.	Imports and exports and total primary production	72
4.1.5.3.	Indices	73
4.1.6.	Impacts of intensified predation	76
4.2.	Discussion	79
Chapter 5: Predation on Intertidal Mussel Beds Around the South African Coast		90
5.1.	Introduction	90
5.2.	Methods	92
5.2.1	Study sites	92
5.2.2	Experimental design	92
5.2.3	Sampling procedures	94
5.2.3.1	Monitoring of cages	94
5.2.3.2	Harvesting of cages	95
5.2.4.	Statistical analyses	95
5.2.5.	Contingencies	96
5.3.	Results	97
5.3.1.	Survival of introduced mussels at harvesting	97
5.3.2.	Monitoring of cages	99
5.3.3.	Predators recorded in cages at harvesting	107
5.3.4.	Other colonisers of the cages	107
5.4.	Discussion	108
Chapter 6: General Conclusions		117
References		120
Appendices A, B, C		129

Chapter One

General Introduction and Aims

There has been a wide variety of studies on processes responsible for regulating community structure in rocky intertidal systems and the importance of predator-prey relationships on the rocky intertidal zone is well documented (Paine 1974, Marsh 1986). Most of these studies consider the direct interactions between predator and prey but there are fewer studies that consider trophic interactions between multiple species or in the whole ecosystem. Indirect interactions between different trophic levels also can induce notable changes in community composition on rocky shores (e.g. Bosman and Hockey 1988). Thus, in determining whether predation contributes substantially to rocky shore community patterns, it is necessary to study the processes within the community in a broad context (Menge 2000).

Mussel beds have long served as the focal point for numerous empirical and theoretical studies on population and community ecology, especially the importance of predation and disturbance events in structuring marine intertidal communities (Seed and Suchanek 1992). However, these studies have dealt almost exclusively with the dominant biomass component, i.e. mussels, with much less reference to the diverse biological community found associated with the mussels. Although, mytilid beds are structurally complex entities that are capable of harbouring a diverse assemblage of associated fauna and flora that interact with one another (Asmus 1987, Griffiths and Hockey 1987).

The structure of the mussel bed is strongly correlated with the physical environment, particularly the degree of wave exposure and air exposure (McQuaid and Branch 1985, Seed and Suchanek 1992, Bustamante and Branch 1996). The variation in mussel beds at different shore heights is affected mainly by intense predation on mussels on the low shore, while at higher tidal elevations predation is reduced, which leads to enhanced survival although growth rates are considerably reduced (Seed and Suchanek 1992).

Wave action on the mussel bed increases disturbance, leading to larger non-predation mortality, which may reduce the diversity in the community (Blanchard and Bourget 1999). Wave action also increases water turnover, replenishing the food source of filter feeders (Bustamante 1994). It has been suggested that mobile predators impact less on their prey on wave-exposed shores due to the rigorous physical environment reducing predation (Menge and Olson 1990).

South African mussel beds are abundant on shores from the cool temperate west-coast province to the sub-tropical shores of the east coast province (van Erkom Schurink and Griffiths 1990). The west-coast marine province has a productive, temperate fauna (Bustamante and Branch 1996) and is ecologically similar to regions such as the Californian coast and the Chilean coast. In South Africa, the west-coast mussel beds are dominated by *Mytilus galloprovincialis* (van Erkom Schurink and Griffiths 1990), which is alien to South Africa and invaded the shores in the 1970s (Griffiths *et al.* 1992), although the mussel has a suite of indigenous predators. In contrast, the east coast marine province is less productive and has a sub-tropical fauna and the indigenous *Perna perna* is the most abundant mussel (van Erkom Schurink and Griffiths 1990).

Studies on intertidal mussels of South Africa have revealed much about their stock size, growth rates, larval biology and physiology (Berry 1978, van Erkom Schurink and Griffiths 1990, 1991, 1992, 1993), although there is little information on the community dynamics of South African mussel beds (Harris *et al.* 1998). Trophic interactions between mussels and their predators have been frequently recorded and many predators include mussels in their diet (e.g. Hockey and Underhill 1984, Griffiths and Blaine 1994). Interactions between drilling whelks and mussels have been studied by Griffiths and Blaine (1994), who showed that drilling by whelks is not always fatal to mussels. Parasitism on local mussels has been the subject of investigation by Calvo-Ugarteburu and McQuaid (1998), who revealed common infections of *P. perna* whereas *M. galloprovincialis* is almost parasite-free. The trophic impact of parasites on the mussels is

unknown. A model of the effects of predation on the local intertidal mussel *Choromytilus meridionalis* was constructed by Griffiths and Hockey (1987), which showed that of the many predators of the mussels, birds and octopus cause the greatest mortality, particularly in older mussel populations, but that the majority of mussel mortality is due to intraspecific competition between the mussels.

In this thesis, the mussel beds were the subjects of two studies on the importance of trophic interactions. Firstly, energy budget models of the trophic flows within a west-coast mussel bed were constructed for network analysis. This was possible due to the large amount of information existing on the biology of the west-coast intertidal fauna and flora associated with the mussel bed. Secondly, the importance of predation on mussels was investigated around the coast of South Africa by field experimentation. This study examined predation, not trophic interactions in general. Since there is a diverse set of South African mussel predators, different types of cage treatments were designed to control access of different predators to the mussels. The caging experiment was repeated around the coast of South Africa in different biogeographical provinces with different species of mussels and predators so conclusions on the predation on intertidal mussels could be generalised for the entire coast. This allowed comparison of the impact of predation on mussels in South Africa with similar international studies, which have often shown the importance of mussel predators (e.g. Paine 1974, Menge 1983). The field study complemented the model since measurements of predation rates upon mussels during the field experiment on the west coast could be compared with predation rates in the model.

This study was designed to investigate whether predation is important to mussel survival compared to non-predatory sources in the mussel bed. It also had the goal of establishing how flows due to secondary production (mostly algae and limpets) compare to the flows associated with filter-feeders, and how predatory and non-predatory losses of this secondary production compare to flows due to the filter feeders. Comparisons were also be made between internal trophic flows and flows that are due to imports and exports

from the system to quantitatively determine how dependant the system is on internal compared to external flows. Patterns of trophic flow were compared under different physical regimes to investigate how flows change in exposed versus semi-exposed shores and how these flows also change with increasing shore height. Trophic models were used to test impacts on the system when predation levels are manipulated. Trophic interactions in the model were considered in the light that the dominant west-coast intertidal mussel species, *Mytilus galloprovincialis*, is an alien invasive to South African shores.

This thesis is split into six chapters. The chapter that follows, Chapter 2, is an introduction to the modelling technique used in simulating the west-coast intertidal mussel bed and how the model was defined to represent the mussel communities in conditions of differing wave exposure and shore height. Chapter 3 gives estimates and sources of the input data required for the living heterotrophic and autotrophic groups in the models. The model required the input of biomass, production, consumption, assimilation efficiency, dietary composition and exports for each species group considered. Chapter 4 describes first how the models were mass-balanced, then gives the outputs and discussion of the models. The model was initially applied to wave-exposed shores at a shore height equivalent to 20% aerial exposure – the situation in which the mussel beds are the most dominant. Since the largest trophic flows were associated directly with the mussel population itself, further more detailed analysis of this group was conducted. Finally, summary statistics and indices allowed comparisons of the models constructed to cover different wave exposures and shore heights including investigating the consequences of an increase in the abundance of selected predators. Chapter 5 comprises experimental field-based tests of the effects of predation on mussel beds around the entire coast of South Africa, which attempted to discern separate the impacts of smaller invertebrates and larger vertebrate predators by varying caging design. The field experiment also provided a “real” test of the model outcomes. Finally, Chapter 6 gives a summary of the conclusions drawn from this research on the importance of trophic interactions in structuring South African mussel beds.

Chapter Two

Construction of the Trophic Models

2.1. Introduction

Many ecosystems have been studied using forms of network analysis whereby energy flows between species or functional groups are modelled as part of or as a whole ecosystem. These models have revealed much about the structure as well as the functioning of the ecosystems. Comparisons between different ecosystems are possible by constructing different models and then comparing a variety of measures and network indices (Field *et al.* 1989). Constructing a model enables a quantitative estimation of the pools, flows between taxa, exports and imports in a system and the degree to which a system is self-contained or linked to other systems. The flows within the system can be traced, giving information about the dependency of taxa on one another, directly or indirectly. It also gives the opportunity to perform validation exercises whereby the measured flows can be checked by summing exercises so that no flows contravene the energy-balance equations.

Network analysis of an intertidal mussel bed system was completed using the modelling software Ecopath 4 (Christensen and Pauly 1992, Christensen *et al.* 2000), based upon a modelling approach by Polovina (1984), which is often applied by fishery biologists. Ecopath requires existing quantitative data on the trophic relationships and then models biomass flows from the apex of the food web to the base within a steady-state, delimited ecosystem. The model is based on the mass equation of a population of a particular species (Equation 2.1) and the energy balance of individuals in that population (Equation 2.2).

Equation 2.1: production of species (i) = sum of all predation on species (i) +
non-predatory losses of species (i) + export of species (i)

Equation 2.2: production = consumption – non-assimilated food – respiration

The mussel bed analysed in the model simulates unharvested, intertidal mussel assemblages on the rocky shores of the west coast of South Africa. The modelled food web contains vertebrate predators consisting of birds and fish as well as invertebrate predators including predatory whelks and anemones, while gastropod grazers consume various epilithic and foliose algal species. The modelled food web also contains various filter-feeders including the mussel *Mytilus galloprovincialis* and the reef worm, *Gunnarea capensis*, and macro-invertebrate deposit-feeders within the mussel-matrix community.

Models of the intertidal mussel bed were constructed under varying conditions of shore height and wave exposure, which are physical parameters known to strongly influence the structure of mussel beds (Seed and Suchanek 1992, Bustamante 1994). The mussel communities under different conditions of wave exposure on the South African west coast differ substantially in their composition, generally with filter-feeding mussels dominating in the exposed locations, while in wave-sheltered locations grazing limpets and algae become more prevalent (McQuaid and Branch 1985, Bustamante and Branch 1996). Predators are more abundant on wave-exposed sites and correlate positively with filter feeder biomass (McQuaid and Branch 1985) and the wave-exposed sites are generally dominated by fewer species with greater biomasses and are more productive than sheltered shores (Bustamante 1994). These notable differences in abundance of functional groups between shores of different exposure implies alterations in the net balance between importation and exportation of production between these communities and the inshore marine system, with exposed shores having a high abundance of filter feeders, necessitating importation of production from the water column to a community in which consumers exhibit considerably larger standing crops than primary producers (McQuaid and Branch 1985).

The modelling software allows the construction and analysis of mass-balanced trophic models of the mussel bed. Mass flows in the mussel bed community can be estimated

over a period of a year and, if constructed under varying conditions of shore height and wave exposure, will allow comparisons between these different physical environments. The initial construction of the model will often show the weaknesses in the model due to difficulties in balancing the mass equations due to poorly known or incorrect estimates of the input parameters. After construction of the model, it is possible to obtain revised estimates and to analyse the trophic flows within the system and the interdependencies between different trophic levels. The model can be compared to other published Ecopath models developed for other ecosystems such as tropical reef systems (e.g. Opitz 1991) and the offshore part of the Benguela upwelling ecosystem (e.g. Jarre-Teichmann *et al.* 1998, Shannon 2001). Comparisons can also be made between the constructs of the mass-balanced models at different wave exposures and shore heights. The comparisons between models are possible by analysing the outputs, which include trophic pyramids, trophic flows, biomass sustained, system throughput, productivity, transfer efficiency and trophic impacts. The modelling software includes a simple form of sensitivity analysis, which accounts for variability in the input parameters, allowing estimates of the robustness of the model.

2.2. Methods

2.2.1. Study Area

The West Coast of Southern Africa extends from the Cape of Good Hope into Namibia. This region is noted for the cold Benguela current with strong coastal upwelling during summer (Shannon 1985). The coast is typically productive with large intertidal biomasses due to the nutrient-rich waters (Bustamante and Branch 1996). The model has been constructed to represent the intertidal mussel beds on these shores.

2.2.2. Definitions

The inputs required in the model and the terminology employed are summarised in Table 2.1.

Table 2.1: Definitions of the terms used in the construction and analysis of the Ecopath model.

Abbre. term	Term	Definition	Units
B	Biomass	Biomass	gAFDM. m ⁻²
WW	Wet weight	Wet weight	grams
DW	Dry weight	Dry weight	grams
AFDM	Ash free dry mass	Ash free dry mass	gAFDM. m ⁻²
Q	Consumption	Consumption	gAFDM. m ⁻² . yr ⁻¹
Q/B	Consumption/ biomass	Ratio of consumption to biomass	yr ⁻¹
P	Production	Somatic production	gAFDM. m ⁻² . yr ⁻¹
P/B	Production/ biomass	Ratio of production to biomass	yr ⁻¹
AE	Assimilation efficiency	The proportion of ingested food consumed by a predator that is absorbed	Unitless
EE	Ecotrophic efficiency	The fraction of production that is consumed by predators	Unitless
GE	Gross efficiency	The ratio of production to consumption	Unitless
	Respiration	Respiration flows include respiration, mucus, excretion and reproductive production	gAFDM. m ⁻² . yr ⁻¹
PP	Primary production	Primary production	gAFDM. m ⁻² . yr ⁻¹
PPR	Pri. Prod. Required	Sum of the flows required for a group from their primary production equivalents	gAFDM. m ⁻² . yr ⁻¹
-	System throughput	Sum of all flows in system i.e., the total consumption, production, exports, respiration and flows to detritus	gAFDM. m ⁻² . yr ⁻¹
-	Connectance index	Ratio of the actual number of trophic links between groups to the number of possible links	Unitless
-	Omnivory index	Measure of the variance of the trophic level of a consumer's prey groups	Unitless

2.2.3. Information Sources

Species included in the Ecopath model are listed in Appendix A at the end of Chapter 4. Sources of data for each species were preferably of local origin although international studies of taxonomically similar species were used to supplement missing data. Ecopath requires input for the following parameters: biomass (B) per unit area, production per unit biomass (P/B), consumption per unit biomass (Q/B), assimilation efficiency, dietary composition, import and export for each species in the ecosystem. The parameter ecotrophic efficiency (the fraction of production that is consumed by predators, EE) was left as unknown and estimated by solving the linear equations. Since models of the mussel bed were constructed under different conditions of wave exposure and tidal height, the input data were modified where information existed for each of these circumstances. Conversions between wet weight, dry weight and ash-free dry masses are listed in Appendix B at the end of Chapter 4

2.2.4. Boundaries of the Ecosystem

The model is intended to simulate the rocky intertidal near Groenrivier on the west coast of South Africa where there are extensive mussel beds on wave-exposed shores. Areas of the rocky shore defined as “mussel bed” were areas with a biomass of mussels greater than 1 kg AFDM m^{-2} , which is approximately equivalent to areas with greater than 50% mussel cover (although percentage mussel cover is not a good measure of biomass due to the layering of mussels (Harris *et al.* 1998)). Rock pools and bare rock patches occurring within areas defined as mussel bed were included as part of the model since energy flows between these patches and the mussel matrix are likely to be highly connected.

2.2.5. Wave Exposure

The presence and extent of the mussel beds are largely dependant on wave exposure. On the west coast mussel beds are absent or thin at the extremes of wave exposure (both sheltered and exposed). At Groenrivier, the wave exposure was measured by Bustamante (1994) concurrently with the biomass surveys. Measurements were obtained with a

Palumbi wave-force dynamometer (Palumbi 1984), which records the maximal wave force per tidal cycle. Mussel beds were present only at shores categorised as “exposed” which experienced maximum wave force readings of about 15000 N. m⁻², and at sites categorised as “semi-exposed” with maximum wave force readings of about 7000 N. m⁻². The mussel beds on the exposed shores were compared with the beds from the semi-exposed sites. The exposed sites at Groenrivier were typically rocky shores lying on the seaward side of headlands while semi-exposed shores were normally open-coast rocky shores situated in the lee of subtidal kelp forests.

2.2.6. Shore Height

Mussel beds on exposed west-coast shores typical extend from the lower to upper balanoid zones (*sensu* Stephenson and Stephenson 1949) and models were constructed at five grades of shore height, derived from unpublished raw data from biomass surveys completed in 1990 by G. M. Branch, R. Bustamante, and S. Eekhout (Zoology Department, University of Cape Town). This data source will henceforth be referred to as the “1990 Surveys”. The shore heights in the 1990 Surveys have been converted to an estimate of air exposure according to the zonation pattern of the shore, following Levitt (1987) (Table 2.2). On semi-sheltered shores, mussel beds with a biomass of greater than 1 kg AFDM m⁻² were only present in two zones with 30 – 40 % air exposure and modelling was restricted to these shore heights in the case of semi-exposed shores.

Table 2.2: The shore heights applied in the Ecopath models, estimated from approximations of the degree of air exposure, the intertidal zonation pattern, and typical algal species occurring in these zones on the west coast derived from Levitt (1987). Transect numbers refer to the shore zones in the 1990 Surveys.

Zone	common algae in zone	air exposure (%) (Levitt 1987)	transect number	estimate of air exposure (%)
Littorina	<i>Porphyra capensis</i>	78.85	-	80
			-	65
Upper balanoid	<i>Ulva</i> sp.	51.37	4	50
			3	40
Lower balanoid	<i>Gigartina</i> sp., <i>Iridaea</i> sp.	28.7	2	30
			1	20
Cochlear	<i>Bifurcaria</i> sp.	8.79	0	10

2.2.7. Derivation of the Input Parameters for the Groups

Groups included in the model consist of the major contributors to biomass in the mussel beds, as recorded in the 1990 Surveys, while rare species with unrecorded biomass were omitted, including the whelk, *Argobuccinum pustulosum* (a predator of *Gunnarea capensis* (J. A. Day, Zoology Department, University of Cape Town, pers. comm.)). Meiofauna associated with the mussel matrix or living within the water column above the mussel bed was also omitted since these taxa were not the focus of the study and their biology is poorly known. Some mobile macro-predators were also omitted including the west-coast rock lobster, *Jasus lalandii*, which has not been documented in South Africa as feeding in the intertidal. The consumption of subtidal reef fish such as the mussel cracker, *Sparodon durbanensis*, and *Octopus vulgaris* was also omitted since the degree to which these species impact on intertidal mussel communities is unknown.

2.2.7.1. Biomass

The biomasses of biota were obtained from the 1990 Surveys, which have been published in a synthesised form in Bustamante and Branch (1996). These biomass surveys were completed during summer of 1990 at Island Point, Groenriver, 600 km north of the Cape Peninsula on the west coast. Four transects were laid perpendicular to the shoreline from mean low spring tide to mean high spring tide at each of three different sites spanning wave exposures categorised as exposed, semi-exposed and sheltered (the latter were excluded from consideration in this thesis as they did not have mussel beds). Each transect extended up the shore to cover the entire extent of the intertidal. Along each transect, between eight and twelve 0.5 m^2 quadrats were randomly placed and the abundances and percentage cover of each species scored on 180 intersect points within each quadrat. From within the mussel bed, 0.075 m^2 subsamples were taken to quantify the abundances of species within the mussel matrix. These measures of abundance and percentage cover were converted to ash free dry mass per m^2 (AFDM. m^{-2}) by conversion ratios, obtained by drying and furnacing subsamples of each species. This method adequately recorded the biomass of the benthic invertebrate and algal groups. For the

more mobile vertebrates, biomass was derived separately from the available literature on their abundance.

2.2.7.2. Dietary Composition

The dietary composition input required for each group consists of the proportional contribution of each prey species in the diet of the consumer. The contribution was derived from weight of prey consumed in the diet or the frequency of prey items in the diet. In cases where the proportional diet was unresolved for all prey species of a predator, the proportional biomass of each prey group available in the field was assumed to reflect the proportional composition of the diet of the predator.

2.2.7.3. Production

Production of intertidal invertebrates consists of somatic and gametic production although for the purposes of this study the production value consisted only of the production of somatic tissues associated with growth. Production of gametes and mucus, forming part of the energy flows from a group, were included in the term 'respiration' by the Ecopath model. Production estimates were in some cases published as production-to-biomass ratios (P/B), which is accepted input for the Ecopath software, but in other cases the P/B was derived by using growth curves, the cohort or size-class composition of the species, or the average number and average mass of the individuals. Estimates of algal growth were either published P/B values or studies of growth of tissue mass in culture or in the field. No separate group was distinguished for suspended phytoplankton nor were estimates of the production of phytoplankton included in the model. Instead, phytoplankton was considered as an import into the system as part of the planktonic "suspended detritus component".

2.2.7.4. Consumption

Ecopath models require estimates of this parameter as a ratio of consumption to biomass (Q/B) for each of the living animal groups. In most cases the consumption had been

directly measured for the species in the model and was available in the literature. Filter feeders also had direct estimates of consumption, obtained from measurement of clearance rates of suspended detritus made in the laboratory. In some cases (e.g. the oystercatcher), consumption was measured indirectly by the balancing of energy budgets.

2.2.7.5. Assimilation efficiency

The proportion of ingested food consumed by a predator that is absorbed is termed the assimilation efficiency. The product of consumption and assimilation efficiency is equal to the sum of production and respiration. The Ecopath model requires this input in the form of the unassimilated proportion ($1 - \text{assimilation efficiency}$), expressed as a percentage. This value has been estimated in the literature for some of the species in the model. In cases where information on assimilation efficiencies was unavailable, estimated values of 80% for carnivores and 60% for herbivores were used. In a few cases absorption efficiency was used to approximate assimilation efficiency where the product of absorption efficiency and consumption is equal to the consumption minus the faeces.

2.2.8. Exports

A recommendation for construction of the Ecopath model is that the sum of transfers between groups in the system should exceed the sum of imports and exports, so that the model represents an ecosystem. In the intertidal, export losses would be expected to be large from dislodged organisms being washed from the rocks. Thus, to reduce the amount of imports and exports from the system to levels required by the model, the non-predatory losses were redirected to a debris and detritus compartment called “dislodged detritus”, and these flows represented export from the ecosystem.

2.2.9. Imports

Import into the mussel bed would include the consumption of suspended detritus by the filterfeeders, the consumption of washed-up plant and animal fragments of subtidal origin by groups such as limpets and anemones and, for the larger mobile carnivores such as

birds, a part of their diet would be derived by foraging in areas external to the mussel bed. Thus import into the mussel bed would be derived from a number of different sources. To distinguish between these, five separate debris and detritus compartments were formed to represent these flows, as specified in the following section. Import would also include the recruitment from the plankton in the form of larvae settling on the rock surface although this import was omitted because of the presumably small energy flows involved. For simplicity, the migration of mobile invertebrates between different zones of the shore and the dislodgement and resettlement of sessile species were also not accounted for within the model.

2.2.10. Detritus Compartments and Detritus Fate

The detritus components include all non-living compartments. In the models five different detritus compartments were represented: suspended detritus, drift algae, drift animal material, mussel-matrix debris and dislodged debris. Suspended detritus represents the non-living material in the water column which is fed on by filterfeeders; drift algae and drift animals are material washed and deposited onto the mussel bed mainly from the sub-tidal zone; mussel-matrix debris is non-living material in the mussel matrix that is fed on mostly by deposit feeders. The dislodged detritus compartment represents material that is dislodged from the mussel bed and exported from the system. These detritus compartments, with the exception of matrix debris, could be considered as import and export from the system, but they were included as constituent compartments in the model in order to meet the requirements of the Ecopath model that the sum of transfers between compartments in the ecosystem should exceed the sum of imports and exports. The fate of non-predatory losses of living groups was modelled as flowing to the detritus compartment termed “dislodged detritus”. An arbitrary biomass of 100 g AFDM. m^{-2} was given to each detritus compartment. This inaccuracy in the biomass parameter is justified since only the flows to and from detritus are of interest and since a change the detritus biomass or availability within an Ecopath model does not result in a change in the consumer diet, production or consumption.

2.2.11. Balancing of the Ecopath model

Often the initial construction of the model creates an unbalanced model, giving unacceptable values of ecotrophic efficiency, which is the fraction of the production that is either passed up the food web or exported. In an unbalanced model the ecotrophic efficiency (EE) of one or more boxes is greater than unity, indicating the production of a component is insufficient to support its predators. It is then necessary to re-evaluate the values so that the model is balanced.

2.2.12. Analysis of the Ecopath model

The mussel bed model was summarised by various statistics calculated by Ecopath, i.e.: total biomass, total consumption, total production, total exports, total respiration, total system throughput (which represents all flows in the entire system: Ulanowicz 1986), flows to detritus, net primary production, net system production as well as connectance and omnivory indices.

For each component in the model the following were calculated and compared: ecotrophic efficiency (EE), the gross efficiency (the ratio of production to consumption or GE), proportion of the P/B due to predation mortality and other mortality losses, flow to detritus, net efficiency which is a conversion efficiency calculated as the fraction of production relative to the assimilated portion of the food, trophic level, omnivory index which is a measure of the variance of the trophic level of a consumer's prey groups, respiration, assimilated food, number of paths from predator to prey, and primary production required to sustain a component.

The impacts of each component upon other components in the ecosystem were measured using the mixed trophic impact assessment technique of Ecopath, where a change in biomass in each group was used to assess the relative changes in biomass of the various other impacted groups. The sensitivity analyses performed by Ecopath individually vary the input parameters of B, P/B and Q/B between -50% and +50% of their original value

and the changes in the EE parameters of each other group are noted. This shows which parameters of which components are sensitive to changes, leading to imbalances in the model.

A trophically aggregated version of the mussel bed model was constructed by grouping the 21 groups into six groups based on functional trophic similarities. The flows, statistics and indices of the groups in the trophically aggregated model were then compared between groups.

Since most of the energy flow in the mussel bed is centred around flows into and out of the *Mytilus galloprovincialis* population, this group in the model was analysed in more detail, comparing models constructed under different shore heights and wave exposures. Comparisons were made of EE values under different model constructs, the consumption of the various predator groups of mussels, and the flows to detritus.

Comparison of the models constructed under different wave exposures and shore heights was undertaken by comparing the summary statistics calculated by Ecopath for each model, including flows, ratios and indices.

The effects of increased predation by the top predators in the system were tested on the balanced models of the mussel bed system at various wave exposures and shore heights. Changes in predation intensity were tested by increasing the biomass of the bird and drilling whelk groups and the resulting changes in the balance of the models components were noted.

2.3. Summary of the Trophic Links in the Modelled Mussel Bed

The components modelled in the mussel bed system are presented in a reduced and simplified trophic diagram in Figure 2.1 with the likely trophic relationships between the groups. Bird groups included in the model are the Oystercatcher and Kelp Gull. *Gunnarea*

capensis is a reef-building worm common on the rocky shores, and *Nucella* spp. are the drilling whelks. Mussels largely comprised *Mytilus galloprovincialis*, but also small amounts of *Aulacomya ater*. The fish group comprised resident intertidal rockfish (families: Clinidae and Gobiesocidae). The model also includes three groups of invertebrates (anemones, limpets and nereid worms), found in the mussel bed. Detritus and debris groups include the debris within the mussel matrix, suspended detritus in the water column, and other debris washed onto the shore from the subtidal.

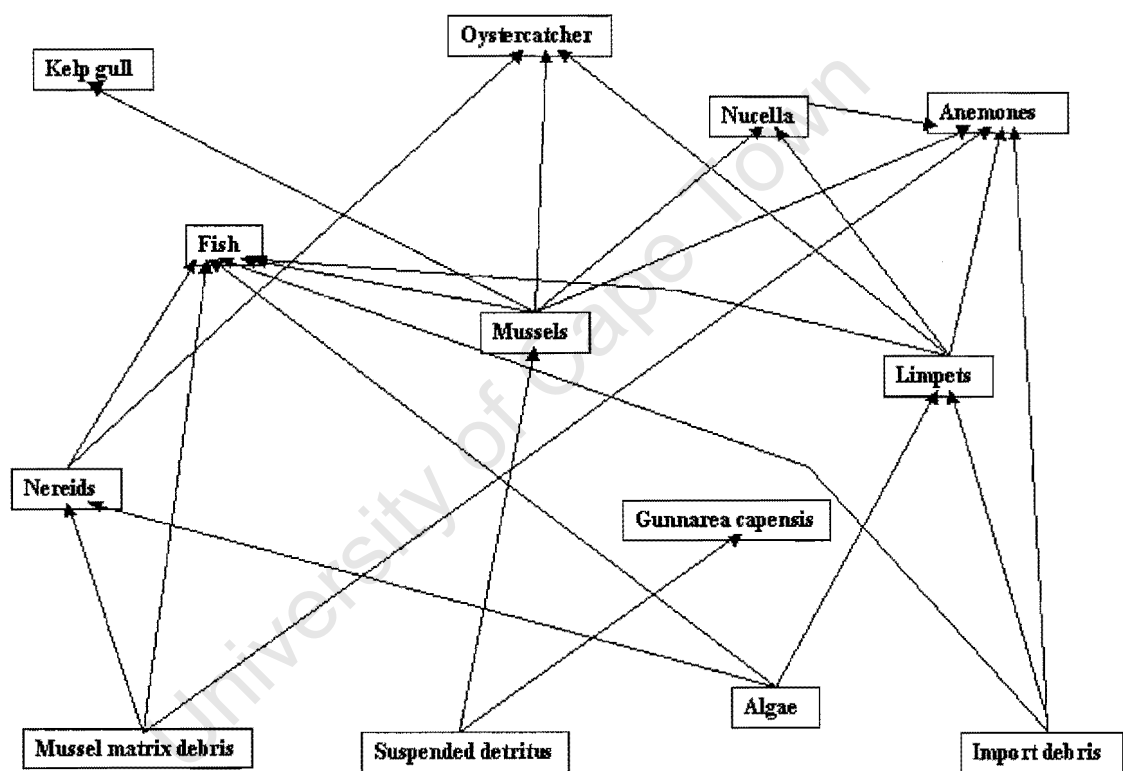


Figure 2.1: Summary diagram of trophic links between components considered in the model of an intertidal mussel bed on the west coast of South Africa. Exports from the system are omitted and the different compartments are explained in the text.

Chapter Three

Input data for the mussel bed models

3. Parameter Estimates for the Living Groups

A general description of each group as well as information on the sources and calculations of biomass, dietary composition, P/B, Q/B, assimilation efficiency, and exports for the 19 living components in the Ecopath model under two conditions of wave exposure and five grades of shore height are detailed in this section.

3.1. Heterotrophs

3.1.1. Group 1: *Haematopus moquini* (African Black Oystercatcher)

Oystercatchers are resident birds of the west-coast intertidal rocky shores that derive most of their nutrition from mussels and limpets.

Biomass: Densities of birds recorded in the literature on the South African west coast vary from 3.6 birds. km⁻¹ of coast on west-coast mainland sites (Bosman and Hockey 1988), to 25 - 78 birds. km⁻¹ on nearshore island sites (Bosman and Hockey 1988). Since the model reflects the mainland mussel beds, a figure of 3.6 birds. km⁻¹ was used. Assuming the area of the shore used for foraging is on average 5 m broad, then there would be 0.00071 birds. m⁻². The mean weight of an adult is 699 g wet weight (Maclean 1985) and the AFDM is approximately 22.5% of the wet weight, which gives a mean biomass of 0.1112 g AFDM. m⁻².

Dietary composition: Hockey and Underhill (1984) investigated the diet of African Black Oystercatcher by inspecting shell middens and by direct observation of items consumed. The survey was done throughout the species range although the dietary information from sites on the south west coast would be expected to most closely match the dietary composition required for the model. Table 3.1 shows the frequency of

occurrence of the various diet items found in the diet. The uncategorised food source, “others”, was assumed to consist of nereids.

Table 3.1: Frequency of occurrence (%) of the dietary items of the African Black Oystercatcher. From Hockey and Underhill (1983).

Diet group	Pelecypoda (mytilids)	<i>Scutellastra</i> <i>granularis</i>	<i>Scutellastra</i> <i>argenvillei</i>	Other limpets	<i>Nucella</i> spp.	Others
frequency in diet (%)	67.5	21.3	4.75	3.38	0.07	3.00

P/B: African Black Oystercatchers raised from chicks grow to 400 g wet weight in their first 35 days (Hockey 1984) thus the maximal P/B value for growth of an oystercatcher would be 10.4 yr^{-1} . Once Oystercatchers reach maximum size they can live for up to 40 years (Goss-Custard 1996). Thus the actual P/B would be considerably lower and was estimated as 5.4 yr^{-1} , which is similar to the value for seabirds on the unexploited tropical French Frigate Shoals (Polovina 1984).

Q/B: A pair of African Black Oystercatchers rearing a single chick require 1473 kJ day^{-1} (Griffiths and Hockey 1987), therefore one breeding oystercatcher requires $269 \times 10^3 \text{ kJ. yr}^{-1}$. The food items consumed would have approximately 23.0 kJ g^{-1} AFDM (Field *et al.* 1980). The mean weight of an adult oystercatcher is 699 g wet weight (Maclean 1985) and the AFDM of vertebrates is approximately 22.5% of the wet weight (Field *et al.* 1980), therefore the Q/B was estimated as 74.3 yr^{-1} .

Assimilation efficiency: The mean assimilation efficiency of growing African Black Oystercatcher chicks was measured as 72% by Hockey (1984).

3.1.2. Group 2: *Larus dominicanus* (Kelp Gull)

The Kelp Gull is a littoral predator and scavenger, which derives a proportion of its nutrition by foraging within the mussel bed.

Biomass: Griffiths and Hockey (1987) specified a density of 0.005 birds. m^{-2} in their model of west-coast, intertidal mussel predation and Hockey and Bosman (1988) recorded a mainland density of 8.3 birds. km^{-1} of shore on the west coast, which is approximately equivalent to 0.00166 birds m^{-2} . Therefore the likely mean density of Kelp Gulls would be 0.00333 birds. m^{-2} . Mean mass of the Kelp Gull is 924 g wet weight (Maclean 1985) and the AFDM of vertebrates is approximately 22.5% of the wet weight (Field *et al.* 1980) therefore there is a mean biomass of 0.69 g AFDM. m^{-2} .

Dietary composition: Griffiths and Hockey (1987) estimated that 25% of the energy requirements of Kelp Gulls was derived from intertidal predation and the rest from scavenging of washed-up animals including large mussels. Regurgitated shells at gull roosts have been noted to contain mainly small mussels consumed whole (Griffiths and Hockey 1987) and Maclean (1985) records dietary items of mussels and limpets, which are likely to originate from mussel beds. Thus a likely dietary composition would be 20% mussels, 5% limpets and 75% imports.

P/B: No local estimate of production of Kelp Gull was available therefore the value for African Black Oystercatcher was used, i.e., 5.4 yr^{-1} .

Q/B: Kelp Gull daily energy expenditure is 800 kJ. day^{-1} (Griffiths and Hockey 1987), which is 292×10^3 kJ. yr^{-1} . The food items would have an energy value of approximately 23.0 kJ. g^{-1} AFDM (Field *et al.* 1980). If the mean density of gulls is 0.00333 birds. m^{-2} , the consumption would be approximately 42.3 g AFDM. m^{-2} , which is equivalent to a Q/B of 61.3 yr^{-1} .

Assimilation efficiency: No local information on this parameter was available for the Kelp Gull, so it was assumed to be same as African Black Oystercatcher, i.e. 72%.

3.1.3. Group 3: Resident Intertidal Fish

The intertidal fish of the South African west coast were surveyed by Prochazka and Griffiths (1992) and they found a total of 14 species in the intertidal rock pools consisting mainly of the two families Clinidae and Gobiesocidae. The most common west-coast intertidal species are: *Clinus acuminatus*, *C. agilis*, *C. heterodon*, *C. superciliosus* and *Chorisochismus dentex*.

Biomass: Prochazka and Griffiths (1992) sampled 30 rock pools totalling 110.2 m² at Groenrivier on the west coast, finding an average abundance of 5.49 fish m⁻² and a total of 35.16 g wet weight fish. m⁻² in pools (thus an average of 6.4 g wet weight per fish). Assuming 10% of rocky shore is in the form of rock pools and using a conversion of 0.27% from wet weight to AFDM (Bennett 1979), gave a biomass of 0.964 g AFDM. m⁻².

Dietary composition: The diet of the littoral fish in the Western Cape was studied by Bennett, Griffiths and Penrith (1983) by stomach content analysis. Over 50 stomachs from each of five fish species listed above were sampled and the percentage volume recorded for each of the following prey items: fish, barnacles, molluscs, nereids, algae, decapods, isopods, copepods, amphipods, tanaids and insects. The dietary composition averaged over the five fish species is: 13.6% nereids, 18.4% mollusc groups, 4.8% barnacles, 1.8% intertidal fish and 1.8% algae; and the remaining prey items were small species considered as mussel matrix debris (59.6%).

P/B: Bennett (1979) calculated the energy budget of *Clinus superciliosus* collected from Oudekraal in the Western Cape from laboratory experiments in which fish ranging in size from 6.19 - 208.4 g were fed mussel mantle tissue. The weight-specific growth rate of the fish calculated by Bennett (1979) is given in Equation 3.1.

Equation 3.1:
$$\text{Production}_{(\text{kJ/day})} = 0.101 \text{ mass}_{(\text{g wet weight})}^{0.140}$$

The average mass of the fish from the biomass estimates above was 6.4 g wet weight therefore the production from Equation 3.1 would be 0.131 kJ. fish⁻¹. day⁻¹. With an average of 0.549 fish. m⁻² and a conversion of 23.0 kJ. g⁻¹ AFDM fish (Bennett 1979), this gives a production estimate of 2.08 g AFDM m⁻². yr⁻¹ or a P/B of 2.16 yr⁻¹.

Q/B: The consumption was also derived from Bennett (1979) (Equation 3.2).

Equation 3.2:
$$\text{Consumption}_{(\text{kJ/day})} = 0.345 \text{ mass}_{(\text{g wet weight})}^{0.7619}$$

The average fish mass at Groenrivier is 6.4 g and therefore the consumption would be 1.42 kJ. fish⁻¹ day⁻¹. Prey items are approximately 23.0 kJ g⁻¹ AFDM (Field *et al.* 1980) and with an average of 0.549 fish. m⁻², the consumption would be 12.4 g AFDM. m⁻². yr⁻¹ which is equivalent a Q/B of 12.8 yr⁻¹.

Assimilation efficiency: Bennett's (1987) study gives the relationship between assimilation efficiency and fish mass so that a fish of wet weight 6.4 g would have an assimilation efficiency of 77%.

3.1.4. Group 4: *Mytilus galloprovincialis*

Mytilus galloprovincialis is the dominant filter-feeding mussel on west-coast intertidal rocky shores in terms of biomass and space occupied.

Biomass: Mass of mussels was derived from the 1990 Surveys (Table 3.2).

Table 3.2: Mean biomass of *Mytilus galloprovincialis* (g AFDM. m⁻²) for different shore heights at wave-exposed sites and semi-exposed sites (1990 Surveys).

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	1939	2892	2300	2256	1362
wave semi-exposed	-	-	1987	952	-

The size, mass and numbers of *Mytilus galloprovincialis* recruits and adults (Table 3.3) were measured by Leeb (1995) in a field survey at Groenrivier. The recruit size class of mussels (defined as 0 - 15 mm shell length) had an approximate average size of 7 mm and a mass of 3.188×10^{-3} g AFDM per individual.

Table 3.3: Mean shell length in mm (size), mass per individual in g AFDM. m^{-2} (mass) and numbers. m^{-2} (numbers) of *Mytilus galloprovincialis* for different shore heights at wave-exposed sites and semi-exposed sites. From Leeb (1995).

		Shore height (% air exposure)				
		10%	20%	30%	40%	50%
wave exposed	Mean adult size (mm)	64	43	44	59	42
	adult mass (g)	2.592	0.777	0.833	2.026	0.724
	adult numbers (m^{-2})	748	3664	2740	1112	1882
	recruit numbers (m^{-2})	784	13558	5136	640	0
wave semi-exposed	Mean adult size (mm)	-	-	41	46	-
	adult mass (g)	-	-	0.673	0.9535	-
	adult numbers (m^{-2})	-	-	2950	998	-
	recruit numbers (m^{-2})	-	-	708	270	-

Dietary composition: *Mytilus galloprovincialis* is a filter feeder consuming bacteria, phytoplankton, fine organic detritus and material of inorganic origin which is suspended in the water column (Seed and Suchanek 1992), represented by the suspended detritus compartment in the Ecopath model.

P/B: Growth of *Mytilus galloprovincialis* at different wave exposures and shore heights was measured by Leeb (1995) at Groenrivier and fitted to a von Bertalanffy growth equation (Equation 3.3). The intermediate values of growth parameters are estimates (Table 3.4).

Equation 3.3: $\text{shell length}_{(\text{mm})} \text{ at age } t_{(\text{yrs})} = \text{maximum shell length}_{(\text{mm})} \cdot (1 - e^{(-K \cdot t)})$

Table 3.4: Values for growth of *Mytilus galloprovincialis* described by a von Bertalanffy equation at different wave exposures and shore heights at Groenrivier. From Leeb (1995).

		Shore height (% air exposure)				
		10%	20%	30%	40%	50%
wave exposed	max. shell length(mm)	92.6	94.4	96.2	98.0	99.7
	K	0.195	0.170	0.145	0.120	0.095
wave semi-exposed	max. shell length(mm)	-	-	124.5	132.5	-
	K	-	-	0.129	0.099	-

The von Bertalanffy growth curves give estimates of changes in shell length of the recruits and adults. These estimates of shell growth were then converted into change in biomass using the relationship between shell length and dry weight derived from van Erkom Schurink and Griffiths (1991, 1993) (Equation 3.4) and a conversion from dry mass to AFDM (Appendix B) and then multiplied by the number of mussels to give production estimates that were used to derive P/B ratios (Table 3.5).

$$\text{Equation 3.4: dry weight}_{(g)} = \text{shell} + \text{flesh} = 5 \times 10^{-5} \text{ shell length}_{(mm)}^{3.028} + 0.328 \times 10^{-5} \text{ shell length}_{(mm)}^{3.075}$$

Table 3.5: Calculated annual P/B values for *Mytilus galloprovincialis* for different shore heights at wave-exposed sites and semi-exposed sites.

		Shore height (% air exposure)				
		10%	20%	30%	40%	50%
wave exposed		0.847	2.39	2.38	2.00	2.46
wave semi-exposed		-	-	2.66	2.63	-

Q/B: The mussels filter out of the water particulate dead organic matter and phytoplankton. Erkom Schurink and Griffiths (1992) collected mussels from Bloubergstrand on the west coast and measured filtration rate with respect to shell length (Equation 3.5) in the laboratory under similar environmental conditions to those experienced by wild mussels. The annual mean particulate organic content of the seston at Groenrivier is 1.14 mg AFDM. l⁻¹ at semi-exposed sites and 1.39 mg AFDM. l⁻¹ at wave

exposed sites (Bustamante 1994). The Q/B values (Table 3.6) were derived by dividing the total consumption by the biomass at each shore height and exposure.

Equation 3.5: Filtration rate_(l./hr) = 1.7×10^{-5} shell length_(mm)^{3.02}

Table 3.6: Estimates of the annual consumption to biomass ratio (Q/B) of suspended detritus in the water column by *Mytilus galloprovincialis* for different shore heights at wave-exposed sites and semi-exposed sites.

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	20.7	18.0	15.9	13.4	11.2
wave semi-exposed	-	-	13.1	11.0	-

Assimilation efficiency: Absorption efficiency, which was used as an approximation of assimilation efficiency, was measured by van Erkom Schurink and Griffiths (1992) for *M. galloprovincialis* and shown to vary with seston concentration. The average suspended detritus concentration at Groenriver at exposed sites is 1.39 mg. l⁻¹ (Bustamante 1994), corresponding to an absorption efficiency of 78%. At semi-sheltered sites where the seston concentration is 1.14 mg. l⁻¹, the corresponding absorption efficiency would have been 81%.

3.1.5. Group 5: *Aulacomya ater*

An indigenous mussel species commonly found subtidally. Adults are now scarce in the intertidal zone due to displacement by *M. galloprovincialis* but large numbers of juveniles inhabit the intertidal mussel matrix.

Biomass: Mass of mussels was derived from the 1990 Surveys (Table 3.7).

Table 3.7: Mean biomass of *Aulacomya ater* (g AFDM. m⁻²) for different shore heights at wave-exposed sites and semi-exposed sites (1990 Surveys).

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	219.2	56.0	237.6	209.4	47.0
wave semi-exposed	-	-	11.4	1.48	-

Dietary composition: *Aulacomya ater* is a filter feeder, and consumes fine particles suspended in the water column, which are represented by the suspended detritus compartment in the Ecopath model.

P/B: The size class composition of *A. ater* has been previously recorded from cores taken from the intertidal mussel beds at Groenrivier on the west coast (Steffani 2001). Each 2 mm shell length size class was converted into dry weight per individual mussel using Equation 3.6, derived from van Erkom Schurink and Griffiths (1991, 1993).

$$\text{Equation 3.6: dry weight}_{(g)} = \text{shell} + \text{flesh} = 1.1 \times 10^{-6} \text{ shell length}_{(mm)}^{3.3865} + 2.3 \times 10^{-5} \text{ shell length}_{(mm)}^{3.276}$$

Griffiths and King (1979) fitted the growth of subtidal *A. ater* populations from Oudekraal in the Western Cape to a Gompertz growth curve (Equation 3.7), which was used to calculate the growth of each size class.

$$\text{Equation 3.7: shell length}_{(mm)} \text{ at age } t_{(yrs)} = 90 \times (1.84 \times 10^{-4})^{0.604 \wedge t}$$

Production (Table 3.8) was calculated for *A. ater* occurring within the *Mytilus galloprovincialis* matrix and then added to the production value for *A. ater* clumps that were separate from the *M. galloprovincialis* matrix. The *A. ater* clumps were assumed to have size distributions similar to the *M. galloprovincialis*.

Table 3.8: The calculated P/B ratios for *Aulacomya ater* for different shore heights at wave-exposed sites and semi-exposed sites.

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	2.05	2.04	1.21	0.72	1.32
wave semi-exposed	-	-	3.07	3.07	-

Q/B: Van Erkom Schurink and Griffiths (1992) measured the relationship between filtration rate of *A. ater* and the dry weight of mussel (Equation 3.8) under laboratory conditions from a sample of intertidal *A. ater* taken from Bloubergstrand in the Western Cape. The filtration rate was calculated for each size class used in the calculation of production and multiplied by the seston concentrations given in the consumption estimate for *M. galloprovincialis*, and then multiplied by the number of mussels in each size class to give estimates of the consumption Table 3.9.

Equation 3.8: Filtration rate_(l./hr) = 0.89 dry weight_(g)^{0.81}

Table 3.9: Estimates of the consumption to biomass ratio (Q/B) for suspended detritus in the water column consumed by *Aulacomya ater* at different shore heights at wave-exposed sites and semi-exposed sites.

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	14.0	11.1	4.74	3.03	13.5
wave semi-exposed	-	-	13.1	11.0	-

Assimilation efficiency: Absorption efficiency, which was used as an approximation of assimilation efficiency, was measured by van Erkom Schurink and Griffiths (1992) for *A. ater* and shown to vary with seston concentration. The average suspended detritus concentration at Groenriver at exposed sites is 1.39 mg. l⁻¹ (Bustamante 1994), corresponding to an absorption efficiency of 60%. At semi-sheltered sites where the seston concentration is 1.14 mg. l⁻¹, the corresponding absorption efficiency would have been 65%.

3.1.6. Group 6: *Aulactinia reynaudi* and other anemones

Aulactinia reynaudi, *Actinia equina*, *Pseudactinia flagellifera*, *Anthopleura michaelsoni* and *Bunodosoma capensis* all occur in the intertidal zone of the west coast although *Aulactinia reynaudi* is by far the commonest anemone. All these species are heterotrophs and the food items consumed by *B. reynaudi* are likely to be other intertidal organisms dislodged from the rock (Kruger and Griffiths 1996).

Biomass: Mass of anemones was derived from the 1990 Surveys (Table 3.10) and consisted solely of the anemone, *Aulactinia reynaudi*.

Table 3.10: Mean biomass of anemones (g AFDM. m⁻²) for different shore heights at wave-exposed sites and semi-exposed sites (1990 Surveys).

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	60.6	157	204	134	23.5
wave semi-exposed	-	-	23.5	13.3	-

Dietary composition: Kruger (1995) sampled the gut contents of *Aulactinia reynaudi* sampled at Blouberg on the west coast and ran laboratory consumption experiments so that the annual consumption of each prey item could be estimated (Table 3.12).

Table 3.12: Dietary composition of *Aulactinia reynaudi* and estimates of annual consumption (from Kruger 1995).

prey item	annual consumption (kJ. m ⁻² . yr ⁻¹)	dietary composition (%)
Isopoda	49.8	0.0273
Amphipoda	17.7	0.00971
Pelecypoda	82483	45.2
Gastropoda	66527	36.5
Nereids	196	0.108
Brachyura	33010	18.1
TOTAL	182284	100

Q/B: Consumption rates of *Aulactinia reynaudi* from Blouberg shores in the Western Cape were investigated by Kruger (1995) in laboratory consumption experiments with various natural prey items. The *A. reynaudi* population was estimated by Kruger (1995) to consume 182284 kJ prey items. $\text{m}^{-2} \cdot \text{yr}^{-1}$. Kruger's (1995) survey of the wild *A. reynaudi* population at Blouberg revealed the population had an average of 712 *A. reynaudi* individuals m^{-2} of shore with 43.8% of the anemones occurring in the mussel bed and 56.2% occurring on rock; the average basal disc width of *A. reynaudi* was 12.2 mm on mussels and 28.2 mm on rock and would have had an approximate energy content of 55.7 kJ on rock and 4.50 kJ on mussels. Thus the biomass on Blouberg shore would be approximately 23684 kJ. m^{-2} and therefore the Q/B ratio for the Blouberg population is likely to be 7.70 yr^{-1} , and this value was applied in the model.

P/B: Local studies of anemone growth rates are lacking although the growth of *Anthopleura elegantissima*, which occurs in intertidal mussel beds on the North American west coast, has been studied by Zamer (1986) (Table 3.11).

Table 3.11: Production values derived from Zamer (1986) in laboratory experiments with laboratory acclimatised *A. elegantissima* fed on *Artemia* sp.

Location on shore	Initial body weight (g AFDM. indv^{-1})	daily growth rate (% by weight)	P/B (yr^{-1})	n
High (1.3 m above LWM, 25% submerged)	0.329	1.48	5.4	15
Low(almost entirely subtidal,95%submerged)	0.247	1.16	4.23	10

The P/B for *A. elegantissima* is probably greater than would be expected for *B. reynaudi* because it was measured for relatively small individuals and P/B declines with size, and possibly also because of the highly nutritious laboratory diet of the *A. elegantissima* individuals. Using the information from Zamer's (1986) study would yield a gross conversion gross conversion efficiency (ratio of P/B to Q/B) greater than 0.5, which would be unreasonable, thus an estimate of 1.5 yr^{-1} (20% of the Q/B estimate) for the P/B value was used in the model.

Assimilation efficiency: Absorption efficiencies were measured by Zamer (1986) for *Anthopleura elegantissima* that were fed *Artemia* sp. in the laboratory. Low-shore intertidal individuals had absorption efficiencies of 79.7 – 90.0 % while individuals in the high-shore had efficiencies of 84.7 - 94.8 %. Thus, for the model the absorption efficiencies (which were used as an approximation of assimilation efficiency) would have likely values of between 85% efficiency at 10 % air exposure and 89% efficiency at 50% air exposure.

3.1.7. Group 7: *Gunnarea capensis*

A reef building, intertidal tubicolous polychaete that filter-feeds on suspended detritus.

Biomass: Mass of *Gunnarea capensis* was derived from the 1990 Surveys (Table 3.13).

Table 3.13: Mean biomass of *Gunnarea capensis* (g AFDM. m⁻²) for different shore heights at wave-exposed sites and semi-exposed sites (1990 Surveys).

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	8:33	1.25	40.5	7.75	0
wave semi-exposed	-	-	198	123	-

Dietary composition: *Gunnarea capensis* is a filter feeder consuming fine particles suspended in the water column, which are represented by the suspended detritus compartment in the Ecopath model.

P/B: The production of *Gunnarea capensis* is unknown, and the P/B was assumed to have a value of 2.0 yr⁻¹.

Q/B: Wells (1988) measured the filtration rate of *Gunnarea capensis* from the Western Cape by feeding the polychaete on a culture of *Chlorella* in the laboratory. *G. capensis* consumed a mean of 117 µg Chl a. g⁻¹ DW of tube-free polychaete every half hour. There

is approximately 1 g of Chl a in 175 g AFDM algae and the shell free AFDM of the polychaete is 0.986 DW (see Appendix B, p. 90). Assuming a 50% submersion time for the polychaete gives a annual consumption figure of 176g AFDM algae consumed per gram AFDM *G. capensis*. This Q/B ratio of 176 yr⁻¹ seems too large to be a reasonable consumption estimate probably because it is derived from laboratory feeding conditions. As the consumption of *Gunnarea capensis* in the field remains unknown, the Q/B was assumed to have a value of 20.0 yr⁻¹ for the purposes of the model.

Assimilation efficiency: The assimilation efficiency was assumed to be 80% since this was unknown for *Gunnarea capensis* and this is the default value suggested by Ecopath.

3.1.8. Group 8: Barnacles

The commonest species of these sessile filter-feeding crustaceans on the rocky shores of west coast of South Africa are *Octomeris angulosa* and *Notomegabalanus algicola*.

Biomass: The biomass of barnacle was not estimated in the 1990 Surveys. Thus, the abundance was approximated as 100 barnacles m⁻² with an AFDM of 0.05g. barnacle⁻¹, giving a biomass of 5g AFDM. m⁻².

Dietary composition: Barnacles are filter-feeders consuming fine particles suspended in the water column, represented by the suspended detritus compartment in the Ecopath model.

P/B: Due to the lack of local studies on the energy budgets of barnacles the values used in this study were derived from Wu and Levings (1978) study on *Balanus gladula*, which inhabits the intertidal of the temperate west coast of North America. Wu and Levings (1978) study on *Balanus gladula* gives monthly production figures for a year of growth of barnacle spat. The production of body tissue was 27.5 calories. barnacle⁻¹. year⁻¹ and the production of shell was 46.2 calories. barnacle⁻¹. year⁻¹. Therefore the somatic production

is 13.4 mg AFDM barnacle⁻¹. year⁻¹ (using a conversion figure of 5.5 calories. mg⁻¹ AFDM). The mean mass of the barnacles averaged over the year was 4.76 mg AFDM barnacle⁻¹ therefore the estimate of P/B is 2.82 yr⁻¹.

Q/B: Wu and Levings (1978) estimated consumption by balancing the energy budget of *Balanus gladula* and calculated it consumed 699.5 calories. yr⁻¹. barnacle⁻¹. Using a conversion figure of 5.5 calories. mg⁻¹ AFDM and the mean mass of the barnacles in the experiment (4.76 mg AFDM barnacle⁻¹) gave a Q/B value of 26.7 yr⁻¹.

Assimilation efficiency: This was measured in the field by Wu and Levings (1978) as 92.5%.

3.1.9. Group 9: *Scutellastra granularis*

This common intertidal herbivorous limpet is often found attached to the shells of large mussels or on rocky patches within the mussel bed.

Biomass: The average AFDM of all limpets was derived from the 1990 Surveys (Table 3.14). The abundances and average weight of the limpets were recorded separately for limpets on bare rocky patches and those on the mussel shells, since the sizes of limpets differ between these habitats.

Table 3.14: Biomass estimates of *S. granularis* on intertidal rocky shores for different shore heights at wave-exposed sites and semi-exposed sites. Biomass has been measured in g AFDM m⁻². The numbers of *S. granularis* and the average weight per limpet are detailed for limpets recorded from the rock surface and from the mussel matrix (1990 Surveys).

Wave exposure	shore height (% air exposure)	Average weight per limpet (g AFDM)		abundance (No. m ⁻²)		Total biomass (g AFDM. m ⁻²)
		rock	mussel	rock	mussel	
exposed	10	0.483	0.0548	4.00	376	22.6
exposed	20	0.139	0.0548	13.8	566	33.0
exposed	30	0.269	0.0548	33.8	408	31.5
exposed	40	0.0959	0.0548	97.0	414	32.0
exposed	50	0.0465	0.0548	109.	328	23.0
semi-exposed	30	0.0230	0.0479	24.2	29.6	7.0
semi-exposed	40	0.100	0.0375	128.	298	24.0

Dietary composition: Branch (1971) studied the gut contents of *S. granularis* collected from the Western Cape intertidal. Individuals from the lower balanoid consume any prostrate or creeping algae and lichen; particles of *Porphyra capensis*, *Ulva* sp. and *Gelidium* were identified in the gut. Thus a likely dietary composition would consist of the following algal groups: thin tubular and sheetlike algae, delicately branched, coarsely branched, and epilithic algae.

P/B: Branch (1974) measured the growth of *S. granularis* with respect to shell length at Kommetjie in the Western Cape (Equation 3.9). The relationship between shell length and wet weight (Equation 3.10) was also calculated for *S. granularis* by Branch (1974). Wet weight flesh mass was converted to AFDM for the whole limpet by assuming half the wet weight is from the shell and half from the flesh and using a conversion figure of 0.0780 to convert wet weight to AFDM (Appendix B).

Equation 3.9: $\text{increment in shell length}_{(\text{mm/yr})} = -0.40 \text{ initial length}_{(\text{mm})} + 37.50$

Equation 3.10: $\text{wet weight flesh mass}_{(\text{g})} = 0.00001100 \text{ Shell length}_{(\text{mm})}^{3.42}$

The average sizes of *S. granularis* upon mussels and on rocks were used to calculate production (Table 3.15). The production of limpets on rock and mussels was calculated separately and then summed, due to the difference in size of the individuals between these habitats.

Table 3.15: The calculated P/B ratios for *S. granularis* for different shore heights at wave-exposed sites and semi-exposed sites on the west coast of South Africa.

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	1.89	2.00	1.64	1.89	2.10
wave semi-exposed	-	-	1.06	1.94	-

Q/B: There are no qualitative studies on the consumption rate of *S. granularis* although it is expected that the consumption values measured in the field for the limpet *S. granatina* on the west coast by Bustamante (1994) would resemble *S. granularis* consumption rates. Bustamante (1994) recorded consumption rates for individuals of 50-60 mm shell length reached a steady grazing rate of 0.68 g wet weight algae day⁻¹, whether fed on kelp or epilithic algae, which is equivalent to 16.7 g AFDM year⁻¹ using a wet weight to AFDM conversion ratio of 0.0672 (Appendix B). *Scutellastra granularis* of 55 mm shell length have a wet weight flesh mass of 9.85 g WW (Branch 1974), which is equivalent to 0.769 g AFDM. The consumption and biomass give an approximate Q/B ratio of 21.69 year⁻¹.

Assimilation efficiency: The assimilation efficiency was assumed to be 60% since this was unknown and this is the default value suggested by Ecopath for herbivores.

3.1.10. Group 10: *Scutellastra argenvillei*

This herbivorous limpet is common on the west coast in the lower balanoid where adults consume mostly kelp blades. This species accounts for 58.2% of the total limpet biomass in the mussel beds although 98.2% of this biomass occurs low on wave-exposed shores at

a level equivalent to 10% air exposure. *Scutellastra argenvillei* was not present on semi-exposed shores at the shore-heights considered here, although it is abundant low on semi-exposed shores (Bustamante and Branch 1995).

Biomass: The average AFDM of *S. argenvillei* was derived from the 1990 Surveys (Table 3.16). The abundances and average weights of the limpets were recorded separately for limpets on bare rocky patches and those on the mussel shells, since limpets differ in size in these habitats.

Table 3.16: Biomass estimates of *S. argenvillei* on intertidal rocky shores for different shore heights at wave-exposed sites and semi-exposed sites. Biomass has been measured in g AFDM m⁻². The numbers of *S. argenvillei* and the average weight per limpet are detailed for limpets recorded from the rock surface and from the mussel matrix (1990 Surveys).

Wave exposure	shore height (% air exposure)	Average weight per limpet (g AFDM)		Abundance (No. m ⁻²)		Total biomass (g AFDM. m ⁻²)
		Rock	mussel	Rock	mussel	
exposed	10	4.09	0.0755	49.2	582	246.0
exposed	20	0.203	-	5.0	0	1.0
exposed	30	0.367	0.0755	6.5	1.59	2.5
exposed	40	0.595	-	1.8	0	1.0
exposed	50	-	-	0	0	0.0
semi-exposed	30	-	-	0	0	0.0
semi-exposed	40	-	-	0	0	0.0

Dietary composition: Bustamante (1994) noted that kelp was consumed by *S. argenvillei* on the west coast and constituted 50.1% of the diet. The kelp consumed by large *S. argenvillei* consists mostly of fronds of live subtidal kelp. The remainder of the gut contents contained: 19.6% ephemeral green algae, 15.8% fleshy red algae and 14.2% calcareous algae by dry biomass. It was assumed that 50% of the diet is derived from subtidal imports of algae and thus the remainder of the diet was composed of algae growing on the rocks, made up of 25.1% kelp, 7.2% corallines and 17.7% of the other algal groups.

P/B: Bosman et al. (1990) calculated the von Bertalanffy growth curve (Equation 3.11) for *S. argenvillei* by measuring changes in shell length of tagged individuals in the field near Groenrivier on the west coast of South Africa. The conversions used for flesh weight to shell length (Equation 3.12a) and gametic weight to somatic weight (Equation 3.12b) are also given in Bosman (1990). Wet weight flesh mass was converted to AFDM for the whole limpet by assuming half the wet weight is from the shell and half from the flesh and using a conversion figure of 0.0881 to convert wet weight to AFDM (Appendix B).

$$\text{Equation 3.11: shell length}_{(\text{mm})} = 81.97 (1 - \exp^{(-0.21 \times t(\text{yrs}))})$$

$$\text{Equation 3.12a: somatic flesh weight}_{(\text{g wet weight excluding shell})} = 5.95 \times 10^{-6} \text{ shell length}_{(\text{mm})}^{3.39}$$

$$\text{Equation 3.12b: gametic flesh weight}_{(\text{g wet weight})} = 0.3252 \text{ somatic flesh weight}_{(\text{g wet weight excluding shell})}^{-2.968}$$

The average sizes of *S. argenvillei* upon mussels and on rocks were used to calculate production (Table 3.17). P/B ratios were distinctly lower in the lowest zone on the shore than in other zones because the population there comprises mainly adults.

Table 3.17: The calculated P/B ratios for *S. argenvillei* for different shore heights at wave-exposed sites and semi-exposed sites on the west coast of South Africa.

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	0.492	2.50	2.31	2.05	-
wave semi-exposed	-	-	-	-	-

Q/B: There were no consumption studies on this species of limpet therefore the consumption to biomass ratio was expected to resemble that described for *C. granatina* by Bustamante (1994). The derivation of a Q/B of 21.69 year⁻¹ is detailed in the estimate for *S. granularis*.

Assimilation efficiency: The assimilation efficiency was assumed to be 60% since this was unknown and this is the default value suggested by Ecopath for herbivores.

3.1.11. Group 11: Other Limpets

A combined grouping of the less common limpet species inhabiting mussel beds included *Cymbula granatina*, *C. miniata*, *Scutellastra barbara*, *S. cochlear* and *Helcion dunkeri*. Energy estimates for this group were from studies on *C. granatina* since the other species lacked energy budget studies. In total, these limpets accounted for 9.81% of the limpet biomass within the mussel bed. *Cymbula granatina* is exceptionally abundant on sheltered shores (Bustamante and Branch 1995) but is relatively uncommon on more exposed shores where mussels occur.

Biomass: The average AFDM of all limpets in this group was derived from the 1990 Surveys (Table 3.18). The abundances and average weight of the limpets were recorded separately for limpets on bare rocky patches and those on the mussel shells.

Table 3.18: Biomass estimates of the limpets: *Cymbula granatina*, *C. miniata*, *Scutellastra barbara*, *S. cochlear* and *Helcion dunkeri* on intertidal rocky shores for different shore heights (% air exposure) at wave-exposed sites and semi-exposed sites. Biomass has been measured in g AFDM m⁻². The numbers of limpets and the average weight per individual are detailed for limpets from the rock surface and from in the mussel bed. Shore heights with zero biomass of a limpet species were omitted (data from 1990 Surveys).

Limpet species	Wave exposure, & shore height (%)	Average mass of limpet (g AFDM)		abundance (No. m ⁻²)		Total biomass (g AFDM. m ⁻²)
		Rock	mussel	rock	mussel	
<i>S. cochlear</i>	wave exposed, 20%	0.25	-	2.00	0	0.50
<i>S. barbara</i>	wave exposed, 10%	0.508	-	4.60	-	1.33
<i>Cymbula granatina</i>	wave exposed, 30%	0.574	0.0548	1.50	3.14	1.0
	wave exposed, 40%	0.470	0.0548	0.50	1.05	0.50
	semi-exposed, 30%	0.413	-	2.42	0	2.0
<i>Cymbula miniata</i>	wave exposed, 10%	2.64	-	2.66	-	3.33
<i>Helcion dunkeri</i>	wave exposed, 10%	-	0.0668	-	20.6	1.33
	wave exposed, 20%	-	0.0668	-	60.0	4.00
	wave exposed, 30%	-	0.0668	-	30.0	2.00
	wave exposed, 40%	-	0.0668	-	22.0	1.50
	wave exposed, 50%	-	0.0668	-	22.0	1.50
	semi-exposed, 30%	-	0.0668	-	164.	11.0
	semi-exposed, 40%	-	0.0668	-	50.0	3.34

Dietary composition: Branch (1971) studied the gut contents of limpets collected from the Western Cape intertidal. *Cymbula granatina* guts were found to contain mostly diatoms but small particles of lithothamnion and possibly also the algal species: *Gigartina radula*, *Caulacanthus* sp. and *Zonaria* species. The guts of *Scutellastra cochlear* mostly contained lithothamnion, *Ralfsia verrucosa* and diatoms. The gut contents of *S. barbara* consisted of *Ralfsia verrucosa*, lithothamnia, corallines, possibly *Ulva* sp. *Gelidium* sp. and *Cladophora* species. The gut contents of *C. miniata* consist mainly of lithothamnia. Bustamante (1994) investigated the gut contents of *C. granatina* stomachs from the west coast and found that drift kelp contributed 54.3% of the dry biomass while the remainder of the gut contents consisted of 42.1% ephemeral green algae, 2.5% fleshy red algae and 0.6% calcareous algae. It was assumed that 50% of the

diet is from imported subtidal algae and the remainder is 0.3% corallines and 49.7% of the other algal groups divided according to their proportional biomass in the field.

P/B: The von Bertalanffy growth curve of *C. granatina* (Equation 3.13) was calculated by Bosman *et al.* (1990) by measuring changes in shell length of tagged individuals in the field near Groenrivier. The growth curves of the limpets: *C. granatina* (Equation 3.14) and also *S. cochlear* (Equation 3.15) were measured separately by Branch (1974) in the field at Kommetjie on the Atlantic side of the Cape Peninsula.

$$\text{Equation 3.13: length of } C. \text{ granatina}_{(\text{mm})} = 67.9 (1 - \exp^{(-0.27 \times t (\text{yrs}))})$$

$$\text{Equation 3.14: } C. \text{ granatina increment in shell length}_{(\text{mm/yr})} = -0.40 (\text{initial shell length}_{(\text{mm})}) + 37.50$$

$$\text{Equation 3.15: } S. \text{ cochlear increment in shell length}_{(\text{mm/yr})} = -0.155 (\text{initial shell length}_{(\text{mm})}) + 7.4$$

The conversions for shell length to flesh weight for the limpet species *C. granatina* (Equation 3.16) and *S. cochlear* (Equation 3.17) were measured by Branch (1974).

$$\text{Equation 3.16: } granatina \text{ somatic flesh weight}_{(\text{g wet weight without shell})} = 1.301 \times 10^{-5} \text{ shell length}_{(\text{mm})}^{3.30}$$

$$\text{Equation 3.17: } cochlear \text{ somatic flesh weight}_{(\text{g wet weight without shell})} = 1.537 \times 10^{-4} \text{ shell length}_{(\text{mm})}^{2.51}$$

For the limpet species *H. dunkeri*, *C. miniata* and *S. barbara* the flesh weight conversions and growth equations used were the same as for *S. granatina*. There was no available information on the size class composition of limpets on mussel beds therefore the average size of the limpets upon mussels and the average size of the limpet species on rocks was used to calculate production (Table 3.19).

Table 3.19: The calculated P/B ratios for *Cymbula granatina*, *C. miniata*, *Scutellastra barbara*, *S. cochlear* and *Helcion dunkeri* combined for different shore heights at wave-exposed sites and semi-exposed sites on the west coast of South Africa.

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	0.998	3.55	3.33	3.51	3.99
wave semi-exposed	-	-	3.66	3.98	-

Q/B: There were no studies on these species of limpet therefore the consumption to biomass ratio was expected to resemble that of the study of *C. granatina* by Bustamante (1994). The derivation of a Q/B of 21.69 year⁻¹ is detailed in the Q/B estimate for *S. granularis*.

Assimilation Efficiency: The assimilation efficiency was assumed to be 60% since this was unknown and this is the default value suggested by Ecopath for herbivores.

3.1.12. Group 12: Nereids

The commonest errant worm in the west-coast mussel beds is *Pseudonereis variegata* although *Lepidonotus* spp. and *Marphysa* spp. are also found there, but contribute little to the overall biomass. No local studies of energy budgets of nereids were available.

Biomass: Mass of nereids was derived from the 1990 Surveys (Table 3.20).

Table 3.20: Mean biomass of nereids (g AFDM. m⁻²) for different shore heights at wave-exposed sites and semi-exposed sites (1990 Surveys).

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	15.3	25.1	8.17	7.50	4.26
wave semi-exposed	-	-	27.9	12.7	-

Dietary composition: G. M. Branch (pers. comm.) has noted that the guts of *P. variegata* always appear to be filled with algal matter although matrix debris and juvenile mussels

are also expected to feature in the diet. It was assumed that the dietary composition would be 20% algae, 5% mussels and 75% matrix debris.

P/B: Cammen (1980) calculated the monthly production of a population of *Nereis succinea* in a salt marsh in North Carolina, USA from cohort and growth data taken from field samples, which resulted in a P/B of 2.0 yr^{-1} . Choi and Lee (1997) measured the production of *Perinereis aibuhitensis* in an intertidal mudflat on the West Coast of Korea and calculated a P/B value of 3.4 yr^{-1} . A study of *Nereis diversicolor* by Chambers and Milne (1975) in an estuary on the north east coast of Britain gave an estimate of P/B as 3.0 yr^{-1} . These P/B values have an approximate mean of 2.8 yr^{-1} although estimates of P/B are likely to include both gametic and somatic growth. The somatic production was estimated by Chambers and Milne (1975) to consist of approximately 60% of the total production, therefore a P/B value of 1.7 yr^{-1} is likely to be most accurate estimation of P/B for the model.

Q/B: The juvenile growth of *Nereis virens* from a salt marsh was measured by Olivier *et al.* (1996) who calculated that individuals of 50 mg wet weight consumed 1.22 – 2.03 mg AFDM slightly degraded *Laminaria longicuris* per day. When fed a diet of fresh *Enteromorpha intestinalis* the polychaete consumed 0.80 - 1.33 mg AFDM algae day^{-1} individual⁻¹. If *Pseudonereis variegata* has consumption rates similar to *Nereis virens*, then one would expect Q/B of 37.0 - 93.8 year^{-1} . In the laboratory, Nielsen *et al.* (1995) studied the feeding of *Nereis diversicolor* and *N. virens*, a species that lives in intertidal mud flats. On a diet of shrimp meat, polychaetes of 0.0906 - 0.573 g wet weight consumed 42 and 50 mg wet weight shrimp per polychaete per day in the case of *N. diversicolor* and *N. virens* respectively. This is roughly equivalent to Q/B values of 46.3 and 55.0. Thus an average from the Olivier *et al.* (1996) and Nielsen *et al.* (1995) experiments gives a Q/B of 58.0, which is possibly the most appropriate estimate of nereid consumption.

Assimilation Efficiency: Olivier *et al.* (1996) studied the assimilation efficiency of *Nereis virens* in the laboratory when it was fed on a range of macro-algae. *Nereis virens* fed on *Laminaria longicruris* had an assimilation efficiency of 55.1% and on a diet of *Enteromorpha intestinalis* it had an assimilation efficiency of 54.8%.

3.1.13. Group 16: *Nucella* spp.

This group of predatory whelks consists of the species *Nucella cingulata*, *N. squamosa* and *N. dubia*, although *N. cingulata* is most common.

Biomass: Mass of whelks was derived from the 1990 Surveys (Table 3.21).

Table 3.21: Mean biomass of whelks (g AFDM. m⁻²) for different shore heights at wave-exposed sites and semi-exposed sites (1990 Surveys).

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	18.7	27.0	22.0	19.0	12.0
wave semi-exposed	-	-	3.50	0.00	-

Dietary composition: *Nucella* spp. feed largely on the mussels *Aulacomya ater* and *Mytilus galloprovincialis* (Griffiths and Blaine 1994) as well as barnacles, limpets and other *Nucella* spp. (personal obs.). The proportional contribution of these prey items to the diet of *Nucella* spp. is unknown therefore it was assumed they were consumed in proportion to the prey species abundance.

P/B: No South African studies of production exist for these whelks. Stickle and Bayne (1987) did an energetic study on *Nucella lapillus* in the laboratory from a population of the whelks near Plymouth, England where the water varies from 6.5 to 18.5 °C. The whelks used were 23 to 28 mm in length and fed on *Mytilus edulis*. In the experiments of Stickle and Bayne (1987), they varied temperature and salinity, but at a temperature of 15°C and a salinity of 30‰ they obtained a mean calculated scope for growth of 46.2 J.

snail⁻¹. day⁻¹. A 25 mm *Nucella lapillus* weighs approximately 2 g wet weight with an AFDM of 0.416 g (Davenport 1996), which is equivalent to an energy biomass of 9.26 kJ snail⁻¹. Thus the growth is equivalent to a P/B of 1.81 yr⁻¹.

Q/B: Similarly, the Stickle and Bayne (1987) energetic study measured consumption of *Nucella lapillus* resulting in a mean ingestion rate of 189.7 J. snail⁻¹. day⁻¹. A 25 mm snail weighs approximately 2 g wet weight with an AFDM of 0.416 g, which is equivalent to an energy biomass of 9.26 kJ snail⁻¹. Thus the ingestion rate is approximately equivalent to a Q/B of 7.48 yr⁻¹.

Assimilation efficiency: The energetic study of *Nucella lapillus* by Stickle and Bayne (1987) referred to above found a mean absorption efficiency of 58%.

3.2. Autotrophs

Over 20 species of foliose algae were recorded from the 1990 Surveys listed in Appendix A, although the list has possible omissions of some of the rarer species of algae occurring in the west-coast rocky intertidal (J. J. Bolton, Botany Department, University of Cape Town, pers. comm.). The species of algae were grouped into a smaller number of categories based upon functional-form groups (Lobban 1994) for inclusion into the model. These five functional-form groups were: Thin Tubular and Sheetlike Algae, Delicately Branched, Coarsely Branched, Kelps, and Coralline and Encrusting algae.

3.2.1. Group 14: Thin Tubular and Sheetlike Algae

This group includes the taxa *Ulva* spp., *Enteromorpha intestinalis*, *Porphyra capensis*, *Aeodes orbitosa* and *Mazzaella (Iridaea) capensis*.

Biomass: Mass of thin tubular and sheetlike algae was derived from the 1990 Surveys (Table 3.22).

Table 3.22: Mean biomass of tubular and sheetlike algae (g AFDM. m⁻²) for different shore heights at wave-exposed sites and semi-exposed sites (1990 Surveys).

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	0.00	0.00	3.50	0.50	0.00
wave semi-exposed	-	-	9.00	0.00	-

P/B: The production of *Porphyra capensis* has been measured by Levitt (1987) in the laboratory. When 79% tidally immersed, *P. capensis* produces 6.283 mg C. g⁻¹ DW. yr⁻¹. The dry weight to carbon ratio is 40% (Levitt 1987), which gives a P/B of 15.7 yr⁻¹. Readjusting this P/B estimate for the lower balanoid (21.15% immersed) gave a P/B of 36.5 yr⁻¹. Similarly, the production of *Ulva rigida* was measured by Levitt (1987). When 51% tidally immersed, it produces 12.1 mg C. g⁻¹ DW. yr⁻¹. The dry weight to carbon ratio is 30% (Levitt 1987), which gives a P/B of 23.7 yr⁻¹. Readjusting this P/B estimate for the lower balanoid (21.15% immersed) gave a P/B of 55.2 yr⁻¹. Waaland (1976) measured the growth of *Iridaea cordata* in culture tanks in running seawater taken from Clam Bay, Washington at temperatures of 8 – 14 °C. Maximal growth was at a biomass of 132 g AFDM. m⁻², with a growth rate of 11.7 g AFDM. day⁻¹ and with 139 growth days in a year this gives a P/B of 32.3 yr⁻¹. The lowest growth rate of tissue was at a biomass of 403 g AFDM. m⁻² with a growth rate of 16.2 g AFDM. m⁻². day⁻¹ and with 139 growth days in a year gives a P/B of 14.7 yr⁻¹. A likely average of these studies would thus be a P/B of 45.9 yr⁻¹.

3.2.2. Group 15: Delicately Branched Algae

Included in this group are the taxa *Cladophora* spp., *Ceramium* spp. and *Aristothamnion collabens*.

Biomass: Mass of thin delicately branched algae was derived from the 1990 Surveys (Table 3.23).

Table 3.23: Mean biomass of delicately branched algae (g AFDM. m⁻²) for different shore heights at wave-exposed sites and semi-exposed sites (1990 Surveys).

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	0.00	0.00	1.00	0.00	0.00
wave semi-exposed	-	-	2.00	3.33	-

P/B: The growth of *Ceramium rubrum* and *Cladophora serica* was measured monthly by Pedersen and Borum (1996) in estuarine waters where the somatic growth rate (ratio of mass produced to biomass) of these two algae was found to vary between 0.006 and 0.251 day⁻¹ with an average of 0.1 day⁻¹, which gives a P/B of 36.5 yr⁻¹.

3.2.3. Group 16: Coarsely Branched Algae

This group includes *Plocamium* spp., *Gigartina* spp., *Gelidium* sp., *Caulacanthus ustulatus*, *Champia lumbricalis*, and *Chordariopsis* sp.

Biomass: Mass of coarsely branched algae was derived from the 1990 Surveys (Table 3.24).

Table 3.24: Mean biomass of coarsely branched algae (g AFDM. m⁻²) for different shore heights at wave-exposed sites and semi-exposed sites (1990 Surveys).

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	11.3	2.00	24.5	0.00	0.00
wave semi-exposed	-	-	6.67	0.00	-

P/B: Levitt (1987) measured *Gigartina radula* growth in the laboratory, for specimens collected from the Western Cape. The species produced 7.96 mg C. g⁻¹ DW. yr⁻¹ and contains 26% DW carbon under a regime of 21% immersion, which gives a P/B value of

30.6 yr⁻¹. Recalculated for lower balanoid (25% immersion), this gave a P/B of 24.8 yr⁻¹. Jackelman and Bolton (1990) did a study on how productivity of *Gigartina radula* varied with wave exposure on the western side of the Cape Peninsula. Productivity of the *G. radula* removed from sites of varying wave exposure was measured in the laboratory. The productivity averaged from two exposed sites and two semi sheltered sites was respectively 1.465 mg C fixed g⁻¹ DW hr⁻¹ and 1.89 mg C fixed g⁻¹ DW hr⁻¹. Thus algae from the semi-exposed sites were a factor of 1.29 greater than the production at exposed sites. The *G. radula* in Levitt's (1987) study was taken from Dalebrook, which is moderately exposed. Thus likely values of production of coarsely branched algae are a P/B of 19.1 yr⁻¹ at exposed sites and a P/B of 24.8 yr⁻¹ at semi-exposed sites.

3.2.4. Group 17: Algae with Thick Blades and Branches (kelps)

Kelps include the species *Ecklonia maxima* and *Laminaria pallida*.

Biomass: Mass of kelps was derived from the 1990 Surveys (Table 3.25).

Table 3.25: Mean biomass of kelps (g AFDM. m⁻²) for different shore heights at wave-exposed sites and semi-exposed sites (1990 Surveys).

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	41.3	18.0	0.00	0.00	0.00
wave semi-exposed	-	-	12.5	0.00	-

P/B: All production studies on kelps have been subtidal. The subtidal growth rates vary mainly due to the effect of light attenuation with depth. A South African study by Dieckmann (1980) measuring the tissue growth of *Laminaria pallida* in the field off Oudekraal recorded that at a depth of 8m, the P/B was 4.7 yr⁻¹ for frond production and 2.0 yr⁻¹ for the entire plant. Mann (1972) measured *Laminaria* sp. somatic production in the field off the East coast of Canada at a variety of wave exposures and depths over one year. At moderately exposed sites at 5m depth, P/B was 11.0 yr⁻¹ while at 8m depth the

P/B was 10.1 yr^{-1} . Thus a likely value of production for the intertidal kelp group would be a P/B of 10.0 yr^{-1} .

3.2.5. Group 18: Coralline Algae

Includes encrusting corallines and articulated corallines such as *Jania* spp. and *Corallina* spp.

Biomass: Mass of articulated corallines was derived from the 1990 Surveys (Table 3.26). There was no estimate of encrusting corallines in the biomass survey thus the biomass of articulated corallines was doubled to include this group of algae in the total biomass estimate of coralline algae.

Table 3.26: Mean biomass of articulated corallines (g AFDM, m^{-2}) for different shore heights at wave-exposed sites and semi-exposed sites (1990 Surveys).

	Shore height (% air exposure)				
	10%	20%	30%	40%	50%
wave exposed	5.00	2.00	2.00	2.00	0.50
wave semi-exposed	-	-	0.50	0.00	-

P/B: No estimates values of P/B were found in the literature although Lobban (1994) cites measurements of productivity for a large range of different seaweeds in mg carbon fixed $\text{gDW}^{-1} \cdot \text{hr}^{-1}$, which were used for comparative purposes to determine the likely production value for corallines. Encrusting corallines all had slow growth rates with production values between 0.1 and 0.2 mg C fixed $\text{gDW}^{-1} \cdot \text{hr}^{-1}$ (5 species sampled). Kelps had productivities between 0.3 and 1.3 mg C fixed gDW^{-1} (13 species sampled). The P/B for South African kelp is likely to be between 4.7 and 11.0 year^{-1} (see kelps above) thus an approximate estimate of the P/B for corallines, adjusted with respect to the estimates of known P/B values for kelp, would be a P/B of 1.33 year^{-1} for corallines.

3.2.6. Group 19: Epilithic Algae

This group consists of various algal species that grow prostrate on the rock surface, including sporelings of *Porphyra capensis*, *Ulva* spp., *Enteromorpha intestinalis*, *Ralfsia verrucosa* and diatoms.

Biomass: The standing stock of epilithic algae was measured monthly on acrylic growth plates over a period of a year in the field at Groenrivier by Bustamante (1994) and thus consists of various rapidly growing forms that are quick to colonise and cover the rock surface. The monthly average was 94 g wet weight. $\text{m}^{-2} \cdot \text{yr}^{-1}$ or 7.76 g AFDM $\text{m}^{-2} \cdot \text{yr}^{-1}$ (assuming the wet weight to AFDM conversion is the same as *Ulva* spp.).

P/B: Bustamante (1994) also measured the monthly production of epilithic algae growing on acrylic growth plates over a period of a year. The monthly average production = 28,8 g wet weight $\text{m}^{-2} \cdot \text{day}^{-1}$, therefore the estimate of P/B is 111.8 yr^{-1} due to the high production and low biomass of algae on the plates.

Chapter Four

The Mussel Bed Models

4.1. Results

4.1.1. Balancing the Models

Twelve out of the ecosystem groups modelled yielded realistic ecotrophic efficiencies (EE) and required no balancing. However, modelling the input data gave EEs greater than unity for seven of the model's ecosystem components. This indicates that model production of these groups was insufficient to support the model consumption by other groups. The models were balanced by modifying the lesser known estimates for these unbalanced groups.

The initial construction of the seven models (five shore levels at exposed shores and two at semi-exposed shores) had values for EE varying between 1 and 4 for each of the gastropod groups (the limpet groups and *Nucella* spp. group). The most inaccurate and least known input to the models was the dietary compositions of the predators of gastropods, i.e. the oystercatcher, kelp gull, intertidal fish and anemones. On varying the biomasses of the various predators it was found that anemones had by far the greatest effect on gastropod mortality. Thus the contribution of gastropods to the anemones diet was reduced 10 fold and the proportion of subtidal imports consumed by anemones was correspondingly increased. The justification for this adjustment is that many of the anemones (including *A. reynaudi*) are likely to rely on wave-tumbled prey, some of which are swept into the intertidal zone.

Highly imbalanced EE values were found for coralline algae for the model constructed on exposed shores at 10% air exposure, which had an EE of 28, showing a wide error in the balancing of flows for this group. The imbalance may be due to an underestimate of the biomass or production of corallines although on recalculating the EE for corallines with double the biomass of corallines and with a 10-fold increase in the production of

corallines still did not balance the group. Therefore, an over-estimate in the amount of coralline consumed by the grazers was probably causing the imbalance. Thus, the dietary composition of corallines in the limpet groups diet was reduced by 10-fold to bring the EE of corallines to below one and the proportion of drift algae in the limpet groups diet was respectively increased. The production value of corallines was also doubled to balance the EE.

The kelp group had an unbalanced EE of between one and three in the initial constructs of the models for 20% air exposure on wave-exposed shores and 30% air exposure on semi-exposed shores. The EE of kelps was reduced by altering the diet of its consumers rather than increasing the biomass or production estimates for kelp. The consumption of kelp by nereids was reduced until the EE for kelps was below one, which required a reduction in the percentage of kelp in the diet of nereids by 3%.

Coarsely branched algal group in the model for 10% air exposure on wave-exposed shores had an unbalanced EE of 2.07, which was corrected by reducing the dietary composition of coarsely branched algae in the limpet consumers diet by half; the proportion of drift algae in the limpet groups diet was correspondingly increased.

4.1.2. General model of the Mussel Bed

Initially, a general model was constructed to represent the mussel bed on exposed shores (maximum wave force readings of 15000 N. m^{-2}) and at a shore height with an air exposure of approximately 20%, equivalent to the lower balanoid zone. This rocky shore environment is where the mussel beds have the greatest biomass on the west coast, averaging $3.24 \text{ kg AFDm. m}^{-2}$ (excluding detritus and debris). Although some species were omitted, 99.7% of the total biomass of organisms recorded from the 1990 Surveys was included in the model. The trophic flows for this general model are summarised graphically in Figure 4.1 although some of the smaller flows between groups have been omitted.

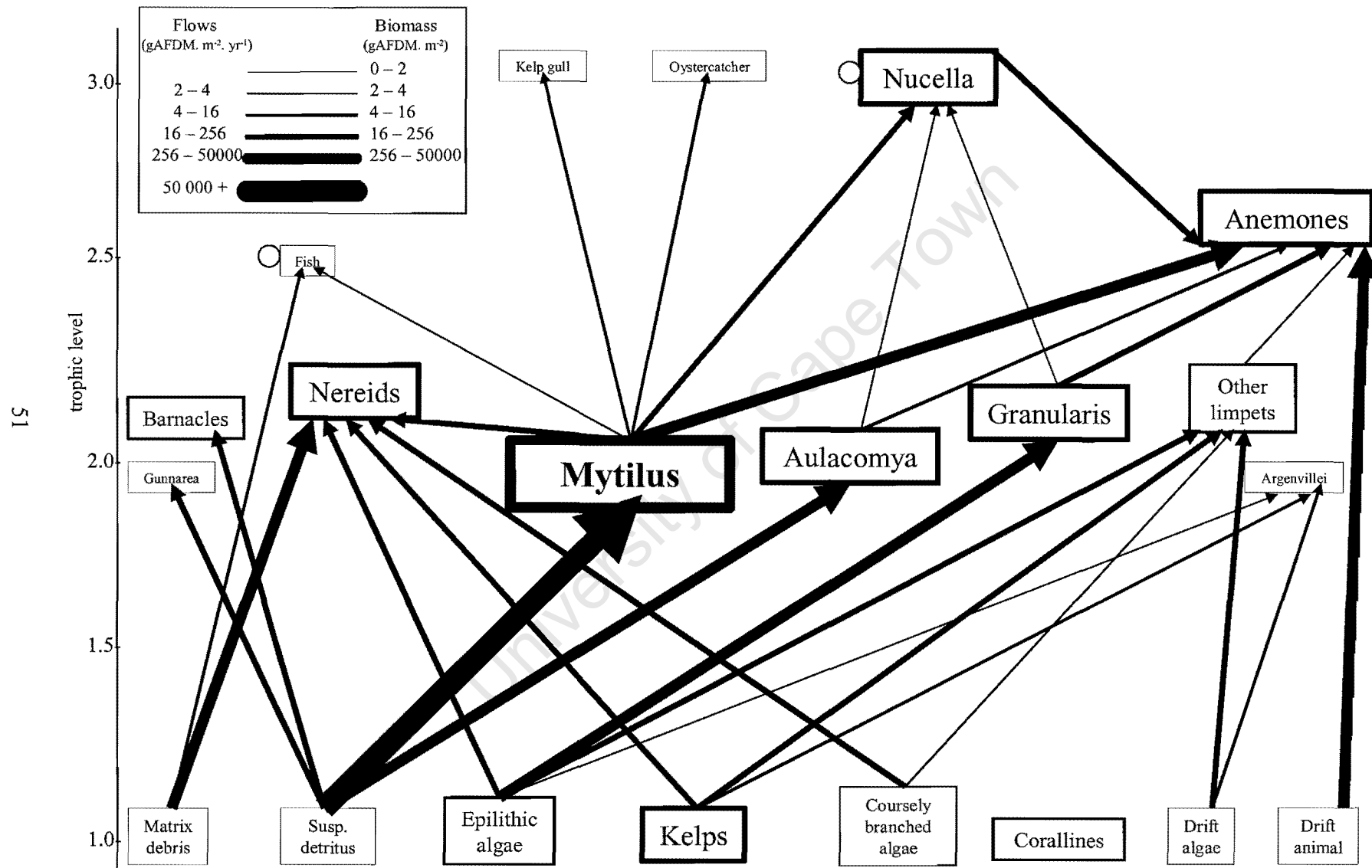


Figure 4.1: Trophic diagram of flows in a South African west coast mussel bed. Boxes are arranged along the vertical axis by trophic level. The magnitudes of flows and biomass are symbolised by the thickness of the arrows and lines boxing the components (see key). Flows less than 2 gAFDM. m⁻². yr⁻¹ were omitted. Circles indicate cannibalism.

4.1.2.1. Dietary Composition Matrix

The input dietary data for the general model of a mussel bed on wave exposed lower-balanoid shores are given in Table 4.1, which summarises the dietary composition of the heterotrophs and shows the trophic links between species. Most groups feed on a range of prey items with the vertebrates, *Nucella* spp. and anemones feeding on a wide range of the heterotrophic groups, and the herbivorous gastropods feeding on various algal groups. The diet of filter-feeding mussels and barnacles is apparently restricted because they are limited to consuming suspended detritus from the water column.

Table 4.1: Balanced proportional dietary composition of groups from the intertidal mussel-bed system of exposed shores at 20% air exposure on west-coast rocky shores. The connectivity matrix summarises the proportional flows from row groups (prey) to column groups (predators).

PREDATOR	Oystercatcher	Kelp Gull	Fish	Mytilus	Aulacomya	Anemones	Gunnarea	Granularis	Other limpets	Argenvillei	Barnacles	Nucella	Nereids
PREY													
1. Oystercatcher	0	0	0	0	0	0	0	0	0	0	0	0	0
2. Kelp Gull	0	0	0	0	0	0	0	0	0	0	0	0	0
3. Fish	0	0	0.018	0	0	0	0	0	0	0	0	0	0
4. Mytilus	0.661	0.196	0.178	0	0	0.443	0	0	0	0	0	0.958	0.049
5. Aulacomya	0.013	0.004	0.003	0	0	0.009	0	0	0	0	0	0.019	0
6. Anemones	0	0	0	0	0	0	0	0	0	0	0	0	0
7. Gunnarea	0	0	0	0	0	0	0	0	0	0	0	0	0
8. Granularis	0.213	0.043	0.002	0	0	0.018	0	0	0	0	0	0.011	0
9. Other limpets	0.034	0.006	0	0	0	0.003	0	0	0	0	0	0.001	0
10. Argenvillei	0.048	0.001	0	0	0	0.001	0	0	0	0	0	0	0
11. Barnacles	0	0	0.048	0	0	0	0	0	0	0	0	0.002	0
12. Nucella	0.001	0	0.001	0	0	0.015	0	0	0	0	0	0.009	0
13. Nereids	0.03	0	0.136	0	0	0.001	0	0	0	0	0	0	0
14. Epilithic algae	0	0	0.005	0	0	0	0	0.993	0.177	0.141	0	0	0.055
15. Coarsely branch	0	0	0.001	0	0	0	0	0	0.048	0.032	0	0	0.014
16. Kelps	0	0	0.01	0	0	0	0	0	0.272	0.255	0	0	0.1
17. Corallines	0	0	0	0	0	0	0	0.007	0	0.009	0	0	0
18. Susp. detritus	0	0	0	1	1	0	1	0	0	0	1	0	0
19. Drift animal	0	0	0	0	0	0.51	0	0	0	0	0	0	0
20. Dislodged debris	0	0	0	0	0	0	0	0	0	0	0	0	0
21. Drift algae	0	0	0	0	0	0	0	0	0.503	0.563	0	0	0
22. Matrix debris	0	0	0.598	0	0	0	0	0	0	0	0	0	0.782
Import	0	0.75	0	0	0	0	0	0	0	0	0	0	0

4.1.2.2. Basic Input and Output Parameters

Summaries of the input for the balanced general model of a mussel bed on exposed, lower-balanoid shores are detailed in Table 4.2 as well as the EE for each group and the ratio of production to consumption (gross efficiency, GE). The highest GE value was 0.25, which is equivalent to a production rate that is one fourth of the consumption rate, which is within the range of normal GE values. The low GE value for nereids is likely due to the detrital diet. The mortalities of each group due to predation and other (non-predation) sources of mortality are also detailed in Table 4.2. *Mytilus galloprovincialis* dominates the biomass, followed by anemones. The anemones have a high trophic level and a large total consumption but because they are sit-and-wait predators that rely on wave-tumbled prey, their impact on the other groups is likely to be small. *Nucella* spp. has the highest biomass of the 'active' predators, but its biomass is small compared with *M. galloprovincialis*.

After mussels and anemones, limpets collectively form the third largest biomass component, larger than the standing stock of algae. This is possible since the algae have large P/B values, particularly epilithic algae with their high growth potential. The big EE values for algae reflect intense limpet grazing. Of the heterotrophs, the two biggest P/B and Q/B ratios are for the birds, which are the only endotherms in the model. The EE is zero for some groups since there are no known predators for these groups in the modelled system.

Table 4.2: Summary of the parameters of the living groups in the balanced Ecopath model of an intertidal mussel bed on the west coast of South Africa. Input into the model consisted of the type of organism (0 – heterotrophs, 1 – autotrophs), the biomass, the ratio of production to biomass (P/B), the consumption to biomass ratio (Q/B) and the unassimilated portion of the diet. From the output of the model the following were derived: the ecotrophic efficiency (EE), the gross efficiency (the ratio of production to consumption or GE) and proportions of the P/B due to predation mortality and other mortality losses. An EE value of zero indicates that there were no known predators of these species within the system.

Group Name	type	Biomass	P/B	Q/B	Unassim.	EE	GE	Other mortality	Predation mortality
		(gAFDM.m ⁻²)	(yr ⁻¹)	(yr ⁻¹)	(%)			(yr ⁻¹)	(yr ⁻¹)
1. Oystercatcher	0	0.083	5.40	74.3	0.28	0.000	0.073	5.40	0.00
2. Kelp Gull	0	0.690	5.40	61.3	0.20	0.000	0.088	5.40	0.00
3. Fish	0	0.964	2.16	12.8	0.23	0.107	0.169	1.93	0.23
4. Mytilus	0	2892	2.39	17.9	0.22	0.118	0.133	2.11	0.28
5. Aulacomya	0	56.0	2.04	11.1	0.40	0.131	0.184	1.77	0.27
6. Anemones	0	157	1.50	7.70	0.10	0.000	0.195	1.50	0.00
7. Gunnarea	0	1.25	2.00	20.0	0.20	0.000	0.100	2.00	0.00
8. Granularis	0	33.0	2.00	21.7	0.40	0.411	0.092	1.18	0.82
9. Other limpets	0	4.50	3.55	21.7	0.40	0.269	0.164	2.50	0.95
10. Argenvillei	0	1.00	2.50	21.7	0.40	0.619	0.115	0.95	1.55
11. Barnacles	0	5.00	2.82	26.7	0.26	0.071	0.106	2.62	0.20
12. Nucella	0	27.0	1.88	7.48	0.20	0.393	0.251	1.14	0.74
13. Nereids	0	25.1	1.64	58.0	0.45	0.075	0.028	1.52	0.12
14. Epilithic algae	1	7.75	111	-	-	0.936	-	7.21	104.59
15. Coarsely branch	1	2.00	24.8	-	-	0.520	-	11.91	12.89
16. Kelps	1	18.0	10.0	-	-	0.988	-	0.12	9.88
17. Corallines	1	4.00	1.33	-	-	0.978	-	0.03	1.30

The magnitudes of the flows due to predation and non-predatory mortality can be found from the products of biomass and the ratio of predation to other mortality, which are detailed in Table 4.3. The sum of all unconsumed production and unassimilated food of all the groups that flows to detritus totals 19547.2 g AFDM.m⁻².yr⁻¹. *Mytilus galloprovincialis* contributes massively to detritus flows via storm damage and

intraspecific competition. These non-predatory mussel losses remove many of the other groups in the model because they are swept away with the mussels. For all heterotrophs, the flows to detritus far exceed the flows to predators. For all the autotrophic groups, flows due to consumption exceed the flows to detritus.

The product of production and EE is equivalent to that part of production that is consumed by predators. The single group with the highest consumed production is *Mytilus galloprovincialis*, due to its large biomass and many predators (Table 4.3). Relative to its biomass, however, only a minor proportion is consumed. Collectively, algae have a small biomass but total consumption of algae exceeds that of *M. galloprovincialis*, largely because of heavy grazing on epilithic algae by limpets. The net efficiency is the ratio of production to assimilated food, and varies between 5% and 31% depending on the group. The trophic level of each component was calculated by assigning detritus and algae as level 1, and assigning other groups to a trophic level of one plus the average of the group's prey trophic level weighted by dietary composition. This ranking of trophic levels gives oystercatchers, Kelp Gulls and *Nucella* spp. the highest trophic-level ranking and the herbivores and filter-feeders have trophic levels of two (Table 4.3). Fish and anemones have intermediate values as they have mixed diets. The omnivory index is a dimensionless, comparative estimate of the variance of the trophic level of a consumer's prey and is calculated by Ecopath; it is highest for the Kelp Gull, anemones and fish since these groups consume prey from a wide range of trophic levels. Low omnivory index values indicate the component specialises on one prey component in the model or due to the predator consuming prey all at a similar trophic level (i.e. limpets). The square root of the omnivory index is the standard error of the trophic level. Food mass that is assimilated sums to 43,6 kg AFDM.m⁻².yr⁻¹.

The respiratory energy flows were calculated for each group by Ecopath using the equation: respiration = consumption – non-assimilated food – somatic production, and are detailed in Table 4.3. Respiratory flows for each living group in the model thus

include respiration, losses of mucus, excretion and reproductive production. The total “respiration” loss is 36187.7 g AFDM.m⁻².yr⁻¹ and 93% of this loss comes from *Mytilus galloprovincialis*. Van Erkom Schurink and Griffiths (1991) calculated a reproductive production to biomass ratio of 0.16 year⁻¹ for local *M. galloprovincialis*, which converts to a reproductive output of 463 g AFDM.m⁻².yr⁻¹ for lower balanoid exposed shores. The entire gametic output of the modelled mussel bed is likely to be similar to this figure for *M. galloprovincialis* due to this mussel comprising such a large portion of the total biomass in the model.

Table 4.3: Summary of flows to detritus, the flow to predators (product of production and EE), the net efficiency, the trophic level, the omnivory index, and flows as respiration and assimilated food for each of the living groups in the Ecopath model of an intertidal mussel bed on the west coast of South Africa.

Group Name	Flow to Detritus	Flow to Predators	Net Efficiency	Trophic Level	Omnivory Index	Respiration	Assim. food
	(gAFDM.m ⁻² .yr ⁻¹)					(gAFDM.m ⁻² .yr ⁻¹)	
1. Oystercatcher	2.18	0.00	0.101	3.0	0.001	3.99	4.44
2. Kelp Gull	12.18	0.00	0.110	3.0	0.562	30.11	33.83
3. Fish	4.70	0.22	0.219	2.4	0.259	7.42	9.50
4. Mytilus	17536.00	814.90	0.170	2.0	0	33646.00	40558.00
5. Aulacomya	347.80	15.00	0.306	2.0	0	258.70	372.90
6. Anemones	356.30	0.00	0.216	2.5	0.280	852.50	1088.00
7. Gunnarea	7.50	0.00	0.125	2.0	0	17.50	20.00
8. Granularis	325.10	27.13	0.154	2.0	0	363.40	429.40
9. Other limpets	50.72	4.29	0.273	2.0	0	42.58	58.56
10. Argenvillei	9.63	1.55	0.192	2.0	0	10.51	13.01
11. Barnacles	47.81	1.00	0.143	2.0	0	84.69	98.79
12. Nucella	71.18	19.97	0.314	3.0	0.009	110.80	161.50
13. Nereids	693.20	3.0720	0.051	2.0	0.047	759.50	800.70
14. Epilithic algae	55.89	811.20	-	1	-	-	-
15. Coarsely branch	23.82	25.77	-	1	-	-	-
16. Kelps	2.22	177.70	-	1	-	-	-
17. Corallines	0.11	5.21	-	1	-	-	-
Totals	19546	1907	-	-	-	36187	43649

The fraction of a group's production that is consumed by that group's predators is called the ecotrophic efficiency (EE) and the values of EE for each living group in the general mussel-bed model are detailed in Figure 4.2, in which the groups are arranged by trophic level. The proportion of production of a group that is not consumed but flows to detritus is (1-EE). The birds and *Nucella* spp. have a trophic level of 3 and an average EE of 0.13. The fish and anemones group have a trophic level around 2.5 and an average EE of 0.05. The other invertebrate groups had a trophic level of 1 and their EE values varied from 0.00 to 0.62. The algal groups, with a trophic level of 1, had higher EE values between 0.52 and 0.99. Generally the proportion of production consumed of each group decreases with increasing trophic level with the exception of *Nucella* spp. Ecotrophic Efficiency is zero for the birds, anemones and *Gunnarea capensis* since there is no predator group included in the model that feeds upon them although these higher predator groups possibly do experience predation outside the model.

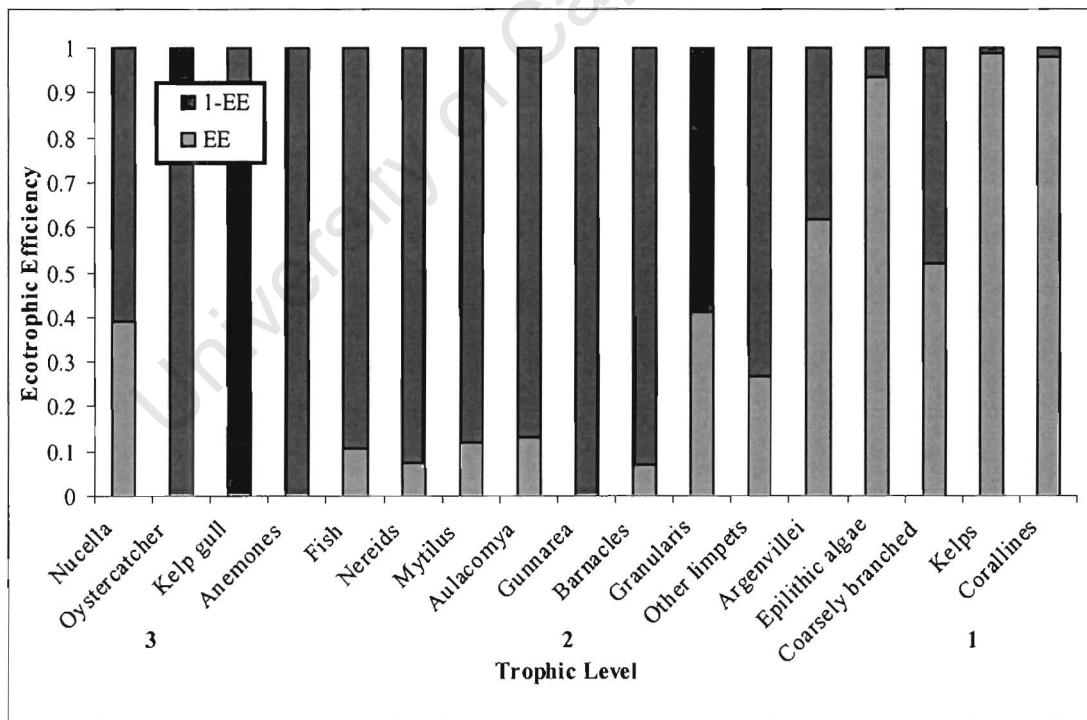


Figure 4.2: Ecotrophic efficiencies (EE) and unconsumed portions of production (1-EE) for the living groups in the Ecopath model of a mussel bed on the west-coast intertidal. The groups have been ordered by decreasing trophic level.

Flows to detritus in terms of production that is not consumed by the group's predators and unassimilated food are detailed in Figure 4.3. These flows represent the qualitative estimates of the amounts of material that are dislodged from the mussel bed for each living group including the production of faeces; the *Mytilus galloprovincialis* group contributes 89.8% of this flow in terms of biomass. The remainder of the biomass consists mostly of nereids, *Aulacomya ater*, anemones and *Scutellastra granularis*. Only small quantities of primary-producer biomass are washed off the mussel bed, reflecting their low biomass and the heavy predation on these groups. The low biomass of the vertebrates accounts for the small flows of these groups to detritus and debris.

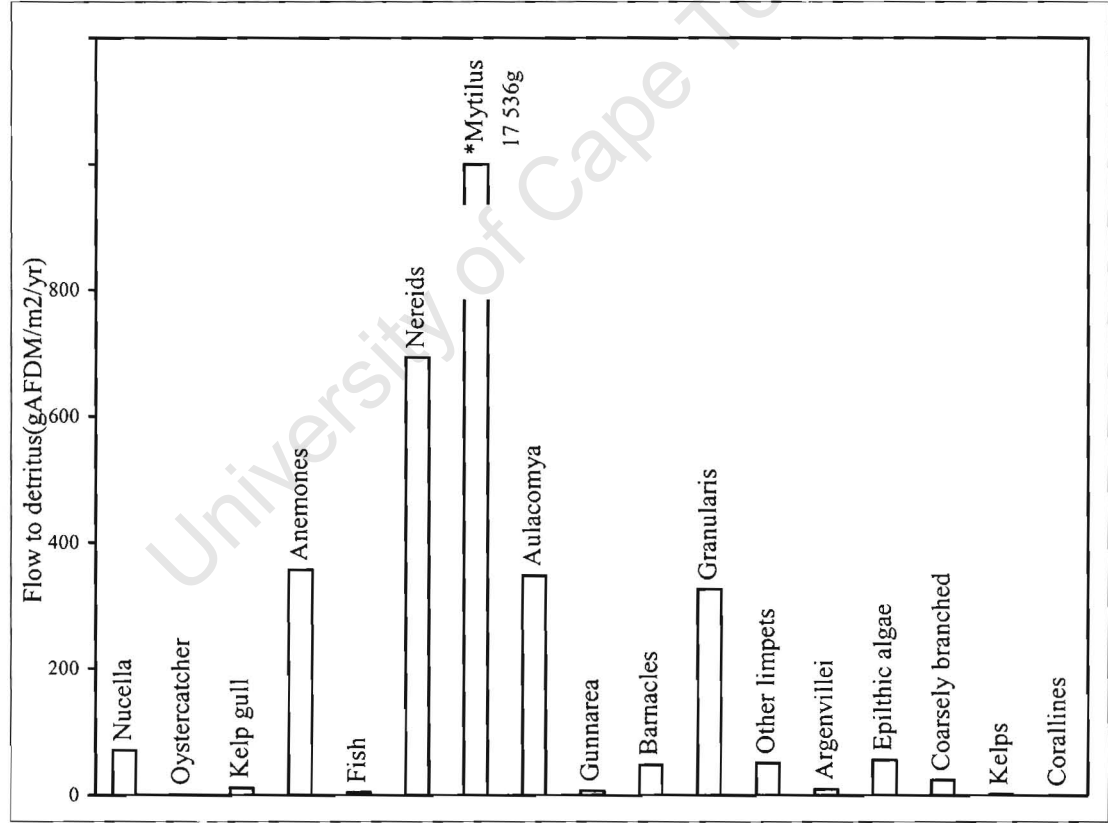


Figure 4.3: Flows to detritus of unconsumed production and faeces from the living groups in the Ecopath model of an intertidal mussel bed on the west coast of South Africa. The groups have been arranged by trophic level. * For graphical purposes, the *Mytilus galloprovincialis* group is shortened from 17 536 g AFDM.m⁻². yr⁻¹.

4.1.2.3. Summary Statistics and Major Flows

The mussel bed community was summarised by calculating various statistics from the balanced Ecopath model, as detailed in Table 4.4. The sum of exports is zero since all material dislodged from the rock was modelled as flowing to a detritus and debris compartment and there was no harvesting of any of the components. The sum of flows to detritus represents the sum of material washed from the rocky shore and the sum of all non-assimilated portions of consumed food. The total system throughput is the sum of all flows in the system i.e., consumption, exports, respiration and flows to detritus. Net system production (or yield) is the difference between total primary production and total respiration. Systems with large imports may have a negative system production, as in this case. Christensen and Pauly's (1992) connectance index is defined as the ratio of the actual number of trophic links between groups to the number of possible links. The system omnivory index is defined as average omnivory index of all consumers, weighted by the logarithm of food intakes.

Table 4.4: Summary statistics for the general trophic model of an intertidal mussel bed on exposed, lower balanoid shores on the west coast of South Africa.

Statistic	Value
Total biomass excluding detritus (g AFDM. m ⁻²)	3235.343
Flows (g AFDM m⁻².yr⁻¹)	
Sum of all consumption	56540.787
Sum of all exports	0.000
Sum of all respiratory flows	36188.524
Sum of all flows into detritus	74149.081
Total system throughput	166878.392
Sum of all production	8562.917
Calculated total net primary production	1102.04
Net system production	-35086.483
Ratios and Indices	
Total primary production/total biomass	0.341
Total biomass/total throughput	0.019
Total primary production/total respiration	0.030
Connectance Index	0.197
System Omnivory Index	0.069

4.1.2.4. Required Primary Production

The total primary production required (PPR) to sustain each heterotrophic group in the Ecopath model was calculated. For each network path to a group, the flows from the primary production equivalents were summed using the formula: consumption/production ratio of each path element times the proportion the next element of the path contributes to the diet of the given path element. The basal path elements are algae, debris and detritus. The origin of debris and detritus is mainly from subtidal primary production and there would be losses due to decay of this subtidal primary production that are unaccounted for in the model. The number of paths to each group calculated by Ecopath is given in Table 4.5 and the trophic level is derived from Table 4.3. The ratio of PPR to consumption reflects the degree to which a group is dependant upon lower trophic levels to sustain itself and thus parallels the calculation of trophic level. The filterfeeders and herbivores derive all energy requirements directly from the trophic level below them, although the vertebrates require up to nine times more energy generated basally in the food web than they directly consume because of the inefficiency of energy transfer up a food web. Predators, with the highest trophic level, the largest number of paths and the highest PPR to consumption ratios, still have comparatively small PPR levels due to their small biomass. The largest PPR is required by *Mytilus galloprovincialis* (needing 52.0 kg AFDM. m⁻². yr⁻¹) even though the group is situated basally in the food web.

Table 4.5: Number of paths from prey to predator, trophic level of the group, total primary production required (PPR), consumption, and PPR to consumption ratio of the living consumer groups in the Ecopath model of an intertidal mussel bed on the west coast of South Africa.

Group Name	No. of paths	Trophic level	PPR (g AFDMm ⁻² . yr ⁻¹)	Consumption (g AFDMm ⁻² . yr ⁻¹)	PPR/cons.
1. Oystercatcher	27	3.0	58.0	6.2	9.4
2. Kelp Gull	13	3.0	339.7	42.3	8.0
3. Fish	23	2.4	110.9	12.3	9.0
4. Mytilus	1	2.0	51998.2	51998.2	1.0
5. Aulacomya	1	2.0	621.6	621.6	1.0
6. Anemones	28	2.5	5572.4	1208.9	4.6
7. Gunnarea	1	2.0	25.0	25.0	1.0
8. Granularis	2	2.0	715.8	715.8	1.0
9. Other limpets	4	2.0	97.6	97.6	1.0
10. Argenvillei	5	2.0	21.7	21.7	1.0
11. Barnacles	1	2.0	133.5	133.5	1.0
12. Nucella	9	3.0	1519.2	202.0	7.5
13. Nereids	5	2.0	1921.1	1455.8	1.3

4.1.2.5. Mixed Trophic Impact Assessment

Indirect and direct interactions were assessed by Ecopath's mixed trophic impact assessment whereby the changes in the biomass of all groups are noted after an consecutive equal proportional increase in biomass of 10% of each group (Figure 4.4). The reduction in the biomass of each group upon itself is due to the group lowering the biomass of its prey and thus increasing intraspecific competition for food. Most of the top predator groups (oystercatcher, kelp gull, rockfish and *Nucella* spp.) have little impact on other groups except anemones (*Aulactinia reynaudi*), which appear in the impact assessment as strongly linked to the "drift animal" debris compartment.

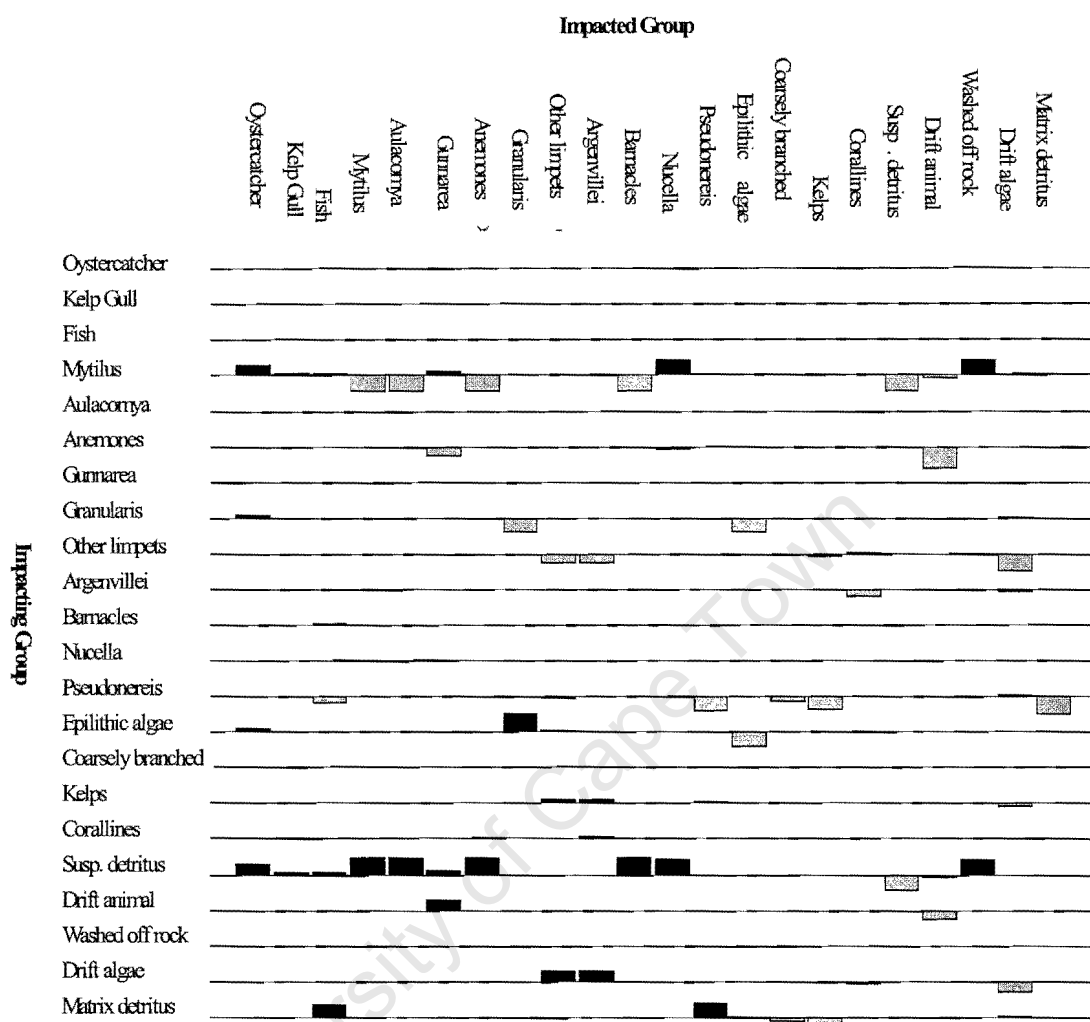


Figure 4.4: Mixed trophic impacts of selected groups in the mussel bed system on the west coast of South Africa (output of Ecopath model). The bars indicate relative net impact of increasing the impacting species (scaled between zero and unity). Positive impacts are shown above the zero line for each group, and negative impacts below. Impacted groups are arranged along the horizontal axis and impacting groups down the vertical axis.

Mytilus galloprovincialis has large impacts on many of the groups. An increase in *M. galloprovincialis* biomass seems to induce strong negative impacts on other filterfeeders and increases in *M. galloprovincialis* biomass mostly favour the predators *Nucella* spp. and oystercatcher, although in this trophic model, *M. galloprovincialis* shows no interaction with the limpets. The suspended detritus compartment also has notable

impacts on most groups from filterfeeders to the top predators. The algal groups of most significance to grazers are epilithic algae and the “drift algal” debris compartment.

4.1.2.6. Sensitivity analysis

The balanced general model of mussel beds on wave-exposed, lower-balanoid shores was tested using sensitivity analysis in which each of the values of input parameters of B, Q/B and P/B were reduced or increased by increments of 10% to a total of 50% and the subsequent proportional change in the EE noted. If the incremental change of 50% in the input parameter caused a proportional change of 0.40 or greater in the output parameters then it was considered to have a large effect and was detailed in Table 4.6. The groups that were most sensitive to changes in their input parameters were anemones, nereids and *Scutellastra granularis*. Only in the case of anemones, *S. granularis* and nereids did changes in inputs for each group result in changes in the EE output of other groups. Reduced B or Q/B for anemones reduced the EE (proportion of production consumed) for *S. granularis*, the other limpets and *Nucella* species. Reductions of these inputs for *S. granularis* reduced the EE for epilithic algae and corallines, and reductions of these same inputs for nereids led to reduced EE for kelps and coarsely branched algae. Changes in the inputs of other groups rarely seriously affected the balance of the model.

Table 4.6: Results of sensitivity analyses performed on the balanced general model of mussel beds on wave exposed, lower balanoid shores. The table details the name of the group and parameter (whether biomass (B), P/B or Q/B) of the group tested in the first column and the name of the group with an affected EE is in the second column. Values are proportional changes in the affected group's EE. The table covers only those combinations of parameters and groups for which a change of up to 50% in the input parameter caused a 0.40 or larger proportional change in the EE.

Changed group & parameter	Affected group & parameter	Percentage change in parameter						
		-50%	-30%	-10%	0%	10%	30%	50%
Fish, P/B	Fish, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Fish, Q/B	Fish, EE	-0.5	-0.3	-0.1	0	0.1	0.3	0.5
Mytilus, B	Mytilus, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Mytilus, P/B	Mytilus, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Aulacomya, B	Aulacomya, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Aulacomya, P/B	Aulacomya, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Anemones, B	Granularis, EE	-0.4	-0.24	-0.08	0	0.08	0.24	0.4
Anemones, B	Other limpets, EE	-0.42	-0.25	-0.08	0	0.08	0.25	0.42
Anemones, B	Nucella, EE	-0.45	-0.27	-0.09	0	0.09	0.27	0.45
Anemones, Q/B	Granularis, EE	-0.4	-0.24	-0.08	0	0.08	0.24	0.4
Anemones, Q/B	Other limpets, EE	-0.42	-0.25	-0.08	0	0.08	0.25	0.42
Anemones, Q/B	Nucella, EE	-0.45	-0.27	-0.09	0	0.09	0.27	0.45
Granularis, B	Granularis, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Granularis, B	Epilithic algae, EE	-0.44	-0.26	-0.09	0	0.09	0.26	0.44
Granularis, B	Corallines, EE	-0.48	-0.29	-0.1	0	0.1	0.29	0.48
Granularis, P/B	Granularis, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Granularis, Q/B	Epilithic algae, EE	-0.44	-0.26	-0.09	0	0.09	0.26	0.44
Granularis, Q/B	Corallines, EE	-0.48	-0.29	-0.1	0	0.1	0.29	0.48
Other limpets, B	Other limpets, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Other limpets, P/B	Other limpets, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Argenvillei, B	Argenvillei, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Argenvillei, P/B	Argenvillei, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Barnacles, B	Barnacles, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Barnacles, P/B	Barnacles, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Nucella, B	Nucella, EE	0.91	0.39	0.1	0	-0.08	-0.21	-0.3
Nucella, P/B	Nucella, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Nereids, B	Nereids, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Nereids, B	Coarsely branched, EE	-0.4	-0.24	-0.08	0	0.08	0.24	0.4
Nereids, B	Kelps, EE	-0.41	-0.25	-0.08	0	0.08	0.25	0.41
Nereids, P/B	Nereids, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Nereids, Q/B	Coarsely branched, EE	-0.4	-0.24	-0.08	0	0.08	0.24	0.4
Nereids, Q/B	Kelps, EE	-0.41	-0.25	-0.08	0	0.08	0.25	0.41
Epilithic algae, B	Epilithic algae, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Epilithic algae, P/B	Epilithic algae, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Coarsely branched, B	Coarsely branched, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Coarsely branched, P/B	Coarsely branched, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Kelps, B	Kelps, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Kelps, P/B	Kelps, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Corallines, B	Corallines, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33
Corallines, P/B	Corallines, EE	1	0.43	0.11	0	-0.09	-0.23	-0.33

4.1.3. Trophic Aggregation of the General Model of the Mussel Bed

The 21 groups in the general model were reduced to six groups by trophic aggregation so that the model could be represented in a simpler form that detailed the flows between the main functional trophic groups. The groups in the general model were reduced to the following functional groups: Vertebrate predators (oystercatcher, Kelp Gull, fish), Limpet grazers (*S. argenvillei*, *S. granularis*, other limpets), Filter Feeders (*Mytilus galloprovincialis*, *Aulacomya ater*, *Gunnarea capensis*, barnacles), Detritus and debris feeders (nereids), and Anemones (anemones). A single detritus and debris component was formed, and named 'Import Detritus' (drift algae, drift animal, suspended detritus, dislodged detritus and debris). The biomass of the trophically aggregated groups was derived by summation of the single groups; whereas the values for production, consumption and dietary composition were derived by biomass weighted averaging the single groups. The condensed model had similar summary statistics to the general model of a mussel bed on wave exposed, lower balanoid shores.

4.1.3.1. Basic Input and Output Parameters

Similar summaries to those of the unaggregated general model of the mussel bed are given in Table 4.7, which details most of the input parameters and the calculated EE and sources of mortality, and in Table 4.8, which details the calculated flows to detritus and flows due to respiration and amount of food assimilated for each group. The Filter-feeder group has the largest production of somatic tissues with 21061 g AFDM. m⁻¹. yr⁻¹ being dislodged off the rock and 846 g AFDM. m⁻¹. yr⁻¹ being consumed by predators (Table 4.8).

Table 4.7: Summary of the parameters of the living groups in the trophically aggregated Ecopath model of an intertidal mussel bed on the west coast of South Africa. Input into the model consisted of the type of organism (0 – heterotrophs, 1 – autotrophs), the biomass, the ratio of production to biomass (P/B), the consumption to biomass ratio (Q/B) and the assimilated portion of the diet. Derived from the output of the model were the ecotrophic efficiency (EE), the gross efficiency (the ratio of production to consumption or GE) and proportion of the P/B due to predation mortality and other mortality losses.

Group Name	type	Biomass (gAFDM. m ⁻²)	P/B (yr ⁻¹)	Q/B (yr ⁻¹)	Unassim. (%)	EE	GE	Other mortality (yr ⁻¹)	Predation mortality (yr ⁻¹)
1. Algae	1	31.8	37.0	-	-	0.707	-	10.8	26.1
2. Limpets	0	38.5	2.68	21.7	0.40	0.555	0.124	1.19	1.49
3. Filter feeders	0	2954	2.31	18.9	0.27	0.124	0.122	2.03	0.29
4. Vertebrates	0	1.74	4.32	49.5	0.24	0.069	0.087	4.02	0.30
5. Anemones	0	157	1.50	7.70	0.10	0	0.195	1.50	0.00
6. Nucella	0	27.0	1.88	7.48	0.20	0.085	0.251	1.72	0.16
7. Nereids	0	25.1	1.64	58.0	0.45	0.144	0.028	1.40	0.24

Table 4.8: Summary of flows to detritus, the product of production and EE, the net efficiency, the trophic level, the omnivory index, and flows as respiration and assimilation for each of the living groups in the Ecopath model of an intertidal mussel bed on the west coast of South Africa.

Group Name	Flow to Detritus	Production * EE	Net Efficiency	Trophic Level	Omnivory Index	Respiration	Assim.
	(gAFDM.m ⁻² .yr ⁻¹)					(gAFDM.m ⁻² .yr ⁻¹)	
1. Algae	344.3	830.2	-	1	-	-	-
2. Limpets	380.0	57.2	0.206	2	0	397.9	501.0
3. Filter feeders	21061	846.0	0.168	2	0	33923	40756
4. Vertebrates	27.6	0.52	0.115	2.7	0.30	57.8	65.3
5. Anemones	356.4	0	0.216	2.5	0.25	852.5	1088
6. Nucella	86.8	4.32	0.314	3.0	0.01	110.8	161.6
7. Nereids	690.3	5.94	0.051	2.1	0.05	759.5	800.7

4.1.3.2. Trophic Flows between Groups

A matrix of the consumption of each of the groups in the trophically aggregated model is detailed in Table 4.9. The total consumption of *Nucella* spp. is more than twice that of the combined vertebrate groups. Anemones are the largest consumer of filter-feeders. A total of 55.8 kg AFDM. m⁻². yr⁻¹ of suspended detritus from the water column (Import Detritus) is required to sustain the filter-feeders.

Table 4.9: Matrix summarising the food intake of trophically aggregated groups of predators to prey in the intertidal mussel bed on the west coast of South Africa. Prey groups are listed in rows and predators in columns. Flow of energy passes from a row component to a column component. Flow is in (g AFDM. m⁻². yr⁻¹).

Predator Prey	Vertebrates	Nucella	Anem.	Filter-feeders	Limpets	Nereids	Algae	Matrix detritus	Import detritus
Vertebrates	0.516	0	0	0	0	0	0	0	27.6
Nucella	0.086	1.82	2.42	0	0	0	0	0	86.8
Anemones	0	0	0	0	0	0	0	0	356
Filter-feeders	31.6	198	544	0	0	72.8	0	0	21061
Limpets	9.89	2.63	44.7	0	0	0	0	0	380
Nereids	4.73	0	1.21	0	0	0	0	0	690
Algae	0.43	0	0	0	539	291	0	0	344
Matrix detritus	17.1	0	0	0	0	1092	0	0	0
Import detritus	0	0	617	55831	296	0	0	0	0
Import	21.6	0	0	0	0	0	0	1109	33798
Sum	86.0	202	1209	55831	835	1456	0	1109	56744

The trophic flows in the aggregated model of the mussel bed are diagrammatically represented in Figure 4.5 with the flows between boxes quantified and the biomass of each box represented.

4.1.4. Trophic Flows specific to the *Mytilus galloprovincialis* group

The *Mytilus galloprovincialis* group has the largest biomass, consumption and production values in the model, although it consisted of a single species. Consequently, the flows in and out of this group were studied in detail using uncondensed models with 21 groups, and separately exploring differences between five zones on wave-exposed shores and two zones on semi-exposed shores.

4.1.4.1. Ecotrophic efficiencies

The Ecotrophic efficiencies for *Mytilus galloprovincialis* for each of the seven models are detailed in Figure 4.6. This is a comparison of the proportions of energy that flow through the *Mytilus galloprovincialis* group and are consumed by predators (EE), and the proportions flowing to detritus (1 – EE). The proportion of consumed *Mytilus galloprovincialis* decreases with increasing shore height and is greater at wave-exposed than semi-exposed shores in the models.

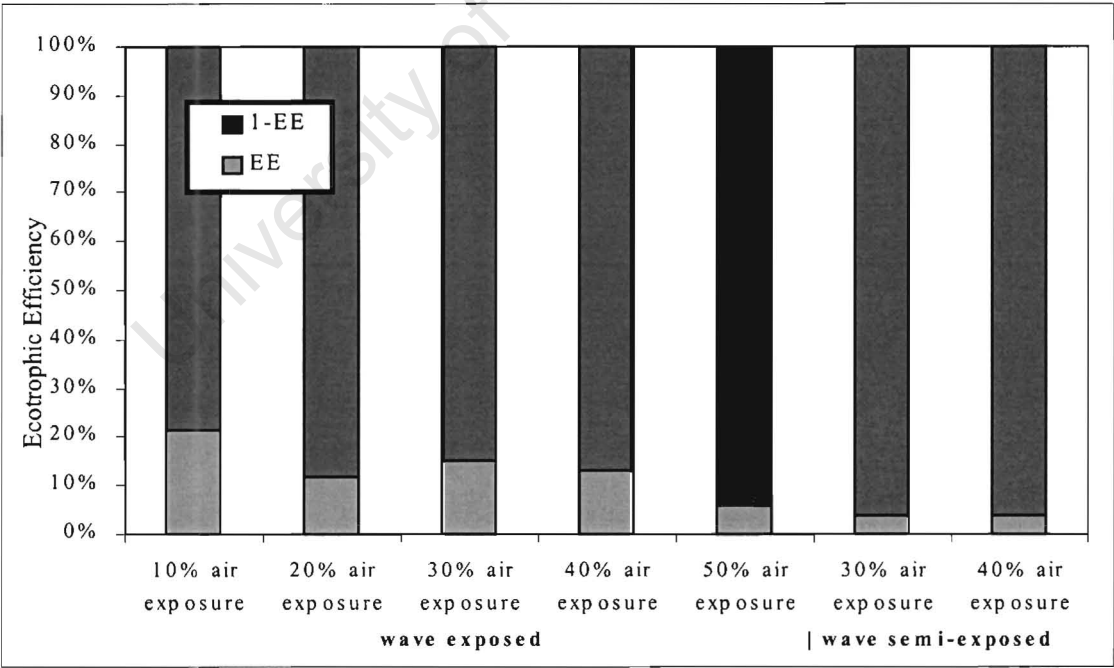


Figure 4.6: Ecotrophic efficiencies (EE) for the group *Mytilus galloprovincialis* at different shore heights and wave exposures in an intertidal mussel bed on the South African west coast.

4.1.4.2. Food Intake by *Mytilus galloprovincialis* predators

The mass of mussels consumed by different species or groups varied with wave exposure and shore height (Figure 4.7) although anemones (*Aulactinia reynaudi*) consistently consumed the largest biomass of mussels. *Nucella* spp. consumed the second largest proportions of mussels on wave-exposed shores but not on semi-exposed shores. Nereids were modelled by assuming that mussels constitute 5% of their diet, and were notable consumers of mussels on semi-sheltered shores only. Vertebrates consumed minor proportions. Overall, consumption was greater on exposed than semi-exposed shores and peaked midway up the vertical gradient examined.

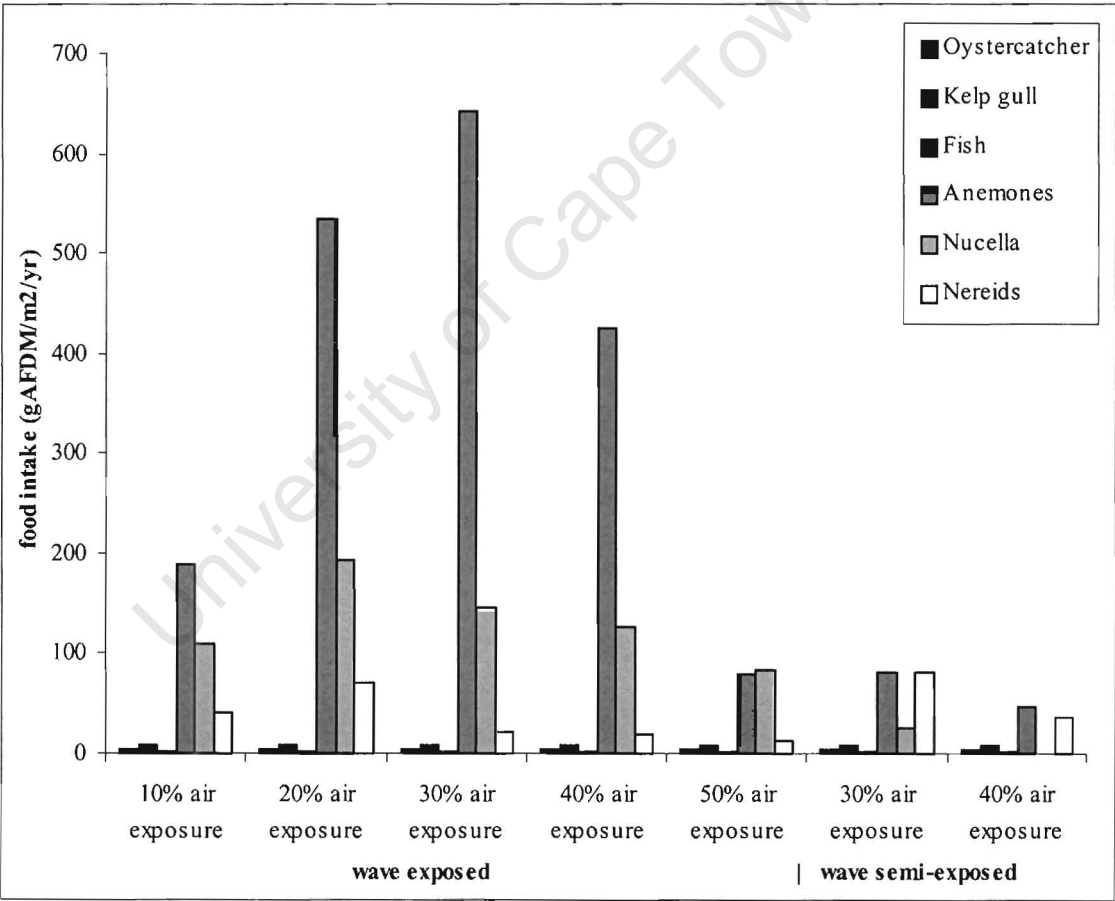


Figure 4.7: Consumption of *Mytilus galloprovincialis* by its predators: African Black Oystercatcher, Kelp Gull, intertidal rockfish, anemones, *Nucella* spp. and nereids at different wave exposures and tidal heights.

4.1.5. Comparison of Wave Exposures and Shore Heights

Comparisons of changes in the overall trophic structure of the models at different shore heights and wave exposures were possible by comparing summary statistics and indices. These comparisons were made using the seven uncondensed models with 21 groups.

4.1.5.1. Total Flows

Estimated total flows include total flows to detritus, total consumption, total respiratory flows, and total production (Figure 4.8). These four total flow terms sum to the Total system throughput (Table 4.10). The sums of flows peak at 20% air exposure and then decrease with shore height and are greater at exposed than semi-exposed shores.

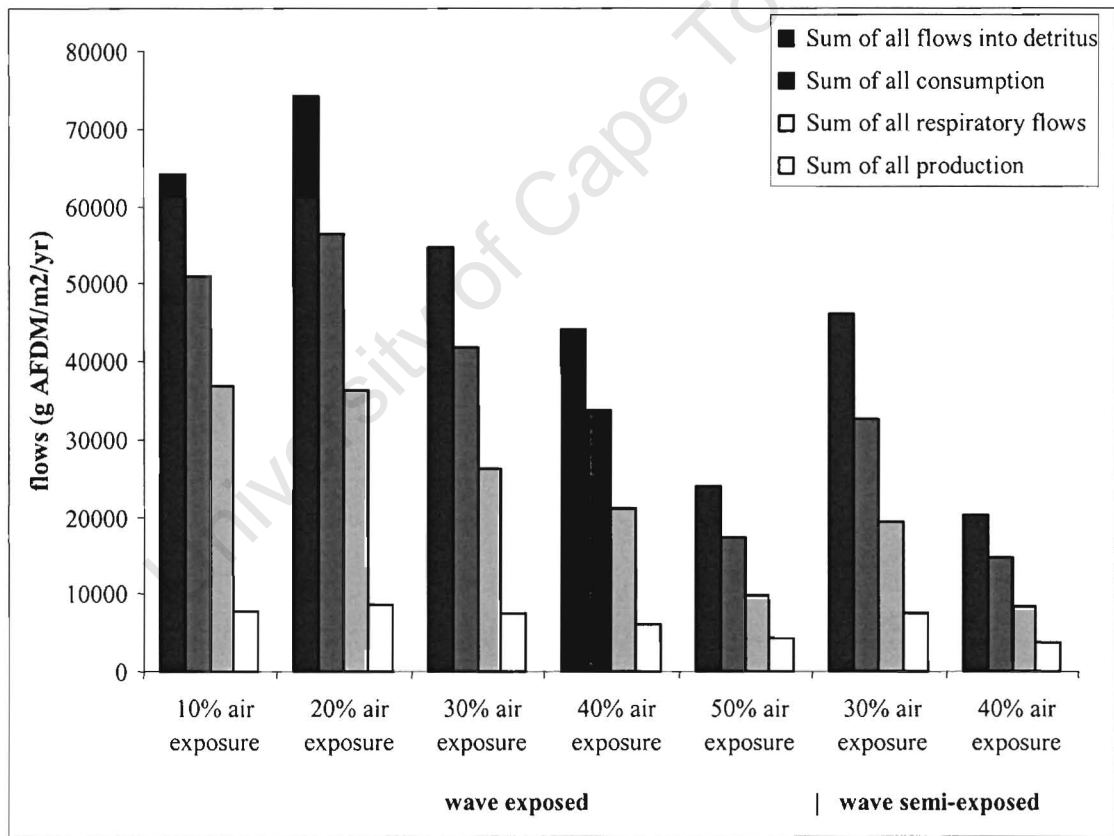


Figure 4.8: Sums of flows in the seven models: detritus, consumption, respiration and production in intertidal mussel beds at different wave exposures and tidal heights. Flows are in gAFDM. m⁻².yr⁻¹.

Table 4.10: Total biomass (g AFDM. m⁻²) and total system throughput (g AFDM. m⁻². yr⁻¹) in intertidal mussel beds at different wave exposures and tidal heights on the South African west coast.

Wave exposure	Wave exposed shores					wave semi-exposed	
Tidal height (% air exposure)	10%	20%	30%	40%	50%	30%	40%
Total biomass	2977	3235	2873	2687	1488	2316	1147
Total system throughput	152075	166878	122333	98583	50689	97899	43169

4.1.5.2. Imports and Exports and Total Primary Production

Totals of imports into the models include the sum of all suspended detritus consumed, drift algal debris, drift animal debris, any matrix debris consumed and the consumption of kelp gulls outside the modelled system. For all the models, suspended detritus consumption contributed more than 90% of all imports. Exports from the model are represented by unconsumed production which is dislodged and washed from the mussel bed as debris, and unassimilated consumption or faeces. If gametic outputs were added to exports these would add not much more than 463 g AFDM.m⁻².yr⁻¹ outputs (see respiration for general model above).

These imports and exports were compared along with *in situ* primary production in Figure 4.9, which shows the importance of imports in maintaining the system compared to primary production, and that faecal production contributes more mass into the water column than dislodged detritus. Generally all these sums of flows decrease with shore height and increase with wave exposure and follow the trends in biomass.

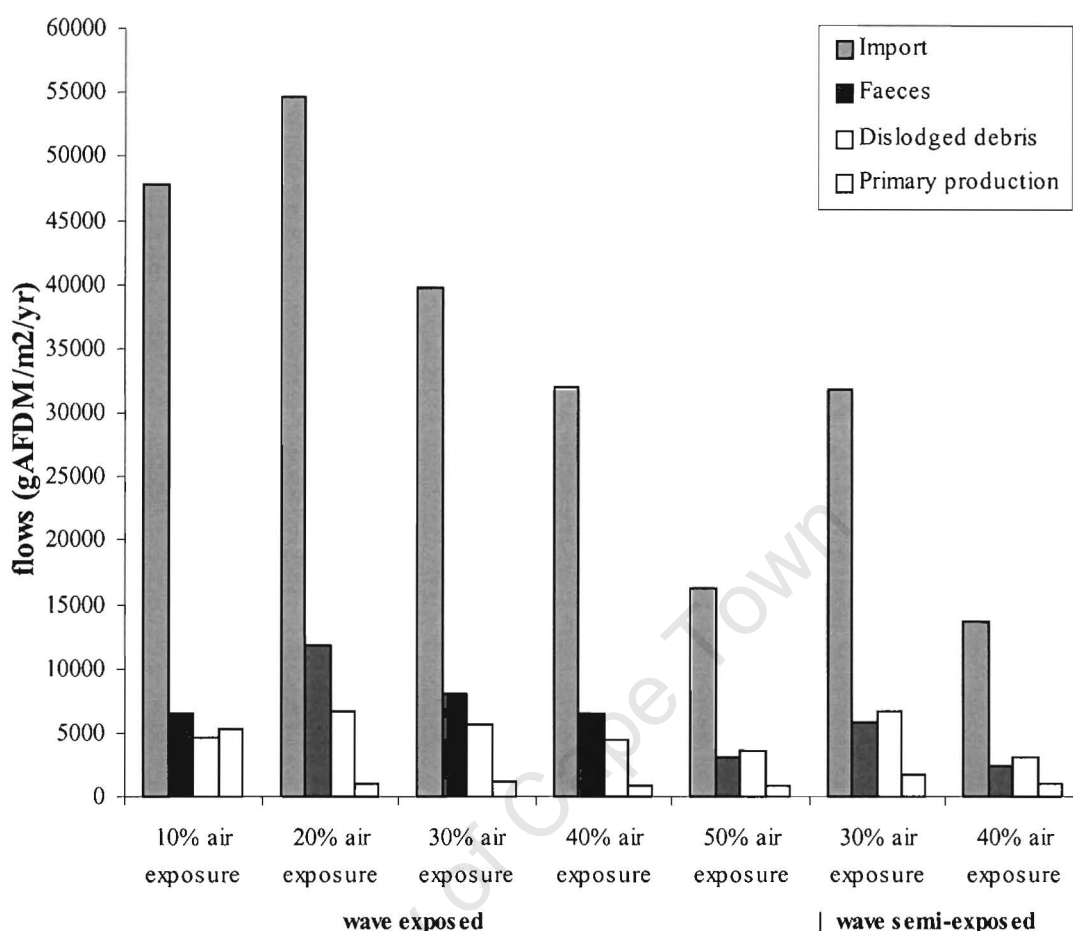


Figure 4.9: Sums of flows in the seven models: imports of consumed suspended detritus and other imports, unassimilated waste (faeces), unconsumed production washed from the rocky shore (dislodged detritus) and total primary production in intertidal mussel beds at different wave exposures and tidal heights on the South African west coast. Measurements are in g AFDM. m⁻². yr⁻¹.

4.1.5.3. Indices

4.1.5.3.1 Cycling Indices

These are proportions of trophic flows that are recycled within the system. Ecopath has two indices of cycling, Finn's cycling index and a predatory cycling index. Both of these compute as zero for all constructs of the model because flows to detritus all accumulate in the "dislodged detritus" box and energy flowing into the system is regarded as imported, so that there is no recycling of energy within the models.

4.1.5.3.2 Average Path Length Indices

This is a measure of the average number of steps energy flows from one group to another before exiting the system or flowing to detritus. Ecopath calculates Finn’s mean path length shown in Figure 4.10. The mean path length increases with shore height and is relatively lower on wave-exposed shores. These patterns are the inverse of those shown by biomass.

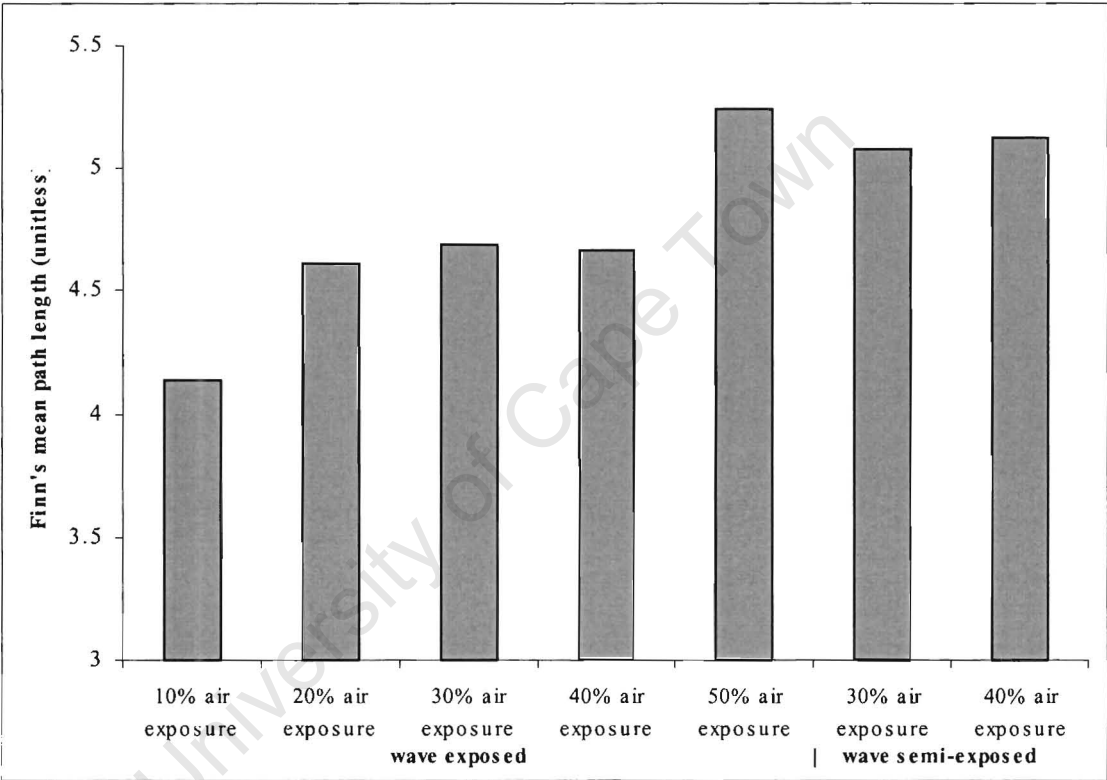


Figure 4.10: Finn’s mean path length at different wave exposures and tidal heights on the South African west coast.

4.1.5.3.3 Ascendency Indices

Ascendency is a measure of systems’ mutual information and is scaled by system throughput (Ulanowicz and Norden 1990). It is the product of total system throughput and the diversity of flows in a system, and is a measure representing size of flows as well as the organisation of flows in a system (Field *et al.* 1989). There are three measures: total ascendency (A); total capacity or developmental capacity (C) which is the upper limit of

the size of ascendancy for an ecosystem or the potential of an ecosystem to develop (Kay *et al.* 1989); and total overhead (system overhead) which is the difference between total capacity and total ascendancy. A high system overhead may suggest a system is stable despite external perturbations. System overhead generally increases with system maturity, and ecosystem maturity is expected to decrease when it is disturbed. The ratio of A/C is the relative ascendancy. The ascendancy indices of total overhead and total ascendancy and the sum of these (i.e. total capacity) are given in Figure 4.11, and all decrease with shore height and are slightly lower at the lower level of wave exposure.

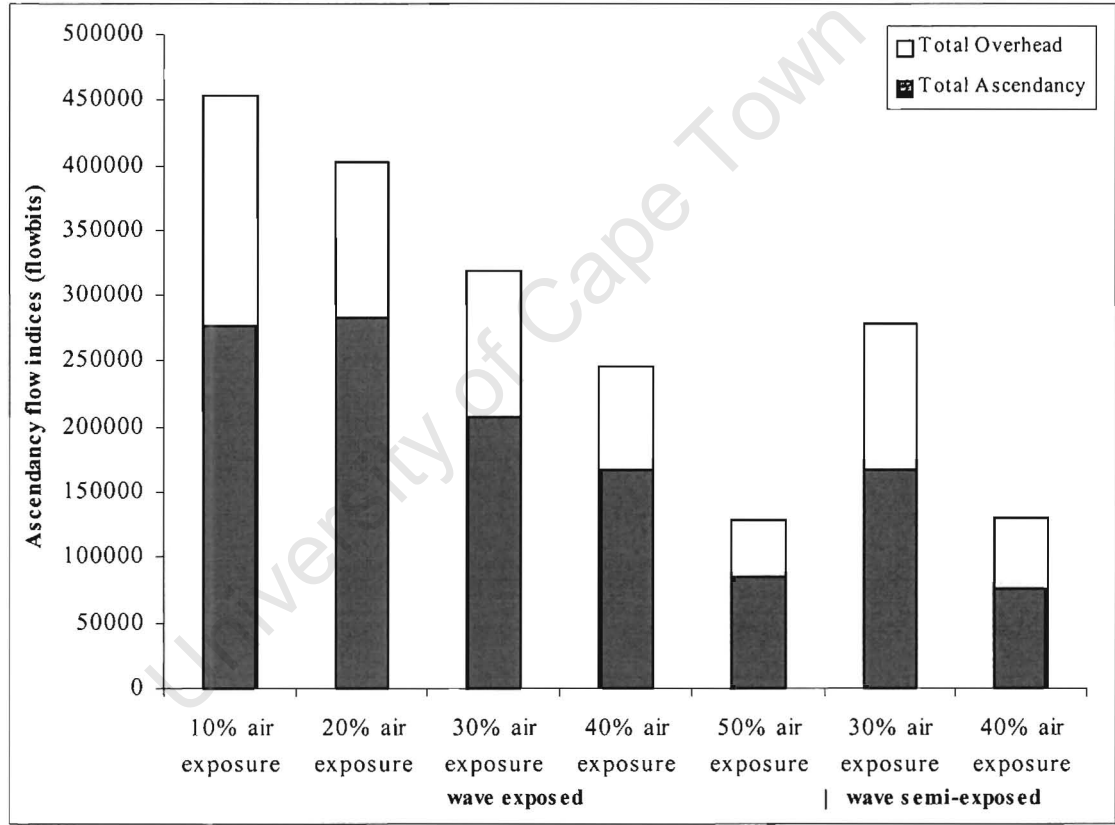


Figure 4.11: Ascendancy indices at different wave exposures and tidal heights on the South African west coast. The sum of total overhead and total ascendancy is the total capacity.

4.1.6. Impacts of Intensified Predation

The models were exercised under intensified predation levels to test the effects of relatively higher predation by the top carnivores in the system. Firstly, oystercatcher biomass was increased from 3.6 birds per km of shore to 78 birds per km of shore (the highest densities of oystercatcher reported from west-coast nearshore island sites: Bosman and Hockey 1988), representing an increase of 20 times the original biomass. The changes in the EE of all the groups in the seven models were noted (Table 4.11). The proportional change in EE was calculated as $((\text{new EE} - \text{original EE}) / \text{new EE})$. Positive values therefore reflect that the new EE is greater than the old one. In Table 4.11, cases on which resultant changes in EE caused the group to be imbalanced in mass flows ($\text{EE} > 1$) the proportional change in the EE is marked in bold. Thus increases in Oystercatcher density frequently imbalanced the limpet groups and, occasionally, the nereids. The impact of heavy oystercatcher predation changed the mussel EE by smaller proportions, with the greatest change at the highest shore level. Changes in the predator density were insufficient to cause effects lower in the food web, which could affect the EE of algae.

Table 4.11: Impacts of intensified African Black Oystercatcher predation on the trophic model of a South African west-coast rocky shore intertidal mussel bed for different shore heights in wave-exposed sites and semi-exposed sites. Oystercatcher biomass was increased 20-fold and the changes expressed as proportional change of the EE of each group. Changes are marked in bold if they caused the impacted group EE to exceed one.

	wave-exposed					semi-exposed	
Air exposure	10%	20%	30%	40%	50%	30%	40%
1. Oystercatcher	0.000	0.000	0.000	0.000	0.000	0.000	0.000
2. Kelp gull	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3. Fish	0.000	0.000	0.000	0.000	0.000	0.000	0.000
4. <i>Mytilus</i>	0.229	0.119	0.118	0.156	0.367	0.367	0.547
5. <i>Aulacomya</i>	0.219	0.132	0.114	0.155	0.376	0.476	0.974
6. <i>Aulactinia</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000
7. <i>Gunnarea</i>	1.000	0.000	0.000	0.000	-	0.000	0.000
8. <i>Granularis</i>	0.899	0.576	0.502	0.587	0.827	0.909	0.867
9. Other limpets	0.855	0.578	0.615	0.639	0.893	0.562	0.883
10. <i>Argenvillei</i>	0.213	0.843	0.686	0.851	-	0.000	-
11. Barnacles	0.000	0.000	0.000	0.000	0.000	0.156	0.000
12. <i>Nucella</i>	0.078	0.010	0.007	0.012	0.059	0.715	-
13. <i>Pseudonereis</i>	0.690	0.627	0.602	0.642	0.717	0.000	0.726
14. Epilithic algae	0.000	0.000	0.000	0.000	0.000	0.000	0.000
15. Sheetlike algae	-	-	0.000	0.000	-	-	-
16. Delicately branched	-	-	0.000	-	-	0.000	0.000
17. Coarsely branch	0.000	0.000	0.000	-	-	0.000	-
18. Kelps	0.000	0.000	0.000	-	-	0.000	-
19. Corallines	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Likewise, the drilling whelk predator group *Nucella* spp. was increased in biomass by 10 times its original biomass in each of the seven models. This had the effect of occasionally imbalancing the limpet groups but the most notable effect of this biomass change was a large change in the EE of the mussel groups. Both *Mytilus galloprovincialis* and *Aulacomya ater* had much larger proportions of the mussels being consumed by intensifying whelk abundance than intensifying oystercatcher abundance although the

increase in whelks only once unbalanced the mussels. The decrease in the EE of *Nucella* spp. is due to proportionally less *Nucella* spp. being consumed since the predators of the whelk do not increase their consumption in the model. Changes in the predator density were insufficient to cause effects lower in the food web, which could have affected the EE of the algal groups.

Table 4.12: Impacts of intensified *Nucella* spp. predation on the trophic model of a South African west-coast rocky shore intertidal mussel bed for different shore heights in wave-exposed sites and semi-exposed sites. *Nucella* biomass was increased to 10-fold its original biomass, and the changes expressed as proportional change of the EE of each group. Changes are marked in bold if they caused the impacted group EE to exceed one (NB: no recorded biomass for *Nucella* on semi-exposed shores with 40% air exposure).

Air exposure	wave-exposed					semi-exposed	
	10%	20%	30%	40%	50%	30%	40%
1. Oystercatcher	0.000	0.000	0.000	0.000	0.000	0.000	
2. Kelp gull	0.000	0.000	0.000	0.000	0.000	0.000	
3. Fish	0.000	0.000	0.000	0.000	0.000	0.000	
4. Mytilus	0.738	0.681	0.615	0.661	0.799	0.537	
5. Aulacomya	0.737	0.698	0.615	0.664	0.797	0.651	
6. Aulactinia	0.000	0.000	0.000	0.000	0.000	0.000	
7. Gunnarea	0.000	0.000	0.000	0.000	-	0.000	
8. Granularis	0.731	0.424	0.328	0.391	0.585	0.138	
9. Other limpets	0.716	0.296	0.288	0.278	0.495	0.208	
10. Argenvillei	0.803	0.000	0.284	0.000	-	-	
11. Barnacles	0.742	0.784	0.764	0.746	0.738	0.418	
12. Nucella	-0.686	-4.458	-5.624	-4.861	-2.122	-5.636	
13. Pseudonereis	0.000	0.000	0.000	0.000	0.000	0.000	
14. Epilithic algae	0.000	0.000	0.000	0.000	0.000	0.000	
15. Sheetlike algae	-	-	0.000	0.000	-	0.000	
16. Delicately branched	-	-	0.000	-	-	0.000	
17. Coarsely branched	0.000	0.000	0.000	-	-	0.000	
18. Kelps	0.000	0.000	0.000	-	-	0.000	
19. Corallines	0.000	0.000	0.000	0.000	0.000	0.000	

4.2. Discussion

Steady state multi-species ecosystem models were successfully constructed to simulate the major trophic flows in South African west-coast rocky shore intertidal mussel beds using the Ecopath software. The ecosystem, although delimited, does represent over 99% of the sessile fauna and flora biomass within the mussel bed, as well as the majority of mobile predators feeding within this zone.

4.2.1. Model Inputs

The biomass estimates for the mussel bed were the best known input parameters entered, which differs from other Ecopath models that have been mostly constructed around fish-dominated ecosystems where the biomass is often one of the least known inputs (e.g. Opitz 1991, Toral-Granda *et al.* 1999). This model used the 1990 biomass surveys that were completed in the summer season, which may have affected the size and condition of some of the fauna and flora (e.g. growth of west-coast algae *Iridaea capensis* is seasonal and its biomass peaks in summer - Bolton and Joska 1993). However the dominant biomass component, *Mytilus galloprovincialis*, has no notable seasonal trends in spawning (van Erkom Schurink and Griffiths 1991) or seasonality in recruitment (Harris *et al.* 1998) that might have seasonally altered mussel biomass.

Values of production, consumption, assimilation efficiency and diet composition were generally less well-known than biomass for some of the components' inputs. Local estimates for some species that are important in mass flows were missing, particularly for the production of anemones, all aspects of the physiology of *Gunnarea capensis*, the assimilation efficiencies of limpets, the production of *Nucella* spp. and all aspects of the physiology of nereids. The diet composition of the major predators would also benefit from refinement, particularly the relative importance of consumption of *in situ* intertidal production compared to consumption of subtidal imports.

4.2.2. Balancing and sensitivity of the model

The sums of the trophic flows between different groups in the models were largely balanced on initial construction due to many of the groups having large flows of unconsumed production to detritus. The exceptions were when the production of a group was insufficient to support its consumers, such as in the case of corallines in the lower balanoid zone on wave-exposed shores. This imbalance is probably caused by the consumption of corallines by limpets being overestimated, due to the indigestible nature of corallines prolonging gut-retention time. Many of the gastropod groups were also initially unbalanced; on varying the biomass of the various predators it was found that the anemones had by far the largest effect on gastropod mortality, thus the contribution of gastropods to anemones diet was reduced. The overestimate of gastropods in the anemones diet is probably due to an overestimate in the numbers of gastropods that are snared by the anemones within the mussel bed, and an underestimate of the contribution to the anemone's proportional diet by wave-tumbled prey originating subtidally.

4.2.3. Similarity between this model and other mussel beds

The mussel beds simulated in the model had a maximal total biomass of 3.2 kg AFDM. m⁻² which is typical of mytilid aggregations on rocky shores that often have large biomasses (e.g. mussels have a maximum standing crop of 1.5kg AFDM. m⁻² in Morecamp Bay (England) and biomasses of 0.9 - 1.4 kg AFDM. m⁻² have been recorded in the northern Wadden Sea (North Sea) - cited in Seed and Suchanek 1992). Mussel beds on the east coast of South Africa are dominated by *Perna perna* and are typically less dense than on the west coast. The east coast beds are thickest on the low shore where they have an average biomass of 0.865 kg AFDM. m⁻² (biomass conversions in Appendix B) (McQuaid *et al.* 2000). The highest productivity of the mussel community simulated in this model was 8.5 kg AFDM. m⁻² which is more than an order of magnitude larger than productivities of 0.2 - 0.6 kg AFDM. m⁻² that were recorded for mussel beds in the northern Wadden Sea, North Sea (cited in Seed and Suchanek 1992). This difference in productivity is probably due to the mussels in the North Sea experiencing lower

temperatures and stronger seasonal growth periods. Thus the west-coast mussel beds modelled in this study represent intertidal mussel beds with large standing stocks and very large productivities compared to other shores.

The predation of mussels in a South African mussel bed was modelled by Griffiths and Hockey (1987). The model investigated the mortality losses of the intertidal mussel, *Choromytilus meridionalis* which is indigenous to South African shores although it is not as abundant as the alien *Mytilus galloprovincialis* has become on the west coast. The Griffiths and Hockey (1987) model produced similar results to this model in that non-predatory mortality was the dominant source of mortality for the mussels and predation was responsible for minimal mortality due to the consistently low ecotrophic efficiencies of the mussels. Among the predators of mussels of the Griffiths and Hockey (1987) model, it was demonstrated that the African Black Oystercatcher and octopus induced the largest predatory losses especially among older mussels, which differs from this study's model where the invertebrate anemones and whelks caused the largest mussel mortality. This difference is probably due to the varying abundance of the predators, since African Black Oystercatchers are relatively scarce on the mainland (Bosman and Hockey 1988) and there are no available references to octopus feeding on *Mytilus galloprovincialis* in the west coast intertidal zone.

4.2.4. Comparison of this mussel bed model to other Ecopath trophic models

The Ecopath modelling package has been applied to various ecosystems internationally and has been particularly widely applied in modelling trophic flows in aquatic systems, often with a strong fisheries focus. Ecopath models built to represent other marine systems were compared to the model constructed in this study. The other marine models used for comparison were, firstly, a system including both pelagic and demersal biota in an offshore South African west-coast ecosystem (Shannon 2001) and, secondly, a model of a tropical inshore reef system by Opitz (1991). These systems had flows measured in tonnes wet weight. km⁻² which requires an approximate conversion ratio of 0.274 to

convert to g AFDM. m⁻² (Appendix B). Comparisons of these three models (Table 4.13) show much larger biomasses, consumption, respiratory flows and total system throughput in the mussel bed than the inshore tropical reef or the offshore upwelling system. Although, primary production was considerably less and the overall production was roughly comparable to the tropical reef system and the offshore upwelling marine system. This low level of primary production is attributable to the lack of algal biomass in mussel beds and the large import “subsidy” caused by wave action and transport of matter. Overall production is low due to the large non-predatory mortality losses at each trophic level and the short average food web length in the mussel bed.

Table 4.13: Comparison of Ecopath models constructed for an inshore subtidal tropical reef (Opitz 1991), an offshore west-coast upwelling system (Shannon 2001), and the west-coast mussel intertidal mussel bed on exposed lower balanoid shores modelled in this study. Tonnes wet weight. km⁻² in other fishery studies was converted to g AFDM. m⁻² using a conversion ratio of 0.274 (Appendix B).

	tropical reef	offshore upwelling	mussel bed
Total biomass (excluding detritus) (gAFDM m⁻²)	1069	60.5	3235
Sum of all consumption (gAFDM m⁻². yr⁻¹)	10355	4721	56540
Sum of all respiratory flows (gAFDM m⁻². yr⁻¹)	8020	2579	36188
Sum of all flows into detritus (gAFDM m⁻². yr⁻¹)	0.295	2403	74149
Total system throughput (gAFDM m⁻². yr⁻¹)	12203	10405	166878
Sum of all production (gAFDM m⁻². yr⁻¹)	8327	4447	8563
Total net primary production (gAFDM m⁻². yr⁻¹)	5471	3281	1102

In most ecosystems, the mean transfer efficiency at each trophic level is commonly around 10% although it was 12-15% for the west coast offshore upwelling system (Shannon 2001). In my study the transfer efficiency between the main biomass component (mussels) and its predators was 2% (since *Mytilus galloprovincialis* assimilates 40.7 kg AFDM m⁻². yr⁻¹ and 0.8 kg m⁻². yr⁻¹ is consumed by its predators). The low transfer efficiencies and low ecotrophic efficiency values of the mussel bed system may infer that the system is not food limited and that trophic interactions are relatively unimportant in determining the mussel bed's structure.

4.2.5. Important energy flows between living groups

Anemones (almost entirely composed of the species *Aulactinia reynaudi*) are the greatest consumers of mussels, although they rely on wave-tumbled prey that may die anyway, so that the effects of anemones on mussel population structure may be minimal. The greatest active predators of mussels in the model are *Nucella* spp. (mainly *Nucella cingulata*) although their consumption is also still small compared to the non-predatory mortality loss of mussels, so that they are unlikely to control mussel numbers. The vertebrate predators in the system, i.e. birds and fish, have minimal levels of intake when compared to the invertebrates even though the consumption to biomass ratio of vertebrates is consistently greater. The small energy flow to the vertebrates is due to their small combined biomass.

The proportional consumption of each group's production by predators (ecotrophic efficiency) is generally minimal compared to non-predatory losses, except for the algal groups: most of the algal production is consumed. Also, the combined biomass of algae is lower than the combined mass of the limpets and this unusual biomass ratio between predator and prey is only sustainable due to the high production to biomass ratio of the algae, and because the limpets' dietary requirements are supplemented by imported sub-tidal algae (Bustamante 1994). Thus, algae are likely to be controlled by limpet grazing at such high levels of herbivory. The high levels of nutrients on the west coast (Bustamante 1994) should be theoretically be capable of supporting an abundant biomass of foliose algae, and the fact that algal biomass is relatively low increases the likelihood that the limpets control algal growth in the mussel bed.

4.2.6. Imports and exports

The mussel bed imports consist mostly of suspended detritus (90% of the total imports) that is consumed by the filter-feeders. The remaining imports consist of large debris fragments consumed in the mussel bed, or are introduced by large mobile predators that

also feed outside the bounds of the model. At Groenrivier on the South African west coast, Bustamante (1994) measured the composition of the suspended detritus from monthly samples of the water column (Table 4.14). Assuming unselective consumption of the available suspended detritus, quantitative estimates of the sources of the suspended detritus can be made. In situations where mussel biomass is high, such imports total to 55.0 kg AFDM $\text{m}^{-2} \cdot \text{yr}^{-1}$ and the majority is attributable to consumption of production originating from sub-tidal kelps (36.0 kg AFDM kelp consumed per m^{-2} mussel bed. yr^{-1}).

Table 4.14: Average percentages by weight of suspended detritus over a year of monthly samples taken from low and high tide conditions (from Bustamante 1994). PIM is particulate inorganic matter and POM is particulate organic matter. Although a semi-sheltered location was not sampled, the values given for semi-sheltered are averages of the values from exposed and sheltered locations.

	Total PIM (%)	kelp (%)	faecal pellets (%)	other algae (%)	diatoms (%)	Total POM (%)
Wave-exposed	10.68	72.72	17.05	4.57	0.83	91.04
Wave semi-exposed	9.04	71.67	14.74	6.14	2.71	91.75

Water clearance rates by the mussel bed were calculated using Bustamante's (1994) estimate of the mean annual concentration of particulate organic matter (POM) of 1.39 mg AFDM. l^{-1} at wave-exposed sites at Groenrivier on the west coast of South Africa. In situations where imports total to 55.0 kg AFDM $\text{m}^{-2} \cdot \text{yr}^{-1}$, clearance rates would total to $3.96 \times 10^4 \text{ m}^3$ sea water per yr per m^2 of mussel bed. Imports of sub-tidal algae washed up onto the rocky shore have also been estimated by Bustamante (1994) as 100 g WW $\text{m}^{-2} \cdot \text{day}^{-1}$ of drift kelp and about one tenth of this value by other algal species, which converts to an input of 2.96 kg AFDM $\text{m}^{-2} \cdot \text{yr}^{-1}$ (Appendix B). The limpet groups are the main consumers of washed up algae and require 0.617 kg AFDM $\text{m}^{-2} \cdot \text{yr}^{-1}$ of sub-tidal imports. Thus, there seems to be adequate imports to support the limpet biomass.

The majority of production in the mussel bed is exported and only a small proportion of this component's production is consumed. Exports from the mussel bed are greatest where the mussel bed is most abundant and total to 7.0 kg AFDM $\text{m}^{-2} \cdot \text{yr}^{-1}$, which

includes unconsumed production and faeces. The 'respiration' term in the model includes some production terms that would be considered as exports from the mussel bed, i.e. gametes, excretion and mucus. Estimates of excretion and mucus were not calculated and may be significant for components such as the anemones. Gamete loss was calculated, and would total approximately $463 \text{ g AFDM m}^{-2} \text{ yr}^{-1}$.

4.2.7. Effects of shore height

The mussel-bed model was constructed at five levels of tidal height on wave-exposed rocky shores, which allowed for comparisons and manipulations of the trophic flows using the models from different shore heights. Total sums of flows in the mussel bed decreased with increasing shore height, which generally followed changes in overall biomass of the mussel bed. The mussel bed had the greatest biomass at a shore height of about 20% air exposure where imports, exports, heterotrophic production and flows between components were the greatest, although primary production was greatest at the lowest grade of air exposure of the models (10% air exposure) due to the greater abundance of algae there.

Consumption of *Mytilus galloprovincialis* is greatest where anemones are most abundant in the lower balanoid at approximately 30% air exposure, although anemones consume only dislodged mussels. The peak consumption by active predators, mainly by drilling whelks, occurs lower on the shore (at 20% air exposure) where there is also the largest abundance of mussels. Predation by birds was low at all shore heights but may have been increased if all bird foraging is concentrating in the upper shore. However the model with intensified bird predation did not suggest that the mussel bed would be unable to support the mussel consumers on the upper shore. The models adjusted with intensified predation both showed stronger effects of predators on the mussels at the lower and upper limits of the bed since the mussels were less numerous at the borders of the mussel bed.

4.2.8. Effects of wave exposure

Models representing wave-exposed and semi-exposed rocky shores were constructed using the available information on input parameters for two grades of wave exposure. Wave-exposed shores had greater total overall system throughput including imports and exports, generally following the changes in biomass on the shore. The contribution of primary production to flows in the mussel bed was marginally higher on semi-exposed shores than exposed shores due to a higher abundance of algae there.

Average trophic path lengths were larger on semi-exposed shores, due to the additional algae and limpet groups that occurred at the more wave sheltered sites. The reduced diversity and path lengths at more wave-exposed sites fits the observation of Carroll and Highsmith (1996) that increasing wave exposure is associated with increasing disturbance and gap formation, and lower diversity.

Consumption of mussels is twice as large on wave-exposed shores than on semi-exposed shores, although much of this is passive consumption by anemones. *Nucella* spp. have the greatest predatory impact on mussels and consume more mussels on exposed shores because their biomass is greater there contrasting with the observations of Menge and Olson (1990) who suggested mobile species will decrease in numbers with increasing wave action. Generally, a greater proportion of mussel production flows to the predators on wave-exposed shores because predators are more abundant there and the proportional losses of mussels due to other non-predatory sources of mortality are greater on semi-exposed shores. Possibly this is an artifact arising from the fact that the model lacked information on how growth rates of whelks differ with exposure, as has been shown in the case of *Nucella emarginata* on North American shores, where growth rates are greater at sheltered sites due to longer foraging time (Brown and Quinn 1988). The higher mortalities and greater turnover of mussels on wave-exposed shores agree with the field observations of McQuaid and Lindsay (2000) on *Perna perna* mussel beds on the east coast of South Africa.

Under simulated conditions of intensified bird predation, the impact on mussel mortality due to predation is greater at less exposed sites due to the smaller biomass of mussels there, although the intensified bird predation never resulted in a situation where mussel production was unable to support the rate of predator consumption. The simulated increase in the intensity of drilling whelk predation induced a higher predation mortality in the whelk's prey groups on exposed shores since the whelks were less numerous at semi-exposed shores.

4.2.9. Limitations and improvements to the model

Real ecosystems are more complicated than the linearly related, mass-balanced fluxes of trophic models, and it is important that the models allow sufficient representation of the basic features of the mussel bed. A significant limitation of the trophic model is the assumption that mass flows are homogeneous both spatially and temporally (e.g. it was assumed that the models had no biomass accumulation although this effect is likely to occur, considering that patches of the mussel bed go through successional stages). Since the model was designed to represent the state of the mussel bed averaged over a large area with a similar environment and assuming no wide-scale disturbances, the mussel bed is likely to fit to the model's assumptions of homogeneity. Further developments in the model could include considering different time and spatial scales.

The models focus on the trophic interactions in the mussel bed but the effects of competition, physical factors and behavioural interactions are also likely to play an important role in structuring the communities and are not necessarily confined to trophic effects. Effects of intraspecific competition for space are intense particularly for mussels (Griffiths and Hockey 1987, Seed and Suchanek 1992) and are important in determining mussel survival. Interspecific competition for space is also important in the mussel bed (e.g. between mussels and limpets on the west coast of South Africa (Steffani 2001)) and would also contribute to explaining changes in trophic flow patterns.

The design of this trophic model does not include the effect of changes in the availability of the lowest trophic groups such as the algae and detritus. Limitations in the availability of seston could effect mussel growth (Griffiths and Griffiths 1987) and would alter the energy flows in the model. Changes in the diet of the heterotrophic groups are also not factored into the model and dietary changes might occur depending on factors other than prey availability. Thus, a future model could include how consumption of the groups changes with prey availability, which would be particularly useful when attempting to predict changes in the mussel bed. Alterations in the behaviour of the living groups, such as the byssal binding of predatory whelks by *Mytilus galloprovincialis* may also change trophic flows in the model (Day, Barkai and Wickens 1991).

An increase in the complexity and resolution of the model could be made by including additional living groups such as the microfauna and meiofauna which occupy the mussel matrix. Although the model focused on the macro-fauna and flora, more detailed analysis of flows through groups such as bacteria and protozoa could be included, which are also likely to have large energy flows associated with them (e.g. Wulff and Field 1983). Parasites were not considered in the model although they possibly are important for trophic flow in some groups. However, the alien mussel, *Mytilus galloprovincialis*, is relatively free of parasites in South Africa (Calvo-Ugarteburu and McQuaid 1998) and thus there is no major energy flow to parasites for the most abundant group included in the model. Greater taxonomic resolution including multiple size and age classes would increase the detail of the model although available local input data would be needed for these model improvements, and are currently lacking for many of the species.

4.2.10. Conclusions

The models constructed enabled quantitative representation of biomass flows between species as well as modelling the imports and exports from the intertidal mussel beds on the west coast of South Africa. The strengths of the interactions between species in the community were measured by the size of the trophic flows and comparing predatory mortality with non-predatory mortality. The west-coast mussel bed community is

dominated by the alien invasive mussel, *Mytilus galloprovincialis*, in terms of biomass and flows. Most of the production of groups in the mussel bed is lost as non-predatory mortality and is washed off the rock. Relatively little production is consumed by predators, even when simulating the effects of increased invertebrate and vertebrate predation. The largest heterotrophic consumers are the anemones, consisting almost entirely of the species *Aulactina reynaudi* although its consumption consists of mussels already dislodged from the mussel bed. The largest consumption by an active predator is by the predatory whelks, mainly *Nucella cingulata*, which feeds most entirely on the mussels. The grazers appear to have the strongest trophic impact on their feeding groups and nearly all algal production is consumed by the limpet grazers. Overall, predators seem to have a little importance in terms of directing energy flow in the mussel-bed system and it is likely that predators are not of great consequence in South African intertidal west-coast mussel beds, in contrast to what has been suggested for other mussel bed systems (see review in Seed and Suchanek 1992).

The mussel bed is supported almost entirely by subtidal imports mainly in the form of degraded kelp material that is consumed by the mussels. The abundance of the mussels at different shore heights and wave exposures is the main determinant in the magnitude of total overall trophic flows. Predation is most intense on wave-exposed shores near the lower end of the mussel bed, although elevated levels of predator abundance increases the predation mortality of mussels at the edges of the mussel beds.

These trophic models would benefit from refinement in terms of additional information on the input parameters that could be fed into the ecosystem analysis. Trophic interactions do not seem to be major causes of mortality for many of the system components, so alternative modelling or field studies that consider other potential ecosystem effects will be needed to expand our understanding of the factors controlling mussel-bed dynamics. The field experiment in the following chapter focuses upon the interactions between mussels and their predators and did serve to partially test the model in this respect.

Chapter Five

Predation on Intertidal Mussel Beds around the South African Coast

5.1. Introduction

Mussels are a dominant feature of intertidal rocky shores worldwide at temperate latitudes in both the southern and northern hemispheres (Seed and Suchanek 1992). At wave-exposed and semi-exposed sites, these filterfeeding, sessile molluscs are normally not only the most abundant and productive invertebrate, but also form a structural habitat within which a diverse rocky-shore community survives (Suchanek 1985). Predation has been experimentally demonstrated to strongly influence mussel population size (Hunt and Scheibling 1995) and the lower limits of mussel beds have been shown to be controlled by predators on temperate shores in North America, Europe, New Zealand and Chile among others (Paine 1966, 1969; Castilla and Durán 1985; Seed and Suchanek 1992). These predators of mussels are diverse, ranging across crabs, predatory gastropods, seastars, fish and birds and the pattern of predation on the mussels varies from strongly monospecific to diffuse - when a number of predators are required to limit mussel abundance. Despite heavy predation pressure, extensive beds of mussels persist on intertidal rocky shorelines due to a combination of mussel life-history characteristics such as dense settlement, rapid growth and high fecundity and the ability to survive in environments away from the greatest predator impact (Carroll and Highsmith 1996).

South African intertidal rocky shores have extensive mussel beds from the temperate west and south coasts to the subtropical east coast (van Erkom Schurink and Griffiths 1990, Bustamante 1994). The west-coast intertidal is influenced by cold, upwelling Benguela current and the east coast by the sub-tropical Indian Ocean. There are substantial geographic differences in the species composition of rocky-shore biota around the southern African coast with the south and east intertidal communities containing almost twice as many species as those on the west coast although abundance is greater in the west coast than the south and east coasts (Bustamante and Branch 1996). South African shores are inhabited by four species of mussel although the commonest are the introduced

Mytilus galloprovincialis on the west and south coast and *Perna perna* on the east coast (van Erkom Schurink and Griffiths 1990). Although studies on these intertidal mussels have revealed much about their stock size, growth rates, larval biology and their physiology (Berry 1978, van Erkom Schurink and Griffiths 1990, 1992), there is little information on the community dynamics of South African mussel beds (Harris *et al.* 1998). The trophic structure of the rocky shore intertidal, in terms of autotrophs, filter feeders and predators, does not change around the coast, although there is variation in productivity around the coast with higher values of production associated with the west-coast flora and fauna (Bustamante *et al.* 1995). The predators of mussels on the South African coast are diverse and vary with geographical location. They include the mussel-drilling whelks (*Nucella cingulata* and *Natica tecta*), intertidal birds (*Larus dominicanus* and *Haematopus moquini*), rock lobsters (*Jasus lalandii*) a species of starfish (*Marthasterias glacialis*), and reef fish (*Cymatoceps nasutus* and *Sparadon durbanensis*) (Griffiths and Hockey 1987).

In this study, a field caging experiment was conducted to quantitatively measure the impact of predation on intertidal mussels concurrently at several study sites spanning different South African marine biogeographical provinces, from the temperate west coast to the sub-tropical east coast. By varying cage design to exclude particular predators, the intention was to resolve the degree of predation caused by a range of predators, from large vertebrates to smaller invertebrates. The densities of one of the mussels' principal predators, drilling whelks (*Nucella* spp.), were also varied between cages to determine their impact on the mussel populations. Most previous studies are biased because they are limited to temperate shores (reviews in Connell 1972, Paine 1994), or limited because they are site-specific or difficult to compare because they were run in different seasons. This study attempts to overcome such limitations and to broaden our understanding of large-scale spatial variations in predation patterns and links with the trophic model constructed in the first chapters of this thesis since comparisons can be made between the predator-prey interactions in the field on the west coast and the simulated model.

5.2. Methods

5.2.1. Study Sites

The predator caging experiments were conducted at five sites (each 100 – 1000 km apart) around the coast of South Africa (Figure 5.1), namely “Groenrivier” at Island Point near the mouth of the Groenrivier on the northwest coast of South Africa (west-coast cool temperate Namaqua biogeographical province), “Scarborough” on the Atlantic side of the Cape Peninsula in the Western Cape (southern end of the west-coast Namaqua biogeographical province), “Transkei” at Dwesa Nature Reserve on the Transkei coast (south coast warm temperate Agulhas biogeographical province), “Natal” at Mdloti near Durban in central KwaZulu-Natal (subtropical east-coast Natal biogeographical province), and “Zululand” at Railway Ledges alongside the Mapelane Nature Reserve on the northern KwaZulu-Natal coast (also in the east-coast Natal biogeographical province). All localities were selected to represent exposed rock platforms on the open coast. Topographic information on the sites is available in Harris *et al.* (1998). The dominant intertidal mussel species differ between regions, with *Perna perna* being the dominant in terms of biomass at sites on the south and east (Transkei, Natal and Zululand) while at Groenrivier and Scarborough, *Mytilus galloprovincialis* is the most abundant mussel (van Erkom Schurink and Griffiths 1990, Bustamante 1994, Bustamante and Branch 1996).

5.2.2. Experimental Design

The design of the field experiments was the same at each of the five study sites, with six different treatments that were replicated three times, and positioned in the centre of the intertidal mussel bed (lower to mid-balanoid intertidal zone). Effort was made to select areas of rock for each cage that were similar in terms of the rock surface, wave action, inclination, direction the slope faced, and the degree of colonisation of mussels. The cages were situated between low spring tides and mid-tide and at each site they were distanced from each other by not less than a half a metre. Five of the treatments consisted of cages but the sixth treatment consisted of a control with no cage associated. The cage

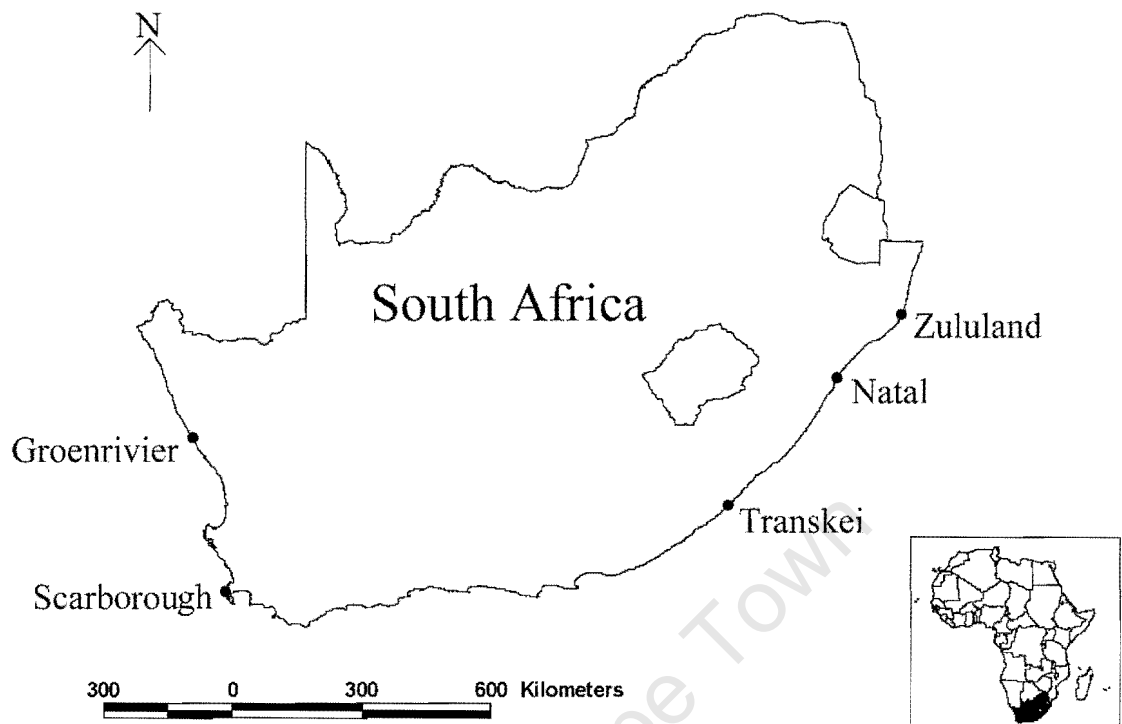


Figure 5.1: Outline of the South African shoreline. The five marked localities on the coast correspond to the study sites mentioned in the text.

treatments were as follows: (1) a cage consisting of four walls and a roof, which had drilling whelk predators introduced as described below; (2) a cage consisting of four walls and a roof excluding all predators; (3) a cage with only a roof supported by the steel frame, which allowed small invertebrate predators access from the surrounding mussel bed but impeded larger vertebrate predators from gaining access to the mussels; (4) a cage with four walls but no roof which was designed to exclude benthic invertebrate predators but allow mobile vertebrate predators access to the mussels; and (5) a cage consisting of only two walls which was to allow all predators of mussels access to the cages but served as a control for the effects of the cages (Figure 5.2). The cages were 25 x 25 cm square in base and 10 cm high with a galvanised steel frame. The walls and a removable roof were made of galvanised steel netting with a mesh size of 5 mm. An area only slightly larger than the size of the cage was scraped clean of mussels and other organisms using a chisel, and the cages were attached to the rock using drilled holes, wall plugs and screws at 8 points around the base of the cage, where metal lugs had been attached. Where the cage

base was not flush with the rock surface, hard foam-rubber filling was bound to the cage to fill the gaps. The control area was also scraped clean of mussels. One hundred mussels of a size of 30 to 50 mm shell length, collected from the mussel bed a short distance from the caging experiment, were allowed to attach to the rock in each plot by placing the mussels under 3-mm nylon mesh netting. The nylon netting was tightly stretched over the mussels in each of the cages and pinned down by the cage frame. In the case of the control treatment, batons were screwed to the rock to hold the nylon netting and mussels firmly against the rock surface to allow the mussels to reattach by growing new byssus threads.

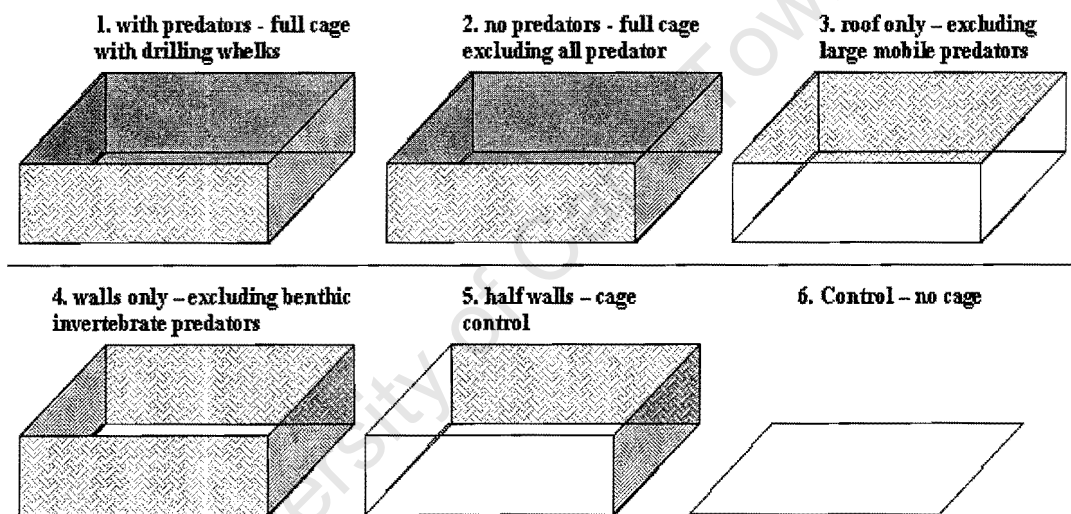


Figure 5.2: Diagram showing the designs of the six treatments used in the mussel caging experiment to quantify predation on mussels around the coast of South Africa.

5.2.3. Sampling Procedures

5.2.3.1. Monitoring

The experiments at each site were initiated between March and May 1999 and run for a period of seven months. After an initial period of a month the cages were revisited and since the mussels had by then reattached to the rock, the nylon netting from all cages and the nylon netting and batons from the control were removed. Ten drilling whelk predators of 15 – 25 mm in shell length (*Nucella cingulata* on the west coast sites and *N. capensis*

on the east coast sites) were collected from the mussel bed a short distance away from the caging experiment and introduced to the enclosed cage treatment intended to include predators. This density was selected to represent the highest density recorded at any site. The cages and control were monitored subsequently at periods of one month, three months and six months. During the monitoring, the lids of the cages were temporarily removed and the numbers of live mussels counted, the percentage cover of mussels, numbers of dead mussel shells with drill holes, numbers of other dead mussels, percentage cover of each species of alga attached to the rock surface (primary algae), percentage cover of each species of alga attached to the biota (secondary algae), numbers of gastropod species, percentage cover of anemone species, percentage total cover of biota and percentage bare rock were recorded in the plots. Growths of algae on the cage walls and roofs were removed and any predators discovered in the treatments intended to exclude predators were removed.

5.2.3.2. Harvesting

The harvesting took place between September and November 1999, when all the contents of the treatments were scraped off the rock, frozen and taken to the lab for processing. In the lab, the mass of the sample, the mass of the mussels, the numbers and sizes of all mussels including newly settled recruits, the numbers and sizes of the predator *Nucella* spp., the mass of each algal species, and the numbers and masses of any other species in the samples were recorded. Organisms were identified to species where possible and all macrofaunal species (> 1 mm length) were counted and weighed to the nearest 0.5 g.

5.2.4. Statistical Analyses

ANOVAs with crossed factors and replications (Zar 1984) were used to examine the effects of site and cage type on the variables recorded in the final monitoring period: numbers of mussels surviving, percentage mussel cover, numbers of drilled dead mussels, other dead mussel shells, cover of algae, numbers of limpets and whelks and snails, and percentage bare rock cover; and from the harvesting: total biomass, numbers and mass of

adult and juvenile mussels, numbers and mass of adult and juvenile whelks and limpets, and mass of the algal species growing in the plots. Normality of the variables was judged by graphically examining categorised normality plots and homogeneity of variances was judged graphically by examining scatterplots of the variances plotted against the means. If a factor was significant ($p < 0.05$) then multiple pairwise post hoc comparison tests were carried out using Tukey's Honest Significant Difference Test (Zar 1984) at a significance level of $p < 0.05$. All statistical analyses were conducted using the STATISTICA 95 software package (StatSoft 1995).

5.2.5. Contingencies

There was a failure to establish mussels in the third replicate at Scarborough and thus this site had only 12 experimental plots. Loss of roofs from some of the treatments occurred due to wave action during the progress of the experiment, although these were replaced during the periodic monitoring (Table 5.1) as well as the replacement of any whelk predators that had escaped the cages designed to include predators. These plots that temporarily lost roofs were included in the analysis.

Table 5.1: Number of plots with roofs that were lost during the experiment, although the roofs were replaced during the monitoring periods.

SITE	Monitoring period	Treatment type		
		with predator	no predator	roof only
Groenrivier	Third	0	1	2
Scarborough	Second	1	1	0
Natal	Second	3	3	2

5.3. Results

5.3.1. Survival of Introduced Mussels at Harvesting

Numbers of adult mussels remaining in the plots at the time of harvesting were recorded at the Groenrivier, Scarborough, Transkei and Natal sites. Of the 100 mussels initially introduced, virtually no mussels were left in the Natal control plots and reduced numbers of mussels were left in the cages that contained whelk predators at Groenriver on the west coast (Figure 5.3). No other noticeable differences occurred between the mussels remaining in the various treatment types at the different sites. Categorised normal probability plots of the variable “adult mussel numbers” were graphed separately for the factors “site” and “cage type” for graphical examination, which appeared to follow normality and homoscedasticity assumptions. A two factor ANOVA was then performed on the variable mussel numbers (Table 5.2).

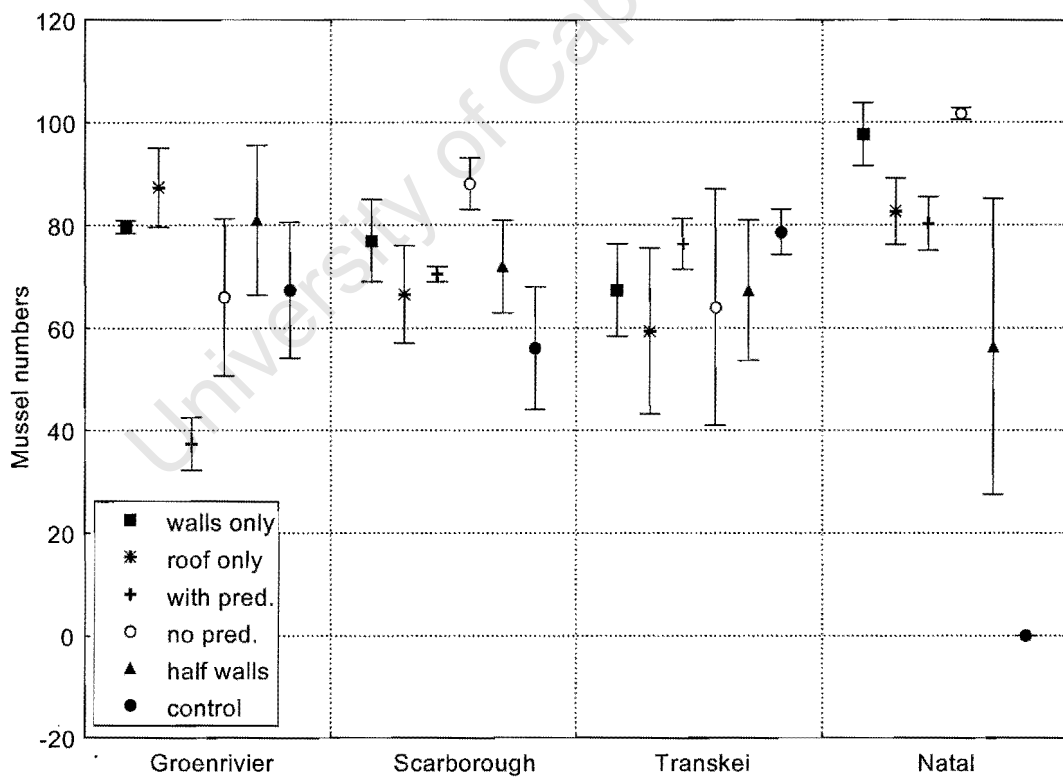


Figure 5.3: Numbers of adult mussels (+/- one S. E.) remaining in the cages at harvesting of the cages at all sites except Zululand which lacked data. The cage types and sites are described in the text.

Table 5.2: Results from the two factor ANOVA of the mussel numbers recorded from the final harvesting of the different cage types and sites around the coast of South Africa (excluding Zululand which lacked data). Significant effects are marked with an asterisk.

Source	D.F. Effect	M.S. Effect	D.F. Error	M.S. Error	F	p-level
Site	3	19.46	42	412.7	0.04715	0.9862
Cage Type	5	1319.	42	412.7	3.197	0.01555*
Site X Cage Type	15	1406.	42	412.7	3.406	0.000869*

The ANOVA shows a strong interaction effect between site and cage type on mussel numbers harvesting (Table 5.2), which means that no significance can be attached to the main effects of site and cage type. This interaction was further analysed with a post hoc Tukey honest significant difference test, which revealed significant differences ($P < 0.05$) were caused by the lack of mussels remaining in the control plots at Natal. Thus, to avoid the impact of the Natal control plots on the interaction effect in the ANOVA, one way ANOVAs were run separately for each site (Table 5.3). A strong significant treatment effect was detected at the Natal site due to the control having no mussels surviving and an almost significant interaction effect was found at the Groenrivier site (Table 5.3) probably due to the lower number of mussels recorded in the cages that included whelk predators. No treatment effects were detectable at the other two sites.

Table 5.3: Results of the one way ANOVA of the mussel numbers recorded from the final harvesting of the different cage types and sites around the coast of South Africa (except Zululand which lacked data). Significant interactions are marked with an asterisk.

Site	Source	D.F. Effect	M.S. Effect	D.F. Error	M.S. Error	F	p-level
Groenrivier	cage type	5	962.9	12	354.7	2.714	0.07261
Scarborough	cage type	5	227.5	6	135.5	1.679	0.2721
Transkei	cage type	5	162.6	12	552.8	0.2942	0.9070
Natal	cage type	5	4273.	12	469.3	9.106	0.0008991*

5.3.2. Monitoring of Cages

The numbers of adult mussels surviving in the cages were recorded during the three monitoring periods and plotted in Figure 5.4. These time-series graphs show a relative decrease in mussel numbers in the cage with predators at Groenrivier and the Natal control plots, although differences in the reduction in numbers of mussels between treatment types was not discernible at all of the five sites.

A two factor ANOVA was performed on the monitoring data collected on the final monitoring period for each of the 12 recorded variables (Table 5.4). The variables followed normality and homoscedasticity assumptions. Post Hoc comparisons using the Tukey honest significant difference (Tukey HSD) test ($p < 0.05$) were used to compare the sites and cage types within the multiple ANOVAs of the data. Zululand lacked data from the final monitoring period, so data from the second monitoring period were used.

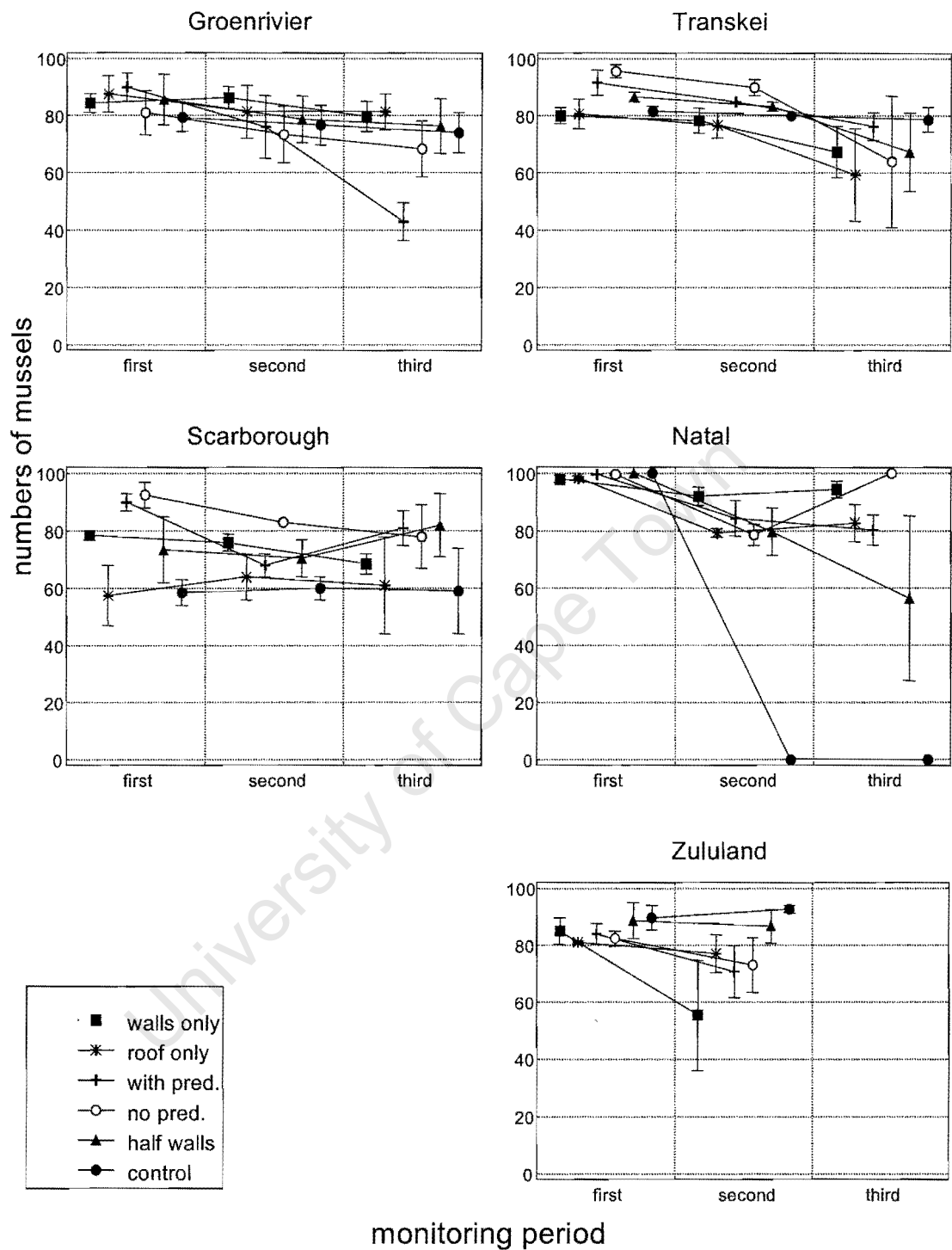


Figure 5.4: Time series graph of the mean live mussel numbers ($\pm$ one S. E.) per plot (y axis) counted during each of the three (first, second and third) monitoring periods over 6 months (x axis) at each site. The y-axis is the mussel numbers per treatment, the treatment types are explained in the text. The data in each time period are displaced to avoid overlap and increase clarity.

Table 5.4: Two factor ANOVAs of variables measured in the last period of monitoring of the cages at the five sites around the coast. The variables are further explained in the text. Snails and anemones lacked data for the Natal site. The Zululand site also had missing data for the 3rd monitoring period therefore data from the 2nd monitoring period were used. Significant effects and interactions are marked with an asterisk.

Variable	Source	Df	MS	Df	MS		
		Effect	Effect	Error	Error	F	p-level
Percentage mussels	Site	4	978.84	54	251.62	3.89	
	Cage Type	5	1170.71	54	251.62	4.65	
	Site X Cage Type	20	934.05	54	251.62	3.71	0.0001*
drilled mussels	Site	4	65.90	54	7.34	8.97	
	Cage Type	5	40.35	54	7.34	5.50	
	Site X Cage Type	20	35.46	54	7.34	4.83	0.0000*
other dead mussels	Site	4	1040.74	54	69.38	15.00	0.0000*
	Cage Type	5	53.59	54	69.38	0.77	0.5738
	Site X Cage Type	20	56.26	54	69.38	0.81	0.6900
algae primary	Site	4	698.54	54	57.76	12.09	0.0000*
	Cage Type	5	31.82	54	57.76	0.55	0.7369
	Site X Cage Type	20	88.84	54	57.76	1.54	0.1063
algae secondary	Site	4	1523.12	54	20.17	75.50	0.0000*
	Cage Type	5	37.88	54	20.17	1.88	0.1134
	Site X Cage Type	20	31.25	54	20.17	1.55	0.1026
limpets primary	Site	4	124.87	54	4.14	30.15	
	Cage Type	5	21.76	54	4.14	5.25	
	Site X Cage Type	20	9.86	54	4.14	2.38	0.0060*
limpets secondary	Site	4	271.90	54	9.84	27.63	0.0000*
	Cage Type	5	19.57	54	9.84	1.99	0.0951
	Site X Cage Type	20	11.89	54	9.84	1.21	0.2840
bare rock	Site	4	3301.01	54	235.10	14.04	
	Cage Type	5	942.82	54	235.10	4.01	
	Site X Cage Type	20	1109.95	54	235.10	4.72	0.0000*
Snails	Site	3	5.11	42	8.98	0.57	0.6380
	Cage Type	5	4.38	42	8.98	0.49	0.7837
	Site X Cage Type	15	4.90	42	8.98	0.55	0.8982
Anemones	Site	3	14.59	42	1.85	7.89	0.0003*
	Cage Type	5	1.64	42	1.85	0.88	0.4998
	Site X Cage Type	15	1.72	42	1.85	0.93	0.5410

The percentage mussel cover recorded during the final monitoring period was similar between sites with approximately 55 - 65% of the surface area of the plots covered by the mussels. Very low values of mussel cover were, however, recorded in control plots at the east coast Natal site and relatively low values of cover in the cages with whelks at the west coast Groenrivier site (Figure 5.5).

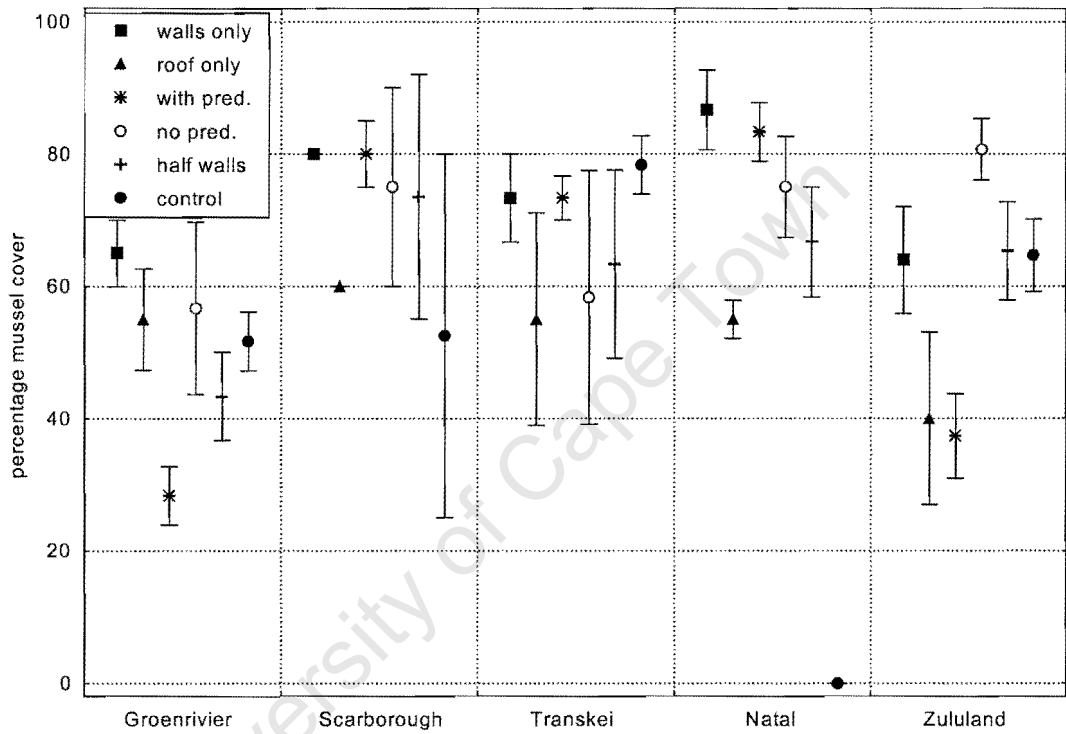


Figure 5.5: Mean percentage mussel cover (+/- one S. E.) recorded from the final monitoring of the treatments at each site. The Zululand site had missing data for the 3rd monitoring period therefore the 2nd monitoring period was used.

The percentage mussel cover in the plots had a significant 2 way interaction between the effects of site and cage type ($F_{20,54} = 3.71$, $p = 0.0001$) (Table 5.4). This was due to the cages with predators at Groenrivier and the Natal control plots having significantly less mussel percentage cover than other combinations of treatments and sites (Tukey HSD test, $p < 0.05$). The drilled dead mussel shells that were found within the plots (which had drill holes caused by attacks from drilling whelks) also had a strong interaction between

site and cage type ($F_{20,54} = 8.97$, $p < 0.0001$) (Table 5.4). These drilled shells differed among sites only in one treatment, being the cage with predators, where it was higher at Groenrivier than elsewhere (Tukey HSD test, $p < 0.05$). Other dead mussel shells found in the plots differed significantly only with respect to site ($F_{20,54} = 15.0$, $p < 0.0001$) (Table 5.4) and, on comparison of the sites, it was found that Transkei had significantly greater numbers of dead mussel shells than the other sites (Tukey HSD test, $p < 0.05$).

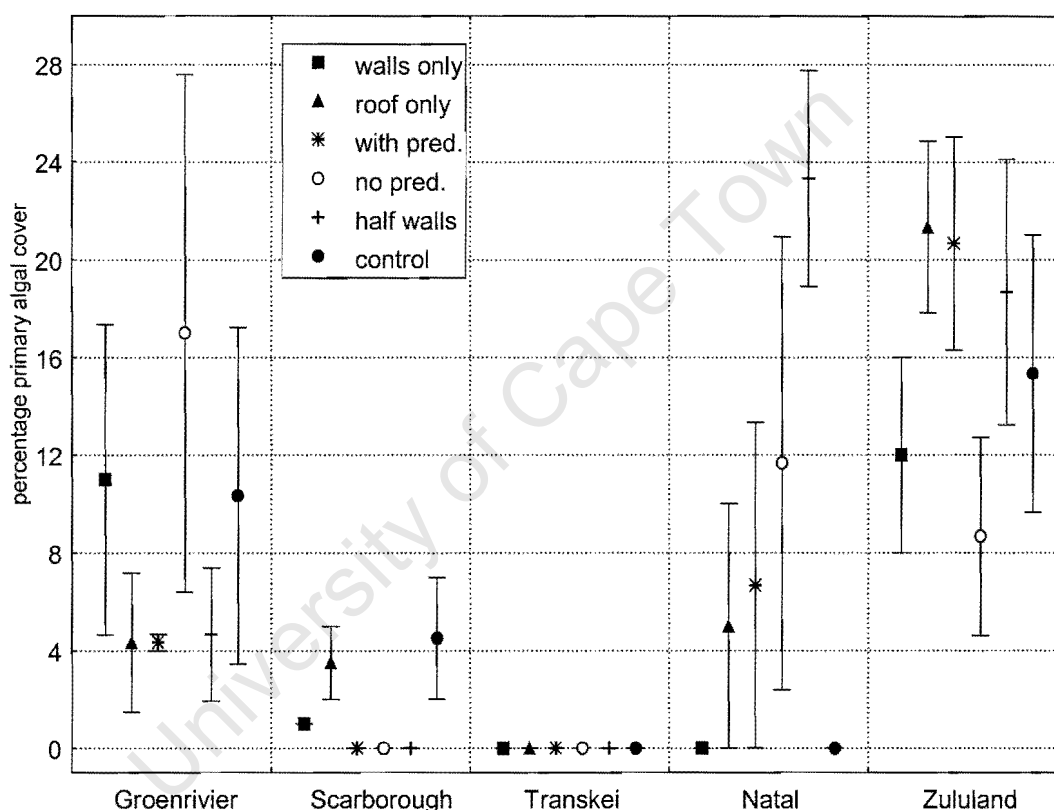


Figure 5.6: Percentage cover ($\pm$ one S. E.) of algae occurring on the primary rock surface in the final monitoring of the cages at all sites. The cage types and sites are described in the text. The Zululand site had missing data for the 3rd monitoring period therefore the 2nd monitoring period was used.

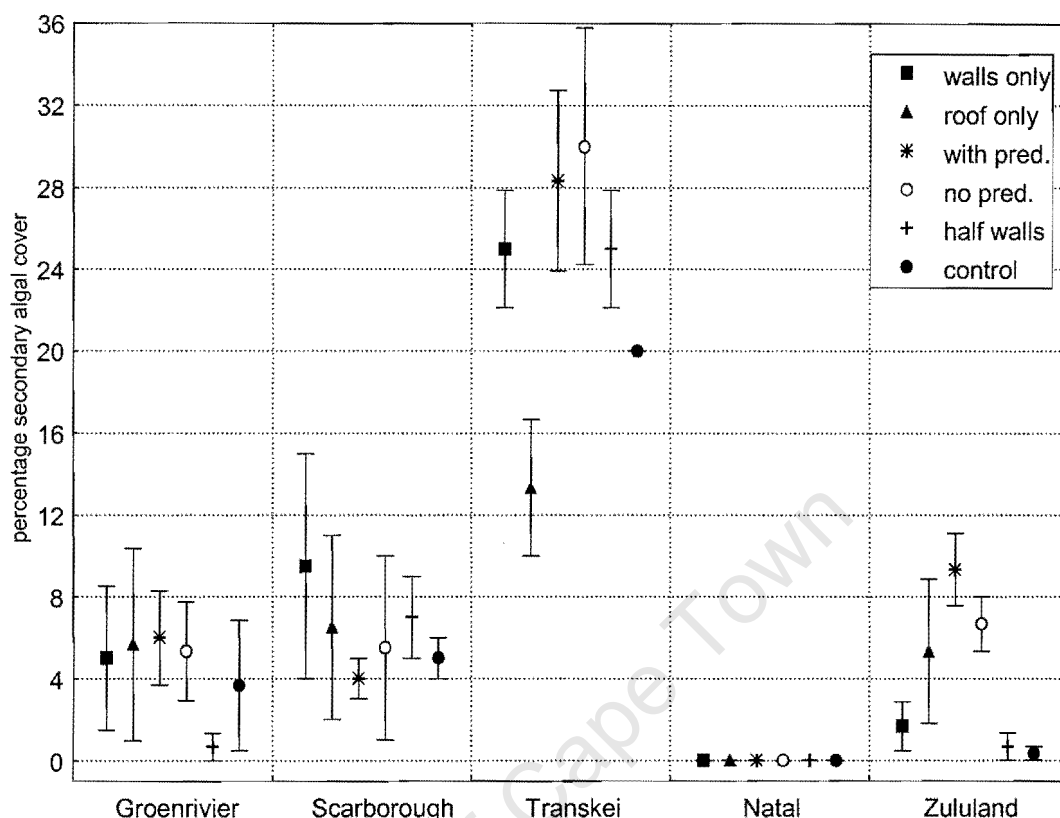


Figure 5.7: Percentage cover ($\pm$ one S. E.) of algae occurring on the biota (secondary substrate) in the final monitoring of the cages at all sites. The cage types and sites are described in the text. The Zululand site had missing data for the 3rd monitoring period therefore the 2nd monitoring period was used.

Percentage of primary algae (attached to the rock surface) differed significantly only with respect to site ($F_{20,54} = 12.09$, $p < 0.0001$) (Table 5.4) and on comparison of the means it was found the primary algae seemed to vary irregularly around the coast, with Zululand > Groenrivier > Natal > Scarborough > Transkei (Figure 5.6). Also, the percentages of secondary algae (growing on other biota, mostly mussels) differed significantly only with respect to site ($F_{20,54} = 75.50$, $p < 0.0001$) (Table 5.4) and on comparison of the means, secondary algae also seemed to vary irregularly around the coast although more or less in a reverse order to primary algae with Transkei >> Scarborough > Groenrivier > Zululand > Natal (Figure 5.7).

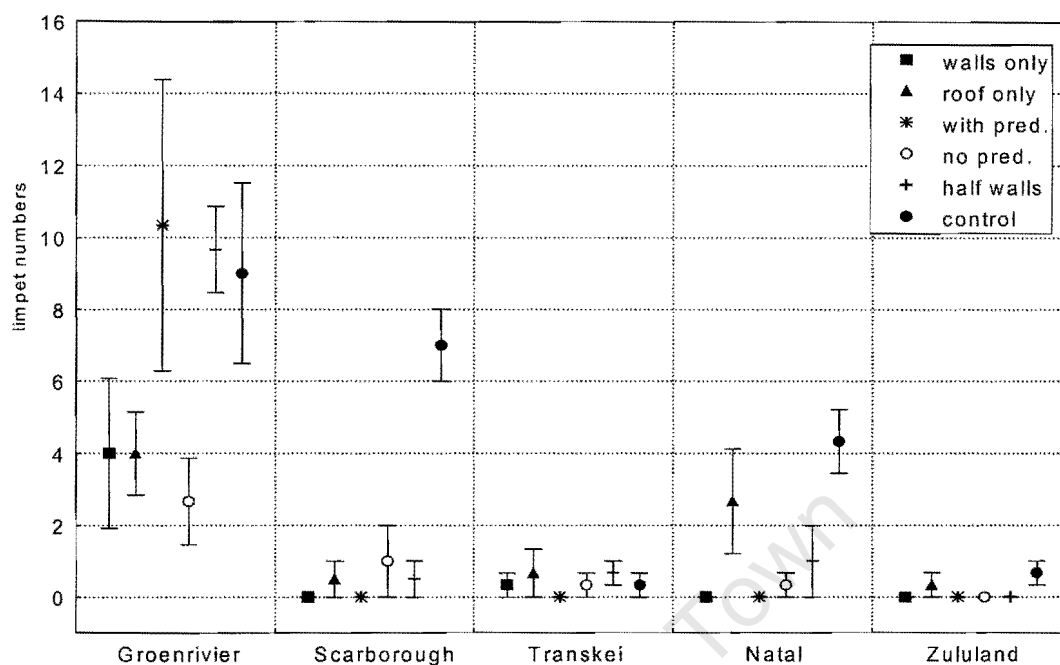


Figure 5.8: Numbers ($\pm$ one S. E.) of limpets occurring on the primary rock surface in the final monitoring of the cages at all sites. The cage types and sites are described in the text. The Zululand site had missing data for the 3rd monitoring period therefore the 2nd monitoring period was used.

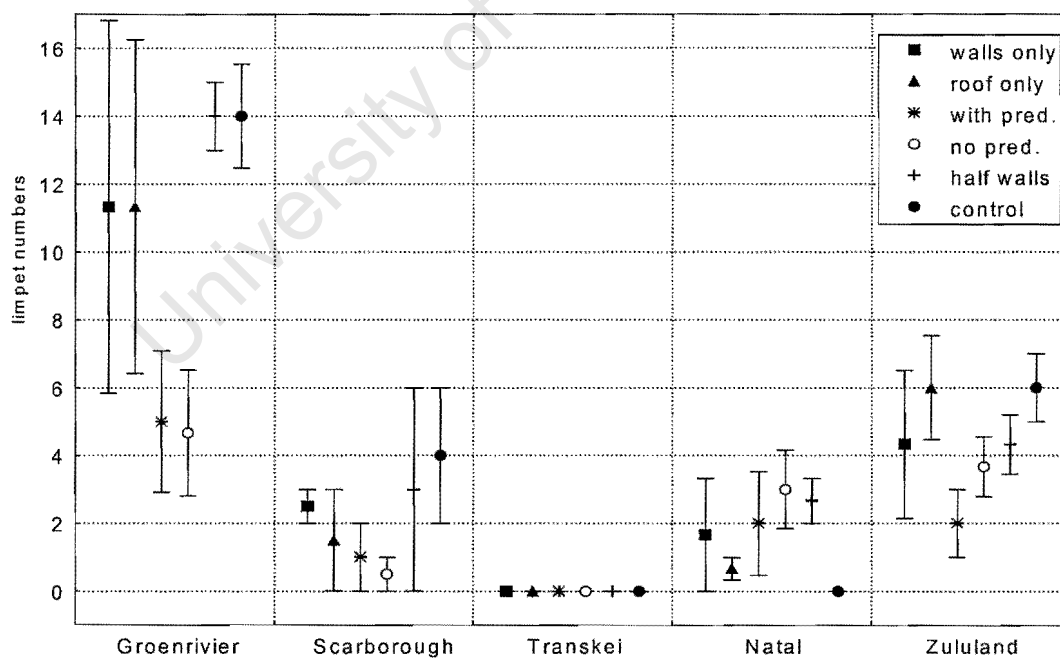


Figure 5.9: Numbers ($\pm$ one S. E.) of limpets occurring on the biota (secondary substrate) in the final monitoring of the cages at all sites. The cage types and sites are described in the text. The Zululand site had missing data for the 3rd monitoring period therefore the 2nd monitoring period was used.

Numbers of limpets recorded from the primary rock surface varied widely between treatments and sites with high numbers recorded from the west coast Groenriver site (Figure 5.8). There was a significant 2 way interaction between the effects of site and cage type ($F_{20,54} = 2.38$, $p = 0.0060$) (Table 5.4). The post hoc (Tukey HSD) analysis of the treatments and sites showed large number of significant variations between sites and treatments although differences were mainly due to the variable and large numbers of limpets recorded from Groenriver treatments and because limpets in controls were more abundant than in other treatments at two sites. The abundance of limpets attached to secondary substrate differed significantly only with respect to site ($F_{20,54} = 27.63$, $p < 0.0001$) (Table 5.4) and on comparison of the means it was found the limpets abundance tended to decrease around the coast with Groenriver > Zululand > Scarborough > Natal > Transkei (Figure 5.9).

A significant 2 way interaction was detected for the variable bare rock, which represents areas within the treatment with no visible colonisations of biota ($F_{20,54} = 4.72$, $p < 0.0001$) (Table 5.4). The interaction was caused by both the Natal control and Groenrivier cage with predators having significantly higher patches of bare rock than other combinations of treatments and sites (Tukey HSD test, $p < 0.05$).

The numbers of snails (whelks) and anemones were not detailed for the monitoring data from the Natal site. For the other sites, there were no significant differences between cage types, site ($F_{3,42} < 0.57$, $p > 0.63$) or the interaction ($F_{15,42} < 0.56$, $p > 0.89$) between these factors (Table 5.4). Anemones differed significantly only with respect to site ($F_{3,42} = 7.89$, $p = 0.0003$) (Table 5.4) and on comparison of the means it was found the anemones abundance decreased around the coast being highest at Groenriver > Scarborough > Zululand > Transkei.

5.3.3. Predators recorded in cages at harvesting

The whelk survival in the cages in which whelk predators were enclosed was noted as 96.6% at Groenrivier, 75.0% at Scarborough and 73.3% at Natal (but unrecorded at Transkei and Zululand) over the six months. Few adult whelks of a size similar to those introduced into the cages with predators were recorded in any of the other treatments, averaging 0.22 adult whelks per plot at Groenriver, none at Scarborough, and 0.17 adult whelks per plot at Natal at the time of harvesting (unrecorded at Transkei and Zululand). Small juvenile whelks were more commonly encountered at the time of harvesting: 2.7 whelks per plot at Groenrivier, 6.8 at Scarborough, and 0.22 whelks per plot at Natal. At Transkei, in one of the cages intended to exclude predators, a single *Octopus* sp. individual had entered and apparently decimated the mussels in that cage. The remains of 82 dead mussel shells were found in that particular plot at the end of the 6 months, while the other plots had on average 14.1 (range of 6-30) dead mussel shells.

5.3.4. Other colonisers of the cages

Juvenile mussels of a size smaller than the introduced mussels were moderately scarce or not recorded from the cages at most sites, but at Scarborough there was a large settlement with on average 856.6 juvenile mussels per plot on harvesting and notable mats of mussel recruits recorded during the monitoring (Figure 5.10). A layer of 0.5 – 2 cm of sand was present in seven of the 18 cages at the Natal site and also covered 2% to 20% of the area of the cages in Zululand.

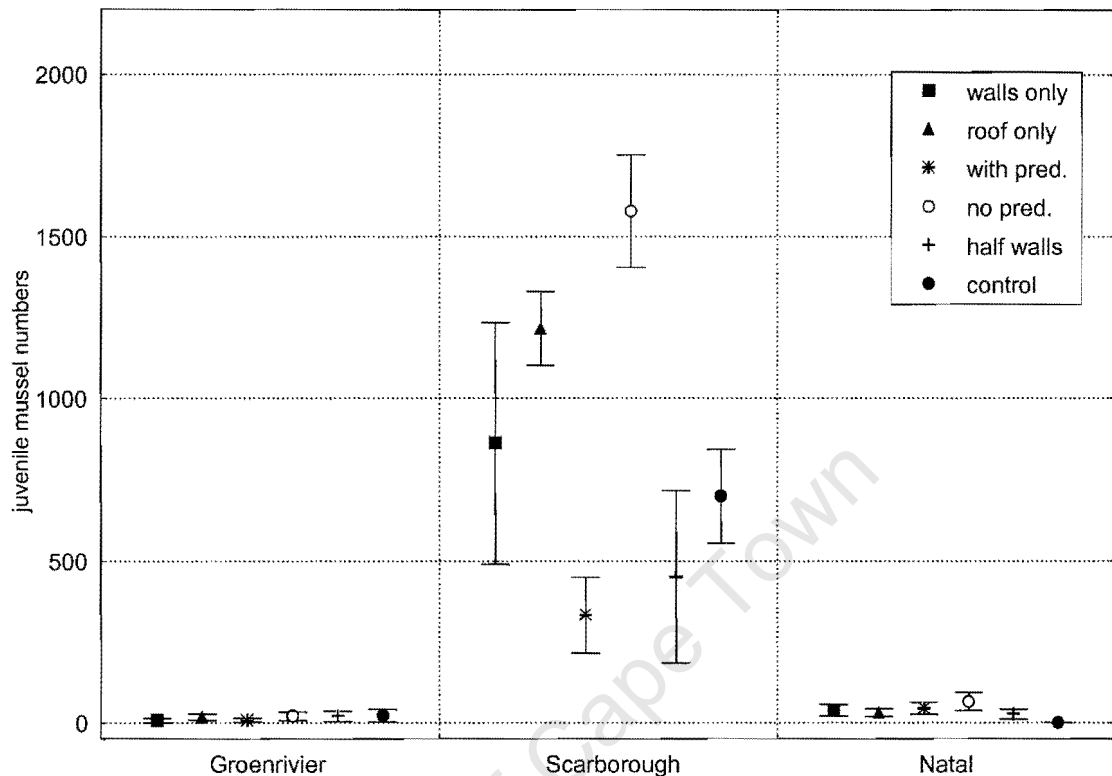


Figure 5.10: Numbers ($\pm$ one S. E.) of juvenile mussels recorded at harvesting of the cages at all sites. The cage types and sites are described in the text. Data was lacking for the Zululand and Transkei sites.

5.4. Discussion

Based on field exclusion-experiments, predation has been concluded to be one of the most important sources of natural mortality for various mussel species in many localities worldwide. Mussel distribution and abundance are controlled by seastars in Washington state, New Zealand and Chile (Paine 1971, 1974, Paine *et al.* 1985). Mussel-bed structure has been shown to be controlled by seastars and drilling whelks on the east coast of England; by seastars, drilling whelks and crabs in Ireland (Kitching and Ebling 1967); and by two species of seastar, drilling whelks and three crab species in New England (Menge 1983). All these studies show the importance of predators of mussels in influencing population size structure as well as overall abundance and local distribution patterns of mussels (Seed and Suchanek 1992). This overall conclusion was thus drawn from numerous field-based predator-exclusion experiments in many different localities

worldwide, although the importance of bottom-up regulation has also been suggested by McQuaid and Lindsay (2000) as a structuring force in mussel beds.

5.4.1. Impact of predatory whelks in South Africa

The results of the predator caging experiment around the South African coast performed in this study generally failed to detect any significant effect of predators on the survivorship of mussels. Only in a single case, at Groenrivier, were there significant differences between the mussel numbers remaining at the time of harvesting in cages with and without introduced predators. The monitoring of the percentage mussel cover in the cages showed a significant decrease in the mussel cover, significantly larger batches of bare rock, and significantly more dead drilled mussel shells in the cages with introduced predators compared to the other cages at Groenrivier. This indicates that the introduced whelk predators were able to reduce mussel numbers to some extent and to create patches of bare rock. These effects were, however, only evident on the cages containing whelks, which were stocked at densities equal to the highest densities recorded. At the other four sites around the South African coast, there were no significant differences in mussel mortalities in the cages with introduced whelk predators compared to cages that excluded whelks.

5.4.2. Large vertebrate predators

Apart from mussel predation by the whelks at Groenrivier other effects of predation were largely unnoticeable. The treatments control, walls only, and half walls were designed to allow unrestricted access for large predators to the mussels but no significant reductions in mussel abundance occurred in these treatments compared to predator-exclusion cages at any site. The *Octopus* sp. individual that inhabited one of the cage plots in the Transkei did decimate the mussels in that particular plot although it did not cause a statistically significant effect among the treatments overall and the predation seemed to be an isolated incident.

The predation rate upon the mussels could have been affected by shading artefacts of the cage design, since shading lowers desiccation and temperature extremes, which possibly favour greater predation rates (Menge 2000). There were, however, no differences in mussel mortality between roof only, control and full cage treatments, so this is unlikely.

5.4.3. Survival of introduced whelks

Mytilus galloprovincialis is known to trap *Nucella* spp. by immobilising the whelks with byssus threads (Day *et al.* 1992, Davenport *et al.* 1996). Some of the dead whelk shells in the caging experiments were observed to be bound to the mussels although it is unknown if binding was the cause of the death or there were other reasons for their mortality. From the 100 adult mussels and the 10 whelks introduced into the cages with predators, no more than 30% of the whelks succumbed over the six month period at the sites where their survival was recorded. Thus, the majority survived until the experiment's completion.

5.4.4. Size of mussels and prey

The caging experiment performed in this study was designed in such a way that it focused on predation upon adult mussels of shell length of 30-50 mm. In general, mussel survival is enhanced by mussels growing out of the size range normally taken by the predators (Seed and Suchanek 1992). Therefore, the possibility exists that the low predation levels on the mussels could have been due to the mussels having already out-grown their predators. Large adult South African *Nucella* spp. can, however, drill and kill mussels up to almost 60 mm in length although it is possible for large mussels (greater than 35 mm) to survive several attacks (Griffiths and Blaine 1994). A model of predation on the South African mussel *Choromytilus meridionalis*, by Griffiths and Hockey (1987), indicated that large mussels of sizes 25 to 90 mm are among the preferred prey of large predators (octopus and oystercatchers). Thus, many of the mussel predators on the South African coast are capable of consuming mussels of the size used in this caging experiment.

5.4.5. Colonisation of the cages by predators

Although visitation of treatments by the larger predators could not be accurately assessed, colonisation by benthic invertebrate predators was measured at harvesting. Three treatments (control, half cage and roof only) were designed to allow unrestricted access by benthic invertebrate predators (e.g. the drilling whelks, *Nucella* spp.), although they were only colonised by some juvenile whelks and very few adults. Overall, the colonisation by whelk predators from the surrounding mussel bed was marginal. Possibly the patches of bare rock created around the cages acted as a barrier to whelk colonisation, although Hunt and Scheibling (1995) showed that when *Nucella lapillus* reduces mussel beds to small patches, movements of the whelk between patches in tidal pools seems unrestricted by the bare rock separating the mussel patches. The effects of the cages on altering the predator's behaviour is unknown. However, the fact that there were no significant differences in the numbers of *Nucella* spp. colonising controls, half cages and roof-only cages suggests that they had no effect, as does the fact that mussel survival was generally not significantly different between these three treatments. If larger mobile predators such as birds and fish avoided cages designed to allow them access to mussels (i.e. the half-walls cage and walls-only treatment), then differences in the survival of mussels would have been expected between these treatments and the controls. Again, because no differences were detected, cage avoidance seems unlikely.

5.4.6. Other colonisers of cages

The cages were colonised by various other intertidal species, apart from mussel recruits and mussel predators, most notably by algae and limpets. Algal growth differed significantly between the sites although it followed no clear pattern around the coast. Heavier growths might have been expected on the west coast than the east coast since the potential primary production on the west coast is higher (Bustamante *et al.* 1995), but this was not the case. Possibly herbivore interactions would have resulted in the differences in growths of the algae in the plots between sites, although there was no indication that grazer densities were correlated with algal growth in either a negative or positive manner.

There were no significant differences between the treatments with respect to algal growth, even though the cages might have been expected to alter growth due to factors such as canopy-shading by the roofs.

Limpets are common in rocky intertidal mussel beds and colonised the Groenriver plots in high numbers and the control plots at Scarborough and Natal. The high limpet abundance at Groenrivier may have reduced the development of algae at this site. Limpets possibly found migration into the control plots easier than the caged plots due to the lack of obstructing cage frames in the controls, which may have resulted in the abundance of limpets in the control plots at Scarborough and Natal. Limpets on mussel beds are sometimes important in preventing fouling of the mussel beds by algae (Seed and Suchanek 1992). The initial transplanting of the mussels might have disrupted this influence although fouling of the mussels by heavy growths of algae was not observed.

Other common intertidal invertebrates noted in the cages were snails (excluding the introduced predators) and anemones. Neither of these groups of invertebrates differed significantly between treatment types and the differences between sites were only noticeable with anemones, which decreased in abundance from the west to the east coast. Overall differences in the fauna and flora colonising the cages through the duration of the experiment did not result in many significant differences between the cage types, although the different sites were significant in affecting the abundance and types of colonisers entering the cages.

5.4.7. Mussel recruitment in the cages

Recruitment of mussels around the coast of South Africa is significantly higher on the west coast than the south and east coasts, although there is significant spatial variation in mussel recruitment over smaller scales between 100 and 1000 km (Harris *et al.* 1998). Juvenile mussels, of a size smaller than the introduced mussels, were moderately scarce or not recorded at all the sites except at Scarborough where there was a large settlement

settlement with an average of 856.6 juvenile mussels per plot at the time of harvesting, and notable mats of mussel recruits recorded during the monitoring. *Nucella* spp. prefer to consume the smaller size classes of mussels (Hunt and Scheibling 1995, Griffiths and Hockey 1987) and the lack of predation on the adult mussels at the Scarborough site was possibly due to the introduced whelks preferring to consume the fast-growing juvenile mussels than the introduced adult mussels. Artificial canopy cover by the cage roofs might have been expected to increase recruitment due to the sheltered conditions the canopy provide (Menge 2000), although the numbers of recruits per cage were not significantly different between treatments at Scarborough (where the only large mussel recruitment occurred).

5.4.8. Non-predator loss of mussels

High wave forces, which are typical at the wave-exposed locations of the intertidal mussel beds, damaged the cages by breaking off some of the roofs. This damage to the cages was most notable at Natal where all the roofs except one had to be replaced between the second and third periods of the experiment. The heavy wave action was also expected to wash some of the introduced mussels from the experimental plots. The control treatments had no cage structure associated that might offer a degree of protection from wave exposure and thus were expected to be most vulnerable to non-predatory loss of mussels. All of the control plots at Natal had large patches of bare rock formed between the first and second monitoring period coinciding with the damage to the Natal cage roofs, and wave action is the most likely reason why the Natal control plots were stripped clean of mussels by the end of the experiment. Apart from at Natal, however, the control plots did not differ significantly from the other treatments in terms of losses of mussels. Differences in the losses of mussels between controls and cages with half walls were not significant at all sites, which indicates that any effects of the cage walls on wave action did not affect the survival of the mussels.

A layer of 0.5 – 2 cm of sand was abundant in seven of the 18 cages at the Natal site and also covered 2% to 20% of the area of the cages at Zululand. Sand covering mussel beds is a common occurrence and influential in structuring rocky shore communities on the east coast of South Africa (McQuaid and Dower 1990, Sink 2001) and may cause significant mortalities of mussels although its impact in the survival of the mussels in the cages was unknown in this experiment. Another cause of mortality could be mussel parasitisation, which has been investigated by Calvo-Ugarteburu and McQuaid (1998), who found high infection rates in east coast *P. perna* but that *M. galloprovincialis* was parasite-free. Possibly this could cause differences in mussel survival rates around the coast.

5.4.9. Tidal height of the mussel bed

Predation on mussels on intertidal rocky shores usually exhibits a gradient, with predation levels on mussels increasing down the shore, while a reverse gradient of mussel mortality exists up the shore due to physical stress increasing with shore height (Seed and Suchanek 1992). The mussel bed exists in the zone where there is a balance between predation and the physical factors. Both *Mytilus galloprovincialis* and to a greater extent *Perna perna* have high resistance to desiccation, high temperatures and survival during long anaerobic periods (van Erkom Schurink and Griffiths 1992), and can become established in the middle zones of shores where they are distanced from the low shore where predation is most intense. If the cages had been positioned lower on the shore, it is possible that predation might have had greater effects.

5.4.10. Effects of cage design

The mussel habitat was recreated in the cages, which involved the mussels being removed from the mussel bed and then allowed to reattach in the plots. To standardise the design, mussel size was restricted to a particular range (30-50 mm) and mussel density was fixed at 100 per cage. This will have altered the composition of the mussels relative to that in the surrounding natural mussel beds, even though, the mussel plots did come to visually

which is particularly obvious on the west coast where the abundance of mussels is high (Harris *et al.* 1998). The hummocks are important for the whelk predators since they provide a favourable microclimate for the whelks, sheltering them from abiotic extremes of the intertidal and providing protection from large predators (Davenport *et al.* 1998) although possibly restricting the movements of large whelks trapped below the hummocks. The monolayer of mussels created in the treatments may have lowered the impact of predators on the west coast in the cages since the whelks could not shelter in the hummocks. Possibly larger or smaller cage designs may have changed the impact of the predators, although Fernandes *et al.* (1999) ran caging experiment with shore crabs, using cages of different sizes, and showed that crab predation did not differ with cage size.

5.4.11. Biogeographical influence of predators of mussels

Even though mussels differ in species, abundance and growth rates around the South African coast (van Erkom Schurink and Griffiths 1990, 1993) and the species of predators differ between the east and west coasts, the influence of mussel predators at all sites was minimal. If this study had been conducted at only Groenrivier, the conclusion might have been that drilling whelks are an important predator of mussels, but by studying the influences of predation around the coast it is clear that conclusion cannot be generalised. The results of high non-predatory mussel losses from the modelling experiment reaffirm the limited influence of the predators of mussels in structuring the beds on the west coast. Indeed, this multi-site caging experiment showed that in general predators are not influential in structuring the mussel populations over wide biogeographical scales within South Africa.

5.4.12. Conclusions

From the results, *Nucella* spp. cannot be considered as a significant predator in mussel beds on South African shores. Only at one site (Groenrivier) did *Nucella*-inclusion cages yield lower mussel survival than predator-exclusion cages. The experiment also failed to

5.4.12. Conclusions

From the results, *Nucella* spp. cannot be considered as a significant predator in mussel beds on South African shores. Only at one site (Groenrivier) did *Nucella*-inclusion cages yield lower mussel survival than predator-exclusion cages. The experiment also failed to detect significant effects of bird or fish predation, although the confident interpretation of caging experiment results requires detailed knowledge of the behaviour of the predators (Fernandes *et al.* 1999), which is lacking for some of the South African mussel predators. The heavy recruitment of mussels at one site (Scarborough) may have saturated the *Nucella* spp. predation rate and reduced the impact of the predators on the adult mussels, but this effect would have high temporal and spatial variability due to the sporadic and patchy nature of mussel recruitment around the coast. Effects of wave action, sand inundation and parasitism may be more important for the survival of the mussels in South African intertidal mussel beds than mortality losses due to predation.

Chapter Six

General Conclusions

Trophic flows in South African intertidal mussel beds were investigated in this thesis, focussing on the energy flows associated with west-coast rocky shore mussel beds and the influences of mussel predators around the coast of South Africa. The west-coast mussel beds have a large sessile biomass of up to 3.24 kg AFDM. m⁻², which is largely maintained by imports of detritus of up to 55 kg AFDM m⁻². yr⁻¹, of which 36 kg originates from subtidal kelp production. The alien mussel, *Mytilus galloprovincialis*, dominates the system contributing to over 90% of the total biomass, consumption and production. Predators in the west-coast system appear to have a low importance in controlling their prey, since 85% or more of the production of most components is lost from the system as non-predatory mortality. A strong trophic link appears to exist between algae growing in the mussel bed and limpet grazers, since nearly all algal production is consumed by limpets and the limpet biomass exceeds that of the standing stock of algae. Imports are important in sustaining these grazers.

From the results of the caging experiment, the impact of predators around the coast of South Africa appears to be minimal. Only at one site on the west coast, under conditions of intensified predation from drilling whelks, was there a significant reduction in mussel numbers due to predation. A comparison of mussel predation rates by whelks in the field experiment and the trophic model is possible by normalising the two measurements of consumption rates. In the field experiment at the Groenrivier site on the west coast, consumption of *Mytilus galloprovincialis* in three cages with the whelk predator was compared to the mortality in three cages that excluded all predators over a six month period. On average, 9.57 mussels of 40 mm shell length (0.724 g AFDM. mussel⁻¹) would have been consumed by each whelk of 21 mm (0.295 g AFDM. snail⁻¹) in a year. Thus, mortality rates of *Mytilus galloprovincialis* caused by *Nucella cingulata* were approximately 23.5 g AFDM mussel per g AFDM whelk. yr⁻¹, which is about a three

times greater consumption by whelks in the field experiment than estimated in the balanced trophic model. The mostly likely reason for this difference is that the cages that included whelks in the field experiment were stocked to densities corresponding to the maximum recorded levels (equivalent to 47.2 g AFDM whelks. m⁻²), whereas the trophic model was based on average levels of biomass. However when tests of the effects of elevated whelk consumption were performed on the model by increasing consumption of whelks by a factor of 10 (corresponding to an increase in whelk biomass to 270 g AFDM whelks. m⁻² on wave-exposed lower shores), the model was still not imbalanced nor were flows change sufficiently that predation became the main cause of mortality. In comparison, an intertidal predator-caging experiment measuring predation between barnacles and *Nucella* sp. on the Cape Peninsula of South Africa by McQuaid (1985) revealed higher predation rates in which whelks consumed 46% of the standing biomass of barnacles each year. In the model I developed, whelks consumed 6.8% of the biomass each year (since 198 g AFDM mussel was consumed by whelks each year and there was a standing biomass of 2892 g AFDM of mussel). This difference is, however, not unexpected, as the standing stocks of mussels were substantially greater than those of the barnacles on which McQuaid worked.

The lack of a noticeable impact of predators from the field experiment I described and from the models of the west coast mussel beds is strong evidence that mussel predators are not very influential in structuring the mussel beds. Possibly the mussel predators limit the extent of the mussel bed, although modifications of the model with high levels of either bird or whelk predation at the borders of the mussel bed were still insufficient to consume even the majority of the mussel production. Thus, generally predation on mussels is not large enough to prevent mussels from dominating the shore and utilizing by far the majority of trophic resources, nor is predation a factor that exerts more than a minor influence on mussel abundance in the mussel beds. In the field experiment, other effects such as dense episodic mussel recruitment, heavy wave action and sand inundation often induced greater effects on the survival of the mussels.

Noticeable effects were also associated with the two environmental factors investigated in the model, namely shore height and wave exposure. Total flows, imports and exports in the mussel bed generally follow changes in the total biomass per unit area, which generally decreases with shore height and increases with wave exposure. Mussel predation decreases with shore height and increases with wave exposure due to changes in the standing stocks of the invertebrate predators. Primary production is slightly higher on semi-exposed shores due to the greater abundance of algae. The changes in mussel abundance with shore height and wave exposure did not appear to be strongly affected by predation rates and is more likely to be linked to differences in immersion, desiccation, removal of mussels by wave action and enhancement of food supply for mussels by wave action.

Generally, within the mussel beds of South African shores, the community structure of mussel beds seems to be largely uninfluenced by the effects of predation. The relatively small importance of predators as controlling agents in South Africa mussel beds contrasts with the important role mussel predators have in other mussel beds (such as studies by Kitching and Ebling 1967; Paine 1971, 1974; Paine *et al.* 1985; Menge 1983; Castilla and Durán 1985; Castilla 1999). The trophic modelling suggests that South African west-coast intertidal mussel beds are dominated by mass flows associated with filter feeders and this has formed a community that is dependant mostly on subtidal imports. The west-coast mussel beds are also characterised by very inefficient flows between a short series of trophic levels with most of the production being washed from the rocks.

References

- ASMUS, H. 1987. Secondary production of an intertidal mussel bed community related to its storage and turnover compartments. *Marine Ecology Progress Series*. 39: 251-266.
- BENNETT, B. 1979. An energy budget for *Clinus superciliosus* (L.) based on laboratory estimates of consumption, assimilation efficiency and faeces production. Honours project. University of Cape Town. 33 pp.
- BENNETT, B., C. L. GRIFFITHS & M. PENRITH. 1983. The diets of littoral fish from the Cape Peninsula. *South African Journal of Zoology*. 18: 343-352.
- BERRY, P. F. 1978. Reproduction, growth and production in the mussel, *Perna perna* Linnaeus), on the east coast of South Africa. Oceanographic Research Institute. *Investigational Report*. 48:1-28.
- BLANCHARD, D. & E. BOURGET. 1999. Scales of coastal heterogeneity: influence on intertidal community structure. *Marine Ecology Progress Series*. 179: 163-173.
- BOSMAN, A. L., S. EEKHOUT & G. M. BRANCH. 1990. *The Exploitation Potential of Limpets on the Coast of Namaqualand*. Final Report to the Chief Director, Marine Development. Sea Fisheries Research Institute.
- BOSMAN, A. L. & P. A. R. HOCKEY. 1988. The influence of primary production rate on the population dynamics of *Patella granularis*, an Intertidal limpet. *Marine Ecology*. 9(3): 181-198.
- BRANCH, G. M. 1971. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. I. Zonation, movements and feeding. *Zoologica Africana*. 6(1): 1-38.
- BRANCH, G. M. 1974. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa, 3. Growth-rates. *Transactions of the Royal Society of South Africa*. 41(2): 161-193.
- BROWN, K. M. & J. F. QUINN. 1988. The effect of wave action on growth in three species of intertidal gastropods. *Oecologia*. 75: 420-425.
- BUSTAMANTE, R. H. 1994. Patterns and causes of intertidal community structure around the coast of Southern Africa. PhD Thesis, University of Cape Town.

- BUSTAMANTE, R. H., G. M. BRANCH, S. EEKHOUT, B. ROBERTSON, P. ZOUTENDYK, M. SCHLEYER, A. H. DYE, N. HANEKOM, D. KEATS, M. JURD. & C. D. McQUAID. 1995. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia*. 102: 182-201.
- BUSTAMANTE, R. H. & G. M. BRANCH. 1996. Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. *Journal of Biogeography*. 23: 339-351.
- CALVO-UGARTEBURU, G. & C. D. McQUAID. 1998. Parasitism and introduced species: epidemiology of trematodes in the intertidal mussels *Perna perna* and *Mytilus galloprovincialis*. *Journal of Experimental Marine Biology and Ecology*. 220: 47-65.
- CAMMEN, L. M. 1980. The significance of microbial carbon in the nutrition of the deposit feeding polychaete *Nereis succinea*. *Marine Biology*. 61: 9-20.
- CARROLL, M. L. & R. C. HIGHSMITH. 1996. Role of catastrophic disturbance in mediating *Nucella-Mytilus* interactions in the Alaskan rocky intertidal. *Marine Ecology - Progress Series*. 138: 125-133.
- CASTILLA, J. C. 1999. Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends in Ecology and Evolution*. 14: 280-283
- CASTILLA, J. C. & L. R. DURÁN. 1985. Human exclusion from the rocky intertidal zone of central chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos*. 45: 391-399.
- CHAMBERS, M. R. & H. MILNE. 1975. Life cycle and production of *Nereis diversicolor* O. F. Müller in the Ythan Estuary, Scotland. *Estuarine and Coastal Marine Science*. 3: 133-144.
- CHRISTENSEN, V. & D. PAULY. 1992. ECOPATH II - A software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modeling*. 61: 169-185.

- CHRISTENSEN, V., C. J. WALTERS & D. PAULY. 2000. *Ecopath with Ecosim – A User's Guide*. University of British Columbia, Fisheries Centre, Vancouver, Canada and ICLARM, Penang, Malaysia. (in press).
- CHOI, J-W. & J-H LEE. 1997. Secondary production of a nereid species, *Perinereis aibuhitensis* in the intertidal mudflat of the west coast of Korea. *Bulletin of Marine Science*. 60(2): 517-528.
- CONNELL, J. H. 1972. Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics*. 3: 169-192.
- DAVENPORT, J., P. G. MOORE & E LeCOMTE. 1996. Observations on defensive interactions between predatory dogwhelks, *Nucella lapillus* (L.) and mussels, *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology*. 206: 133-147.
- DAY, R. W., A. BARKAI, & P. A. WICKENS. 1991. Trapping of three drilling whelks by two species of mussel. *Journal of Experimental Marine Biology and Ecology*. 149: 109-122.
- DIECKMANN, G. S. 1980. Aspects of the ecology of *Laminaria pallida* (Grev.) J. Ag. off the Cape Peninsula (South Africa) I. Seasonal growth. *Botanica Marina*. 23: 579-585.
- FERNANDES, T. F., M. HUXAM & S. R. PIPER. 1999. Predator caging experiments: a test of the importance of scale. *Journal of Experimental Marine Biology and Ecology*. 241: 137-154.
- FIELD, J. G., C. L. GRIFFITHS, R. J. GRIFFITHS, N. JARMAN, P. ZOUTENDYK, B. VELIMIROV & A. BOWES. 1980. Variation in structure and biomass of kelp communities along the south-west cape coast. *Transactions of the Royal Society of South Africa*. 44(2): 145-203
- FIELD, J. G., F. WULFF & K. H. MANN. 1989. The need to analyze ecological networks. In: Wulff, F., Field, J. G. and Mann, K. H. (Eds). *Network analysis in marine ecology*. *Coastal and Estuarine Studies* 32: 3-12, Springer-Verlag, Germany. 3-14.

- GOSS-CUSTARD, J. D. 1996. *The oystercatcher from individuals to populations*. Oxford University Press. Oxford.
- GRIFFITHS, C. L. & M. J. BLAINE. 1994. Non-fatal cropping of large mussels by drilling whelks, *Nucella cingulata* (Linnaeus, 1771). *Journal of Molluscan Studies*. 60: 346-348.
- GRIFFITHS, C. L. & R. J. GRIFFITHS. 1987. *Bivalvia*. In: Animal Energetics, Volume 2. Academic Press Inc. pp 1-88.
- GRIFFITHS, C. L. & P. A. R. HOCKEY. 1987. A model describing the interactive roles of predation, competition and tidal elevation in structuring mussel populations. In: Benguela and Comparable Ecosystems. Payne, A. I. L., J. A. Gulland & Brink, K. H. (Eds). *South African Journal of Marine Science*. 5: 547-556.
- GRIFFITHS, C. L., P. A. R. HOCKEY, C. VAN ERKOM SCHURINK & P. J. LE ROUX. 1992. Marine invasive aliens on South African shores: implications for community structure and trophic functioning. In: Benguela Trophic Functioning. Payne, A. I. L., Brink, K. H. & R. Hilborn (Eds). *South African Journal of Marine Science*. 12: 713-722.
- GRIFFITHS, C. L. & J. A. KING. 1979. Energy expended on growth and gonad output in the ribbed mussel *Aulacomya ater*. *Marine Biology*. 53: 217-222.
- HARRIS, J. M., G. M. BRANCH, B. L. ELLIOT, B. CURRIE, A. H. DYE, C. D. MCQUAID, B. J. TOMALIN & C. VELASQUEZ. 1998. Spatial and temporal variability in recruitment of intertidal mussels around the coast of southern Africa. *South African Journal of Zoology*. 33(1): 1-11.
- HOCKEY, P. A. R. 1984. Growth and energetics of the African Black Oystercatcher *Haematopus moquini*. *Ardea*. 72: 111-117.
- HOCKEY, P. A. R. & L. G. UNDERHILL. 1984. Diet of the African Black Oystercatcher *Haematopus moquini* on rocky shores: spatial, temporal and sex-related variation. *South African Journal of Zoology*. 19: 1-11.

- HUNT, H. L. & R. E. SCHEIBLING. 1995. Structure and dynamics of mussel patches in tide-pools on a rocky shore in Nova Scotia, Canada. *Marine Ecology Progress Series*. 124: 105-115
- JACKELMAN, J. J. & J. J. BOLTON. 1990. Form variation and productivity of an intertidal foliose *Gigartina* species (Rhodophyta) in relation to wave exposure. *Hydrobiologia*. 204/205: 57-64.
- JARRE-TEICHMANN, A., L. J. SHANNON, C. L. MOLONEY & P. WICKENS. 1998. Comparing trophic flows in the Southern Benguela to other upwelling ecosystems. In *Benguela Dynamics: Impacts of Variability of Shelf-Sea Environments and their Living Resources*. Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *South African Journal of Marine Science*. **19**: 391-414.
- KITCHING, J. A. & F. J. EBLING. 1967. Ecological studies and Lough Ine. *Advances in Ecological Research*. 4: 198-291
- KRUGER, L. M. 1995. *Feeding biology of intertidal sea anemones in the south-western Cape*. MSc Thesis. University of Cape Town. 98 pp.
- KRUGER, L. M. & C. L. GRIFFITHS. 1996. Sources of nutrition in intertidal sea anemones from the south-western Cape, South Africa. *South African Journal of Zoology*. 31 (3): 110-119.
- LEEB, A. 1995. *Patterns of Recruitment, Growth and Mortality of the Mussel, Mytilus Galloprovincialis in Relation to Wave Exposure and Tidal Elevation*. MSc Thesis. University of Cape Town.
- LEVITT, G. J. 1987. Studies on the seasonal primary production of Cape Peninsula littoral and sublittoral seaweeds. M.Sc Thesis. University of Cape Town. 196 pp.
- LOBBAN, C. S. 1994. *Seaweed ecology and physiology*. Cambridge University Press.
- MACLEAN, G. L. 1985. Roberts' birds of Southern Africa. CTP Printers. Cape Town.
- MANN, K. H. 1972. Ecological energetics of the sea-weed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of the seaweeds. *Marine Biology*. 14: 199-209.

- MARSH, C. P. 1986. Rocky intertidal community organization: the impact of avian predators on mussel recruitment. *Ecology*. 67:771-786.
- MCQUAID, C. D. & G. M. BRANCH. 1985. Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Marine Ecology Progress Series*. 22: 153-161.
- MCQUAID, C. D. & K. M. DOWER. 1990. Enhancement of habitat heterogeneity and species richness on rocky shores inundated by sand. *Oecologia*. 84: 142-144.
- MCQUAID, C. D. & T. L. LINDSAY. 2000. The effects of wave exposure on growth and mortality rates of the mussel *Perna perna*: bottom-up regulation of intertidal populations. *Marine Ecology Progress Series*. 206: 147-154.
- MCQUAID, C.D., J. R. LINDSAY & T. L. LINDSAY. 2000. Interactive effects of wave exposure and tidal height on population structure of the brown mussel *Perna perna*. *Marine Biology*. 137: 925-932.
- MENGE, B. A. 2000. Testing the relative importance of positive and negative effects on community structure. *Trends in Ecology and Evolution*. 15(2): 46-47.
- MENGE, B. A. 1983. Components of predation intensity in the low zone of the New England rocky intertidal region *Oecologia*. 58: 141-155.
- MENGE, B. A. & A. M. OLSON. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution*. 5: 52-57.
- NIELSEN, A. M., N. T. ERIKSEN, J. J. L. IVERSEN & H. U. RIISGÅRD. 1995. Feeding, growth and respiration in the polychaetes *Nereis diversicolor* (facultative filter-feeder) and *N. virens* (omnivorous) - a comparative study. *Marine Ecology Progress Series*. 125: 149-158.
- OLIVIER, M., G. DESROSIERS, A. CARON & C. RETIÈRE. 1996. Juvenile growth of the polychaete *Nereis virens* feeding on a range of marine vascular and macroalgal plant sources. *Marine Biology*. 125: 693-699.
- OPITZ, S. 1991. *Quantitative models of trophic interactions in Caribbean coral reefs*. PhD Thesis. Universität du Kiel.

- PAINE, R. T. 1966. Food web complexity and species diversity. *American Naturalist*. 100: 65-75.
- PAINE, R. T. 1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference and intertidal community structure. *Ecology*. 50: 950-961.
- PAINE, R. T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology*. 52: 1096-1106.
- PAINE, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*. 15: 93-120.
- PAINE, R. T. 1994. Marine rocky shores and community ecology: an experimentalist's perspective. *Excellence in Ecology Series*. Volume 4. Ecology Institute. Olendorf. Germany.
- PAINE, R. T., J. C. CASTILLA & J. CENCINO. 1985. Perturbation and recovery patterns of starfish dominated intertidal assemblages in Chile, New Zealand and Washington State. *American Naturalist*. 125: 679-691.
- PALUMBI, S. R. 1984. Measuring intertidal wave forces. *Journal of Experimental Marine Biology and Ecology*. 81: 171-179.
- PEDERSEN, M. F. & J. BORUM. 1996. Nutrient control of algae growth in estuarine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen storage among phytoplankton and species of macroalgae. *Marine Ecology Progress Series*. 142: 261-272.
- POLOVINA, J. J. 1984. Model of a coral reef ecosystems I. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* 3(1):1-11.
- PROCHAZKA, K. & C. L. GRIFFITHS. 1992. The intertidal fish fauna of the west coast of South Africa - species, community and biogeographic patterns. *South African Journal of Zoology*. 27 (3): 115-120.
- SEED, R. & T. H. SUCHANEK. 1992. Population and community ecology of *Mytilus*. *The Mussel Mytilus: Ecology, Physiology, Genetics and Culture*. E. Gosling (Ed). Elsevier. Amsterdam. 87-169.

- SHANNON, L. V. 1985. The Benguela ecosystem. Part 1. Evolution of the Benguela. Physical features and processes. *Oceanography and Marine Biology, an Annual Review*. 23: 105-187.
- SHANNON, L. J. 2001. *Trophic models of the Benguela upwelling system: towards an ecosystem approach to fisheries management*. PhD Thesis. University of Cape Town. 318 pp.
- SINK, K. J. 2001. *A hierarchical analysis of abiotic determinants and harvesting impacts in the rocky intertidal communities of KwaZulu-Natal*. PhD Thesis. University of Cape Town. 277 pp.
- STATSOFT, Inc. 1995. *STATISTICA for Windows (computer program manual)*. StatSoft, Inc., 2300 East 14th Street, Tulsa, Oklahoma.
- STEFFANI, C. N. 2001. *Interactions between an indigenous limpet, Scutellastra argenvillei, and an alien invasive mussel, Mytilus galloprovincialis – moderation by wave action*. PhD Thesis. University of Cape Town. 190 pp.
- STEPHENSON, T. A. & A. STEPHENSON. 1949. The universal features of zonation between tidemarks on rocky coasts. *Journal of Ecology*. 49:1-29.
- STICKLE, W. B. & B. L. BAYNE. 1987. Energetics of the muricid gastropod *Thais (Nucella) lapillus* (L.). *Journal of Experimental Marine Biology and Ecology*. 107: 263-278.
- SUCHANEK, T. H. 1985. Mussels and their rôle in structuring rocky shore communities. In: *The Ecology of Rocky Coasts*. Moore, P. G. & R. Seed (Eds). Hodder and Stoughton. London. 70-96.
- TORAL-GRANDA, M. V., C. L. MOLONEY, J. M. HARRIS & B. Q. MANN. 1999. *Ecosystem impacts of the KwaZulu-Natal Reef Fishery, South Africa: an exploratory model*. P211-230. In: *Ecosystem approaches for fisheries management*. University of Alaska. Sea Grant, AK-SG-99-01. Fairbanks. 765 pp.
- ULANOWICZ, R.E. 1986. *Growth and Development: ecosystem phenomenology*. Springer Verlag, New York. 203 pp.

- ULANOWICZ, R. E. & NORDEN, J. S. 1990. Symmetrical overhead in flow and networks. *International Journal of Systems Science*. 21(2): 429-437.
- VAN ERKOM SCHURINK, C. & C. L. GRIFFITHS. 1990. Marine mussels of Southern Africa - their distribution patterns, standing stocks, exploitation and culture. *Journal of Shellfish Research*. 9 (1): 75-85.
- VAN ERKOM SCHURINK, C. & C. L. GRIFFITHS. 1991. A comparison of reproductive cycles and reproductive output in four southern African mussel species. *Marine Ecology Progress Series*. 76: 123-134.
- VAN ERKOM SCHURINK, C. & C. L. GRIFFITHS. 1992. Physiological energetics of four South African mussel species in relation to body size, ration and temperature. *Comparative Biochemical Physiology*. 101A (4): 779-789.
- VAN ERKOM SCHURINK, C. & C. L. GRIFFITHS. 1993. Factors affecting relative rates of growth in four South African mussel species. *Aquaculture*. 109: 257-273.
- WAALAND, R. J. 1976. Growth of the red algae *Iridaea cordata* (Turner) Bory in semi-closed culture. *Journal of Experimental Marine Biology and Ecology*. 23: 45-53.
- WELLS, J. 1988. *Orientation, tube construction and feeding in Gunnarea capensis (Schm.) (Polychaeta)*. Honours Thesis. University of Cape Town 23 pp.
- WU, R. S. S. & C. D. LEVINGS. 1978. An energy budget for individual barnacles (*Balanus glandula*). *Marine Biology*. 45: 225-235.
- ZAMER, W. E. 1986. Physiological energetics of the intertidal sea anemone *Anthopleura elegantissima*. *Marine Biology*. 92: 299-314.
- ZAR, J. H. 1984. *Biostatistical Analysis*. Prentice-Hall Inc. Englewood Cliffs. New Jersey. 718 pp.

Appendix A

The phylogenetic affinities of the species included in the Ecopath model of the intertidal, rocky shore mussel bed on the west coast of South Africa.

HETEROTROPHS

Class	Species
Anthozoa (sea anemones)	<i>Aulactinia reynaudi</i> <i>Actinia equina</i> <i>Pseudodactinia flagellifera</i> <i>Anthopleura michaelsoni</i> <i>Bunodosoma capensis</i>
Polychaeta	<i>Marphysa</i> sp. <i>Pseudonereis variegata</i> <i>Terebella</i> sp. <i>Lepidonotus semitecta</i> <i>Gunnarea capensis</i>
Cirripedia	<i>Notomegabalanus algalicola</i> <i>Octomeris angulosa</i> <i>Tetraclita serrata</i>
Bivalvia (mussels)	<i>Mytilus galloprovincialis</i> <i>Aulacomya ater</i>
Gastropoda (limpets)	<i>Scutellastra argenvillei</i> <i>Scutellastra barbara</i> <i>Scutellastra cochlear</i> <i>Cymbula granatina</i> <i>Scutellastra granularis</i> <i>Cymbula miniata</i> <i>Helcion dunkeri</i>
(whelks)	<i>Nucella cingulata</i> <i>Nucella dubia</i> <i>Nucella squamosa</i>

Teleostomi	<i>Clinus acuminatus</i>
	<i>Clinus agilis</i>
	<i>Clinus heterodon</i>
	<i>Clinus superciliosus</i>
	<i>Chorisochismus dentex</i> .
Aves	<i>Larus dominicanus</i>
	<i>Haematopus moquini</i>

AUTOTROPHS

Division	Family	Species
Chlorophyta	Cladophoraceae	<i>Cladophora</i> spp.
	Ulvaceae	<i>Enteromorpha intestinalis</i>
	Ulvaceae	<i>Ulva</i> spp.
Phaeophyta	Chordariopsidaceae	<i>Chordariopsis capensis</i>
	Ectocarpaceae	<i>Ectocarpus</i> sp.
	Lessoniaceae	<i>Ecklonia maxima</i>
	Lessoniaceae	<i>Laminaria pallida</i>
Rhodophyta	Bangiaceae	<i>Porphyra capensis</i>
	Caulacanthaceae	<i>Caulacanthus ustulatus</i>
	Ceramaceae	<i>Ceramium</i> spp.
	Ceramaceae	<i>Aristothamnion collabens</i>
	Chamaceae	<i>Champia lumbricalis</i>
	Corallinaceae	Encrusting Corallines
	Corallinaceae	Articulated Corallines
	Gelidiaceae	<i>Gelidium micropterum</i>
	Gigartinaceae	<i>Gigartina radula</i>
	Gigartinaceae	<i>Gigartina stiriata</i>
	Gigartinaceae	<i>Mazzaella (Iridaea) capensis</i>
	Halymeniaceae	<i>Aeodes orbitosa</i>
	Plocamiaceae	<i>Plocamium</i> spp.
	Ralfsiaceae	<i>Ralfsia verrucosa</i>

Appendix B

Table B: Mass conversion co-efficients between wet weight (WW), dry weight which includes the shell in invertebrates (DW), and ash free dry weight (AFDM). The details of the location where the ashed organisms originated are given. From unpublished data by G. M. Branch, Zoology Department, University of Cape Town.

Species	DW / WW	AFDM/DW	Location
<i>Mytilus galloprovincialis</i>	0.412	0.824	Groenrivier
<i>Aulactinia reynaudi</i>	0.206	0.268	Groenrivier
<i>Gunnarea capensis</i>	0.67	0.968	Groenrivier
<i>Octomeris angulosa</i>	0.701	0.916	Cape Infanta
<i>Scutellastra granularis</i>	0.605	0.871	Cape Infanta
<i>Scutellastra cochlear</i>	0.67	0.863	Cape Infanta
<i>Scutellastra barbara</i>	0.605	0.88	Cape Infanta
<i>Scutellastra argenvillei</i>	0.634	0.861	Cape Infanta
<i>Cymbula miniata</i>	0.47	0.779	Cape Infanta
<i>Burnupena</i> spp.	0.628	0.831	Groenrivier
<i>Pseudonereis variegata</i>	0.937	0.831	Groenrivier
<i>Helcion dunkeri</i>	0.609	0.872	-
<i>Nucella cingulata/dubia</i>	0.638	0.67	Groenrivier
Kelps (<i>Laminaria</i> & <i>Ecklonia</i>)	0.125	0.351	Groenrivier
Upright corallines	0.417	0.845	Cape Infanta
<i>Aeodes orbitosa</i> (Rhodophyta)	0.184	0.298	Groenrivier
<i>Champia lumbricalis</i> (Rhodophyta)	0.136	0.628	Cape Infanta
<i>Gigartina stiriata</i> (Rhodophyta)	0.131	0.42	Groenrivier
<i>Iridaea capensis</i> (Rhodophyta)	0.176	0.303	Groenrivier
<i>Ulva</i> spp. (Chlorophyta)	0.337	0.842	Groenrivier
<i>Cladophora</i> spp. (Chlorophyta)	0.143	0.423	Groenrivier
<i>Plocamium</i> sp. (Rhodophyta)	0.128	0.567	Cape Infanta
<i>Ralfsia verrucosa</i>	0.128	-	Groenrivier
<i>Caulacanthus ustulatus</i> (Rhodophyta)	0.216	0.783	Tsitsikamma
<i>Ceramium</i> spp. (Rhodophyta)	0.145	0.696	Groenrivier
<i>Gelidium micropterum</i> (Rhodophyta)	0.674	0.37	Cape Infanta
<i>Gigartina radula</i> (Rhodophyta)	0.131	0.42	Groenrivier
<i>Porphyra capensis</i> (Rhodophyta)	0.21	0.309	Groenrivier

Appendix C

Table C: Summary statistics calculated by Ecopath for the seven trophic models of an intertidal mussel bed at different wave exposures and shore heights on the west coast of South Africa. Export values are zero since all detritus and debris washed from the shore was modelled as flowing into a detritus group.

wave exposure	Exposed					semi-exposed	
shore height (% air exposure)	10%	20%	30%	40%	50%	30%	40%
Biomass total excl. detritus (gAFDM/m ²)	2977	3235	2873	2687	1488	2316	1147
Flows (gAFDM/m ² /yr)							
Sum of all consumption	51016	56540	41617	33556	17132	32612	14612
Sum of all exports	0	0	0	0	0	0	0
Sum of all respiratory flows	36763	36188	26077	21083	9669	19264	8419
Sum of all flows into detritus	64295	74149	54638	43942	23887	46023	20137
Total system throughput	152075	166878	122333	98583	50689	97899	43169
Sum of all production	7734	8562	7409	5910	4420	7524	3863
Calculated total net primary prodn	5284	1102.04	1119.19	895	868	1644	988
Net system production	-31478	-35086	-24958	-20188	-8800	-17619	-7430
Ratios (dimensionless)							
Total primary prodn/total respiration	0.144	0.03	0.043	0.042	0.09	0.085	0.117
Total primary prodn/total biomass	1.775	0.341	0.389	0.333	0.583	0.71	0.861
Total biomass/total throughput	0.02	0.019	0.023	0.027	0.029	0.024	0.027
Connectance Index	0.218	0.197	0.204	0.219	0.26	0.179	0.207
System Omnivory Index	0.052	0.069	0.067	0.069	0.07	0.059	0.063
Network Flow Indices (Flowbits)							
Total Ascendency: Import	79813	87998	64464	51937	26678	51581	22692
Total Ascendency: Internal Flow	138797	138637	102152	82401	43729	85462	39600
Total Ascendency: Respiration	58260	56602	40720	32865	15154	30640	13236
Total Ascendency: Totals	276886	283238	207337	167218	85561	167684	75528
Total Overhead: Import	25478	13962	9744	7477	2891	10320	4566
Total Overhead: Internal Flow	94457	62146	62304	42282	24490	63858	30810
Total Overhead: Respiration	57052	42683	39262	29009	15829	36139	18969
Total Overhead: Totals	177098	118792	111310	78874	43212	110318	54346
Total Capacity: Import	105291	101960	74208	59414	29570	61902	27258
Total Capacity: Internal Flow	233254	200784	164457	124683	68220	149320	70410
Total Capacity: Respiration	115313	99286	79982	61874	30984	66779	32205
Total Capacity: Totals	453985	402031	318648	246093	128774	278002	129875
System Throughput							
Total system throughput (gAFDM/m ² /year)	152084	166878	122333	98592	50689	97899	43169
Information content (bits)	1.821	1.697	1.695	1.696	1.688	1.713	1.75
Cycles and Pathlengths							
Throughput cycled (excl. detritus) (gAFDM/m ² /yr)	1.3	2	1.5	1.4	0.9	0.3	0.2
Finn's mean path length(dimensionless)	4.14	4.61	4.69	4.67	5.24	5.08	5.13
Finn's straight-through path length(without detritus)	1.09	1.05	1.07	1.07	1.08	1.04	1.1
Finn's straight-through path length(with detritus)	4.14	4.61	4.69	4.67	5.24	5.08	5.13