Ecosystem effects of a rock-lobster 'invasion': comparative and modelling approaches

Laura Kate Blamey

Supervisors: Emeritus Professor George M. Branch and Dr Éva Plagányi-Lloyd

Thesis presented for the Degree of
Doctor of Philosophy
In the Department on Zoology
Faculty of Science
University of Cape Town
February 2010

“For in the end, we will conserve only what we love,

we will love only what we understand,

and we will understand only what we are taught.”

~ Baba Dioum, 1968.

This thesis is dedicated to my parents
Campbell and Ursula Blamey

And to my grandfather
Donald Currie

Declaration

I hereby declare that all the work presented in this thesis is my own, except where otherwise stated in the text. This thesis has not been submitted in whole or in part for a degree at any other university.

Laura Kate Blamey

Date

Table of Contents

Chapter 1

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

Chapter 7

Chapter 8

Acknowledgements

This project would not have been possible without the financial support I received from the NRF (National Research Foundation), the Andrew W. Mellon Foundation, the History of the Nearshore Project and the South African Research Chairs Initiative of the Department of Science and Technology and the National Research Foundation, through the Research Chair in Marine Ecology and Fisheries.

To my supervisors - George Branch and Éva Plagányi-Lloyd - I am forever indebted.

George – It has been a great privilege to be able to work with you. A word that sums up everything you have taught me is 'passion'. Your passion for your family, for marine science, for your students and for life in general is unparalleled. Thank you for your guidance, your enthusiasm, your patience and for pushing me that much further.

Éva – Stepping into your mathematical modelling world was one of the biggest challenges I faced during this thesis. I could never have done it without you. Thank you for your patience and for going the extra mile when it came to explaining maths to a biologist. Thank you for your guidance and enthusiasm, for replying to my endless emails and for allowing me to invade your new home.

To Margo Branch and Penn, Sabrina and Isabella Lloyd – thank you for allowing your husband/wife/mom to spend all those late nights going over my thesis, particularly during this last month.

To all those who helped me on what seemed like endless dive trips: Andrea Plos, Maya Pfaff, Peter Southwood, Steven Horsley, Andrew Jones, Marc Cornwell, Case Bakker, Kate Watermeyer, Alli Craig, Jock Currie, Megan Laird, Karen Tunley, Debbie Robertson-Andersson, Eleanor Yeld-Hutchings, Ken Hutchings, Riaan Crous and the MCM team - Bradley, Neil, Chris, Steve, Rick, Brett and Corné and anyone else I have forgotten!

The diving trips often involved early morning starts, cold waters, long days spent in wetsuits and time away from home. Thank you for giving up your time and energy to help with the data collection. I could not have done this without your help.

A special thanks in particular to Andrea Plos, Peter Southwood, Steven Horsley, Andrew Jones, Marc Cornwell and Eleanor Yeld-Hutchings who dived on numerous occasions and would not rest until I had the data.

Technical and logistical support was received from Andrea Plos, George DuPlessis, Granville Faulmann, Paul Hanekom, Pieter Truter, Peter Southwood, Petra Muller and Gilly Smith. Thank you for your ideas and enthusiasm.

Rob Anderson and Charles Griffiths are thanked for their help in algal and invertebrate identification. Thanks to Rob Tarr, Andy Cockcraft, Danie van Zyl, Sven Kerwath and Colin Attwood for providing the necessary data for the model.

To my friends and colleagues: the GMB lab, Paula de Coito, Tammy Robinson, Janine Basson, Ros Crookes, Lisa Nupen, Eleanor Yeld-Hutchings, Kath Potgieter, Maya Pfaff, Rachel Cooper, the UCT pub and my home group. Without you I would not have survived this monster that is a PhD. Thank you for being there when I needed to talk shop. Thank you for being there when I couldn't face another dive, another spreadsheet, another p-value, another model-crash.

And finally to my family:

Mum and Dad – thank you for taking me to the beach all those years ago. Thank you for always believing in me and giving me the opportunity to fulfil my dream. Without you I would be lost.

Ross – thank you for the friendly sibling rivalry that comes with doing our PhDs at the same time. I am grateful for the discussions, arguments, encouragement and most of all the laughs. I just beat you.

Jo – how I have missed you these last three years. Thank you for always being a phone call away and for supporting me from afar…and for trying so hard to share my enthusiasm in marine stuff!

Tom – thank you for your sense of humour, your sarcasm and for always being the party-starter. You are a legend.

Gramps – thank you for the fishing lessons and for sharing your knowledge of the ocean. I miss you.

Riaan – my love, thank you for being you. I am so grateful for your endless support, encouragement, understanding, patience and love…especially during these last few months. Thank you for helping me to keep some perspective on my life.

Above all, thanks to the Lord God Almighty.

Abstract

An eastward shift in the West Coast rock lobster *Jasus lalandii* took place in the early 1990s along the south-west coast of South Africa in an area known as East of Cape Hangklip (EOCH). Given the predatory capabilities of *J. lalandii*, an intricate relationship between the urchin *Parechinus angulosus* and juvenile abalone *Haliotis midae*, and an already over-exploited ecosystem, the lobster 'invasion' is assumed to have had serious consequences on the benthic community and associated fisheries.

To investigate these effects, I used both empirical and modelling approaches. Based on field studies, I first analysed temporal changes in rock lobsters and the benthic community at two lobster-invaded sites EOCH. Prior to 1990, rock lobsters were rare EOCH, but from the mid 1990s onwards they achieved densities of 0.4-0.8 m^{-2}. The pre-invaded benthic community was significantly different from the post-invaded community at both sites. Three major changes followed the lobster invasion: (1) a decline or even a disappearance of herbivores (a direct effect), (2) macroalgal proliferation (an indirect effect) and (3) increases of a range of sessile taxa (unknown effect). This was followed by a detailed spatial analysis of *J. lalandii* densities and the benthic community EOCH, in which I surveyed six sites (three invaded and three non-invaded) at three different depth zones (<5 m, 6-12 m and 13-20 m). At all three depth zones *Jasus lalandii* was significantly more abundant in invaded areas than in non-invaded areas, and invaded and non-invaded benthic communities were significantly different. Invaded sites were characterized by higher densities of rock lobsters, macroalgae and sessile species, whereas non-invaded sites had greater amounts of herbivores and encrusting corallines. Abalone abundance reflected their previously-recorded dependency on urchins and the effects of rampant poaching. Floral species diversity was on average greater at invaded sites and increased with depth, whereas faunal species diversity was greater at non-invaded sites but also increased with depth. The depths in which strongest effects of *J. lalandii* were felt coincided with the depth of maximum abundance of the urchin *Parechinus angulosus*, the abalone *Haliotis midae*, the kelp *Ecklonia maxima* and encrusting corallines.

In line with an ecosystem approach to fisheries management and to better understand the ecosystem dynamics EOCH, a lobster-urchin-abalone Minimally Realistic Model was developed for a lobster-invaded area, and an adjacent non-invaded area. A key feature of the model is that its focus was restricted to the critical interactions of interest and was fitted to all available data. An existing abalone stock-assessment model formed the foundation of this multispecies model, to which rock lobsters and urchins were added. Abalone and rock lobsters were modelled using age-structured production models and urchins were modelled using a simpler surplus production model because of data limitations. The model estimated a lobster starting biomass (in 1985) of 314 tonnes (MT) and a carrying capacity of 1511 MT. Species-interaction parameters, particularly the lobster-abalone interaction, were difficult to estimate and the model was unable to estimate the urchin intrinsic growth rate parameter because the data had insufficient contrast. Results from the model suggest that the lobster invasion was probably caused by an influx of adult lobsters as opposed to increased larval settlement. Future projections suggest that given the virtual disappearance of urchins, complete removal of rock lobsters would be needed to allow the urchin population to re-establish itself. Recovery of urchins could take up to 50 years and recovery of abalone would take even longer. The model-predicted differences in lobsters, abalone and urchins between invaded and non-invaded areas paralleled empirical data.

Further model explorations included (1) a hypothetical lobster invasion into a currently non-invaded zone EOCH and (2) the addition of a top fish predator into a lobster-invaded zone. Various hypothetical lobster invasions into the non-invaded zone all resulted in the eventual disappearance of urchins and, consequently, juvenile abalone. Available catch and effort data for fish indicated that a major decline in linefish has taken place, but that this occurred prior to the 1980s and was thus not the direct cause of the rock-lobster invasion. This was supported by outputs of a model incorporating fish predation, which demonstrated that the presently over-exploited fish biomass has very little effect on the rock lobster population, but that at historical pristine levels, fish would have been capable of preventing the establishment of a dense rock-lobster population and the consequent disappearance of urchins and abalone. These results indicate that the over-fishing of top-predators would have had massive ramifications for the rest of the ecosystem. Through dual empirical and modelling approaches, my study highlights the complexity of ecosystem interactions and the need for multispecies models in developing an ecosystem approach to fisheries management, and adds to the understanding of the causes and implications of human- and environmentally-induced shifts in community structure.

Glossary

AIC	- Akaike Information Criterion
ANOSIM	- Analysis of Similarity
ANOVA	- Analysis of Variance
ASPM	- Age-Structured Production Model
CL	- Carapace Length
CV	- Coefficient of Variation
CPUE	- Catch per Unit Effort
DEAT	- Department of Environmental Affairs and Tourism (South Africa)
EAF	- Ecosystem Approach to Fisheries
EOCH	- East of Cape Hangklip
EwE	- ECOPATH with ECOSIM
FIAS	- Fishery-Independent Abalone Survey
FIMS	- Fishery-Independent Monitoring Survey
HDI	- Historically Disadvantaged Individual
MCM	- Marine and Coastal Management
MDS	- Multi-dimensional Scaling
MPA	- Marine Protected Area
MRM	- Minimally Realistic Model
MT	- Metric Tonne
NMLS	- National Marine Linefish System
OM	- Operating Model
OMP	- Operational Management Procedure
PERMANOVA	- Permutational Multivariate Analysis of Variance

PERMDISP - Permutational analysis of Multivariate Dispersions

PRIMER - Plymouth Routines in Multivariate Ecological Research

TAC - Total Allowable Catch

SCUBA - Self Contained Underwater Breathing Apparatus

SIMPER - Similarity Percentage

SL - Shell Length

SST - Sea Surface Temperature

UCT - University of Cape Town

WCRL - West Coast Rock Lobster

Chapter 1

Setting the scene: introduction and overview of thesis

1.1 Kelp Forest Ecosystems

1.1.1 Global kelp forests and trophic cascades

Kelp forest ecosystems have received enormous attention due to the complexity of biological interactions that structure them, their immense productivity, and their inclusion of species that contribute to global fisheries. Dominating shallow temperate reefs in upwelled regions, they form highly diverse systems. Much research has focused on trophic interactions within these ecosystems (Estes 2007, Branch 2007, Fariña *et al*. 2007, Graham *et al*. 2007), spanning the ecological effects of kelp (Reed and Foster 1984, Ojeda and Santelices 1984, Santelices and Ojeda 1984, Kennelly 1989, Kennelly and Underwood 1993, Edwards 1998, Melville and Connell 2001, Connell 2003, Irving *et al*. 2004, 2005, Toohey *et al.* 2007), including the effects of intense grazing – predominantly by sea urchins (Lawrence 1975, Lang and Mann 1976, Dayton 1985a, Harold and Reed 1985, Andrew 1993, Hagen 1983,1995), top-down control by predators (Estes and Duggins 1995, Estes *et al*. 1998, Tegner and Dayton 2000, Shears and Babcock 2002, 2003, Byrnes *et al*. 2006, Halpern *et al.* 2006), and the ecosystem effects of overfishing these systems (Babcock *et al.* 1999; Steneck 1997, 1998, Tegner and Dayton 2000, Götz *et al*. 2009a, 2009b, Ling *et al*. 2009b).

The idea of top-down control was first put forward by Hairston *et al*. (1960), and concerns control of ecosystem structure and functioning by predators, which alter prey abundance, with indirect effects on lower trophic levels that are referred to as ‘trophic cascades’. The removal or reduction of higher trophic levels shifts the dominance and impact of consumers to lower trophic levels (Steneck 1998). A classic example of a coastal marine trophic cascade is the ‘otter-urchin-kelp’ interaction in the western Alaskan Aleutian Islands, in which sea otters feed on urchins, and urchins graze on kelps. Before humans influenced the relationship, sea otters prevented urchins from over-grazing the kelp. However, during the 18th and 19th centuries, the fur trade led to the over-exploitation of sea otters, resulting in an increase in urchins and a subsequent collapse of kelp forests. It was only during the 20th century that legal protection of sea otters allowed their recovery, thus reversing the trophic cascade (Simenstad *et al*. 1978, Estes and Palmisano 1974, Estes and Duggins 1995, Estes *et al*. 1998). Recently, this ecosystem interaction was further complicated by killer whales switching their diet to sea otters, probably as a result of declines in other prey species such as seals and sea lions. As a result, sea otter numbers declined once more, removing the pressure on urchins, which in turn led to kelp deforestation and ultimately an urchin-dominated system (Estes *et al*. 1998, 2004, Pace *et al*. 1999, Williams *et al*. 2004).

1.1.2 Predators vs. Grazers

Sea urchins are well known in many parts of the world for their grazing abilities (Lawrence 1975, Mann 1977, Hay 1984, Carpenter 1986, 1988, Andrew 1993, Andrew and Underwood 1993, Ling and Johnson 2009) and have frequently been demonstrated to play a major role in controlling kelp communities (Estes and Palmisano 1974, Vadas 1977), despite their broad algal diets (Vadas 1977, Harrold and Reed 1985). They are particularly infamous for their role in kelp deforestation, predominantly in the Northern Hemisphere (Breen and Mann 1976, Mann 1977, Tegner and Dayton 1991, Watanabe and Harrold 1991, Estes and Duggins 1995, Steneck 1997; Dayton *et al.* 1998), where they are known to transform kelp forests into coralline-dominated ‘urchin barrens’. In the Southern Hemisphere, several species of urchins feed more on drift algae than on attached plants (Castilla and

Moreno 1982, Santelices and Ojeda 1984a, Dayton 1985b, Day and Branch 2002b; Vanderklift and Kendrick 2005) and thus urchin-induced kelp deforestation is not as common as in the Northern Hemisphere (see review by Steneck *et al.* 2002), but is known to occur in Australia (Andrew 1993, Andrew and O'Neill 2000, see review by Andrew and Byrne 2001, Johnson *et al*. 2005, Ling 2008, Ling and Johnson 2009) and in New Zealand (Choat and Schiel 1982, Babcock *et al*. 1999).

The intense grazing pressure exerted by sea urchins on kelp communities is often controlled by the top-down effects of predators. Notable sea urchin predators that structure communities through top-down effects include the already-mentioned sea otters (Estes and Palmisano 1974, review by Estes *et al.* 1989, 1998), fish (Cowen 1983, Sala and Zabala 1996, Sala *et al*. 1998, Shears and Babcock 2002, 2003, Steneck *et al*. 2004), clawed lobsters (Mann and Breen 1972, Breen and Mann 1976) and rock (or spiny) lobsters (Tegner and Dayton 1981, 1991, Tegner and Levin 1983, Babcock *et al*. 1999, Mayfield and Branch 2000, Shears and Babcock 2002, 2003, Ling *et al*. 2009b). In southern California, the spiny lobster *Panulirus interruptus* and the Sheephead *Semicossyphus pulcher* are know to prey on urchins (Tegner and Levin 1983, Cowen 1983) and probably control their populations (Tegner and Dayton 1981). On the east coast of North America, urchin populations in Maine were probably controlled by large predatory fish before overfishing of these stocks took place (see reviews in Steneck *et al.* 2002, 2004) and in Nova Scotia, the clawed lobster *Homarus americanus* is a key predator of urchins and was linked directly to urchin declines and indirectly to kelp forest expansion in the 1970s (Breen and Mann 1976).

1.1.3 South African kelp forests

Extensive kelp forests, comprising mostly *Ecklonia maxima* and *Laminaria pallida*, dominate the shallow subtidal zone along the temperate west and south-west coasts of South Africa, extending from southern Namibia in the north, to as far as Cape Agulhas on the south coast (Field *et al.* 1977, Velimirov *et al.* 1977). This stretch of coastline falls within two distinct biogeographical provinces – the cool temperate Namaqua Province, extending from Lüderitz to Cape Point, and a part of the warm temperate Agulhas Province, running from Cape Point to East London (Emanuel *et al.* 1992). Moving southwards down the Namaqua Province, kelp standing stocks increase, with *E. maxima* typically forming a floating canopy and dominating depths shallower than 9 m, while *L. pallida* forms an understory bed and penetrates to greater depths (Field *et al.* 1980a, Branch and Griffiths 1988). The section of coast between Cape Point and Cape Agulhas (hereafter referred to as the south-west coast) has also been termed a transition zone (Bolton 1986) and differs from the west coast in terms of kelp-forest community composition. The west coast has long been recognized for its large numbers of the West Coast rock lobster *Jasus lalandii* (Field *et al.* 1980a, Branch and Griffiths 1988) and mussels, particularly the black mussel *Choromytilus meridionalis* and the ribbed mussel *Aulacomya ater* (Van Erkom Schurink and Griffiths 1990, Bustamante and Branch 1996), as well as dense red algae covering most of the substratum in the shallows (Anderson *et al.* 1997). In contrast, the south-west coast has a greater abundance of herbivores, predominantly the Cape urchin *Parechinus angulosus* but also the abalone *Haliotis midae*, two turban snails *Turbo sarmaticus* and *Turbo cidaris* and the winkles *Oxystele* spp (Field *et al.* 1980a). The mussels *C. meridionalis* and *A. ater* are more scarce (Field *et al.* 1980b) and foliar algae decrease and are replaced by extensive beds of encrusting corallines (Anderson *et al.* 1997).

1.2 The South African Abalone *Haliotis midae*

The abalone *Haliotis midae* is a large, compressed, slow-growing marine mollusc that occurs on shallow temperate reefs along the west and south coasts of South Africa. It was once particularly abundant along the south-western Cape coast, but has been decimated by intense illegal fishing (Hauck and Sweijd 1999, Hauck 2009). *H. midae* is herbivorous, feeding predominantly on kelps and red algae, often trapping drift weed under its foot. Its planktonic larvae settle preferentially on encrusting corallines (Day and Branch 2000a), and their juveniles take shelter in crevices, or on the south-west coast, beneath urchins (Tarr *et al.* 1996, Day and Branch 2000a, 2000b), emerging to live on open rock faces only once they have attained a size large enough to be less prone to predation. *H. midae* is slow growing, taking about 7 years to reach sexual maturity and 8-9 years to reach the minimum legal size limit of 114 mm shell length (Tarr 1993). Given their slow growth rate and accessibility, they are highly susceptible to overfishing.

1.3 The Cape Urchin *Parechinus angulosus*

Along the South African temperate coastline, the most abundant herbivore is the urchin *Parechinus angulosus*, which feeds mainly on drift kelp (Velimirov *et al.* 1977, Velimirov and Griffiths 1979). Occasional dense patches of this urchin may be found in deeper water (8-15 m) along the west coast (Velimirov *et al.* 1977, Field *et al.* 1980a), but on the south-west coast, *P. angulosus* is far more abundant and extends into the shallows (2-5 m) (Anderson *et al.* 1997). Turbulent sea conditions along this coastline prevent the urchins from feeding on live kelp fronds or ascending the plants to graze (Fricke 1979, Anderson *et al.* 1997) and thus typical ‘urchin barrens’ do not form. Experimental removal of urchins in such shallow waters has been shown to have no effect on the abundance of foliar algae (Day and Branch 2002a). However, other urchin-exclusion experiments in deeper waters (Fricke 1979) have demonstrated that experimental removal of *P. angulosus* can lead to an increase in the abundance of sporelings of *E. maxima*, suggesting that at least under certain conditions *P. angulosus* grazes on juvenile kelp and curtails their establishment. Anderson *et al.* (1997) found that in the presence of herbivores (predominantly urchins), kelp sporelings settle mainly on the holdfasts of adult plants – out of reach of grazers. Day (1998) found that exclusion of all benthic herbivores (including urchins) led to a proliferation of foliar algae at the expense of encrusting corallines. It seems likely that *P. angulosus* acts as a drift-feeder if sufficient drift material is available (and will have no influence on attached algae under these conditions), but may switch to grazing if drift algae are scarce. Comparable switches of behaviour have been suggested or demonstrated for other urchins (Mattison *et al*. 1977, Reed and Foster 1984, Dayton 1985a, Harrold and Reed 1985, Konar 2001, Rodríguez 2003).

1.4 Urchin-Abalone Interactions

Parechinus angulosus also plays a crucial role in sheltering juvenile abalone (Day and Branch 2000a, 2000b), specifically on the south-west coast. Both *P. angulosus* and small *H. midae* can be consumed by *J. lalandii* (Mayfield *et al*. 2000a, 2000b, Van Zyl *et al.* 2003). However, although the gut contents of field-sampled rock lobsters frequently reveal sea urchin remains, they rarely contain juvenile abalone (Mayfield and Branch 2000). This suggests that sea urchins provide some form of protection for juvenile abalone, which supports findings by Day and Branch (2000a, 2000b), showing that juvenile abalone decline radically if urchins are experimentally removed. This relationship between *P. angulosus* and juvenile *H. midae* takes on an additional role when *P. angulosus* traps kelp debris, as the juvenile abalone can feed on this trapped drift, obviating the need for them to leave the shelter of urchins to feed (Day and Branch 2002a, 2002b).

1.5 The West Coast Rock Lobster *Jasus lalandii*

1.5.1 Effects as a predator

Jasus lalandii is a significant predator, known to feed on a wide variety of prey including mussels, winkles, urchins, juvenile abalone, barnacles, sponges, algae and even their own species (Pollock 1979, Mayfield *et al*. 2000a, 2000b, 2001, Van Zyl *et al*. 2003). Despite such a broad diet, *J. lalandii* is a selective forager, specifically seeking out preferred prey items, particularly mussels and urchins (Mayfield *et al*. 2000a, 2000b, 2001, Haley 2008). However, when these are in short supply, they switch their attentions to unorthodox prey such as barnacles, sponges and even mysids (Barkai and Branch 1988c). Because of this, their populations are not necessarily limited by depletion of preferred prey (Barkai and Branch 1988a, 1988b, Barkai and McQuaid 1988). As a consequence, any radical change in the abundance of *J. lalandii* could have substantial effects on benthic invertebrate communities.

The sizes and prey species that *J. lalandii* can consume are related to the size of the rock lobsters. So, for example, individuals less than 68 mm carapace length (CL) are incapable of consuming urchins whereas those above 75 mm CL can consume even the largest of urchins (Mayfield *et al*. 2001). Nevertheless, despite such limitations on what *J. lalandii* may consume, it plays a powerful role in structuring benthic communities.

1.5.2 Shifts in rock lobster abundance

A decline in the catches of *J. lalandii*, partly due to reduced growth rates, occurred along the West Coast in the late 1980s. No single explanation satisfactorily explains the cause of this slow growth but Mayfield *et al.* (2000b) have suggested that a diminishment of preferred food sources caused the rock lobsters to expend more time and effort on foraging, and that this adversely affected their growth even though they were able to fill their guts. Another suggestion is that because rock lobsters congregate inshore when there are oxygen-deficient waters along the shelf of the west coast, ensuing competition due to over-crowding could explain the decrease in growth rate (Pollock and Shannon 1987). A decade later, Pollock *et al.* (1997) linked reduced growth rates of *J. lalandii* to environmental anomalies in the southern Benguela. Primary production was low in this area during 1988 and 1989 (Shannon *et al.* 1992) and is thought to have further decreased during the 1990-1993 *El Niño* years (Pollock *et al.* 1997). This episode, together with oxygen-depleting red tides and a collapse in 1990 of one of the most important rock lobster food sources – the ribbed mussel, *A. ater* (unpublished information reported in Shannon *et al.* 1992) – may, in combination, explain the decreases in growth rate and abundance of *J. lalandii* along the west coast since the late 1980s. However, at the time that *J. lalandii* was decreasing along the west coast, a substantial increase in their abundance took place along the south-west coast in an area known as 'East of Cape Hangklip' (or 'EOCH') (Cockcroft *et al.* 2008). Tarr *et al.* (1996) reported a considerable increase in *J. lalandii* in the early 1990s between Cape Hangklip and Hermanus (Fig 1.01), with a progressive decrease in abundance from west to east. This increased abundance of *J. lalandii* EOCH has been termed a 'lobster invasion', because although rock lobsters were present there prior to 1990 they were sufficiently scarce that they were not even recorded in detailed benthic surveys done at the time (Field *et al*. 1980a, Jackleman 1996). Throughout this thesis, the area between Cape Hangklip and Hermanus where *J. lalandii* has increased dramatically is referred to as a rock lobster 'invaded' area, whereas the area between Hermanus and Quoin Point lying to the east of this, where its densities remain low, is referred to as a 'non-invaded' area.

1.5.3 Explanations for the eastward shift

Reasons for the increase in rock lobsters along the south-west coast are uncertain, but various hypotheses have been put forward:

(1) Rock-lobster migration

Initial reports of an increase in *Jasus lalandii* East of Cape Hangklip (EOCH) included the fact that rock lobsters were relatively large, implying that their appearance was perhaps the result of adult rock lobsters migrating inshore from deeper waters (Cockcroft *et al*. 2008). An alternative was that a south-eastward migration of adults had taken place. Atkinson and Branch (2003) examined the incidence of longshore movements by large male rock lobsters and they concluded that longshore migration of adults was very unlikely to explain the invasion EOCH, as less than 1% of tagged lobsters moved further than 10 km. However, their study was limited to adult males (which had been tagged for growth studies and could incidentally be used to study their movements). Studies from Australia and New Zealand have demonstrated that a sister-species, *Jasus edwardsii*, also does not move significant distances (Kelly 2001, Gardner *et al*. 2003, Barrett *et al*. 2009b). However, small proportions of *J. edwardsii* populations in New Zealand have been reported to undergo large-scale migrations in response to changes in environmental conditions (McKoy 1983, Annala and Bycroft 1993).

(2) Increased larval settlement

Another hypothesis is that improved larval settlement EOCH allowed the rock lobster population to expand. Rock lobster phyllosoma larvae are capable of dispersing over large distances as they spend 9-11 months in the plankton before metamorphosing into the benthic puerulus stage (Pollock and Melville-Smith 1993). Pollock (1989, 1990, 1992) has suggested that specific environmental triggers initiate metamorphosis and that larvae may delay this transformation until exposed to such triggers.

Jasus lalandii larvae hatch in spring and have been suggested to disperse rapidly offshore in a northerly direction, entering the South Atlantic gyre where they remain until they are circulated back towards the Western Cape (Pollock 1986, Pollock and Melville-Smith 1993). Their sister species, *Jasus tristani*, which is found at Tristan da Cunha Islands, is proposed to have a similar dispersal pattern. The larvae appear to enter the South Atlantic Gyre where they must travel vast distances if they are to return to their natal grounds via this route. It is thought that the Vema Seamount population of *J. tristani* was established by larvae travelling this route (Lutjeharms and Heydorn 1981).

Variations in ocean currents could affect the distribution of larvae and fluctuations in sea temperatures or other environmental cues could determine where and when they settle.

Set against the arguments that larval dispersal established the population EOCH is the absence of any records indicating arrival of juveniles.

(3) Environmental change

It seems likely that there has been a change in environmental conditions during the 1980s/1990s. Rouault *et al*. (2009) report a warming in the Agulhas Current system since the 1980s, although this was largely offshore and it appears as though the inshore shallow waters along the south coast have cooled, particularly east of Cape Agulhas (Roy *et al*. 2007, Rouault *et al*. 2009). It is possible that inshore cooling on the south coast created more favourable conditions for *J. lalandii*, which is known to prefer the colder waters found along the west coast. Long-term inshore data sets quantifying factors such as sea temperature and bottom oxygen are inadequate to rigorously test this concept (Cockcroft *et al*. 2008). However, *J. lalandii* is not the only species to have shifted eastwards, and the distributional shifts of other species have also been linked to environmental change.

Two of the earliest organisms observed to have extended their range were the kelps *Ecklonia maxima* and *Laminaria pallida*, which are a feature of the South African west coast, where they thrive in the cold Benguela waters (Velimirov *et al*. 1977). Initially abundant only on the west coast, *E. maxima* has extended further eastwards. Historical photographs and early unpublished surveys in False Bay show that it was absent from Froggy Pond in the 1930s, and from Dalebrook and Fish Hoek up to the 1970s, but by the late 1980s, it was well established in False Bay (G.M. Branch unpublished data). Both species of kelp have always been present at Cape Hangklip – an upwelling centre – but only in the last two decades have they formed dense forests at Betty's Bay and further eastwards. Since the turn of the millennium, a substantial increase in kelp beds just east of Danger Point has been reported (W. Chivell, Marine Dynamics, Gansbaai, pers. comm.).

The warm-water brown mussel *Perna perna* has also recently shifted eastwards (A. Mead, University of Cape Town, pers. comm.) in keeping with the concept that coastal waters on the south coast have cooled.

The commercially important pilchard or sardine *Sardinops sagax* has also shifted eastwards. The fishery for this species was established along the west coast in the 1950s, where the bulk of initial catches were made. As the fishery developed, fishing grounds expanded southwards and then eastwards, and by the early 1990s, catches made around Cape Agulhas were comparable to those made off the west coast. However, in the late 1990s, the mean location of sardine catches shifted further eastwards (van der Lingen *et al.* 2001, Fairweather *et al.* 2006b), and as catches increased on the south coast, they declined dramatically on the west coast. In 2004, no sardines were caught west of Cape Point (van der Lingen *et al.* 2005). In addition, van der Lingen *et al.* (2002) reported that the spawning area of the anchovy *Engraulis encrasicolus*, another important pelagic species, has also shifted eastwards. Reasons for these eastwards shifts are not known, but may be linked to changes in environmental conditions (van der Lingen *et al.* 2001, Roy *et al*. 2007, Crawford *et al.* 2008d, Cockcroft *et al*. 2008).

The eastward shift in sardines, combined with their virtual disappearance from the west coast, has had a profound effect on predators, particularly seabirds such as the African Penguin (*Spheniscus demersus*) and the Cape Gannet (*Morus capensis*). These seabirds nest on coastal islands, feeding predominantly on pelagic fish, upon which they rely heavily during their breeding season, when foraging distance is limited. The shift in sardines from the west coast to the south coast is correlated with observed decreases in penguin and gannet populations on the west coast, and increased gannet populations on the south coast (Underhill *et al*. 2006, Crawford *et al.*

2007, 2008b, 2008c, Pichegru *et al*. 2007). Although penguin populations have remained relatively stable on the south coast, a new colony formed on the mainland at De Hoop Nature Reserve in 2003 (Underhill *et al*. 2006). Another bird that appears to have shifted its distribution is the Bank Cormorant (*Phalacrocorax neglectus*), which feeds predominantly on West Coast rock lobsters (Hockey *et al.* 2005). Crawford *et al.* (2008a) link the decrease in rock lobsters on the west coast and their increase EOCH to respective decreases and increases in *P. neglectus* breeding colonies in these areas. Other sea birds have also shifted (see review in Crawford *et al.* 2008d).

A change in environmental conditions, probably associated with a cooling of inshore waters on the south-west coast, seems to be the most plausible explanation for the observed south and eastwards shifts, although no conclusive links have been established (Cockcroft *et al*. 2008). There have been anecdotal suggestions that *J. lalandii* was common EOCH in the 1960s, and then went through a period of scarcity there until the ‘invasion’ of the area in the 1990s – implying that geographic shifts in this region are cyclical. Data do not extend far back enough in time to verify this. However, the issue is not whether or not these shifts have occurred repeatedly, but rather what are the consequences for the already heavily-fished and unstable ecosystem?

1.6 An Ecosystem Approach to Fisheries (EAF)

Since the mid 20th century, technological advances have improved fishing techniques and capture rates, leading to ‘fishing down the food web’ (Pauly *et al*. 1998). Combined with other anthropogenic and climatic effects, this has resulted in complex changes in ecosystem structure (Pauly *et al.* 1998, 2000b). With an ever-expanding human population, the demand for fisheries resources continues to grow and although aquaculture now contributes a significant proportion of the fish produced for human consumption, it cannot alone meet global demands, and capture fisheries continue to supply the majority of the world's fish resources (FAO 2007). Traditionally, fisheries management has been based on a single-species approach, but the fact that many of these fisheries are now fully or even over-exploited has led to the motivation for a complementary approach, focusing on entire ecosystems, rather than just on individual species (Pauly *et al*. 2000a). This new approach has been termed an Ecosystem Approach to Fisheries – EAF – and has already been adopted by some of the world's leading fishing nations, including South Africa (Cochrane *et al.* 2004). It aims to examine the ecosystem as a whole, taking into account the direct and indirect effects of fisheries on the rest of the ecosystem, and incorporates the effects of environmental change. Although current methods such as operational management procedures (OMPs) and total allowable catches (TACs) are still based on single species stock assessments (and more than likely will continue to be so), multispecies models that consider whole ecosystems or subsets of interacting species are now being taken into account. However, these types of models are difficult to apply, largely due to the amount of data required, and there are often disagreements as how best to begin implementing such models (Crowder *et al.* 2008). Nevertheless, South Africa has taken the necessary steps to begin developing an EAF, specifically dealing with the southern Benguela region (Shannon *et al*. 2004).

1.6.1 Commercial fisheries east of Cape Hangklip

The Benguela region is a cold-water, wind-driven coastal upwelling system, bounded by two warm water currents – the Agulhas in the south-east and the Angola in the north-west. In the southern Benguela, upwelling is seasonal, pulsed and highly variable. The cold upwelled waters are rich in nutrients, fuelling a high productivity and supporting large commercial fisheries, including two major invertebrate fisheries for the abalone *Haliotis midae* and the West Coast rock lobster *Jasus lalandii* and, on a smaller scale, a fishery for the kelp *Ecklonia maxima*, which is used largely to supply food for abalone farms (Troell *et al*. 2006).

1.6.1.1 Abalone fishery

Haliotis midae occurs on shallow subtidal reefs along the west and south coasts of South Africa. It is a highly sought-after resource that is predominantly exported to the Far East where it is enjoyed as a delicacy. The abalone fishery was once the smallest South African fishery in terms of yield but the most lucrative in terms of unit value (Hauck and Sweijd 1999, Hauck 2009), and it comprised both a commercial and recreational sector. The heart of the commercial fishery was situated along the south-west coast, where fishing took place from small boats in shallow water (<10 m). Divers used a hookah breathing apparatus and pried abalone off the reef using a blunt instrument. Fishing regulations were introduced in 1970, after which harvesting remained relatively stable at around 650 tonnes for about 20 years (Hauck and Sweijd 1999). However, by the mid 1990s, illegal fishing of the resource had begun to spiral out of control and fishing quotas were cut drastically. Continued illegal fishing, combined with the indirect negative effect of increased rock lobsters in the area East of Cape Hangklip, meant a desolate future for the abalone stock. Eventually the recreational fishery was closed in 2003, followed by closure of the commercial fishery in 2008 (Hauck 2009).

In addition to the economic importance of *H. midae*, it is also ecologically important. Although *H. midae* is a herbivore, it is not considered a grazer as it mostly traps drift algae (Velimirov *et al.* 1977, Velimirov and Griffiths 1979). Consequently, it does not necessarily have any direct grazing effect on algal abundance; however, it does have an effect on algal diversity. Abalone shells provide a habitat for algal species that is different from the surrounding rock face, and Farrell (2010) demonstrated that species composition on *H. midae* shells differed significantly from that on rocks adjacent to abalone, thus enhancing biodiversity. This important ecological role has undoubtedly diminished with the decline in abalone stocks.

1.6.1.2 West Coast rock lobster fishery

The West Coast rock lobster (*Jasus lalandii*) occurs in water shallower than 200 m, from about 23°S, just north of Walvis Bay in Namibia, to about 28°E, near East London, South Africa. Its fishery comprises two separate sectors, a commercial fishery and a recreational fishery. The commercial fishery exists predominantly along the west coast (Fig 1.01) from about 25°S in Namibia to Gansbaai (34°40′ S) in South Africa (Pollock 1986; Cockcroft and Payne 1999; DEAT 2005a, 2005b). Within this stretch of coast, various marine protected areas (MPAs) exist, either in the form of rock-lobster sanctuaries protecting only rock lobsters, or marine reserves that protect all species (Mayfield *et al.* 2005). The commercial fishery is split into two sectors, namely the West Coast Rock Lobster (WCRL) offshore fishery (industrial or large-scale commercial) and the WCRL inshore fishery (small-scale commercial). The WCRL inshore fishery replaced a temporary WCRL subsistence fishery in 2001 (DEAT 2005a). There are two major differences between the two sectors: (i) the gear utilized and (ii) the percentage allocation of the total allowable catch (TAC). The WCRL offshore fishery uses traps or hoopnets or a combination of both to catch rock lobsters, whereas the inshore fishery uses hoopnets only. Hoopnets are restricted to the shallower waters and are seldom used at depths greater than 30 m, whereas traps, and thus offshore vessels, can operate in deeper waters. The fishing-vessel length ranges between 8-30 m in the offshore fishery, but is restricted to less than 8 m in the inshore fishery. Vessels in the offshore fishery may move between areas around the coast, whereas in the inshore fishery they are restricted to particular fishing areas. The offshore and inshore fisheries receive 80% and 20% of the total TAC respectively. This split is based on the distribution of rock lobsters, with 80% occurring in deeper waters and 20% in shallow waters (DEAT 2005a, 2005b).

The recreational WCRL fishery theoretically covers the same geographic range as that of the species, but the bulk of recreational fishing takes place in the South-Western Cape (Cockcroft and Mackenzie 1997) and is legally restricted to the period mid November to mid April.

Regulations for managing the WCRL fisheries include gear restrictions, commercial TACs, recreational and commercial fishing seasons, a recreational bag limit of four per person per day, minimum size limits (carapace length (CL) in millimetres), rock lobster sanctuaries, recreational prohibition on selling catch, and a ban on taking either soft-shelled individuals or ovigerous females (Loewenthal *et al.* 2000, Mayfield *et al.* 2005). The commercial Total Allowable Catch (TAC) is set using a stock assessment in the form of an operating model (OM), which then feeds into an operational management procedure (OMP) developed by both scientists and stakeholders.

The vast increase during the 1990s in the abundance of West Coast rock lobsters along the South-Western Cape coast, particularly EOCH (Tarr *et al.* 1996, Mayfield and Branch 2000), has led to the introduction of small-scale commercial fishing rights EOCH during 2003. The majority of these rights were allocated to

Historically Disadvantaged Individuals (HDIs)[*] to compensate for the initially reduced and finally abolished abalone fishing permits (DEAT 2005a).

1.6.1.3 Kelp fishery

The South African kelp fishery is largely based on *Ecklonia maxima*, and was first established in the mid 20th century when kelp was collected and exported to alginate-producing countries. These days, fresh *E. maxima* is harvested and used mainly as feed for cultured abalone (Troell *et al*. 2006). The harvesting of fresh kelp along the south-western cape is a vital requirement for the abalone farms, and Levitt *et al.* (2002) calculated that in order to produce 100 tonnes (MT) of abalone (50-70 mm diameter), 5 MT of fresh kelp fronds are required daily. This is likely to put severe pressure on existing kelp beds as the abalone culture industry expands.

1.6.2 The importance of an EAF east of Cape Hangklip

Three major benthic resources either have been or are currently exploited EOCH: the West Coast rock lobster *Jasus lalandii*, the abalone *Haliotis midae* and the kelp *Ecklonia maxima*. All three are constituents of the kelp forests that exist in the region. Given the broad diet of *J. lalandii* (Mayfield *et al*. 2000a, 2000b, 2001, Van Zyl *et al*. 2003), its ability to survive on unusual foods (Barkai and Branch 1988c, Haley 2008), and its role in structuring benthic communities (Barkai and Branch 1988a, 1988b, Barkai and McQuaid 1988), the influx of rock lobsters EOCH can be expected to have major effects on the benthic community. Following the large increase in rock lobsters, an initial decline and then virtual disappearance of sea urchins occurred (Tarr *et al*.

---

[*] Historically Disadvantaged Individual (HDI) refers to a non-white South African citizen who, due to the Apartheid policy that was in place, was socially, economically, educationally and otherwise, deprived.

1996), which is likely to have had a negative effect on the abalone population, given the relationship between juvenile abalone and urchins (Day and Branch 2000a, 2000b). In addition, the abalone stock was hit hard by illegal fishing during the mid-to-late 1990s (Hauck and Sweijd 1999), leading to the legal closure of the entire fishery in 2008. With a heavily depleted parent stock as well as a near-absence of urchins to provide refuges to juvenile abalone, abalone recruitment failure is imminent if not already in effect. This is probably compounded by the fact that depletion of urchins and other herbivores results in a proliferation of foliar algae and increased siltation. These, in turn, diminish encrusting corallines that are a settlement site for abalone settlers (Day 1998, Day and Branch 2000a). Kelp – or rather drift fragments of kelp fronds – serve as the major source of food for adults of *H. midae*. A tangled web of interactions thus exists in the kelp beds EOCH (Fig 1.02).

The decline and eventual cessation of all but illegal catches of wild abalone has increased the demand for cultured abalone, which in turn has increased the demand for fresh-cut kelp (*E. maxima*) to feed these abalone. Sustainable harvesting methods have been developed by Levitt *et al*. (2002), but many areas supplying kelp for this purpose are close to the limits of sustainability, and unsustainable depletion of *E. maxima* could have serious ripple effects for the rest of the ecosystem (Anderson *et al*. 1997, 2006).

Although a commercial fishery for *J. lalandii* currently operates EOCH, rock lobster densities there have remained high. The extent to which they may have altered the ecosystem has yet to be determined. However, given the complex interactions within this kelp forest ecosystem, it is vital that local fisheries acknowledge these interactions when deciding on how best to manage the target species. An ecosystem approach to fisheries management is clearly a desirable complement to existing single-species stock assessments.

Against this backdrop, this thesis comprises two parts: the first deals with the documentation of temporal and spatial changes in rock lobsters and benthic invertebrate communities - focusing on areas EOCH 'invaded' by rock lobsters and on adjacent 'non-invaded' areas. The second describes (i) the development of a multispecies model specific to the EOCH area, (ii) results from the model, and (iii) further model developments/improvements. The aim of this model is to provide a better understanding of ecosystem functioning EOCH.

1.7 Breakdown and Overview of Thesis

Chapter 1: Overview of background and introduction

Chapter 2: Temporal changes in rock-lobster densities and kelp-forest benthic communities at two invaded sites EOCH

Chapter 3: Spatial differences in rock lobsters and the benthic community between lobster-invaded and non-invaded areas EOCH

Chapter 4: Development of a base-case multispecies model for the lobster-invaded area EOCH, using past data and new data collected as part of this thesis, and presentation of results for this base-case model

Chapter 5: Sensitivity analyses of the base-case model, and future projections modelled using different scenarios

Chapter 6: Modelling a hypothetical invasion of rock lobsters into a currently non-invaded zone

Chapter 7: Modelling impacts of depleting top predators on the predatory effects of rock lobsters on benthic communities

Chapter 8: Synthesis

Chapter 2

Temporal changes in kelp forest benthic community structure at two sites East of Cape Hangklip

2.1 Introduction

Top-down effects of predators have been demonstrated in coastal ecosystems including intertidal rocky shores (Paine 1974, 1980, Castilla 1999, Menge 2000), kelp-forests (Estes *et al*. 1998, Steneck *et al*. 2002, Halpern *et al*. 2006) and subtidal temperate reefs (Shears and Babcock 2002, 2003, Barrett *et al*. 2009a). Along the South African west coast, the predatory effects of the West Coast rock lobster *Jasus lalandii* can even be responsible for a regime shift in subtidal benthic community structure, and the maintenance of an alternate stable state (Barkai and Branch 1988a, Barkai and McQuaid 1988).

Although *J. lalandii* has historically been concentrated on the west coast, a south-eastward shift in the early 1990s resulted in a massive 'invasion' in rock lobsters along the south-west coast (Tarr *et al*. 1996, Mayfield and Branch 2000) so that the coast is divisible into 'invaded' and 'non-invaded' regions. Similar geographic shifts have also been reported for other coastal species including the kelps *Ecklonia maxima* and *Laminaria pallida* (G.M. Branch unpublished data) the sardine *Sardinops sagax* (van der Lingen *et al.* 2001, Fairweather *et al.* 2006b) and anchovy *Engraulis encrasicolus* (van der Lingen *et al.* 2002). The shift in pelagic fish, in turn, caused changes in the abundance of pelagic-feeding coastal seabirds (see review in Crawford *et al.* 2008d). Reasons for these shifts are largely unknown, but are the likely result of environmental change. Rouault *et al*. (2009) reported a change in the Agulhas Current system since the 1980s, in which offshore waters have warmed and the inshore shallow waters along the south coast have cooled. Roy *et al*. (2007) specifically recorded inshore cooling east of Cape Agulhas. This inshore cooling may explain the eastward shift in the above-mentioned cold-water species (Roy *et al*. 2007), but data are insufficient to rigorously evaluate this proposition.

Environmental changes and geographic shifts in commercially-important species have serious consequences for associated fisheries. The pelagic fishery has incurred huge expenses in transporting fish from the south coast where most of the catch is currently made to the west coast where fish-processing factories are located (Fairweather *et al*. 2006a). The commercial fishery for the West Coast rock lobster was expanded east of False Bay in 2003 following the eastward shift in rock lobsters, which has been termed a ‘lobster invasion’ of the area known as ‘East of Cape Hangklip’ (EOCH). In this same area, the kelp *Ecklonia maxima* is harvested mainly for use as feed for cultured abalone (Troell *et al*. 2006). As about 5 tonnes (MT) of fresh kelp fronds are required daily for an annual production of 100 MT of cultivated abalone (Levitt *et al*. 2002), this is likely to put severe pressure on existing kelp beds as the abalone mariculture industry expands.

Although this same coastline was once the heart of a lucrative wild-caught abalone fishery targeting *Haliotis midae* (Hauck and Sweijd, 1999, Hauck 2009), illegal fishing in the mid-1990s escalated to such levels that the recreational abalone fishery was closed in 2003, and the commercial fishery in 2008. Most abalone are now supplied by mariculture, but illegal fishing remains a problem. The decline in abalone due to poaching was augmented by the invasion of rock lobsters. *Jasus lalandii* is a major predator of the urchin *Parechinus angulosus*, and the increased rock lobster densities EOCH coincided with a significant decrease in urchins (Tarr *et al*. 1996, Mayfield and Branch 2000). At least in the Western Cape, *P. angulosus* feeds largely by trapping drift kelp rather than actively grazing and provides both protection and nourishment to juvenile abalone (Day and Branch 2000a, 2000b), so the collapse of the urchin population EOCH has important repercussions for this region,.

Given the complex relationship between rock lobsters, urchins, abalone and kelp, changes in benthic communities could have severe implications for commercial fisheries. Against this backdrop, this study documents temporal changes in the abundance of rock lobsters and the composition of benthic communities at two sites EOCH, based on comparisons of historical data captured from published and unpublished sources, and surveys of my own.

In making temporal comparisons, I have drawn primarily on three main historical sources of data: Field *et al*. (1980a) for Betty's Bay, Jackleman (1996) for the Cape Hangklip area, and Reaugh (2001) for both Cape Hangklip and Betty's Bay, and additional sources of data are outlined in the Methods. Some of these data are published, some not, but wherever possible, I returned to the original data for comparisons. All the data were quantitative but the level of replication and the taxonomic resolution of identifications varied, imposing limits on statistical comparisons and necessitating pooling of data in some instances.

This chapter is principally comparative due to the nature of past data. Its aim is to compare recent benthic community data with past data from two sites on the south-west cape coast, Cape Hangklip and Betty's Bay both of which experienced large increases in *J. lalandii* during the early 1990s. Therefore I anticipated that the benthic communities would be radically different following this 'lobster invasion'. Three questions are explored: (1) Have *J. lalandii* densities EOCH increased post-1990? (2) Is the 'post-invasion' benthic community different to the 'pre-invasion' community? (3) If so, how is it different and what groups of organisms are responsible for this difference?

2.2 Methods

2.2.1 Study sites

In 2005-2006, I surveyed two kelp beds along the south-west coast of South Africa (Fig 2.01), for which historical data were available: Cape Hangklip (34°23′09″S, 18°51′12″E) and Betty's Bay (34°22′08″S, 18°54′20″E). Both sites regarded as falling within the 'lobster-invaded' region.

2.2.2 Data collection

Data collected prior to 1990 (two sets) were *a priori* considered pre-lobster-invasion and those collected after 1990 (four sets) as post-lobster-invasion. Table 2.01 summarises these data, including sampling dates, taxa sampled, sampling methods, replication and data units.

In my study, I sampled three different depth zones (<5 m, 6-12 m and 13-20 m). However, Jackleman (1996) and Reaugh (2001) sampled only in the 0-5 m zone, so from the sources listed in Table 2.01, I extracted only data for the 0-5 m depth interval, over which I could make valid temporal comparisons. As data were recorded in different units, they were all converted to g.m^{-2} wet weight using conversion tables provided in Field *et al*. (1980a) or in Appendix 1 Table A1.01 of this thesis.

2.2.3 Taxonomic/Functional Groups

Data were recorded either to species level or to functional- or taxonomic-group level (Table 2.01). However, for temporal comparisons, the lowest resolution (taxonomic or functional groups) was used, with the exception of the 'major species', which were examined at species level: *Jasus lalandii*, *Parechinus angulosus*, *Haliotis midae*, *Ecklonia maxima* and *Laminaria pallida*. All other invertebrates were grouped into taxonomic groups (e.g. asteroids, holothuroids, cnidarians etc) and all other algae were grouped into functional groups (e.g. turf, foliar, encrusting). In some cases where turf and foliar algae were not separated they were grouped as understory algae.

2.2.4 Statistical analyses

Multivariate analyses

Data for different periods of sampling at Cape Hangklip and Betty's Bay were analysed using PRIMER (Plymouth Routines in Multivariate Ecological Research version 6.1.5) (Clarke and Gorley 2006) and PERMANOVA+ for PRIMER (Anderson *et al*. 2008). The data were fourth-root transformed to create a Bray-Curtis similarity matrix. From the similarity matrix, an ANOSIM (analysis of similarity) and a semi-parametric PERMANOVA (permutational analysis of variance) were performed *a priori* to test for a difference between pre-invaded and post-invaded groups. The PERMANOVA was an unrestricted permutation of raw data using a Type III sum of squares.

Following this, hierarchical clustering (using Bray-Curtis co-efficients) and multidimensional scaling (MDS) were carried out to compare community structure before and after the lobster invasion. A SIMPER (similarity percentage) analysis (with a cut-off of 90%) was then performed on the untransformed data to determine which taxa were responsible for any emergent dissimilarities between the pre-invaded and post-invaded groups. Due to small sample sizes or lack of replication in some of the historical data, univariate statistical analyses could not be validly performed, and the data are treated descriptively.

2.3 Results

2.3.1 Temporal changes in Jasus lalandii

Data collected from Betty's Bay in 1978/1979 showed a complete absence of *Jasus lalandii* during this period (Fig 2.02a). By 1996/1997, *J. lalandii* were present at 125 g.m^{-2}, equating to roughly 0.4 lobsters per m^2. Abundance remained relatively steady over the next ten years, peaking in 1998 at 257 g.m^{-2} (0.8 lobsters per m^2). A similar pattern occurred at Cape Hangklip – prior to 1990, no lobsters were recorded (Fig 2.02b), but by the mid-1990s, *J. lalandii* was abundant and has remained so since, although its biomass was slightly less than that found at Betty's Bay.

The central message is that rock lobsters were absent in 1980 but present at high densities of about 0.4-0.8 per m^2 from 1996 onwards. No valid statistical test of this change was possible because of the zero variance attached to the absence of lobsters in 1980 but the change is clearly 'significant'.

2.3.2 Changes in community composition at Betty's Bay

Both the *a priori* ANOSIM (R = 0.85, p<0.001) and PERMANOVA (Pseudo-F = 10.84, P(perm)<0.0004, SS=13707) revealed a significant difference in the benthic community assemblage before and after the rock-lobster invasion. This was supported by a cluster analysis (Fig 2.03a) and MDS plot (Fig 2.03b), which revealed an obvious split between the pre-invaded (Group 1) and post-invaded (Group 2) benthic community. The post-invaded group was further divided into two sub-groups – a 2001 benthic community (Group 2a) and a 2005/2006 benthic community (Group 2b) in which divergence from the 1980 condition was even greater than in 2001.

SIMPER analysis revealed an average dissimilarity of 91.60% between the pre- and post-invasion communities. The taxa responsible are shown in Fig 2.04. The pre-invaded benthic community was dominated by herbivores - mostly echinoderms, including *Parechinus angulosus* with a mean of 82.5 g.m^{-2}, gastropods including *Haliotis midae* with a mean of 1396.7 g.m^{-2}, and scavengers (decapods excluding *J. lalandii*). There was a notable absence of *J. lalandii*, understory algae and Porifera. The post-invaded benthic community was dominated by *J. lalandii*, understory algae and sponges. *Haliotis midae* and other gastropods were greatly reduced, and *P. angulosus* and all other echinoderms were absent. Understory algae, which were absent prior to the lobster invasion, reached substantial levels, and *Ecklonia maxima* (but not *Laminaria pallida*) increased by almost an order of magnitude subsequent to the rock-lobster invasion.

Fig 2.05 shows temporal trends of the key role players considered influential in structuring the kelp forest benthic ecosystem (in addition to *J. lalandii*). As already noted, *Jasus lalandii* was entirely absent during the late 1970s, but achieved a mean of 257 g.m^{-2} in the 1990s/2000s (Fig 2.02a). The opposite was seen with *P. angulosus* (Fig 2.05a), which had a mean of 82 g.m^{-2} in the late 1970s, collapsing to undetectable levels in surveys carried out in 1998, 2001 and 2005/2006. *Haliotis midae* followed a similar trend (Fig 2.05b), with a high mean abundance in the late 1970s (1400 g.m^{-2}), declining rapidly in the late 1990s/early 2000s and being completely absent in the 2005/2006 survey. *Ecklonia maxima* (Fig 2.05c) showed no long term trend. *Laminaria pallida* (Fig 2.05d) remained stable until the 2005/2006 survey when it was not observed. Understory algae increased between the late 1970s, when they were completely absent, to a peak of 338 g.m^{-2} in 2001, after which it remained fairly constant (Fig 2.05e). Encrusting coralline (Fig 2.05f) were not recorded in the survey by Field *et al*. (1980a) but increased from 586 g.m^{-2} in 1998, to 3562 g.m^{-2} in 2005/2006.

2.3.3 Changes in community composition at Cape Hangklip

An *a priori* ANOSIM revealed significant differences in the Cape Hangklip benthic community structure before and after the rock-lobster invasion (R= 0.763, p<0.001). This result was supported by the semi-parametric PERMANOVA (Pseudo-F = 22.98, P(perm)<0.0001, SS=18115) as well as the cluster and MDS analyses (Fig 2.06) which separated the pre-invaded community data (Group 1) and the post-invaded community data (Group 2). The post-invaded data were split into three sub-groups; Groups 2a and 2b containing a mix of 2001 and 2005/06 data, and Group 2c comprising only those from 2005/06.

Pre-invaded and post-invaded community assemblages were 83.6% dissimilar. Fig 2.07 shows that the pre-invaded benthic community was again dominated by herbivores, with high densities of *P. angulosus* (604 g.m^{-2}) *H. midae* (288 g.m^{-2}) and other gastropods and echinoderms. Understory algae were also abundant, with mean abundances of 523 g.m^{-2} for foliar algae and 231 g.m^{-2} for turf algae. There was a notable absence of *J. lalandii* and other scavengers as well as sessile species. Following the rock-lobster invasion, surveys in 2001 and 2005/2006 revealed that *J. lalandii* had become established, although its mean abundance was low. The dominant organisms comprising the post-invaded benthic community were kelps and understory algae, as well as sessile species. *E. maxima* increased from a mean of 185 g.m^{-2} to a mean of 2772 g.m^{-2} and *L. pallida* from being absent to a mean of 821 g.m^{-2}. Although understory algae were present prior to the rock-lobster invasion, they increased from a collective value of 754 to 1440 g.m^{-2}. Sessile species, which were absent prior to the invasion, had become common, with sponges reaching an average of 347 g.m^{-2}. *P. angulosus* and *H. midae*, which were abundant before the invasion, were not observed. Other grazing gastropods were present but at a reduced abundance, and neither asteroids nor holothuroids were evident.

The analyses for Cape Hangklip were re-run using only data from Jackleman (1996) and my current surveys because these two data sets allowed analyses of algae at species level. The resultant ANOSIM again revealed a very strong significant difference between pre-invaded and post-invaded communities ($R = 0.897$, $p<0.001$). Cluster and MDS analyses (Fig 2.08) showed a more clear-cut division between communities than previously seen when all data sets were included and algae grouped into functional categories, with SIMPER revealing a 97.27% average dissimilarity between the pre- and post-invasion samples.

Temporal changes in the abundances of important benthic species based on all available data sets for Cape Hangklip are shown in Figs 2.02 and 2.09. As noted above, *Jasus lalandii* (Fig 2.02b) was absent in 1988/1989 but abundant from 1996 onward. In contrast, both *P. angulosus* (Fig 2.09a) and *H. midae* (Fig 2.09b) were present in 1988/1989 with mean abundances of 604 $g.m^{-2}$ and 288 $g.m^{-2}$ respectively. From 2001 onward, they were both absent. *Ecklonia maxima* and *L. pallida* were both more abundant in 2001 and 2005/2006 compared to 1988/1989. *Ecklonia maxima* (Fig 2.09c) increased from a mean of 185 $g.m^{-2}$ in 1988/1989 to 4133 $g.m^{-2}$ in 2005/2006 and *L. pallida* (Fig 2.09d) went from being absent in 1988/1989 to 968 $g.m^{-2}$ in 2005/2006. Understory algae (Fig 2.09e) were relatively unchanged between 1988/1989 and 2001, but then doubled in 2005/2006 to 1867 $g.m^{-2}$.

2.4 Discussion

2.4.1 Changes in rock-lobster densities

The increase in *Jasus lalandii* density East of Cape Hangklip was first reported by Tarr *et al*. (1996), based on increased landings in the rock-lobster recreational fishery during the early 1990s, and increased sightings on dive surveys. For the mid-to-late 1990s, Mayfield and Branch (2000) added support for this conclusion. The temporal data presented here (Fig 2.02), show that rock lobsters were absent from both Betty's Bay and Cape Hangklip prior to 1990. By the mid 1990s they had become abundant. Both Tarr *et al*. (1996) and Mayfield and Branch (2000) outline the implications that this increase in rock lobsters could have for the rest of the ecosystem, given the broad diet of *J. lalandii* (Mayfield *et al*. 2000a, 2000b, 2001, Van Zyl *et al*. 2003) and its well-known ecosystem-altering predatory capabilities (Barkai and Branch 1988a, 1988b, Barkai and McQuaid 1988).

Lobster predation has often been linked to changes in kelp-forest communities (Breen and Mann 1976, Tegner and Dayton 1991, Shears and Babcock 2002, 2003, Barrett *et al*. 2009a). In north-eastern New Zealand, the establishment of 'no take' marine protected areas (MPAs) led to an increased abundance and mean size of two important predators: the demersal predatory fish *Pagrus auratus* and the rock lobster *Jasus edwardsii* (Babcock *et al*. 1999). Shears and Babcock (2002, 2003) demonstrated top-down control on community structure in these MPAs, where increased densities of rock lobsters and fish limit destructive grazing of the urchin *Evechinus chloroticus*. As a result, encrusting-coralline habitat was transformed into a macroalgal-dominated habitat. A similar situation has been observed in Tasmania where Barrett *et al*. (2009a) have reported changes in invertebrate and macroalgal populations inside MPAs. Protection of *Jasus edwardsii* inside these MPAs resulted in increases in its abundance and mean size. Following this, significant declines in the urchins *Centrostephanus rodgersii* and *Heliocidaris erythrogramma* and the black-lip abalone *Haliotis rubra* were observed in MPAs relative to adjacent areas that were not protected.

2.4.2 Changes in benthic communities

At both Betty's Bay and Cape Hangklip, multivariate analyses revealed significant shifts in community composition pre- and post-invasion. Cluster analyses and MDS (Figs 2.03 and 2.06) provided supporting evidence. Prior to the increase in *J. lalandii* density, communities were dominated by herbivores and deposit feeders. Adult kelp plants were also abundant. Algal turf and foliar algae ranged from being absent at Betty's Bay to relatively abundant at Cape Hangklip. Following the increase in rock lobsters, herbivores declined dramatically – with *P. angulosus* and all deposit-feeding echinoderms completely disappearing. Kelps increased from a pooled averaged value of 1062 to 3658 $g.m^{-2}$. Sessile species such as sponges were also significantly more abundant, increasing over 1000-fold. The overall picture is that following the increase in *J. lalandii*, herbivores (and in particular urchins) disappeared, or decreased significantly, kelps increased, and understory algae and sessile animals proliferated enormously. These conclusions held true irrespective of whether the analyses were based on algae being divided into functional groups or treated as individual species, although the differences were more pronounced when employing the latter approach.

2.4.3 Causes and consequences of changes in benthic communities

These data and analyses suggest that three main changes took place after lobsters invaded the area EOCH. First, herbivores declined significantly, with some species even disappearing. This was almost certainly due to increased top-down predation by rock lobsters, and similar effects have been documented in many other predator-controlled systems (Paine 1974, 1980, Estes *et al*. 1998, Steneck *et al*. 2002, Shears and Babcock 2002, 2003, Halpern *et al*. 2006, Barrett *et al*. 2009a). However, the decline or disappearance of the abalone *Haliotis midae* would have been partly human-induced as the period of decline coincided with the intensification of poaching directed at this species (Hauck and Sweijd 1999, Tarr 2000).

The second change was the proliferation of macroalgae, particularly understory foliar and turf forms, although kelp also increased. This is likely an indirect ripple effect of lobster predation following declines in herbivores. This line of thought could be challenged on the grounds that the most dramatic decline of a herbivore was that of the urchin *Parechinus angulosus*. Although many urchins are well known for their ecological role in structuring temperate kelp forests through intense grazing, often transforming these forests into bare coralline-covered barrens (Breen and Mann 1976, Mann 1977, Tegner and Dayton 1991, Estes and Duggins 1995, Steneck 1997, Dayton *et al*. 1998, review in Steneck *et al*. 2002), *P. angulosus* fulfils a different role. First, because this species is much smaller than many other urchins it is not able to ascend adult kelp plants in the turbulent coastal waters (Fricke 1979, Anderson *et al.* 1997). It is therefore prevented from removing whole adult kelp plants. Secondly, *P. angulosus* traps drift kelp rather than actively grazing on attached algae (Velimirov *et al.* 1977, Velimirov and Griffiths 1979). Nevertheless, Day (1998) has shown that exclusion of all benthic herbivores (including *P. angulosus*) does enhance macroalgal growth.

Parechinus angulosus does, however, fulfil another role. Day and Branch (2000a, 2000b) showed that along the south-west coast, juveniles of the abalone *H.*

midae are dependant on *P. angulosus* for survival as they take refuge under urchins, gaining both protection from the spiny canopy, and nourishment from the trapped drift-algae.

Finally, a range of sessile taxa increased in the post-invasion period, including hydroids, sponges, solitary hard corals and bryozoans. Causes of their increases are obscure.

Data sets from the EOCH region do not extend back far enough in time to detect if similar changes have occurred in the past. It is possible that shifts in *J. lalandii* abundance have happened before, changing the benthic community from a herbivore-dominated system into one dominated by sessile species and algae. However, this is questionable given that the changes now taking place in the ecosystem are additional to the pressures being exerted by ever-expanding human influences. For this reason, the changes are likely to be prolonged and intensified. During the course of the 20th century, commercial catch rates for the majority of linefish species along the south and west coasts (including temperate-reef sparids that are known to feed on *J. lalandii*) have declined by 75-99%, and many of these stocks are now considered over-exploited (Griffiths 2000). Illegal fishing of the abalone resource is more recent and intensified in the 1990s - roughly the same time at which the *J. lalandii* invasion and *P. angulosus* decline is believed to have occurred (Tarr *et al*. 1996). With depressed densities of predatory fish, rock lobsters are likely to remain abundant, and herbivores rare, unless environmental conditions change and force a retraction of lobsters. Specifically, the current near-absence of urchins will perpetuate. This, in combination with (1) a depleted abalone parent stock due to over-exploitation and (2) the reliance of juvenile abalone on *P. angulosus* for protection and nourishment (Tarr *et al.* 1996, Day and Branch 2000a, 2000b, Day and Branch

2002a, 2002b), constitutes a severe threat to the abalone population, and it is not surprising that abalone recruitment is at an all-time low (Tarr *et al*. 1996, Tarr 2000).

While this chapter was necessarily comparative, given the nature of the historical data available, it is obvious that *J. lalandii* densities have increased significantly post-1990, and that following this increase, the benthic communities at both Betty’s Bay and Cape Hangklip are now substantially different. The next chapter provides a detailed spatial comparison of (1) rock lobster densities and (2) benthic communities between invaded and non-invaded sites East of Cape Hangklip during the post-invasion period.

Chapter 3

Spatial differences in kelp forest benthic community structure: impacts of an ‘invasion’ by the rock lobster *Jasus lalandii*

3.1 Introduction

Kelp forest ecosystems are both diverse and highly productive, and a large amount of research has focused on the trophic interactions within them (see reviews in Estes 2007, Branch 2007, Fariña *et al*. 2007, Graham *et al*. 2007), particularly on algal-herbivore-predator interactions (Lawrence 1975, Lang and Mann 1976, review in Dayton 1985a, Harold and Reed 1985, Andrew 1993, Hagen 1983 1995, Estes and Duggins 1995, Estes *et al*. 1998, Tegner and Dayton 2000, Shears and Babcock 2002, Byrnes *et al.* 2006, Halpern *et al*. 2006).

Sea urchins are among the most notable herbivores in kelp forest ecosystems, and with their considerable grazing abilities (Lawrence 1975, Mann 1977, Andrew 1993, Andrew and Underwood 1993, Ling and Johnson 2009), they have become renowned for their role in kelp deforestation, transforming kelp forests into coralline-dominated 'urchin barrens' (Breen and Mann 1976, Mann 1977, Tegner and Dayton 1991, Watanabe and Harrold 1991, Estes and Duggins 1995, Steneck 1997, Dayton *et al.* 1998, review in Steneck *et al.* 2002). Most examples of kelp-deforestation are from the Northern Hemisphere, partly because in the Southern Hemisphere, several species of urchins feed more on drift algae than on attached plants (Castilla and Moreno 1982, Santelices and Ojeda 1984a, Dayton 1985b, Day and Branch 2002b, Vanderklift and Kendrick 2005) and thus urchin-induced kelp deforestation is not as common there (see review in Steneck *et al.* 2002), but is know to occur in Australia (Andrew 1993, Andrew and O'Neill 2000, see review by Andrew and Byrne 2001, Johnson *et al*. 2005, Ling 2008, Ling and Johnson 2009) and in New Zealand (Choat and Schiel 1982, Babcock *et al*. 1999).

The intense grazing pressure exerted by sea urchins on kelp communities is often controlled by the top-down effects of predators. Notable predators of urchins that structure communities through top-down effects include sea otters (Estes and Palmisano 1974, Estes *et al.* 1989, 1998), fish (Cowen 1983, Sala and Zabala 1996, Sala *et al.* 1998, Shears and Babcock 2002, 2003, Steneck *et al.* 2004), clawed lobsters (Mann and Breen 1972, Breen and Mann 1976) and rock (or spiny) lobsters (Tegner and Dayton 1981, Tegner and Levin 1983, Babcock *et al.* 1999, Mayfield and Branch 2000, Shears and Babcock 2002, 2003, Ling *et al.* 2009b).

Along the South African coastline, forests of the kelps *Ecklonia maxima* and *Laminaria pallida* are restricted to the cool temperate shallow sub-tidal waters off the west and south-west coasts (Field *et al.* 1977, Velimirov *et al.* 1977). These two coasts do, however, differ in terms of kelp-forest community structure. Forests along the productive but low-diversity, upwelling-fuelled west coast (Shannon 1985) have been recognized for their large numbers of West Coast rock lobsters *Jasus lalandii*, mussels, and dense red algae cover most of the substratum in the shallows (Field *et al.* 1980a, Branch and Griffiths 1988, Anderson *et al.* 1997). In contrast, the south-west coast, which is less productive because upwelling is diminished but supports a higher number of species and endemics (Turpie *et al.* 1999), has a greater abundance of herbivores, such as the Cape urchin *Parechinus angulosus*, the abalone *Haliotis midae* and two turban snails *Turbo sarmaticus* and *Turbo cidaris* (Field *et al.* 1980a), but mussels are scarce (Field *et al.* 1980b) and foliar algae less abundant, being replaced by extensive beds of encrusting corallines (Anderson *et al.* 1997).

As documented in Chapter 2 and by Tarr *et al.* (1996) and Mayfield and Branch (2000), the West Coast rock lobster *Jasus lalandii* shifted south-eastward in the early 1990s, declining on the west coast, and substantially increasing in kelp beds along the south-west coast in an area known as East of Cape Hangklip (EOCH). This increased abundance has been termed an ‘invasion’. Reasons for this shift are largely unknown, but it is thought to be linked to changes in environmental conditions. Roy *et al*. 2007 and Rouault *et al*. 2009 have recorded a cooling of inshore waters on the south coast, particularly east of Cape Agulhas, but long-term data are inadequate to test whether this could have accounted for the expansion of the lobster population (Cockcroft *et al*. 2008).

The potential consequences of this invasion are immense, and extend to the economically important abalone, *Haliotis midae*. Day and Branch (2000a, 2000b, 2002a) revealed an intricate relationship between the urchin *Parechinus angulosus* and juvenile abalone, and in describing it, coined the phrase 'urchin-abalone-kelp effect'. Unlike many other species of urchins that are known to be grazers (Lawrence 1975, Mann 1977, Andrew 1993, Andrew and Underwood 1993), *P. angulosus* feeds mainly on trapped drift kelp (Velimirov *et al*., 1977, Velimirov and Griffiths 1979). Consequently, this urchin remains relatively immobile, allowing juvenile abalone (3-35 mm) to take refuge under its spines and to secure nourishment there from pieces of drift algae trapped by the urchin (Day and Branch 2002a, 2002b). The significant increase in *J. lalandii* EOCH during the early 1990s coincided with a rapid decline and virtual disappearance of *P. angulosus*, associated with a collapse in the densities of juvenile abalone (Tarr *et al*. 1996). In that same decade, the stock of adult abalone EOCH began to be pummelled by illegal fishing (Hauck and Sweijd 1999, Hauck 2009).

This stretch of coastline once supported a major abalone fishery (Tarr *et al.* 1996), but the combined effects of urchin depletion, following the rock lobster invasion, and intense illegal fishing of abalone have led to its demise (Tarr *et al.* 1996). In its place, a fishery for West Coast rock lobster has been developed (DEAT

2005a), and several other resources involved in the kelp-bed foodwebs are also harvested there, including linefish and kelp.

Benthic communities EOCH have clearly been altered by the rock lobster 'invasion' (see Chapter 2 and Mayfield 1998), with profound consequences for the benthic ecosystem, including other harvested species.

Interaction webs were hypothesized *a priori* for both invaded and non-invaded states (Fig 3.01). In the invaded state where *Jasus lalandii* numbers were expected to be high, I anticipated that they would play a dominant and direct predatory role in reducing the abundance of scavengers, herbivores (urchins and grazers), sessile species and encrusting corallines. A decline in herbivores was then expected to diminish their grazing effects, leading to a proliferation of macroalgae (foliar algae, turfs and kelps). Their increase was forecast to have a negative effect on sessile species and encrusting corallines through competition for space and shading (particularly from kelps).

The opposite circumstances were predicted for the non-invaded state. *Jasus lalandii* numbers were expected to be low and their predation effects diminished. As a consequence, I expected scavengers, herbivores (particularly urchins), sessile species and encrusting corallines to be more abundant when compared with the invaded state. A greater abundance of herbivores was predicted to reduce macroalgal cover, thus reducing their negative effects on encrusting corallines. An increase in sessile species was expected to have a negative effect on both encrusting corallines and other algae as a result of competition for space.

The aims of this chapter are two-fold: first, to compare rock lobster densities between six sites – three putatively 'invaded' and three 'non-invaded' - and second, to compare the composition of benthic communities between 'invaded' sites with recently elevated densities of rock lobsters and 'non-invaded' sites at which rock lobsters were absent or their densities low. I hypothesized that (1) rock lobsters would be significantly more abundant at the 'invaded' sites and (2) that the 'invaded' sites would have a different community composition from 'non-invaded' sites.

3.2 Methods

3.2.1 Study sites

Data were collected from six study sites (Fig 3.02) along the south-west coast of South Africa: Cape Hangklip (34°23'09"S, 18°51'12"E), Betty's Bay (34°22'08"S, 18°54'20"E), Mudge Point (34°25'00"S, 19°07'02"E), Romans Bay (34°36'30"S, 19°19'28"E), Kruismans Bay (34°37'28"S, 19°19'00"E) and Quoin Point (34°46'56"S, 19°38'05"E). These sites all fall within the area termed EOCH (East of Cape Hangklip) - the core of what used to be a major abalone fishery. On the basis of fisheries surveys (Cockcroft *et al*. 2008) showing a west to east decline in rock lobster abundance and an abrupt reduction in catches and catch rates east of Hermanus, I regarded the first three of these sites as being invaded by rock lobsters, and the other three as lying just beyond the range of the 'invasion'. Henceforth, I use the terms 'invaded sites' and 'non-invaded sites' to describe these respective sites. This classification was assigned *a priori* and its validity verified by counts of rock lobsters (see below, section 3.2.5). The six sites were chosen on the basis that (1) they all fell in the same biogeographic region, (2) they experienced comparable moderately strong wave action and (3) all except Quoin Point, had been sampled at least once in the past. The Betty's Bay site falls within a marine protected area, which is closed to all types of fishing, although illegal harvesting of rock lobsters and abalone does take place there.

3.2.2 Sampling

Sampling was carried out using SCUBA during 2005 and 2006. Three depth ranges were sampled: <5 m, 6-12 m and 13-20 m. Similar depths were sampled within each depth zone at each site: 2-3 m for the <5-m zone, 8-9 m for the 6-12-m zone and 16-18 m for the 13-20-m zone. In each depth range, three 10-m transects were set out parallel to the shore, at least 5 m apart. Along each transect a swim search was conducted and six replicate 0.25 m^2 quadrats were sampled. The swim search involved a diver counting all rock lobsters, crabs, octopus, large abalone and giant periwinkles within 1 m either side of a 10-m transect chain. The quadrats were placed on bottom with slopes <30° at measured intervals along the transect chain. Within each quadrat algae and invertebrates were identified to the level of species and quantified - either as percentage cover (sessile species) or as counts (mobile species). Any organisms that could not be identified *in situ* were taken back to the laboratory and identified as far as possible. Sponges and compound ascidians were not identified further. The kelps *Ecklonia maxima* and *Laminaria pallida* were counted in 1m^2 quadrats if their stipe length exceeded 30cm; those less than 30cm were recorded as 'juvenile kelp' in the 0.25 m^2 quadrats.

3.2.3 Definition of functional groups

For some analyses the data for individual taxa were pooled into functional groups defined specifically for this study. *Jasus lalandii* was the dominant predator in the EOCH kelp forest ecosystem and the functional group 'predator' refers only to *J. lalandii*. All other predatory/carnivorous species were grouped as 'scavengers'. 'Urchins' refer to the urchin *Parechinus angulosus*, and 'grazers' to all other herbivores. ‘Herbivores’ are the combination of ‘urchins’ and ‘grazers’. ‘Sessile species’ refer to all those faunal species that are not mobile, including mussels, barnacles, hydroids, sponges, ascidians and crinoids. The term ‘macroalgae’ incorporates all erect algae – turfs, foliar algae and kelps – as distinct from encrusting corallines which are treated as a separate functional group. A list of all the taxa in these functional groups appears in Appendix 1 Table A1.01.

3.2.4 Statistical analyses

Data from the quadrats and transects were converted from percentage cover or counts into biomass (grams wet weight per m^2) either by weighing entire samples that were brought back to the laboratory or by using conversions (Appendix 1 Table A1.01) derived from my surveys or previous research in the area.

Multivariate analyses

For each depth range, biomass data were analysed using PRIMER (Plymouth Routines in Multivariate Ecological Research version 6.1.5) (Clarke and Gorley 2006) and PERMANOVA+ for PRIMER (Anderson *et al*. 2008). The data were fourth-root transformed to down-weight the dominance of abundant species, and then used to generate a Bray-Curtis similarity matrix. From the similarity matrix, an ANOSIM (analysis of similarity) was performed to test for *a priori* differences between invaded and non-invaded groups. In addition, a semi-parametric PERMANOVA (permutational analysis of variance) was performed to test for the significance of any difference between invaded and non-invaded groups, using the similarity matrix created from fourth-root transformed data. A Type III sum of squares was employed and the permutation method was an unrestricted permutation of raw data. A

PERMDISP analysis was employed to test for the homogeneity of within-group dispersions between invaded and non-invaded groups.

Hierarchical clustering (using Bray-Curtis co-efficients) and multidimensional scaling (MDS) were used to compare community structure between sites. SIMPER (similarity percentage) analysis (with a cut off of 90%) was performed on untransformed data to determine which species were responsible for the dissimilarity between invaded and non-invaded groups. The taxa identified by SIMPER were then tested for normality using the Kolmogorov-Smirnov test. As normality could not be achieved even after transformation of the data, a non-parametric Mann-Whitney U test was used to compare mean abundances of each species between invaded and non-invaded groups. Some of the identified species were absent from either the invaded or non-invaded states and thus had zero variance, but Mann-Whitney U tests were nevertheless performed. Due to the large sample size, the Mann-Whitney U statistic rapidly approached the normal distribution, so Z-values (normal distribution variate values) were reported. The Mann-Whitney U test provides p-values that are adjusted for ties, as well as exact p-values. The adjusted p-values were used rather than the exact p-values because, although they are not always conservative, they are often more accurate (Visch and Hudson 2000).

Correlations

Species were placed in functional groups and then Pearson Product-moment correlations run between functional groups using STATISTICA (version 7). Correlations were considered significant at $p<0.05$. Abalone were not included in these analyses because illegal fishing has diminished the population to such an extent that their numbers are now unlikely to reflect biological interactions.

Univariate analyses

(i) Rock lobster data

Jasus lalandii counts that I recorded at each site were grouped as either invaded or non-invaded according to the site. These data were tested for normality using a Kolmogorov-Smirnov test, and for homogeneity of variances using Levene's test. The <5-m depth zone (non-invaded) data were not normally distributed and the variance non-homogenous, even after transformation, and were thus compared using a non-parametric Mann-Whitney U test. The 6-12-m and 13-20-m data had normal distributions and homogeneous variances and were analysed with t-tests for differences between invaded and non-invaded areas. A nested ANOVA could not be used to test for differences between and within sites due to an absence of *J. lalandii* at some of the sites.

(ii) Data for urchins, kelp and understory algae

Even after transformation of the data, normality and homogeneity of variances could not be met because of large numbers of zero values, and therefore no univariate statistical tests could validly be carried out.

Species Diversity

Total, floral and faunal species diversity was calculated for each site at each depth using the Shannon Diversity Index ($H' = -\sum_{i=1}^{S} p_i(\log_2 p_i)$), based on mean biomass as a measure of abundance. Species dominance curves were created by calculating the mean percentage biomass for each species and then plotting the cumulative percentage biomass of these species against their ranked order of importance (on a log *x*-axis).

3.2.5 Fishery Independent Monitoring Survey (FIMS) data

Annual West Coast rock lobster inshore monitoring surveys were conducted EOCH by MCM (Marine and Coastal Management) for 2002-2005 at set stations (Fig 3.02). These surveys were undertaken annually during November and December. At each station, 15 hoopnets were set in groups of five at three depth intervals: 0-10 m, 11-20 m and 21-30 m. The soak time was standardized to 15-20 minutes for each hoopnet, and the sex and length of each lobster caught was recorded (Glazer and Brouwer 2005). I employed the data for Stations 61-71 (invaded) and Stations 77-90 (non-invaded). Stations 73-76 were ignored because they are dominated by sandy bottom unsuitable for rock lobsters. Data from the non-invaded stations were not normally distributed and variances were not equal because of numerous zero counts. A non-parametric Mann-Whitney U test was used to test for a significant difference between invaded and non-invaded stations, despite the violation of these assumptions, so the analyses need to be interpreted in this light. CPUE was defined as the number of lobsters caught per hoopnet per soak period.

3.3 Results

3.3.1 Spatial differences in Jasus lalandii distribution

Annual inshore fishery-independent monitoring surveys (FIMS) undertaken over the period 2002–2005 revealed a significant difference in rock lobster CPUE (lobsters.hoopnet^{-1}.soak period^{-1}) between invaded and non-invaded stations (adjusted Z = 10.79, $p<0.001$). Mean CPUE for *J. lalandii* in the area EOCH (Fig 3.03) was significantly greater between stations 61 (Cape Hangklip) and 70 (Hermanus) than between stations 71 to 80, including Romans Bay (station 78) and Kruismans Bay (station 79), and then dropped to zero or close to zero east of Danger Point (stations 84 to 90). The data were averaged for all depths and all years, but a similar trend was evident for all three depth ranges examined. The relative abundance of lobsters coincided with the 'invaded' and 'non-invaded' status of areas I designated in these categories, respectively west and east of Hermanus (Fig 3.02).

The size-frequencies for *J. lalandii* over the years 2002-2005, recorded as a percentage of the total sample taken in each year on inshore FIMS surveys, showed that females were smaller than males, had a narrower size range, and few exceeded the legal catch size of 75 mm CL (Fig 3.04).

In addition to the FIMS, I sampled rock-lobster abundance during the 2005-2006 dive surveys at three different depth ranges (Fig 3.05). At all three depths, *J. lalandii* was significantly more abundant at the invaded sites - Cape Hangklip, Betty's Bay and Mudge Point – than at the non-invaded sites – Romans Bay, Kruismans Bay and Quoin Point: <5 m (adjusted Z = 3.694, p<0.001), 6-12 m (t = 3.453, p< 0.01) and 13-20 m (t = 2.682, p <0.01). At depths of 13-20 m, numbers of *J. lalandii* at the non-invaded sites were greater than in the shallower depths, but still less than at the invaded sites. Taken across all depths, Kruismans Bay had more lobsters than the other non-invaded sites.

3.3.2 Community composition at a species level

Multivariate analyses

An *a priori* ANOSIM based on the biomass of individual species revealed significant differences in community composition between invaded and non-invaded areas at each depth zone (<5 m: R = 0.412, p<0.001; 6-12 m: R = 0.414, p<0.001 and 13-20 m: R = 0.301, p<0.001). The semi-parametric PERMANOVA also indicated significant differences between invaded and non-invaded areas for each depth zone (<5 m: Pseudo-F = 22.41, P(perm)<0.001, SS=43491; 6-12 m: Pseudo-F = 21.10, P(perm)<0.001, SS=50739 and 13-20 m: Pseudo-F = 13.51, P(perm)<0.001, SS=30398). Cluster and multi-dimensional scaling analyses were applied to the average values per transect per site for each depth zone. In the <5-m depth zone (Fig 3.06a), two of the invaded sites (Cape Hangklip and Mudge Point) separated as a primary cluster (Group 1). A second cluster consists of mostly non-invaded sites and could be sub-divided into a sub-cluster (Group 2a) consisting of the Betty's Bay invaded site and the Kruismans Bay non-invaded site and another sub-cluster (Group 2b) made up of the two remaining non-invaded sites (Romans Bay and Quoin Point).

In the 6-12-m depth zone (Fig 3.06b) four groups were identified, three of which (Romans Bay, Quoin Point and Kruismans Bay) were non-invaded areas – and a fourth group containing all the invaded sites. The most obvious pattern was that the invaded sites were tightly clustered, whereas the non-invaded sites were not.

In the 13-20-m depth zone (Fig 3.06c) two main clusters emerged - the first (Group 1) consisted of two non-invaded sites and the second (Group 2) comprised the invaded sites plus one non-invaded site (Kruismans Bay).

Overall, two patterns emerged. First, the invaded and non-invaded sites always separated out, with the exception that Kruismans Bay tended to cluster with the invaded sites. Second, the invaded sites clustered more closely together – particularly in the 6-12 and 13-20-m depth ranges – reflecting greater homogeneity. This was partly supported by the PERMDISP analysis which revealed a significant difference in the within-group dispersion between invaded and non-invaded groups for the 6-12-m depth zone (P(perm)<0.0001) and a borderline non-significant difference at the 13-20-m depth zone (P(perm)<0.068).

Characteristic species

At all three depth ranges there were clear patterns for predators and foliar macroalgae (more abundant at invaded sites), and grazers and encrusting corallines (more abundant at non-invaded sites, most obviously so at the two shallowest depth ranges). Sessile organisms showed more mixed patterns, being more abundant at non-invaded sites except in the most shallow depth range. Overall, invaded sites had more predators, macroalgae and sessile species, whereas non-invaded sites had more grazers and encrusting corallines.

<5-m depth zone

SIMPER analyses revealed 75.82% dissimilarity between invaded and non-invaded sites. Fig 3.07a shows that invaded sites had a significantly greater biomass of rock lobsters and were dominated by algae – in particular the kelp *Ecklonia maxima* and two red algae, *Plocamium corallorhiza* and *Hypnea ecklonii* - all significantly more abundant in invaded than non-invaded sites. The ascidian *Pyura stolonifera* was also significantly more abundant at invaded sites. However, the most striking observation was the complete absence of the urchin *Parechinus angulosus* at invaded sites, whereas it achieved 900 g.m^{-2} at non-invaded sites. The non-invaded sites had a greater cover of encrusting corallines, particularly *Heydrichia woelkerlingii*.

6-12-m depth zone

An average dissimilarity of 86.35% was revealed by a SIMPER analysis. Of the species contributing most to this dissimilarity (Fig 3.07b), *Jasus lalandii*, was significantly more abundant at invaded (240.4 g.m^{-2}) than non-invaded sites (8.9 g.m^{-}

^{2}). The urchin *P. angulosus* was abundant at non-invaded sites whereas it was absent at invaded sites, which were dominated by kelps and understory algae, several species of which were significantly more abundant there. Sponges were significantly more abundant at invaded sites, but the ascidian *Pyura stolonifera* reversed the pattern seen at 0-5 m and was more abundant at non-invaded sites. The non-invaded areas were again characterized by a greater abundance of encrusting corallines, particularly *Heydrichia woelkerlingii*.

13-20-m depth zone

Invaded and non-invaded sites were on average 81.58% dissimilar. Fig 3.07c shows that invaded sites were again dominated by *J. lalandii* and understory macroalgae, which were most frequently significantly more abundant there. Kelps were less abundant at this depth interval and did not differ significantly between invaded and non-invaded sites. The encrusting coralline, *Leptophytum foveatum* was also significantly more abundant at invaded sites, but overall the encrusting algae were no longer clearly different between invaded versus non-invaded sites. Non-invaded sites were predominantly characterized by significantly greater abundances of sessile species and *P. angulosus* (although the latter occurred in lower densities than at the shallower depths).

3.3.3 Community composition at a functional group level

The *a priori* ANOSIM, based on functional groups rather than species, again revealed a significant difference in community structure between invaded and non-invaded areas at each depth zone: <5 m (R=0.522, p<0.01), 6-12 m (R=0.494, p<0.01) and 13-20 m (R=0.388, p<0.01). This was supported by the semi-parametric PERMANOVA:

<5 m (Pseudo-F=12.63, P(perm)<0.0002, SS=3159), 6-12 m (Pseudo-F=10.29, P(perm)<0.0004, SS=2676) and 13-20 m (Pseudo-F=7.62, P(perm)<0.002, SS=2179).

Cluster and MDS analyses performed on the functional groups (Fig 3.08) showed similar trends to those emerging from data at the species level. Once again, three general patterns were apparent: (1) Invaded and non-invaded sites clustered separately except for Kruismans Bay, which merged with the invaded sites despite being classed as non-invaded. (2) Non-invaded sites were more distinct from each other than invaded sites, which were more homogeneous. This was quantified using a PERMDISP analysis, which revealed that invaded sites were significantly more homogenous at the 6-12 m (P(perm)<0.0003) and 13-20 m (P(perm)<0.04) depth zones; and (3) the Kruismans Bay site was unexpectedly grouped with the invaded sites, being most similar to Betty's Bay.

Univariate analyses

In contrast to non-invaded sites, scavengers and grazers were rare at invaded sites (Fig 3.09a, b) and urchins were completely absent (Fig 3.09c). Similar trends were observed at all three depth zones for all three invaded sites. Of the non-invaded sites, only Kruismans Bay had low biomasses of grazers and urchins, explaining its grouping among invaded sites in the cluster analyses.

Sessile species (Fig 3.09d) were relatively uniform in their abundance and no obvious trends emerged, but at the <5-m depth zone at Mudge Point, their biomass was extremely high (20340g.m^{-2}).

Kelps (Fig 3.09e) were more abundant at invaded sites and their biomass decreased with depth. Because of this, the differences between invaded and non-invaded sites diminished with depth. Understory algae (Fig 3.09f) were also more abundant at invaded sites, but surprisingly showed no obvious pattern with depth.

Encrusting corallines (Fig 3.09g) generally had a low biomass at the invaded sites, almost regardless of depth. At the non-invaded sites, encrusting coralline biomass was greater, especially at Romans Bay, and decreased with depth, with very little encrusting coralline biomass in the 13-20-m depth zone, where distinctions between invaded and non-invaded sites were not evident. For all three algal groups, Kruismans Bay again differed from the other non-invaded sites, either resembling the invaded sites or being intermediate between invaded and non-invaded sites.

3.3.4 Species Diversity

At a depth of <5 m (Fig 3.10a), faunal diversity at the non-invaded sites was double that of the invaded sites. Floral diversity did not differ in an equivalent manner, but was greater than the faunal diversity in the invaded sites and less than the faunal diversity in the non-invaded sites. In the 6-12-m depth zone (Fig 3.10b), faunal diversity was once more greater in the non-invaded sites, whereas floral diversity was greater in the invaded sites. Again, floral diversity exceeded faunal diversity in the invaded sites and this was reversed in the non-invaded sites. In the 13-20-m depth zone (Fig 3.10c), faunal diversity was still greater at the non-invaded sites, but the difference was not as obvious as it was at the other two depth intervals. Faunal diversity at the non-invaded sites remained fairly constant as depth increased, but in the invaded sites, it increased with depth. Floral diversity was, on average, again greater at the invaded sites and tended to increase with depth. Differences between invaded and non-invaded sites became less obvious with depth for both faunal and floral species.

In brief: (1) faunal diversity was greater at non-invaded than invaded sites, whereas floral diversity showed either no pattern or the reverse trend; (2) floral diversity increased with depth, but faunal diversity did so at invaded sites only.

3.3.5 Impacts

Pearson Product-moment correlations were used to examine the strength of positive and negative relationships between functional groups, shown in the form of 'impact graphs' for each depth interval (Fig 3.11).

<5-m depth zone

At depths <5 m (Fig 3.11a), the rock lobster *Jasus lalandii* had a significantly negative impact on the urchin *P. angulosus*, grazers and encrusting corallines and a negative but non-significant impact on scavengers. It also had a non-significant positive impact on macroalgae (foliar, turf and kelp) and a significant positive impact on sessile species. Scavengers were indirectly positively associated with urchins. *Parechinus angulosus* additionally had a significantly positive impact on encrusting corallines and probably an indirect, but also significant, positive association with grazers. A non-significant negative impact was exerted by *P. angulosus* on foliar and turf algae and a significant negative impact on kelp. Grazers additionally promoted encrusting corallines and were (most likely indirectly) associated with scavengers, and non-significantly negatively correlated with all macroalgal groups and sessile species. The three macroalgal groups (foliar, turf and kelp) were negatively associated with urchins, grazers and encrusting corallines, mostly positively associated with sessile species, and had a mixture of positive and negative correlations amongst themselves. Encrusting corallines were positively associated with *P. angulosus* and grazers, and negatively associated with all three groups of algae – although only significantly so in the case of kelp. The sessile species had a significant negative impact on the encrusting corallines and non-significant negative associations with grazers and scavengers.

6-12-m depth zone

With rare exceptions, the patterns in the 6-12-m depth zone paralleled those in the <5-m depth zone (Fig 3.11b). The most notable departure was that scavengers and sessile species were now significantly positively correlated.

13-20-m depth zone

At depths of 13-20 m, there were far fewer significant correlations among the functional groups: 6 as opposed to 19 at 0-5 m and 16 at 6-12 m (Fig 3.11c). Most of the diminishment was accounted for by the fact that urchins were too scarce for meaningful relationships to be sought for them, but even allowing for this, there was still a substantial decline in the number of significant associations among other groups. *Jasus lalandii* was again negatively correlated with grazers and scavengers, and positively with foliar and turf algae. Unlike the shallower depths, *J. lalandii* now had a significant positive association with encrusting corallines and a (non-significant) negative effect on sessile species. Other departures from the patterns at shallower depths included the fact that impacts exerted by grazers were all now non-significant, and they were negatively correlated with encrusting corallines, contrasting with the situation observed in shallower depths. Both foliar and turf algae were now positively correlated with encrusting coralline, and foliar algae had a significant negative correlation with sessile species, which was intuitively more logical than the (marginally) positive nature of these associations in shallower zones. Kelps were scarce and their associations much weaker than in 0-5 m where they strongly influenced several other groups, and the signs of their correlations were reversed from those in the shallows in almost all cases. Finally, sessile species were again significantly and positively associated with scavengers as was the case in 6-12 m.

3.4 Discussion

This chapter addressed two primary questions: (1) Was there a significant difference in *J. lalandii* numbers between invaded and non-invaded areas? (2) Was the invaded benthic community composition different from the non-invaded benthic community composition in different depth zones? Additionally, potential causes of the emergent patterns were sought.

3.4.1 Rock lobsters: a notorious predator

Depending on their density and size structure, rock lobsters have the ability to radically alter community structure and functioning. This has been reported both elsewhere in the world (Tegner and Dayton 1981, 1991, Tegner and Levin 1983, Babcock *et al*. 1999, Robles 1987, Robles *et al*. 1990) and locally (Barkai and Branch 1988a, 1988b, Barkai and McQuaid 1988), and is underpinned by rock lobsters being opportunistic foragers that feed on a wide variety of prey (Edgar 1990, Goñi *et al*. 2001, Cox *et al*. 1997, Barkai and Branch 1988a, 1988b, Barkai *et al*. 1996, Mayfield *et al*. 2000a, 2000b, Mayfield and Branch 2000). Barkai and Branch (1988c) have shown that in the absence of preferred food substances, *J. lalandii* is capable of switching to unusual foods (e.g. barnacle recruits), and is thus able to maintain high densities even in areas of apparently low food abundance.

Given the reputation of rock lobsters for altering community structure, I expected that in areas where *J. lalandii* had invaded, the community structure would be substantially different from that in areas where *J. lalandii* is still rare.

3.4.2 Spatial changes in Jasus lalandii distribution

Fisheries Independent Monitoring Surveys (FIMS) clearly showed that the mean *J. lalandii* CPUE (lobsters.hoopnet^{-1}.soak period^{-1}) was higher at invaded areas (stations 61-71) than at non-invaded areas (stations 77-90) (Fig 3.04). In addition, size-frequency data (Fig 3.04) showed that at least half the population sampled was ≥ 69 mm CL, which is the minimum size *J. lalandii* needs to achieve to consume *P. angulosus* (Mayfield *et al*. 2001).

My surveys yielded results similar to the FIMS data, with *J. lalandii* numbers significantly more abundant at the invaded sites. The three non-invaded sites had very few if any rock lobsters at the <5-m and 6-12-m depth ranges, although their numbers did increase with depth.

In short, *J. lalandii* was more abundant at invaded sites, where at least half the population exceeded the size required to consume *P. angulosus*. This independently confirmed my *a priori* classification of sites as either ‘invaded’ or ‘non-invaded’.

3.4.3 Invaded vs. non-invaded: are benthic communities different?

Changes in community at a species level

Multivariate analyses revealed that invaded sites were significantly different from non-invaded sites in all three depth zones. Only the non-invaded Kruismans Bay site was anomalous in that it grouped most closely with the invaded Betty’s Bay site, especially at depths of 6-12 m and 13-20 m. One possible reason for this anomaly could be the greater abundance of *J. lalandii* there than at the other non-invaded sites (Fig 3.03 and Fig 3.05), although their numbers were still low there in comparison with the invaded sites. Kelp and understory algal density were also greater at Kruismans Bay than at the other two non-invaded sites, and *P. angulosus* unexpectedly absent. Fig 3.12 shows urchin density plotted against the density of rock lobsters at all sites. Below 0.15 lobsters.m^{-2}, urchins were present except for the sole oddity of the Kruismans Bay <5-m depth zone. Mayfield and Branch (2000) reported that at a density $\geq$ 0.25 lobsters.m^{-2} very few, if any urchins would survive. My surveys support this, with urchins being absent above 0.22 lobsters.m^{-2} (Fig 3.12).

Community composition was relatively homogeneous across invaded sites where lobster densities were high, but at the non-invaded sites it was extremely heterogeneous. This pattern was seen at all three depth zones, but was most evident in the 6-12-m zone. Other research has shown that following disturbance in the form of human harvesting, community composition tends towards homogeneity (Hockey and Bosman 1986). The increase in rock lobster predation in invaded areas evidently reduced community heterogeneity in a similar manner.

At both invaded and non-invaded sites, benthic communities (and species interactions) changed with depth. At invaded sites, *Jasus lalandii* was least abundant in the shallower depth zone, and grazers, sessile species, algae and encrusting corallines all decreased with depth. At non-invaded sites, both *J. lalandii* and sessile species increased with depth, while urchins and grazers, as well as kelp and encrusting corallines decreased. Depth therefore interacted with the effects of rock-lobster predation in influencing community composition.

Characteristic species

SIMPER analyses highlighted the species responsible for the difference in community structure observed between invaded and non-invaded areas. One emergent pattern was that as depth increased, so did the number of species responsible for differences in community structure: the number of species contributing to 90% of the dissimilarity at 0-5, 6-12 and 13-20-m depth zones was respectively 11, 14 and 26; and the number of species with significantly different biomasses between invaded and non-invaded sites similarly increased, being respectively 7, 10 and 19 (Fig 3.07a-c). Thus, an increase in depth led to more heterogeneous benthic communities - particularly in terms of understory algae and sessile species. Community composition was therefore influenced by both invasion status and depth.

At a depth of <5 m, the non-invaded areas were typical of the south-west coast shallow subtidal habitat described by Field *et al*. (1980a) and Anderson *et al*. (1997), supporting coralline-dominated flats, relatively low abundance and diversity of foliar algae, and abundant *P. angulosus* and grazers. At this depth, invaded areas differed in having zero urchins, greater biomass and diversity of foliar algae and sessile species, and less encrusting corallines.

As depth increased through the 6-12-m and into the 13-20-m depth zones, most of these differences between invaded and non-invaded areas were retained, but some depth-related differences were superimposed. *Jasus lalandii* increased in abundance, while always remaining more abundant at invaded sites. Urchins declined with depth at non-invaded sites and were rare at 13-20 m, but were uniformly absent at invaded sites. Kelps diminished with depth, while understory algae increased in diversity although their biomass fluctuated unpredictably with depth; both groups were more abundant at invaded than non-invaded sites. Encrusting corallines became less abundant with depth (contrary to the predictions of Steneck and Dethier 1994, who argued that as productivity diminishes with a reduction in light, encrusting corallines will become proportionally more dominant), and their prevalence at non-invaded relative to invaded sites disappeared at 13-20 m. Sessile organisms such as sponges, ascidians, bryozoans and crinoids became more diverse and more abundant with depth at non-invaded sites, whereas at invaded sites the opposite tended to hold. In the shallows, they were more abundant at invaded areas, but this was reversed in deeper waters. Sponges, however, remained consistently more abundant at invaded areas, which was surprising, given that lobsters feed on sponges in this area (Mayfield and Branch 2000), particularly if their 'normal' food sources such as urchins and mussels are scarce.

Differences in community at a functional group level

Functional-group analyses showed similar results to those done at a species level. The same two patterns emerged. Firstly, invaded and non-invaded sites were largely distinct, although Kruismans Bay was once again an oddity, appearing more similar to the invaded sites, particularly Betty's Bay. Secondly, as depth increased, the divide between invaded and non-invaded sites narrowed.

Species diversity

Fig 3.13 summarises diversity patterns and species dominance, first for all species combined and then split into faunal and floral categories to explore underlying causes of observed patterns.

Total species diversity was greater at invaded sites and increased with depth (Fig 3.13a). Floral diversity was on average, greater at invaded sites whereas faunal diversity was greater at non-invaded sites. Both floral and faunal diversity increased with depth (Fig 3.13b,c). Dominance curves for all species combined (Fig 3.13d,g) indicated a greater dominance by a smaller number of species in the shallows, and this trend was more pronounced at invaded that non-invaded areas.

These trends may be explained as follows. Firstly, top-down predation may account for difference in faunal diversity. Predation can increase diversity (Paine 1966, Menge and Sutherland 1976) if it prevents competitively dominant species from monopolizing the system. However, in the invaded system, where rock lobsters were significantly more abundant, faunal diversity was diminished and dominance curves indicated a greater dominance by relatively few species (Fig 3.13e). There is evidence that top predators such as large fish have been heavily depleted in this area (Attwood and Farquhar 1999, Griffiths 2000; and see Chapter 7). This may have contributed to rock lobsters increasing in the invaded areas and establishing sufficiently intense predation that faunal species diversity is reduced, leaving only a subset of species that are disfavoured as prey and assume greater dominance.

Secondly, an increase in depth leads to a reduction in light and reduces productivity, and I expected algal diversity to decrease with depth. However, this was not the case: floral diversity was lowest in the shallows and increased with depth in both invaded and non-invaded areas (Fig 3.13c). Similar patterns have been observed in coral communities (Loya 1972, Glynn 1976, Huston 1985a, 1985b). Three different reasons may explain the observed trends:

1) It is likely that shallow depths associated with high productivity are monopolized by one or more species and that with an increase in depth, dominance by any one species is reduced, allowing species diversity to increase. For floral species (Fig 3.13f, i), dominance was greatest in the shallows, with few species contributing

to more than 75% of the biomass, and diminished with depth. For faunal species, dominance was greater in invaded areas (Fig 3.13e) where predation would have been more intense than in the non-invaded areas (Fig 3.13h).

2) Wave action decreases with depth, with the most intense physical disturbance occurring in the shallows. The intermediate disturbance hypothesis (Grime 1973, Horn 1975, Connell 1978, Sousa 1979) proposes that maximum diversity will occur at intermediate levels of disturbance. However, disturbance is often difficult to quantify (Reynolds *et al*. 1993) and the term “intermediate levels” is rather subjective, often being defined in terms of the conditions that produce maximum diversity (Huston 1994, Shea *et al*. 2004). One might expect species diversity to be enhanced in the shallow depths, where waves generate physical disturbance. However, if the disturbance there is frequent and severe, wave action may favour only those species that tolerate such conditions. Organisms unable to tolerate this physical disturbance are thus only likely to appear as depth increases and wave action subsides.

3) Floral diversity in the invaded and non-invaded areas was relatively similar in the shallows. However, as depth increased, floral species diversity became greater in the invaded areas (Fig 3.13c). This could reflect a prevalence of physical control in the shallows, giving way to greater biological controls as wave action subsides with depth and the dominance effect diminishes. Herbivore biomass was significantly lower in the invaded areas than in the non-invaded areas, and although increased grazing pressure can increase floral species diversity (Hily *et al*. 1992), it is also known to decrease diversity (Vance 1979, Himmelman *et al*. 1983, Duggins and Dethier 1985, Wootton 1995). This could explain why non-invaded areas, where herbivores are significantly more abundant, support a lower floral diversity.

All of these potential effects of depth, predation and grazing (and their interactions) are speculative, but are amenable to experimental tests and modelling.

3.4.4 Urchin-abalone interactions

Jasus lalandii is an opportunistic forager and feeds on a wide variety of organisms (Mayfield *et al*. 2000a, 2000b, 2001, Van Zyl *et al*. 2003). On the west coast of South Africa, it has large negative effects on its main prey, leading to the development of alternative stable states of community composition in localities where it is abundant versus rare (Barkai and Branch 1988a, 1988b, Barkai and McQuaid 1988). In invaded areas EOCH, the urchin *Parechinus angulosus* was entirely absent, whereas it was abundant both in non-invaded areas and prior to the invasion (Chapter 2). Its disappearance has serious consequences for the abalone *Haliotis midae*, which has declined drastically since the mid 1990s due to both overfishing caused by poaching (Hauck and Sweijd 1999, Hauck 2009), and its critical dependence on urchins (Day and Branch 2000a, 2000b). Associated with the decline of urchins, abalone recruitment in this area is exceptionally low (Tarr *et al*. 1996). Nevertheless, I anticipated finding juvenile abalone sheltering under the urchins at non-invaded sites where urchin densities have remained high, as Tarr *et al*. (1996) have previously recorded. Surprisingly, none were recorded. This strongly suggests that recruitment failure is taking place: that adult stocks have been depleted to the point that reproduction and subsequent recruitment are collapsing. As broadcast spawners, abalone are prone to the Allee effect (Gascoigne and Lipcius 2004), whereby populations need to achieve minimal densities for fertilization to be effective in the face of dilution of sperm and eggs in the water column. Collapse of broadcast-spawning urchins has previously been attributed to this effect (Quinn *et al*. 1993).

3.4.5 Herbivore-algal interactions

The absence of *P. angulosus* and *H. midae* and the low biomass of other herbivores in invaded areas corresponded with a high biomass of understory algae and kelps. The kelp biomass in invaded areas was more than double that of the non-invaded areas in the <5-m depth zone; and the same was true for understory algal biomass in all depth zones.

At sites where rock lobsters were scarce or absent, *P. angulosus* was the dominant subtidal herbivore and there was also a markedly greater biomass of other herbivores such as *Turbo sarmaticus*, *T. cidaris* and *Oxystele sinensis*. Urchins are renowned worldwide for their grazing abilities (Lawrence 1975, Mann 1977, Hay 1984, Carpenter 1986, 1988, Andrew 1993, Andrew and Underwood 1993). However experimental removal of *P. angulosus* by Day and Branch (2002a) on the Cape Peninsula did not lead to significant changes in foliar algae, kelp sporelings or encrusting corallines. They attributed this to the fact that *P. angulosus* traps drift algae (particularly kelp debris) rather than acting as a grazer. Nevertheless, both my study and an earlier survey by Reaugh (2001) showed significant positive correlations between *P. angulosus* and encrusting corallines, and negative correlations between *P. angulosus* and kelp, turf and foliar algae - although only the correlation with kelp was significant. Moreover, the fact that algal abundance in non-invaded areas was less than half that in invaded areas, where urchins were absent and the biomass of other grazers was low, suggests that a combination of high densities of urchins and other grazers collectively controls kelp and understory algal abundance.

Despite the abilities of other species of urchins to transform algal-dominated systems into coralline barrens elsewhere (Breen and Mann 1976, Mann 1977, Tegner and Dayton 1991, Estes and Duggins 1995, Dayton *et al*. 1998, review in Steneck *et al*. 2002), it is unlikely that *P. angulosus* alone can achieve this. Firstly, *P. angulosus* feeds primarily on drift kelp and only in the absence of this drift kelp does it become an active grazer (Velimirov *et al*. 1977; Velimirov and Griffiths 1979). Secondly, turbulent waters in the coastal zone prevent *P. angulosus* from ascending kelp plants. However, Anderson *et al*. (1997) have suggested that should events such as large-scale storms or unsustainable harvesting lead to depletion of kelp beds, then high densities of *P. angulosus* and other grazers in combination might prevent the re-colonization of the kelp beds, resulting in coralline-dominated barrens. Although my data are correlative, they do constitute strong circumstantial evidence that high densities of rock lobsters lead indirectly to proliferation of algae via depletion of herbivores.

3.4.6 Algal-algal interactions

Although kelps achieved a high biomass at invaded sites and spanned a wide range of biomass across all sites and depths, there was no significant negative correlation between them and understory algae, so they did not appear to influence understory algae in the manner seen elsewhere (Reed and Foster 1984, Johnson and Mann 1988, Kennelly 1989, Dayton *et al*. 1992, Melville and Connell 2001, Clark *et al*. 2004). However, there was a significant negative correlation between kelp and encrusting corallines. In Australia, experimental work has shown that canopy cover of *Ecklonia radiata* reduces understory (foliar/turf) algae but increases the abundance of encrusting corallines (Melville and Connell 2001). A similar association has been reported in California (Reed and Foster 1984). In my study, different patterns and processes emerged - there was a decrease in encrusting corallines at invaded areas and an increase in understory algae. It seems likely that predation by rock lobsters, which are more abundant in invaded areas, directly reduces herbivores there, indirectly leading to a cascading positive effect on algae and thence to a negative effect on encrusting corallines. Further studies are needed to determine what role canopy-cover plays, and whether it influences the species composition of understory algae, even if it does not appear to affect their overall biomass.

Encrusting corallines are both resistant to and tolerant of urchin grazing (Breitburg 1984) and in many cases they indirectly benefit from grazing through the removal of erect algae that would otherwise smother them (Steneck 1982, Breitburg 1984, Fletcher 1987, Andrew and Underwood 1993, Bulleri *et al*. 2002). In addition, experimental work has shown that following the removal of erect algae, encrusting corallines can exert a negative effect on their recruitment, out-competing them for space and thus retarding their re-colonization (Johnson and Mann 1986, Keats *et al*. 1994, 1997, Bulleri *et al*. 2002). In my study, there was a strong positive correlation between encrusting corallines and both urchins and grazers, implying that encrusting corallines indirectly benefit from herbivores. This is not surprising given that numerous studies have shown that in productive environments where herbivores are abundant, encrusting corallines dominate (Branch 1975, Lawrence 1975, Menge and Lubchenco 1981, Paine 1984, Steneck 1986, Fletcher 1987, Steneck and Dethier 1994). Furthermore, experimental work has shown that urchins and other grazers are often required to maintain subtidal beds of encrusting corallines (Fletcher 1987, Morrison 1988, Littler *et al.* 1995). The relationship was, however, not straightforward or consistent. Encrusting corallines were (non-significantly) negatively correlated with both turf and foliar algae in the two shallowest zones but positively correlated with them in the deepest zone. Their relationship with kelp was more clear-cut, being consistently negative. This was probably underpinned by negative urchin/grazer effects on kelp, but I cannot rule out the possibility that encrusting corallines themselves exert a direct negative effect on erect algae.

3.4.7 Spatial differences in the kelp forest ecosystem EOCH

Relative abundances of trophic groups within invaded and non-invaded kelp forests and their deduced interactions in the three different depth zones, based on correlations and SIMPER analyses of functional groups, are summarized in Figs 3.14a-c.

<5-m depth zone

Jasus lalandii was 20 times more abundant at invaded areas, and was strongly negatively associated with urchins, grazers and encrusting corallines and, to a lesser extent, scavengers. From my *a priori* flow model (Fig 3.01) I expected urchins to be scarce at invaded sites; in reality, they were absent altogether, whereas they constituted the dominant component of the herbivores at non-invaded sites (Fig 3.14a). Other herbivores (grazers) were also an order of magnitude more abundant at the non-invaded sites. Both outcomes were almost certainly due to intense predation by *J. lalandii* in invaded areas, and ensuing diminished negative effects of grazing on algae, allowing them to proliferate. In turn, the abundant macroalgae at invaded sites had a negative effect on encrusting coralline through competition for space and probably also shading by kelps. Some herbivores such as abalone and certain limpets are known to settle selectively on encrusting corallines (Morse *et al.* 1979, Steneck 1982, Day and Branch 2000a) and urchins are likely to achieve greater tenacity on encrusting corallines rather than on surfaces covered with foliar algae. There may thus be a two-way beneficial relationship between these ‘crusts’ and herbivores.

The greater abundance of sessile species (sponges, ascidians and bryozoans) at invaded sites was not expected. I forecasted that they would be depleted by predation (Fig 3.01) as *J. lalandii* is known to forage on sponges (Mayfield and Branch 2000), which made up a large proportion of the sessile species at the <5-m invaded sites. In reality, sessile species were significantly positively correlated with rock lobster biomass. Potential explanations include an indirect effect of reduced grazer abundance and therefore reduced disturbance of the sessile species, or the possibility that enhancement of macroalgae improves settlement or survival of sessile species (see Wieters 2005). At invaded sites, sessile species were abundant and negatively associated with encrusting corallines, probably through competition for space.

6-12-m depth zone

Again, *J. lalandii* was much more abundant at invaded sites – by a factor of 25 – with comparable strong negative effects on scavengers, urchins, grazers and encrusting corallines (Fig 3.14b). By reducing herbivores, rock lobsters would have had indirect positive effects on macroalgae, cascading to indirect negative effects on encrusting corallines, which were 10-fold more abundant in non-invaded than invaded sites.

There were, however, three departures from the patterns seen in the <5-m depth zone. The strong positive correlation between lobsters and sessile species, and the strong negative association between sessile organisms and encrusting corallines that were evident in the shallows both disappeared in the 6-12-m depth zone. The strong negative (probably shading) effects that kelps had on encrusting corallines at <5 m also diminished as kelps declined with depth, attenuating their proportional influence on light.

13-20-m depth zone

At 13-20 m there were a number of departures from patterns evident at both of the shallower depth zones (Fig 3.14c). First, although *J. lalandii* was still more abundant at invaded than non-invaded sites, the difference was muted. Nevertheless, at invaded sites, *J. lalandii* continued to have strong negative effects on scavengers and grazers and strong indirect positive effects on macroalgae. In contrast to the positive relationship between *J. lalandii* and sessile species displayed in the <5-m depth zone, at 13-20 m they were clearly negatively associated, which is the intuitively more obvious relationship I forecasted *a priori* (Fig 3.01). Despite a reduction in kelp biomass with depth, kelps now exerted a negative effect on sessile species, probably because of the sweeping action of blades of *Laminaria pallida* (Velimirov and Griffiths 1979), which was the dominant kelp at this depth.

Second, kelps, encrusting corallines and urchins were much diminished in this depth zone, and associations among them and other functional groups were weak.

Third, sessile faunal species increased in abundance at non-invaded sites as algae diminished (a pattern previously noted by Velimirov *et al*. 1977), and became strongly positively associated with scavengers. This was probably because sessile organisms constituted a food source for scavengers, although the association may be a purely incidental by-product of both groups increasing due to the combined effects of reduced competition with algae at this depth and reduced predation by *J. lalandii* in the non-invaded areas.

3.4.8 Top-down control, overfishing and climate change

Many marine ecosystems are viewed as resource-controlled (bottom-up control). For instance, when nutrient-limitation of phytoplankton dynamics controls the system (e.g. Richardson and Schoeman 2004; Ware and Thompson 2005; Frederiksen *et al.* 2006). The opposite of this – systems that are consumer driven (top-down control) – has often been thought to be limited to nearshore and intertidal ecosystems (Frank *et al.* 2007). Coastal top-down control has frequently been documented in kelp-forest ecosystems (Estes *et al.* 1998, Steneck *et al.* 2002, Halpern *et al.* 2006), subtidal temperate reefs (Shears and Babcock 2002, 2003, Barrett *et al.* 2009a, Götz *et al.* 2009a, 2009b), and intertidal rocky shores (Paine 1974, 1980, Castilla 1999, Menge 2000). However, it is only in the past decade that evidence for top-down control in exploited ecosystems has risen to prominence as overfishing of top predators has reached critical levels (e.g. Worm and Myers 2003, Frank *et al.* 2005). Strong (1992) suggests that top-down structuring of ecosystems is not typical, but instead indicates a form of biological instability, as reflected in over-fishing that has led to the collapse of many coastal ecosystems (Jackson *et al.* 2001). For example, the removal of top-predators through over-fishing is reported to disrupt predator-prey relationships, allowing prey to now predate on and/or compete for food with the top predator's early life stages, thereby inhibiting the recovery of top-predators (Köster and Möllmann 2000, Swain and Sinclair 2000). A combination of both top-down and bottom-up control is known as wasp-waist control (Rice 1995). This occurs when a species of an intermediate trophic level controls other species at both higher and lower trophic levels – a classic example being small pelagic fish, which exert a top-down control on zooplankton as well as having bottom-up influences on top predators (Cury *et al.* 2000).

So just what effect does the removal of top-predators have on the rest of the ecosystem? In a mesocosm study, O'Conner and Bruno (2007) showed that the removal of predatory fish affected the structure and functioning of the ecosystem.

Despite difficulties in extrapolating from a small, controlled mesocosm experiment to an authentic ecosystem, their results nonetheless alert one to the effect that predator removal can have on lower trophic levels; and just how important predator identity and density may be.

Along the south-western Cape coast, overfishing predatory linefish has led to their collapse (Attwood and Farquhar 1999, Griffiths 2000). Fishing success of both the commercial and recreational fisheries has declined, and catches have shifted from high-value, slower-growing species to low-value, short-lived species (Attwood and Farquhar 1999). It is possible that the depletion of these predatory fish created an unstable ecosystem and opened up a niche for other predators such as *J. lalandii*. Alternatively, or in combination, possible changes in environmental conditions could have allowed *J. lalandii* to increase in density EOCH.

On the southern section of the Australian east coast, increased poleward penetration of the East Australian Current (EAC), has resulted in a 1.5°C increase in SST along eastern Tasmania (Ridgway 2007). The warming of these temperate waters allowed the long-spined sea urchin *Centrostephanus rogersii* to extend its range southwards from New South Wales (NSW) to eastern Tasmania (Johnson *et al*. 2005, Ling *et al*. 2008, 2009a). Consequences of this range-extension are potentially catastrophic for the following reasons: (1) *Centrostephanus rogersii* has the ability to over-graze macroalgal habitats, creating and maintaining alternative stable ‘barren’ states (Fletcher 1987, Andrew & Underwood 1993, Andrew 1993, Johnson *et al*. 2005), and ca. 50% of the rocky reef off NSW is maintained as barrens (Andrew and O’Neill 2000). (2) Ling (2008) demonstrated that barrens formed by *C. rogersii* along Tasmania have resulted in a significant decline in macroalgal cover and habitat-forming invertebrates and hence a loss of species abundance, richness and diversity.

(3) Given the warming of coastal waters, *C. rogersii* is currently capable of reproductively maintaining itself along eastern Tasmania (Ling *et al*. 2008), and the phenotypic plasticity displayed by *C. rogersii* helps facilitate its colonisation of Tasmanian reefs (Ling and Johnson 2009). (4) The rock lobster *Jasus edwardsii* – a major predator of *C. rogersii* – has been over-fished in Tasmanian waters, resulting in both fewer and smaller-sized lobsters, diminishing consumption of *C. rogersii* and heightening its impact on reef habitats (Ling *et al*. 2009b).

Locally, Rouault *et al*. (2009) have reported a significant increase in the sea surface temperature (SST) of the Agulhas Current system since the 1980s. This increase in SST is likely due to an increase in wind-stress curl in the South Indian Ocean (Rouault *et al*. 2009), which is consistent with a poleward shift in westerly winds reported elsewhere (Thompson and Solomon 2002, Gillett *et al*. 2003, Seidel *et al*. 2008). Simultaneous to the warming of offshore waters, inshore coastal waters east of Cape Agulhas have cooled along the south coast (Roy *et al*. 2007, Rouault *et al.* 2009). Cooling of these inshore water temperatures since the 1980s may have contributed to the observed shifts in kelps, rock lobsters and pelagic fish (see Chapter 1), which are all cold-water species. However, the fact that this inshore cooling occurred predominantly east of Cape Agulhas argues against it being the cause of the lobster invasion EOCH, and attempts to link geographic shifts of species to changes in environmental conditions have been problematic because of inadequate long-term datasets (Cockcroft *et al*. 2008).

As Ling *et al.* (2009b) have described, climate-change-induced range-expansion, coupled with ecosystem instability through the over-fishing of top-predators, does not bode well for the maintenance of ecosystems or their ability to recover from perturbations. Given the eastward shift in *J. lalandii* into an unstable over-fished system, as well as its notorious ability to alter benthic communities (Barkai and Branch 1988a, 1988b; Barkai and McQuaid 1988), it is highly likely that *J. lalandii* has initiated a regime shift in the community structure at invaded sites EOCH, through top-down predatory control.

3.5 Conclusions

Numbers of *Jasus lalandii* have increased EOCH since the late 1990s and they are now significantly more abundant at invaded than non-invaded sites. In parallel, the benthic community in invaded areas is significantly different to that in non-invaded areas. My observational and correlative data revealed strong patterns suggesting that *J. lalandii* is responsible for the observed shift in community structure, but they do not test cause and effect, which would require manipulative experiments. However, given the broad diet of *J. lalandii*, the densities it reaches in invaded areas, and its documented ability to alter community structure (Barkai and Branch 1988a, 1988b, Barkai and McQuaid 1988), as well as the observed correlations between lobster increases and urchin decreases in the early 1990s (Tarr *et al*. 1996, Mayfield and Branch 2000), is the accumulative evidence strongly suggesting that *J. lalandii* is the cause of the contrasting benthic communities. The most notable differences in benthic community structure between invaded and non-invaded areas occurred in the <5-m and 6-12-m depth zones, where there was strong evidence that *J. lalandii* was responsible for a trophic cascade in invaded areas, depleting herbivores and consequently releasing macroalgae, ultimately cascading into a reduction of encrusting corallines. At non-invaded sites *J. lalandii* was rare, herbivores abundant and the 'waist of the wasp' had disappeared with macroalgae diminishing and encrusting corallines becoming more abundant (Fig 3.15a). Deeper down at 13-20 m these effects were still detectable but were damped down because (a) differences in abundance of *J. lalandii* between invaded and non-invaded areas were not as obvious, and (b) many of the species were more scarce, reducing their interaction strength (Fig 3.15b). Patterns thus reflected the relative strength of the effects of *J. lalandii* and the influence of depth.

The depths in which strongest effects of *J. lalandii* were felt coincided with the depth of maximum abundance of *Parechinus angulosus*, *Haliotis midae*, *Ecklonia maxima* and encrusting corallines, with ominous repercussions. Firstly, where *J. lalandii* numbers were high, *P. angulosus* had been eliminated and other grazers were greatly reduced. Given that *P. angulosus* provides vital shelter for juvenile abalone (Day and Branch 2000a, 2000b, 2002a), the removal of *P. angulosus* has imminent negative consequences for the abalone fishery. In addition, the cascading effects of *J. lalandii* appear to have diminished encrusting corallines, which are the preferred settlement site of abalone recruits (Day and Branch 2000a), further stressing the fishery for abalone, which is already in turmoil because of illegal fishing. The plummeting fishery has led to a ban on all fishing for wild stocks (Hauck 2009) and the rapid development of abalone mariculture (Troell *et al*. 2006), which has increased the demand for harvested kelp. Levitt *et al*. (2002) discourage the harvesting of whole kelp plants EOCH, considering it unsustainable, with the potential to eradicate current kelp forests, although harvesting fronds can be sustainable. On the other hand, the increase in *J. lalandii* has allowed the development of a commercial rock-lobster fishery EOCH. Balancing the harvesting of these resources will require deft management and a clear understanding of the ecosystem, achieved in part through multispecies modelling that forms the focus of Chapters 4-6 of this thesis.

Chapter 4

A Minimally Realistic Model of lobster-urchin-abalone interactions in a lobster-invaded area East of Cape Hangklip

4.1 Introduction

The unsustainable rate at which many fish populations are harvested has led to the overexploitation of many target species and, as a consequence, entire ecosystems have been altered (Jackson *et al*. 2001). Conventional fisheries management has in the past focused largely on the direct effects of fishing on the target species. However, given the state of fish stocks as well as marine ecosystems, the indirect effects of fishing on the ecosystem can no longer be ignored. The transition from traditional single-species management towards an ecosystem approach to fisheries management has already begun. Single-species stock assessments are still the predominant choice for the management of fisheries, but the development of multispecies models has proven useful in identifying and understanding ecosystem interactions (see Plagányi 2007 for a review).

The most extensively employed ecosystem modelling approach is ECOPATH with ECOSIM (EwE) (Polovina 1984, Christensen and Pauly 1992, Walters *et al*. 1997, 2000). EwE is a mass-balance ‘whole-ecosystem’ model that focuses on the entire ecosystem, taking into account all trophic levels from top-predators down to primary producers. It therefore requires a substantial amount of quality data. Although it was initially criticized by fisheries scientists, improvements and ongoing developments have made it a useful tool in developing hypotheses and providing a better understanding of the structure and functioning of ecosystems (Plagányi and Butterworth 2004). EwE was never intended to replace traditional stock assessment methods, but used judiciously it is a constructive compliment to them. However, there are still some major concerns and limitations relating to EwE, as highlighted by Plagányi and Butterworth (2004), who analyse EwE from a critical perspective, including the practicality of using it in fisheries management.

Considerably simpler than whole ecosystem models are Minimally Realistic Models (MRMs) – first given this label by Butterworth and Harwood (1991). One of the first implementations was by Punt and Butterworth (1995). These models represent a limited number of species believed to have the most important interactions with the target species. Hence, only a small part of the ecosystem is modelled. By reducing the number of species modelled, one ends up reducing the number of interspecific links that need to be modelled, particularly those that can be construed as weak links (Butterworth and Plagányi 2004, Plagányi 2007). A Minimally Realistic Model was chosen for the ecosystem East of Cape Hangklip (EOCH). There were four main reasons for this choice: (1) the existence of known strong links between a limited set of species; (2) the existence of exploratory work of a similar nature on the ecosystem (Plagányi 2004) that provided a platform from which I could build; (3) difficulties in using EwE to answer the types of questions I was posing (see Plagányi and Butterworth 2008); and (4) an absence of necessary data for many of the species that would have had to be incorporated in an EwE model.

The area EOCH has been subject to radical changes in the ecosystem over the past two decades. A kelp forest system once dominated by herbivores – particularly urchins (*Parechinus angulosus*), abalone (*Haliotis midae*) and large winkles (*Oxystele* and *Turbo* spp) has been transformed into a system now dominated by rock lobsters (*Jasus lalandii*), foliar algae and sessile colonial organisms (see Chapters 2 & 3). A combination of factors has been responsible for this change. Firstly, in the early 1990s, rock lobsters increased substantially and this coincided with a rapid decline in urchins (Tarr *et al*. 1996) that was almost certainly directly due to the increase in rock lobsters, which are notorious predators, and are known to feed on urchins (Mayfield and Branch 2000, Mayfield *et al*. 2000a, b). In addition, illegal fishing of the abalone resource reached uncontrollable levels (Hauck and Sweijd 1999, Hauck 2009). Given the critical relationship between juvenile abalone and urchins (Day and Branch 2000a, b), the decline and then virtual disappearance in urchins, combined with a heavily depleted abalone parent stock, has negatively impacted the abalone resource. What was once a lucrative commercial fishery has now been closed legally and a rock lobster fishery has developed in the area instead. Despite this harvesting, rock lobster densities remain high, urchins remain absent and the future for abalone in this region is not promising.

An initial attempt at a multispecies Minimally Realistic Model for the EOCH region was undertaken by Plagányi (2004), focusing on abalone, rock lobsters and urchins, but insufficient data were then available to adequately parameterise the model. The abalone were modelled using an age-structured production model (ASPM), whereas the rock lobsters and urchins were modelled using surplus production models. This served as a useful starting point, but the multispecies model I developed in this thesis has substantially furthered this initial development by introducing (1) a more detailed representation of the rock lobster component using an age-structured model; (2) a better representation of the urchin dynamics; (3) a flexible framework for later explicit inclusion of groups such as encrusting coralline algae and fish; and (4) parameterization of the model using field information collected as part of this thesis. The model developed here is specific for Zone D/Area 12 along the EOCH coast (Fig 4.01), with a non-invaded rock lobster Zone B being simultaneously modelled for comparison and for purposes of parameter estimation.

In this chapter I develop an initial 'base-case' multispecies model for the EOCH 'invaded' area, focusing on rock lobsters, abalone and urchins. The abalone component is based on the same model used in the national abalone stock assessment

(Plagányi 2004, Plagányi and Butterworth in press), whereas the rock lobster, urchin and species-interaction components are new developments and have been added to the existing abalone model. The model is not intended to replace traditional stock assessment methods for either the abalone or rock lobster fisheries. Rather, it compliments these approaches by improving our understanding of the mechanisms behind the recent changes in the kelp forest ecosystem EOCH. Therefore, its aims are strategic rather than tactical.

4.2 Study Area

The west and south-west coasts of South Africa are divided into commercial fishing zones for both the abalone and rock lobster fisheries (Fig 4.01). East of Cape Hangklip, there are four abalone fishing zones (A-D) (Tarr 2000) and one rock lobster zone (F) – which is sub-divided into three areas: Area 12 Kleinmond, Area 13 Hermanus and Area 14 Gansbaai (Cockcroft *et al.* 2008). Based on rock lobster densities, the EOCH area can be divided into an 'invaded' area (high rock lobster density) and a 'non-invaded' area (low rock lobster density). The invaded area incorporates abalone Zones C and D and rock lobster Areas 12 and 13. The non-invaded area includes abalone Zones A and B and rock lobster Area 14.

The model presented here focuses on the invaded area, specifically abalone Zone D, which coincides with rock lobster Area 12. Zone B was simultaneously modelled within the same framework, partly for parameter estimation, but also to allow a direct comparison of invaded and non-invaded ecosystems. This permitted separate estimation of mortality due to biological interactions as distinct from that due to fishing (and in particular illegal fishing) as these mortality sources are confounded if one considers only a single area that has both fishing and lobster effects (Plagányi 2004).

4.3 Data

4.3.1 Abalone data

Data used in the abalone model included both catch data and indices of abundance. The catch data comprised commercial catch data, recreational catch estimates, and confiscation trends – the latter being used to estimate illegal catches. Commercial catch data and recreational catch estimates extend as far back as 1951 (Appendix 2 Table A2.01) and poaching confiscations are available for all years since 1994.

Various indices of abundance were used in the model-fitting process, including standardized commercial CPUE, fishery-independent abalone survey (FIAS) data and various catch-at-age data. Standardized commercial CPUE data were available for the period 1980-2006 and the FIAS data were collected by Marine and Coastal Management (MCM) for the period 1995-2007. Lastly, the catch-at-age data include data from the commercial, recreational and illegal (confiscations) fishery sectors, and also from fishery-independent and industry surveys. All indices of abundance can be found in detail in Tables 3.5-3.14 in Plagányi (2004).

When extending the single-species abalone model to a multispecies model, data were added in the form of rock lobster commercial catch data, as well as recreational and poaching estimates. Additional indices of abundance, to which the model was fitted included rock-lobster non-standardized commercial CPUE, fishery-independent monitoring surveys (FIMS) conducted by MCM, as well as urchin and juvenile abalone surveys that are described below.

4.3.2 Juvenile abalone and urchin data

Counts of juvenile abalone and urchins for the period 1989-1995 were used in the model-fitting process. These data (Appendix 2 Table A2.02) are from Betty's Bay (Area 12, Zone D) and were taken from Tarr *et al.* 1996. As the raw data were not available, the software TechDig (v.2) was used to digitize the data from Figure 3 in Tarr *et al.* (1996). The juvenile abalone and urchin counts were recorded roughly every three months per year and were recorded as counts per 0.25m^{-2}. For purposes of the model, the average number of juvenile abalone and urchins per model year (defined as from October year $y-1$ to September of year y) were used. The associated variances fluctuated throughout the years as well as between years, and therefore the coefficient of variation (CV) for all the years was set at the mean values of 0.155 and 0.460 for urchins and juvenile abalone respectively. Tarr *et al.* (1996) targeted dense aggregations of urchins (and consequently juvenile abalone) and therefore the counts were considered biased and the variances artificially low, particularly for the urchin counts. As a result, an additional variance of 0.05 was incorporated into the model to establish a total variance that was realistic.

4.3.3 Rock lobster data

Since the early 1980s, the West Coast rock lobster commercial fishing grounds have been divided into fishing zones and areas. Prior to 1997, each zone was allocated a Total Allowable Catch (TAC), and a total TAC was achieved by summing across all zones. From 1997 on, an Operational Management Procedure (OMP) has been in place, in which a total TAC has been set and then subdivided into zonal TACs (Johnston and Butterworth 2005). The commercial fishery is divided into offshore and inshore components, with the offshore component receiving roughly 80% of the TAC and the inshore the balance. Offshore fishers use traps deployed from large vessels in deep water and are not restricted to a particular fishing zone. Instead, they use an inter-area schedule agreed upon by all fishers. Inshore fishers use hoopnets deployed from small boats ("bakkies") and are restricted to a particular zone or area (Cockcroft *et al.* 2008). The minimum size limit for both offshore and nearshore sectors is 75 mm carapace length (CL) and fishing seasons vary according to zone, but in most cases the season runs from 15 November of model year $y-1$ until 30 June of model year y. A small-scale commercial fishery was developed East of Cape Hangklip in 2003 and TACs were allocated to historically disadvantaged individuals (DEAT 2005). These new commercial fishing grounds fall under Zone F (Areas 12, 13 and 14). As this fishery is recent, catch data are limited. Commercial catch data for Area 12 were available from the MCM database for the period 2000-2008 (Appendix 2 Table A2.03). No TAC was allocated in 2003 and thus it is assumed no catches were made during that year.

The recreational fishery is managed by various regulations including size limits, bag limits, gear restrictions, closed areas and closed seasons. It operates from 15 November until 15 April the following year. Between 15 November and 31 December, fishing is allowed all days of the week, whereas between 1 January and 15 April fishing is restricted to weekends and public holidays. The current bag limit is four rock lobsters per person in possession of a permit and the minimum size limit is 80 mm CL. Information on catch data from the rock lobster recreational fishery is difficult to obtain. Multi-phase telephonic surveys were initiated in the 1991/1992 fishing season and are now the standard method for estimating annual recreational catch (Cockcroft and Mackenzie 1997, Cockcroft *et al.* 1999). Recreational catches for Area 12 alone were not available; however, estimates of the total recreational catch EOCH were available for the period 1992-1995 and for the area between Gordons Bay and Cape Agulhas for the period 2003-2007. Area 12 was assumed to account for one quarter of these total values (Appendix 2 Table A2.03). Between these periods, recreational catch data are lacking, but the recreational fishery was operational and thus the mean catch of the four preceding years (1992-1995) has been used for the period 1996-2002. Illegal fishing take was assumed to be zero prior to 2000, and thereafter (2000-2008) it was assumed to be 10% of the commercial catch for Area 12, consistent with the approach used in the rock lobster stock assessment (S. Holloway, University of Cape Town, pers. comm.) (Appendix 2 Table A2.03).

Rock lobster data used in the model-fitting process were from two sources (Appendix 2 Table A2.04): (1) non-standardized CPUE data (kg.bakkie^{-1}.day^{-1}), calculated using the commercial catch data from Area 12, were available for the period 2004-2008 and (2) fishery-independent monitoring survey (FIMS) data (number of lobsters.hoopnet^{-1}) for areas EOCH, were available from the MCM database for the period 2002-2005. The FIMS is an annual independent survey, which has been carried out along the west coast for a number of years but only recently EOCH. Unfortunately, the survey was discontinued EOCH after 2005.

4.3.4 Length-at-age data

Male and female West Coast rock-lobster lengths were taken from Johnston and Butterworth's (2001) length-at-age matrix, which includes a period of change in the somatic growth, and then averaged over the model period 1980-2007. This resulted in a mean length-at-age for both females and males. Using Heydorn's (1969) length-weight conversion formula, male and female mass-at-age was calculated. Rock lobsters were treated as one sex in the model and thus a mean length-at-age and mass-at-age was used (Appendix 2 Table A2.05). Although male rock lobsters grow both faster and bigger than their female counterparts, this difference in growth is most noticeable once they have attained the size (or age) required to consume urchins. The rock lobster sex ratio EOCH was assumed to be roughly 50:50. Therefore, the model does not differentiate between sexes.

4.3.5 Data for interactions among species

Data used in the multispecies interactions are largely from published work done in the EOCH area and can be found in Tables 4.01 and 4.02. Details of data collection from my study can be found in Chapter 3.

4.4 Rock Lobster Model Assumptions

Model year

1. The rock lobster model begins in 1985 and the lobster starting age structure is shown in Table 4.03
2. Consistent with the abalone model, the rock lobster model year runs from October year $y-1$ through to September of year y, the catch is assumed to be taken as a pulse at half year (season two). This coincides with the commercial fishing season which runs for approximately the same period.
3. The model year is divided into 4 seasons, where the catch is taken from the second season – i.e. after half a model year, and the numbers left after the 4th quarter of year $y-1$ are the numbers that contribute to season 1 of the next model year y.
4. At the beginning of the model, the rock lobster population was assumed to not be in equilibrium.

Lobster Demographics

5. Rock lobster sex ratio EOCH was assumed to be 50:50 and both sexes are treated as one.
6. Males and females are of similar size up to the age of about 10 years old. Only after they reach sexual maturity, which coincides with the size at which they are able to consume urchins, do males begin to grow faster than females and get larger than them. A mean length- and weight-at-age is thus assumed for both sexes (Appendix 2 Table A2.05).
7. Age-length matrices used were based on the average length-at-age for the years 1980-2008.
8. 50% maturity was reached at 10yrs and 100% maturity at 11yrs.

Lobster recruitment

9. Recruitment contributed directly into the Zone D population. It is acknowledged that rock-lobster larvae are capable of dispersing over large distances (Pollock and Melville-Smith 1993), but the current model assumes local recruitment only.

Lobster Harvesting

10. Commercial harvesting in the area started in the year 2000.
11. Illegal fishing also started in 2000.
12. Recreational catches for Area 12 were 25% of the total recreational catch for the south-west coast.
13. Illegal catches were 10% of the commercial catch.

Model selectivities

14. Illegal fishing took lobsters ≥ 65mm CL (11yrs).
15. The Commercial sector took only legal-sized lobsters ≥ 75mm CL (14yrs).
16. The Recreational sector took legal-sized lobsters ≥ 80mm CL (16yrs).
17. FIMS samples lobsters ≥ 55mm CL (9yrs).
18. Transect counts recorded only lobsters ≥ 55mm CL (9yrs).

Lobsters-urchin-abalone interactions

19. Lobsters ≥ 12 years eat urchins and urchin size was assumed irrelevant as lobsters of this age are capable of feeding on the largest urchins.
20. Lobsters ≥ 11years show 50% selectivity for abalone at age 0, 100% selectivity for abalone at age 1 and 0% selectivity for abalone >1 years.
21. The pristine urchin density estimate was the maximum urchin density recorded in the EOCH area.
22. Juvenile abalone survival is a function of urchin density and below a certain urchin threshold, abalone survival decreases.
23. Juvenile abalone survival rate has a lower bound of 1% per annum.

4.5 Model Description

4.5.1 Abalone

The abalone component of this multispecies model was based on the current model used in the abalone stock assessment. The model is an age-structured production model (ASPM), with five individual zones modelled simultaneously but split into ‘inshore’ and ‘offshore’ components. For purposes of this study, only Zones B (not invaded by rock lobsters) and D (invaded by rock lobsters) are considered. See Plagányi (2004) and Appendix 3 for details of the model.

4.5.2 Rock Lobster

The current stock assessment uses a detailed size-structured model to manage the West Coast rock lobster fishery (Johnston and Butterworth 2005), and functions as an Operating Model (OM) that feeds into an Operational Management Procedure (OMP) (Butterworth 2008). An OMP is a formal method of designing long-term, robust strategies that satisfy multiple conflicting objectives, address uncertainty issues, and assess the consequences of alternative options for management of both the target species and associated fisheries (Rademeyer *et al*. 2007, Plagányi *et al*. 2007).Initially developed by scientists and stakeholders, the OMP is based on pre-specified data and formulae that, given the OM, generates a management recommendation in the form of a total allowable catch (TAC) (Johnston and Butterworth 2005, Butterworth 2008). Although the most common model applied in South African fisheries is an age-structured production model (Plagányi *et al*. 2009), the West Coast rock lobster fishery is based on a size-structured model. This is largely due to the difficulty of aging crustaceans, and because of the fairly large variability in the age of lobsters of a fixed length. However, it is possible to convert size data into age data based on the growth rate of lobsters derived from tagging each year, and to calculate a length-at-age matrix (Johnston and Butterworth 2001). A relatively simple ASPM was used to model the rock lobster component assuming that the mean length at an age approximately captured the overall dynamics. This approach ignores among-individual variation in growth but was considered adequate for current purposes given the other larger uncertainties in representing the ecosystem dynamics. Mean length-at-age was based on values from the age-length key produced by Johnston and Butterworth (2001). They modelled males and females separately, but I treated the two sexes as one in my model, and used a mean length-at-age for the model period 1985-2008.

The abalone model starting year was 1951 for both Zones B and D but the multispecies effects were only added to Zone D as from 1985. The rock lobster invasion EOCH was first noticed in the early 1990s (Tarr *et al.* 1996) and various suggestions have been put forward as to what caused it, resulting in two conflicting hypotheses: (1) a migration of large lobsters into the area, or (2) increased rock lobster recruitment in the area, which eventually led to the observed increase in abundance. Various scenarios of rock lobster starting age-structures were trialled in the model, with reference-case starting values shown in Table 4.03. The rock lobsters were modelled in quarterly time steps, with the remaining numbers from any given season contributing to the following season. As with the abalone model, the rock lobster catch was assumed to have been taken as a pulse at mid-year (season 2). For the first few years, no catches were made; it was only in the early 1990s that recreational catches were made, and commercial catches began in 2000.

A description of the parameters and variables used in the rock lobster component of the model can be found in Tables 4.04 and 4.06 respectively.

4.5.3 Urchins

As with the rock lobsters, the urchin population was introduced into the model in 1985 for Zones B and D. The initial starting populations were assumed to be at carrying capacity, which was approximated as the mean maximum recorded urchin biomass along that stretch of coastline, multiplied by the reef areas of the respective zones. The two urchin populations were then modelled using a surplus production model. The Zone B population remained at carrying capacity in the absence of rock lobsters, whereas in Zone D, the urchins were preyed upon by large rock lobsters. Descriptions of the parameters and variables used in the urchin component of the model appear in Tables 4.05 and 4.06 respectively.

4.5.4 Species interactions

Fig 4.02 summarizes the multispecies interactions occurring within kelp forest ecosystems EOCH, focusing on the positive and negative associations between rock lobsters, urchins and abalone.

Rock lobsters as predators

Rock lobsters forage on a wide range of prey items (Mayfield *et al.* 2000a, 2000b, 2001, Van Zyl *et al.* 2003, Haley *et al.* 2008 unpublished data). Along the south-west coast, their preferred prey includes urchins, winkles, mussels and also juvenile abalone (Mayfield *et al.* 2000a, 2000b, Van Zyl *et al.* 2003). Feeding experiments have shown that rock lobsters need to reach a size of 65 mm carapace length (CL) to be able to consume small abalone (Van Zyl *et al.* 2003) and >68 mm CL to be capable of consuming urchins (Mayfield and Branch 2000). Therefore, in the model, rock lobsters were modelled as an additional ‘fishing fleet’ that would ‘capture’ juvenile abalone and urchins when rock lobsters reached 11 years and 12 years respectively. Predation by rock lobsters was assumed to only affect the dynamics of their prey and not the rock lobsters (predators) themselves. This is largely due to the fact that: (1) urchins and abalone make up a small component of the lobster diet (Pollock 1979, Mayfield *et al.* 2000a), (2) rock lobsters are significant predators with the ability to alter ecosystem structure (Barkai and Branch 1988a) and (3) although they are highly selective foragers (Mayfield *et al*. 2000a, 2000b, 2001, Haley 2008) that readily switch between prey types, they have the ability to maintain dense populations in the absence of preferred prey (Barkai and Branch 1988c). This is also obvious from the fact that they have continued to increase and remain at high densities EOCH despite decreases in urchin and abalone populations (Mayfield and Branch 2000). In order to realistically model two-way predator-prey interactions a complicated ecosystem model would be required and parameter estimation would be highly complex, if not impossible, and would likely not provide any greater insights into the research questions posed (Plagányi *et al*. 2009).

Urchin-abalone relationship

Day and Branch (2000a, 2000b) revealed that the large majority of juvenile abalone (3-35mm) conceal themselves beneath urchins, giving both a food source in the form of drift algae trapped by the urchins, and protection by the urchins' spines against predators such as rock lobsters. Mayfield and Branch (2000) calculated that urchin densities below 25-30 urchins.m^{-2} would limit the survival of juvenile abalone. In the model, survival of juvenile abalone was modelled as a function of urchin density, where below a certain density threshold ($0.3K_u$), abalone survival decreased exponentially. A minimum abalone survival value was applied preventing a complete recruitment failure.

4.6 Model Equations

The abalone model equations are taken from Plagányi (2004) and appear in Appendix 3. They were modelled for five individual zones, simultaneously, within the same framework – although only Zones D and B are considered here. The rock lobster and urchin model equations, as well as the species interactions, are presented below and, in developing the base-case model, are only applied to Zone D, which was ‘invaded’.

4.6.1 Rock Lobster Population Dynamics

Rock lobsters were modelled using a deterministic age-structured production model.

Numbers-at-age

$$J_{y+1,0} = R^J_{y+1} \tag{4.1}$$

$$J_{y+1,a+1} = J^4_{y,a} e^{-M^J/4} \tag{4.2}$$

$$J^2_{y+1,a+1} = (J^1_{y+1,a+1} - C^J_{y+1,a}) e^{-M^J/4} \tag{4.3}$$

$$J^3_{y+1,a+1} = J^2_{y+1,a+1} e^{-M^J/4} \tag{4.4}$$

$$J^4_{y+1,a+1} = J^3_{y+1,a+1} e^{-M^J/4} \tag{4.5}$$

where

y refers to model year which runs from October of calendar year $y-1$ to September of year y.

a refers to age in years

$J_{y,a} = J^1_{y,a}$ for simplicity of notation

$J^q_{y,a}$ is the number of rock lobsters in age class a during quarter q of year y

M^J is the rock lobster annual natural mortality rate

R^J_y is the number of rock lobster recruits to age class 0 at the beginning of year y

$C^J_{y,a}$ is the total catch of rock lobsters from age class a during year y

Spawning biomass – recruitment relationship

The number of rock-lobster recruits, R_y^J was assumed to be related to the spawning biomass, B_y^{sp-J}, through a Beverton-Holt stock-recruitment function:

$$R^J(B_y^{sp-J}) = \frac{\alpha B_y^{sp-J}}{\beta + (B_y^{sp-J})^{\gamma}} \tag{4.6}$$

where α, β and γ are spawning biomass-recruitment parameters. When $\gamma = 1$, the relationship is that of a Beverton-Holt, but if $\gamma > 1$, recruitment mimics a Ricker-type relationship - reaching a maximum recruitment at a certain level of spawning biomass and then declining towards zero. B_y^{sp-J} is the total spawning biomass computed, taking account of the proportion of rock lobster biomass that is mature at the start of the calendar year:

$$B_y^{sp-J} = \sum_{a=1}^{z} f_a^J w_a^J J_{y,a} \tag{4.7}$$

where

w_a^J is the mass of rock lobster of age a in year y

f_a^J is the proportion of rock lobsters aged a that are mature

The stock-recruitment relationship in equation 4.6 can be re-parameterized in terms of the pre-exploitation (virgin) equilibrium spawning biomass K_J^{sp} and the 'steepness', of the stock-recruitment relationship, to work with parameters that are more biologically meaningful. The 'steepness' of the stock-recruitment relationship, *h*, is the fraction of the virgin recruitment obtained when the spawning stock biomass level is 20% of the virgin spawning stock biomass:

$$\beta = \frac{(K_J^{sp})^{\gamma}\left(1-5h0.2^{\gamma}\right)}{5h-1} \tag{4.8}$$

and

$$\alpha = \frac{\beta + (K_J^{sp})^{\gamma}}{SPR0} \tag{4.9}$$

Where SPR0 is the virgin spawner per recruit for a rock lobster population in equilibrium and was calculated as:

$$SPR0 = \sum_{a=1}^{z} f_a^{\ J} w_a^{\ J} J_a^{virg} \tag{4.10}$$

with

$$J_1^{virg} = 1$$

$$J_a^{virg} = J_{a-1}^{virg} e^{-M_{a-1}} \qquad \text{for } 2 < a < z-1$$

$$J_z^{virg} = J_{z-1}^{virg} e^{-M_{z-1}} / \left(1-e^{-M_z}\right)$$

where z is the largest age considered i.e. the 'plus' group (the group containing all lobsters ≥ age z).

The rock lobster starting population was assumed not to be in equilibrium at the start of the model (1985) and a starting age structure of rock lobsters was input into the model (see equations 4.21-4.24). The stock-recruitment relationship for lobsters calculated the spawning biomass-recruitment parameters β and α in terms of the 'pristine' (K_J^{sp}) rather than starting (1985) rock-lobster spawning biomass.

Total Biomass

Total rock lobster biomass at the start of the calendar year was a summation of all numbers-at-age and their corresponding biomass and was calculated as follows:

$$B_y^J = \sum_{a=1}^{z} w_a^J J_{y,a}^q \tag{4.11}$$

Total catch and catches-at-age

The total catch $C_{y,a}^J$ was the sum of catches for each age class in each sector where s indicates the sector of the fishery (commercial, recreational or illegal/poaching).

$$C_{y,a}^J = \sum_s C_{y,a}^{J-s} \tag{4.12}$$

The annual catch by mass (C_y^{J-s}) for sector s is given by:

$$C_y^{J-s} = \sum_{a=11}^{z} w_a^J C_{y,a}^{J-s} \tag{4.13}$$

The summation was taken from age 11 as it was assumed that no rock lobsters younger than 11 years old would be caught by any of the fishing sectors (Table 4.01).

The sector-specific catch by mass in year y is given by:

$$C_y^{J-s} = \sum_{a=11}^{z} w_a^J J_{y,a} e^{\frac{-M^J}{4}} S_a^{J-s} F_y^{J-s} \tag{4.14}$$

Where S_a^{J-s} is the fishing selectivity-at-age for sector s and F_y^{J-s} is the fishing 'mortality' in year y.

The commercial and recreational sectors were both assumed to catch only legal-sized rock lobsters, and so for these sectors, $S_a^{J-s}=0$ for $a<12$ (commercial) and $a<14$ (recreational). The minimum age of rock lobsters caught by the illegal fishing sector was assumed to be 11 years (S. Johnston, University of Cape Town, pers. comm.) and so for this sector, $S_a^{J-s}=0$ for $a<11$.

The sector-specific exploitable or 'available' component of rock lobster abundance is either in terms of exploitable biomass:

$$B_y^{\exp\_J,s}=\sum_{a=11}^{z} w_a^J S_a^{J-s} J_{y,a}^2 \tag{4.15}$$

or population numbers (in the case of FIMS, which is considered as another fishery sector s):

$$J_y^{\exp,s}=\sum_{a=11}^{z} S_a^{J-s} J_{y,a}^2 \tag{4.16}$$

The proportion of rock lobsters harvested each year F_y^{J-s} by sector s is given by:

$$F_y^{J-s}=C_y^{J-s}/B_y^{\exp\_J,s} \tag{4.17}$$

It follows that catch at age a is:

$$C_{y,a}^{J-s}=S_a^s F_y^s J_{y,a} e^{\frac{-M^J}{4}} \tag{4.18}$$

Length-weight conversions (from Heydorn 1969):

$$W_a^m=0.6518\cdot l_a^{m\,2.8990} \tag{4.19}$$

$$W_a^f=0.5869\cdot l_a^{f\,2.9729} \tag{4.20}$$

where

W_a^m is the total body weight (in grams) of a male rock lobster of age a

W_a^f is the total body weight (in grams) of a female rock lobster of age a

l_a^m is the carapace length (in centimetres) of a male rock lobster age a

l_a^f is the carapace length (in centimetres) of a female rock lobster age a

Initial conditions

The rock lobster population was modelled from the year 1985; however, it is unlikely that this initial year would have reflected a population and population age-structure that corresponded to a pre-exploitation equilibrium. Therefore, it was assumed that the stock was not in equilibrium but rather a fraction (θ) of its pre-exploitation biomass:

$$B_{y_0}^{sp-J} = \theta . K_J^{sp} \tag{4.21}$$

with the starting age structure:

$$J_{y_0,a} = J_{start,a} . \phi_a \qquad \text{for } 1 \le a \le z \tag{4.22}$$

where

$$J_{start,a} = B_{y0}^J / \omega_a \qquad \text{for } 1 \le a \le z \tag{4.23}$$

ϕ_a is the proportion of rock lobsters in age class a in 1985

$$\omega = w_a^J . \phi_a \text{ (proportion of rock lobster biomass in age class } a \text{ in 1985)} \tag{4.24}$$

4.6.2 Urchin Population Dynamics

The urchin population is modelled by a simple surplus production model

$$U_{y+1} = U_y + r_u U_y (1 - U_y / K_u) - C_y^{U-J} \tag{4.25}$$

where

U_y is the biomass of urchins in year y

r_u is the urchin intrinsic growth rate parameter, and

K_u is the urchin carrying capacity for a zone

C_y^{U-J} is the biomass of urchins consumed by rock lobsters for year y

Initial starting population

The initial starting population of urchins in 1985 was assumed to be at carrying capacity for both Zone B and Zone D. An estimate of this starting population was calculated as follows:

$$K_u = (U_{pristine} * (Area^x * hfact) * W_u) \tag{4.26}$$

where

K_u is the carrying capacity/initial starting population biomass (MT)

$U_{pristine}$ is the maximum number of urchins per m^2 recorded in Roman's Bay, a non-invaded site (which was assumed to be equivalent to the carrying capacity)

$Area^x$ is the area covered by kelp forest and is specific for Zone B and Zone D (Tarr 1993)

$hfact$ is a habitat multiplication factor which partly accounts for the bottom topography (see Plagányi 2004)

W_u is the mean weight of an adult urchin in MT.

4.6.3 Multispecies Interactions

Lobster-abalone interactions

The rock lobster population was considered as an additional 'fishing fleet'.

The proportion of abalone consumed by lobsters each year ($F_y^{Ab\_J}$) is given by:

$$F_y^{Ab\_J} = C_y^{Ab\_J} / B_y^{prey} \tag{4.27}$$

where the biomass of abalone prey (B_y^{prey}) available for consumption by rock lobsters is:

$$B_y^{prey} = \sum_{a=0}^{1} S_a^{Ab\_J} w_a \left(N_{y,a}\right) e^{\frac{-M_a}{4}} \tag{4.28}$$

where

$S_a^{Ab\_J}$ is the fishing selectivity-at-age for abalone by the rock lobster ‘fishing fleet’

w_a is the abalone weight-at-age

$N_{y,a}$ is the number of abalone in age class a during year y

M_a is the age-dependant abalone annual natural mortality rate

The summation is shown for ages 0 to 1 years as it is assumed that abalone > 1 year are unlikely to be preyed upon by rock lobsters because they are too large. (The selectivity for abalone aged 0 was set at 50% given recruits take time to grow to a size large enough to be eaten and for 1 year olds it was assumed to be 100%).

The total biomass of lobsters comprising the “predator fishing fleet” that prey on abalone B_y^{J-Ab} is given by:

$$B_y^{J-Ab} = \sum_{a=11}^{z} w_a^J \left(J_{y,a}\right) e^{\frac{-M^J}{4}} \tag{4.29}$$

where rock lobsters aged 11 and older are capable of preying on juvenile abalone (Table 4.01).

The consumption of abalone by rock lobsters is then given by a Holling Type II function (Appendix 4):

$$C_y^{Ab\_J} = \frac{\alpha_{Ab\_J} B_y^{J\_Ab} B_y^{prey}}{1+\beta_{Ab\_J} B_y^{prey}} \tag{4.30}$$

where α_{Ab_J} and β_{Ab_J} are the abalone-lobster interaction parameters. Both parameters are positive constants, with α describing the rate at which rock lobsters capture juvenile abalone and β describing the rock lobster's handling time of the juvenile abalone. $C_y^{Ab\_J}$ is the total biomass of abalone consumed by lobsters in year y.

The abalone numbers-at-age consumed by lobsters each year is given by:

$$N_{y,a}^{Ab\_J} = S_a^{Ab\_J} F_y^{Ab\_J} \left(N_{y,a}\right) e^{-M\ /4} \tag{4.31}$$

Lobster-urchin interactions

The biomass of lobsters available to prey on urchins $B_y^{J\_U}$ is given by:

$$B_y^{J\_U} = \sum_{a=12}^{z} w_a \left(J_{y,a}\right) e^{\frac{-M^J}{4}} \tag{4.32}$$

where rock lobsters aged 12 and older are capable of preying on urchins (Table 4.01). The consumption of urchins by rock lobsters is also given by a Holling Type II function:

$$C_y^{U\_J} = \frac{\alpha_{U\_J} B_y^{J\_U} U_y}{1 + \beta_{U\_J} U_y} \tag{4.33}$$

where α_{U_J} and β_{U_J} are the urchin-lobster interaction parameters, with α describing the rate at which rock lobsters capture urchins and β describing the rock lobster's handling time of the urchin captured. $C_y^{U\_J}$ is the total biomass of urchins consumed by lobsters.

The abundance of both abalone and urchins was assumed to have no affect on lobster population dynamics because they make up a relatively small proportion of the diet (Pollock 1979, Mayfield *et al*. 2000a), and lobsters readily switch amongst prey and can maintain high densities even in the virtual absence of preferred prey such as mussels and urchins (Barkai and Branch 1988c).

Urchin-abalone interactions

Abalone natural mortality M_a was assumed age-dependent and was estimated in the original abalone stock-assessment model developed by Plagányi (2004), by estimating the mortality parameter μ. This mortality parameter was then input into an abalone-mortality equation resulting in an estimated mortality-at-age as described by Plagányi (2004):

$$M_a = \mu + \frac{\lambda}{a+1} \tag{4.34}$$

where a = age and λ was set equal to a constant (0.2).

In the base-case multispecies model, μ was fixed, and the focus was instead on estimating the additional mortality due to the urchin-abalone interaction, which was not explicitly represented in the single-species model. Given the relationship between urchins and juvenile abalone (Day and Branch 2000a, 2000b), I then modelled the natural mortality of juvenile abalone using an urchin-abalone interaction.

The urchin-abalone interaction is incorporated into the model in the form of juvenile abalone survival relative to urchin densities. Survival is related to natural mortality as follows:

$$S_{base} = e^{-M_{base}} \tag{4.35}$$

where S_{base} is the juvenile abalone (age $= 0$) survival prior to the lobster invasion and M_{base} is the abalone natural mortality rate prior to lobster invasion.

When urchin densities are above a certain threshold (Table 4.02), juvenile abalone survival S_0 is as follows:

$$S_0 = S_{base} \tag{4.36}$$

When urchin densities fall below the threshold, S_0 is calculated as:

$$S_0 = S_{\min} e^{aU_y / K_u} \tag{4.37}$$

where

$S_{\min}$ is a minimum abalone survival constant of 0.01 (which is input);

U_y is the number of urchins in year y; and

K_u is the urchin carrying capacity

a is a constant which is calculated as: $\dfrac{\ln S_{base} - \ln S_{\min}}{U_{thresh}}$

U_{thresh} is the urchin threshold (relative to urchin carrying capacity), below which juvenile abalone survival declines.

4.6.4 Likelihood Function

The model was fitted to all available data to estimate model parameters. This was achieved by minimizing the negative of the log likelihood function for these data. Various data contribute to the overall likelihood, including the abalone component, which made several contributions by fitting the model to empirical abundance indices and catch-at-age data. These contributions are described above in section 4.3, as well as in Plagányi *et al*. (2001) and Plagányi (2004) and hence, only new contributions to the likelihood, which were added when extending the model to a multispecies model, are described below. The new data that were added included rock-lobster commercial CPUE and FIMS, and counts of juvenile abalone and urchins. All equations listed below were developed based on those in Plagányi (2004) (see Appendix 3).

Abundance data

$$\varepsilon_y^s = \ln\left(I_y^s\right) - \ln\left(\hat{I}_y^s\right) \tag{4.38}$$

where I_y^s is the abundance index for year y and sector s and

$\hat{I}_y^s = q^s B_y^{\exp\_J,s}$ which is the corresponding model estimated value, where $B_y^{\exp\_J,s}$ is the model value for exploitable biomass in sector s (given by equation 4.15). However, if the index refers to numbers, then $B_y^{\exp\_J,s}$ is replaced by $J_y^{\exp,s}$ (see equation 4.16).

The abundance data contribute to the negative of the log likelihood as follows:

$$-\ln L = \sum_s \left[\sum_y \ln \sigma_y^s + \left(\varepsilon_y^s\right)^2 / 2\left(\sigma_y^s\right)^2 \right] \tag{4.39}$$

Variance unspecified (CPUE abundance data)

The standard deviation $\hat{\sigma}^s$ of the residuals for the logarithm of abundance series s was estimated in the fitting procedure by its maximum likelihood value:

$$\hat{\sigma}^s = \sqrt{\frac{1}{n_s}\sum_y \left(\ln I_y^s - \ln \hat{I}_y^s\right)^2} \tag{4.40}$$

where n_s is the number of data points for the abundance series corresponding to sector s.

The catchability co-efficient q^s for the abundance index of sector s was estimated by its maximum likelihood value:

$$\ln \hat{q}^s = \frac{1}{n_s}\sum_y \left(\ln I_y^s - \ln \hat{B}_y^{\exp\_J,s}\right) \tag{4.41}$$

Variance specified (FIMS data, juvenile abalone and urchin data)

The catchability co-efficient q^s for the abundance index of this sector was estimated by its maximum likelihood value:

$$\ln \hat{q}^s = \frac{\sum_y 1/\left(\sigma_y^s\right)^2 \left(\ln I_y^s - \ln \hat{B}_y^{\exp\_J,s}\right)}{\sum_y 1/\left(\sigma_y^s\right)^2} \tag{4.42}$$

Where

$$(\sigma_y^s)^2 = \ln(1 + (CV_y)^2)$$

CV_y is the coefficient of variation of the resource abundance estimate for year y, which is input.

The same equation was used to estimate the abundance index for the juvenile abalone and urchins, except that a δ term (Table 4.06) is added because some of the observed data points (I_y^s) are zero:

$$\ln \hat{q}^s = \frac{\sum_y 1/\left(\sigma_y^s\right)^2 \left(\ln(I_y^s + \delta) - \ln(\hat{B}_y^{\exp\_J,s} + \delta)\right)}{\sum_y 1/\left(\sigma_y^s\right)^2} \tag{4.43}$$

Where

$(\sigma_y^s)^2 = \ln(1 + (CV_y)^2) + \sigma_{AD}$

σ_{AD} is an additional variance term added to the observed variance due to a survey bias and therefore unrealistically low variances.

4.7 Parameters

Given that the abalone model forms the basis for the annual abalone stock-assessment, effort has already been devoted to fitting the model to available data (Plagányi *et al.* 2001, Plagányi 2004, Plagányi and Butterworth in press), so for the purposes of the base-case multispecies model, the focus was on estimating the new parameters and these are summarized as follows:

1. $B_{y_0}^J$ Initial total rock lobster biomass in 1985.
2. α_{Ab_J} Lobster-abalone interaction parameter 1.
3. β_{Ab_J} Lobster-abalone interaction parameter 2 (for a Holling Type II functional response).
4. α_{U_J} Lobster-urchin interaction parameter 1.

5. β_{U_J} Lobster-urchin interaction parameter 2 (for a Holling Type II functional response).
6. K_J^{sp} Rock lobster spawning biomass carrying capacity for Zone D.

4.8 Results and Discussion

Results from the base-case multispecies model are outlined and discussed below. In addition to the pre-existing parameters, six new parameters ($B_{y_0}^J$, α_{Ab_J}, β_{Ab_J}, α_{U_J}, β_{U_J} and K_J^{sp}) were estimated within a maximum likelihood framework using the software AD Model Builder™ (v 7.1.1, Otter Research, Ltd). These parameters are reported in Table 4.07, with associated 90% Hessian-based confidence intervals. The base-case model fits are shown in Fig 4.03 and the negative log likelihoods are summarized in Table 4.08.

The full set of base-case model parameter estimates is given in Appendix 5 Table A5.01, which also shows the results from a model version with all parameters (such as natural mortality, poaching estimates and selectivities) estimated simultaneously. The latter model version results in an improved fit to the data but is problematic from a number of other perspectives as summarised in Appendix 5. For this reason, the previously estimated mortality and poaching parameters are held constant in the extended multispecies model developed here, and the focus is instead on explicitly representing the lobster invasion.

4.8.1 Parameter estimation

Model results suggested an initial rock lobster starting biomass, $B_{y_0}^J$, of 413 tonnes (MT), but this parameter was not well estimated (90% C.I = 0-942) because of the lack of contrast in the indices of abundance (lobster CPUE/FIMS), which are unfortunately not available over the period when lobsters were first increasing (Table 4.07). In the initialization of the model, the starting age structure was kept below the age/size of a rock lobster required to consume juvenile abalone and urchins (predation size limit). This allowed the lobsters time to grow and reach a size at which they were capable of preying on urchins, coinciding with the observed urchin decline. Surveys conducted in Zone D prior to 1990 recorded an absence of rock lobsters (Field *et al*. 1980a, Jackleman 1996). It is highly unlikely that there were absolutely no rock lobsters present in the area, but rather that their numbers were too low for detection in transects or that they were located mainly offshore in deeper waters than those surveyed. Mayfield and Branch (2000) calculated that a density exceeding 0.25 large (>68 mm CL) rock lobsters.m^{-2} is needed to realistically simulate some level of direct interaction between lobsters and abalone. Estimation of the lobster-urchin interaction parameters was made possible because the urchin data reflected a sudden decline that could be directly attributable to lobsters in the model. Similarly, data on the decline in the numbers of juvenile abalone assisted in estimation of lobster-abalone interaction parameters. Estimation of these parameters would improve with additional contrasting data e.g. data to inform on the reverse process whereby lobsters decrease and urchins recover. However, these data are not available.

It is possible that a different functional response may be better suited; in fact, one of the challenges in constructing multispecies models lies in the decision about suitable interaction parameter(s). The simplest functional response (Type I) was first described by Lotka-Volterra (Lotka, 1925; Volterra, 1926) and assumes a linear increase in consumption rate: i.e. the number of prey consumed increases infinitely in proportion to the prey density. However such a model is overly simplistic and rarely occurs in nature. Holling (1959) then improved on this basic model in the form of the Type II and Type III functional responses (Appendix 4). In the asymptotic Type II response, consumption rate increases at a decelerating rate and gradually levels off at a maximum rate when predators become satiated. The Type III response is similar to that of Type II, in that satiation occurs at high levels of prey density, but there is now a sigmoid increase in consumption rate as prey density increases. In these three functional responses (Appendix 4), feeding rate depends only on the density of the prey and not the density of other predators (competition).

Mayfield *et al.* (2000) found that rock lobsters in areas of fast growth, where preferred foods are abundant, had a lower gut-fullness than rock lobsters from areas where preferred foods are scarce. This suggests that in areas where preferred foods are abundant (e.g. Zone D prior to the 1990s) rock lobsters forage until they are satiated and not until they reach gluttony – which might be the case in areas with fewer preferred (lower quality) foods. Rock lobsters are also selective predators, only switching foods when a preferred prey is unavailable. Thus, for purposes of the multispecies model, I used a Holling Type II functional response – consumption of prey (urchins and juvenile abalone) by rock lobsters increases with an increase in prey density up until a certain prey density whereby rock lobsters become satiated and prey consumption levels off (Appendix 4). Sensitivity to alternative functional forms should ideally be tested but was not done here given that the interspecific interactions were dominated by other factors, including the timing and nature of the rock-lobster invasion.

Rock-lobster spawning biomass carrying capacity, K_J^{sp}, was estimated to be 1510 MT (90% CI = 1085-1935) (Table 4.07). A rough calculation involving the area of Zone D, a habitat multiplication factor (Table 4.06) and the mean weight of mature rock lobsters, equates a rock-lobster biomass of 1500 MT to approximately 0.83 rock lobsters.m^{-2}. The greatest mean rock-lobster density recorded in Zone D was 0.94 rock lobsters.m^{-2} (Reaugh 2001), but most of the mean densities recorded (during the mid to late 1990s) range between 0.2 and 0.5 rock lobsters.m^{-2} (Mayfield and Branch 2000, Marine and Coastal Management unpublished data, Chapters 2 & 3), so the estimate is not unrealistic.

In 2002, the West Coast rock lobster size-structured single-species model roughly estimated a total rock-lobster biomass EOCH of approximately 10 500 MT for rock lobsters >65 mm CL and 5500 MT for rock lobsters >75 mm CL (Johnston 2002). These estimates are greater than the estimated K_J^{sp}; equating to some 5000 MT for the entire area EOCH. Given similar habitat areas for Zones C and D, the model estimate could be roughly doubled to yield a K_J^{sp} estimate of 3000 MT of spawning biomass EOCH. Furthermore, my model takes into account only the area covered by kelp forest and not deeper waters where *J. lalandii* also occurs. Given all this, as well as the attendant 90% confidence intervals, the estimated K_J^{sp} seems plausible.

4.8.2 Observed values vs. model predictions

(i) Abalone CPUE and FIAS

Both Zones B and D show an increase in standardized commercial catch rates between 1980 and the mid-to-late 1990s, followed by a decrease over the last decade (Fig 4.03a,b). A general decrease in abalone population density was also evident in the FIAS data over this period (Fig 4.03c,d). The model yielded a reasonably good fit for both these indices (Figs 4.03a-d, Table 4.08); however, during the 1990s the observed CPUE values were higher than the predicted model values for Zone D. These higher CPUE values were the result of area changes made to Zone D. Since

1977 the overall area for Zone D has changed twice through additions and removals of coastline (Dichmont *et al.* 2000). As a consequence, between 1986 and 1993 access to a large proportion of the kelp bed west of this zone was first prohibited, but then permitted again after 1993 (Dichmont *et al.* 2000). This change in access resulted in unusually high CPUE values for 1993 and the next few years. Future model developments should consider omitting these non-representative data.

(ii) Rock lobster CPUE and FIMS

The first commercial catches EOCH were made in 2000, but both these catches and those made in 2001 and 2002 were relatively small (Appendix 2 Table A2.03) compared to those made when the full-scale commercial fishery was opened in 2003. Consequently, the CPUE time series began only in 2004 with the intention of keeping this index as comparable as possible. Although the CPUE data series is limited, the commercial catch rate showed a gradual decline (Fig 4.03e), suggesting a reduction in the rock lobster biomass. The FIMS data showed no trend, because the first survey EOCH was only conducted in 2002, and after 2005 the surveys were discontinued. The model showed a relatively good fit to the observed CPUE (Table 4.08). The best fit for the FIMS data showed no obvious change in the predicted FIMS catch rate over the four years (Fig 4.03f).

(iii) Juvenile abalone and urchins

Tarr *et al.* (1996) recorded urchin counts as well as juvenile abalone sheltering beneath urchins. They revealed a decline in urchin numbers over the years, a striking sudden drop in 1994, and then their virtual disappearance in 1995 and 1996 (Fig 4.03g). There was no clear a trend in juvenile abalone: initially there was a slight increase in numbers, followed by a substantial drop in 1995-1996, although there was considerable sampling variability (Fig 4.03h). The observed crash in juvenile abalone is not surprising as no urchins were found in 1995 and 1996 and, as a consequence, no juvenile abalone were recorded in these years either. Admittedly a small proportion (ca 5%) of juvenile abalone shelter in crevices (Day and Branch 2000b), but there is presumably a limit on the availability of suitable unoccupied crevices.

Trying to fit the model to these urchin and abalone data was challenging for two reasons: firstly, dense aggregations of urchins were specifically targeted during the survey and therefore the numbers recorded are not a true reflection of the mean urchin density. More importantly, this led to the sample variance being particularly low, resulting in the model placing too much emphasis on the urchin data. Secondly, the sudden decline and then total disappearance of both urchin and juvenile abalone made it difficult to fit the model to the observed ‘zero’ data points. To simulate this more realistically, an additional variance was added to both the urchin and abalone observed variance. This reduced emphasis on these data, especially at times when there was a sudden decline. Counts that were recorded as ‘zero’, were changed to ‘one’ for purposes of fitting the model. I considered that even though no urchins or abalone were recorded, it was likely that urchins and abalone were still present – even if very rare. Confirmation of this came from the detection of urchin and abalone remains in the gut contents of lobsters (Haley 2008) despite the failure to record either of these prey species in benthic surveys (Chapters 2 & 3). By replacing the zero values with one, the dramatic decline in urchins and juvenile abalone was still evident, and the model fit improved to the extent that the model was successful in simulating the observed urchin decline (Fig 4.03g).

4.8.3 Population trajectories and catch trends

(i) Abalone

The inshore abalone spawning biomass trajectories for Zones B and D are shown in Fig 4.04a,b. The model calculated a spawning biomass of around 3500 MT for Zone B and 5500 MT for Zone D in 1951. Subsequently, both zones underwent a steep decline in biomass due to high exploitation levels during the 1950s and 1960s. In 1970, fishing regulations were introduced, and as a result the spawning biomass remained relatively stable for the next 20-30 years. However, by the mid 1990s illegal fishing had begun, initially in Zone D, and later on in Zone B. It is for these years that the model yielded a rapid decline in the spawning biomass, particularly for Zone D where the ‘invasion’ of rock lobsters augmented the decline due to overexploitation, culminating in their virtual disappearance by 2007.

Zones B and D had similar abalone catch trends (Fig 4.04c,d): commercial harvesting was recorded as far back as 1951, and by the 1960s exploitation levels reached a maximum and then slowly began to decline. This led to the implementation of fishing regulations in 1970 and, as a result, the catches dropped further and then remained relatively constant up until around 2000 in Zone B. In Zone D however, the commercial catch diminished by 50% by the late 1980s. Despite increased poaching, the catches increased slightly towards the end of the 1990s in response to socio-economic pressures, and subsistence and limited commercial rights were introduced for a few years, but then dropped again post-2000. The commercial fishery was eventually closed throughout its range in 2008. Recreational fishing increased after the 1970s, reaching a peak in the 1990s, but the fishery was then closed in 2003 in an attempt to curb illegal fishing and re-establish sustainability. Illegal catches are thought to have been minor prior to 1980, and the confiscations of illegally-caught abalone from the 1990s and 2000s showed that illegal fishing was at its worst during these periods. Model-derived estimates of illegal catches are shown in Fig 4.04c,d.

(ii) Rock lobster

The model estimated a rock lobster spawning biomass of approximately 50 MT in 1985 (Fig 4.04e). The lobster biomass was then predicted to increase rapidly to a maximum of just less than 1000 MT in 1994. Between 1995 and 2000 there was a decrease in spawning biomass, after which it remained fairly constant between 2001 and 2006 and then dropped slightly in 2007.

There are two probable reasons for the decline in rock lobster biomass during the mid-to-late 1990s. (1) The initial starting biomass comprised 0-10 year olds, of which only a small percentage would have been mature and therefore, recruitment of large individuals would have been limited or absent. By the mid-to-late 1990s, this ‘limited recruitment’ would have had time to allow the lobster to grow and mature, contributing to the spawning biomass, albeit less than in previous years. (2) In addition, large lobsters (16+ years) were being removed by the recreational fishery during the same time period (mid-late 1990s) (Fig 4.04f), further decreasing the spawning stock. Spawning biomass confidence intervals (Fig 4.05a) were extremely wide up until around 2000, after which they narrowed considerably, reflecting the considerable uncertainty in determining rock-lobster population status between 1985 and 2000. Following this period, indices of abundance are available and therefore confidence intervals improve.

Resource depletion (Fig 4.05b) began in the mid 1990s, presumably due to the initial recreational catches. Resource depletion then appears to have levelled off, despite the opening of the commercial fishery. The rock-lobster modelled trends matched the observed trends (Fig 4.03e,f), which suggests resource depletion (Fig 4.05b) between 2001 and 2007, although it must be noted that both CPUE and FIMS datasets do not extend very far back, so it is difficult to evaluate the plausibility of the trends.

The greatest rock-lobster density (0.94 lobsters.m^{-2}) was recorded in 2001 in the Betty's Bay MPA (Reaugh 2001). If only the areas of Zone D that lie outside the MPA are taken into account, the highest recorded density was during the mid 1990s (Marine and Coastal Management unpublished data, Mayfield and Branch 2000), which supports the model prediction of biomass reaching a peak around this period.

Available data from MCM suggest that rock lobster catches by recreational fishers in Zone D began in earnest in the 1990s (Fig 4.04f), and in the model, the available recreational biomass ($B^{exp\_J,rec}$) was thus set at zero until 1991 (Fig 4.05c). However, Mayfield and Branch (2000) reported boat launches made from Hermanus (Zone C) as early as 1987, and that these increased 10 fold between 1987 and 1997. Although no catch data are available between 1987 and 1992, it is thus likely that recreational rock lobster fishing was taking place, although on a small scale. The EOCH coastline was not well known for its rock lobster abundances prior to the early 1990s and therefore, I assumed that the biomass of rock lobsters removed by recreational fishers at that time was negligible. The commercial fishery only expanded EOCH in 2003/2004 after reported increases in rock lobster abundance during the 1990s and experimental commercial catches made in 2000-2002. Since then, catches have increased slightly, reaching a maximum in 2007. The model suggests that lobsters of a sufficient size to be caught by commercial fishers ($B^{exp\_J,comm}$ – commercially available biomass) first became available in 1989 (Fig 4.05d) – a few years prior to the available recreational catch. Estimated confidence intervals for these estimates are, once again, extremely wide. Illegal fishing was assumed to have started only in 2000 when the first commercial catch was made. However, no records exist of illegal harvests and an earlier start-date is probable. The annual West Coast rock lobster stock assessment assumes the illegal take to be 10% of the commercial catch, and this assumption was employed in the model (Fig 4.04f). Prior to 2000, illegal fishing EOCH is assumed to have been concentrated on abalone and therefore the illegal rock lobster catch at that time was assumed to be insignificant.

(iii) Urchins

In the base case model, urchin biomass was modelled for both zones, but rock lobsters would only have had an impact on urchins in Zone D. At the start of the lobster model year (1985), urchins were assumed to be at carrying capacity in both zones (see equation 4.26 for calculations). In Zone B the urchin carrying capacity was calculated to be just over 14 600 MT and with no lobster interactions, it remains at this level (Fig 4.04g). In Zone D, the urchin carrying capacity was calculated to be just under 15 000 MT in 1985 (Fig 4.04h), with an initial decline beginning in the late 1980s. By the early 1990s, this decline was more severe, resulting in very few urchins by 1996 and their complete disappearance in 1997. The observed data from Tarr *et al.* (1996) suggest that the urchins had disappeared by 1995 (Fig 4.03g), and if this was the case, then perhaps an exponential decline in urchin biomass is more appropriate than a linear decline.

4.8.4 Species Interactions

Despite a decline in urchin biomass, juvenile abalone biomass remained relatively constant and only began to decline when urchins dropped below 4000 MT (Fig 4.06a).

The modelled urchin population crashed in 1997 and although abalone recruitment began to decline at around that time, it was only after 2000 that the recruitment failure accelerated (Fig 4.06c). This is not surprising, given that abalone recruitment is not only directly related to urchin biomass, but is also a delayed response reflecting the (illegal) over-exploitation of the abalone stock. As the Beverton-Holt relationship suggests in Fig 4.08a, abalone recruitment increases with spawning stock biomass, eventually reaching an asymptote at large spawning stock sizes. Therefore a decline in spawning biomass would result in decreased recruitment, likely becoming more precipitous at low levels of spawning biomass. Survival of juvenile abalone (0-1 year olds) is extremely sensitive to urchin biomass (Fig 4.06b). Mayfield and Branch (2000) estimated that if urchins fall below a density of 25-30 urchins.m^{-2}, juvenile abalone survival will be limited. Therefore, in the multispecies model, survival of juvenile abalone was set to decline when urchin biomass dropped below a third of the carrying capacity (equivalent to the density calculated by Mayfield and Branch 2000), as seen in Fig 4.06b. Estimating this urchin-abalone relationship was not possible, given that I was already trying to estimate the other interaction parameters using limited data. In future, uncertainties pertaining to this relationship could be better accounted for using e.g. a Bayesian approach.

Lobster recruitment (Fig 4.06d) follows a similar trend to that of the spawning biomass (Fig 4.04e): there is a sharp increase, with maximum recruitment produced at the maximum spawning biomass towards the mid-1990s. After the mid-1990s, recruitment would have decreased with a decrease in spawning biomass. This is reflected by the Beverton-Holt relationship shown in Fig 4.08b, in which recruitment increases with spawning biomass, eventually reaching an asymptote.

Figs 4.06e and 4.06f show the relationship between urchins and lobsters, and abalone and lobsters respectively. As expected, urchin biomass decreased with an increase in rock lobster biomass. Abalone biomass remained fairly constant until rock lobster biomass reached almost 1000 MT, and thereafter abalone biomass declined. However, this is most likely due to the combined effects of increased illegal fishing, and the rapid decline in urchins, and is therefore only indirectly linked to rock lobsters given the relatively small impact from direct predation.

The consumption of juvenile abalone by rock lobsters (Fig 4.07a) followed the same trend as the rock lobster biomass and thus an increase in large rock lobsters resulted in an increase in juvenile abalone consumption (Fig 4.07c). However, the proportion of juvenile abalone consumed was very small in comparison to the biomass available for consumption. As with juvenile abalone, urchin consumption increased with an increase in large rock lobsters (Fig 4.07d), with almost a third of the urchin biomass of 4052 MT being consumed in 1992 (Fig 4.07b). After this, urchin consumption declined – not as a result of a decrease in lobster biomass, but rather due to the diminishing urchin population.

The consumption of abalone by rock lobsters was modelled using a Holling Type II relationship. However, the parameters estimated by the base-case model resulted in a linear (Type I) relationship instead of an asymptotic (Type II) relationship (Appendix 4), probably because lobster biomass never reached the level at which the asymptote would have come into effect. This is, however, unlikely to change conclusions, given that the overall consumption of abalone by rock lobsters is low.

4.8.5 Diagnostics

A useful diagnostic that can be used to assess the validity of the model, is the trend in the lobster fishing mortality rate F_y^{J-s}, which represents the proportion of the stock removed by a given fishery. Fig 4.09 shows the F_y^{J-s} values for the commercial, recreational and illegal fisheries. These values are not directly comparable, however, as each fishery differs in the minimum size limit (age) at which they may harvest. Up until 1992, it was assumed that no (or negligible) catches were made (no data exist) and therefore the F_y^{J-s} values were zero. From 1993 until 1998, catches were made by the recreational fishery only, so during the 1990s, the F_y^{J-rec} values were below 0.15, but began to increase after 2000, when the initial commercial catches and significant illegal catches were taken. From 2000 onwards, the F_y^{J-rec} values fluctuated between 0.12 and 0.24. The EOCH coastline, particularly Zones B and C are infamous for illegal fishing of the abalone resource (Hauck and Sweijd 1999, Hauck 2009). Rock lobsters were not very abundant in these areas until recently and therefore any illegal fishing on lobsters can reasonably be assumed to have taken place on a comparatively small scale. Consequently, the F_y^{J-poa} values are fairly low at around 2%. Before 2003, the commercial rock lobster fishery had not officially opened and therefore catches made prior to this were considered experimental and, as a consequence, fairly low. As a result, the F_y^{J-comm} values were low to begin with, but increased with the opening of the commercial fishery. In 2007, the largest commercial catch was made and the F_y^{J-comm} reached 0.36. Fishing at a level that is ≤30% of the resource biomass is thought to be fairly realistic. The initial lobster starting total biomass (at the given starting age structure), was estimated at just over 300 MT which is considered realistic as it corresponds to reasonable estimates of F_y^{J-s} values. A smaller initial biomass resulted in very high F_y^{J-comm} and F_y^{J-rec} values, resulting in a population crash, which is unrealistic, given actual catch records.

Further diagnostics are the negative penalties – often incorporated into models to prevent unrealistic scenarios e.g. population crashes. If no negative penalties are required to maintain the model (i.e. negative penalties are zero), this increases confidence in the model. In the case of my model, all negative penalties were zero.

4.9 Summary

In the multispecies model presented in this chapter, abalone and rock lobsters were modelled using an age-structured production model and urchins with a simpler surplus production model. The abalone model, which is used in the abalone national stock assessment, was taken from Plagányi (2004) and provided the foundation for the multispecies model, to which the rock lobster and urchin components were added. The original abalone parameters were thus maintained and new parameters added to the model were estimated. These included the initial rock lobster starting biomass B_{y0}^{J}, the rock lobster spawner carrying capacity K_J^{sp}, the abalone-lobster interaction parameters α_{Ab_J} and β_{Ab_J}, and the urchin-lobster interaction parameters α_{U_J} and β_{U_J}. Species interactions between rock lobsters and abalone and rock lobsters and urchins were modelled using a Holling Type II functional response.

Limited rock lobster CPUE time series made it difficult to estimate an initial rock lobster starting biomass and confidence intervals were fairly wide, but the narrow confidence intervals for rock lobster carrying capacity suggested this parameter was well estimated. The interaction parameters were extremely difficult to estimate and confidence intervals were especially wide for the abalone-lobster parameters. Results from experiments such as the lobster exclusion cage experiments could be helpful to assist with parameterisation. One of the problems is that there is a paucity of data on lobster numbers available over the critical 1990s period and it isn't possible to rectify this – the uncertainty in the exact population growth and size composition of lobsters over this period further increases uncertainty in estimating interaction terms involving lobsters. Moreover, the lobster catch and monitoring information contains little contrast. One solution could involve careful monitoring of the current 'non-invaded' Zone B area if an invasion does occur there in the future. Given the lack of data, the urchin-lobster interaction parameter estimates were better than expected. Comparisons between model outputs for Zone B (non-invaded) and Zone D (invaded) yielded outcomes that coincided with empirical data (Chapters 2 & 3), further strengthening confidence in the model.

Essentially, the model described in this chapter is a base-case model, which provides a framework to which additional data can be added, and different scenarios tested, and is a starting point for the exploration of ecosystem interactions EOCH. Specifically it provides the basis for Chapter 5, which explores both future projections and model sensitivity analyses, and Chapter 6 and 7, in which I expand on the base-case model by exploring two different scenarios: (1) the addition of rock lobsters into the non-invaded Zone B, and (2) the addition of a top predator into the lobster-invaded Zone D.

Chapter 5

Sensitivity analyses and future projections for a Minimally Realistic Model in a lobster-invaded area East of Cape Hangklip.

5.1 Introduction

The need for an Ecosystem Approach to Fisheries (EAF) is well recognized (Gislason *et al*. 2000, Pauly 1998), and although this transformation is underway, progress in multispecies models capable of contributing to tactical management advice remains limited largely due to insufficient data and a limited understanding of ecosystem processes. The better represented ecosystem interactions are, the more complex the model becomes, and without adequate data, this leads to scientific uncertainty and imprecise parameter estimation (Plagányi 2007).

Already overfished, the kelp forest East of Cape Hangklip (EOCH) has been transformed by invasion by one species – the rock lobster *Jasus lalandii* – and the severe overexploitation of another – the abalone *Haliotis midae*. To improve understanding of interactions and processes within this ecosystem, a Minimally Realistic Model (MRM) was developed for the area invaded by rock lobsters, which focused on three significant role-players: rock lobsters, urchins and abalone (Chapter 4). Both the abalone and rock lobster components were modelled using an age-structured production model (ASPM), while the urchins were represented by a simple surplus-production model. The abalone component was based on a single-species abalone model used in national stock-assessments of this species (Plagányi 2004, Plagányi and Butterworth in press) and because associated parameters had been previously tested and found reliable they were fixed in the multispecies model. Only parameters for the rock lobster and urchin components of the model (including abalone interactions) were estimated. As highlighted in the previous chapter, there were difficulties in parameter estimation, particularly with the interaction parameters for both abalone and lobsters, and urchins and lobsters. Due to uncertainty in both estimated and input parameters, sensitivity analyses were conducted and the results compared with the base-case model. In addition to testing sensitivity to model inputs and parameters, sensitivity to alternative model structures was explored by, for example, testing alternative hypotheses – in particular the model was used to interrogate alternative hypotheses about the magnitude of the original increase in lobsters EOCH.

In this chapter, I perform sensitivity analyses on the base-case model and explore future biomass projections. Sensitivity analyses were carried out under the following categories: (1) estimated parameters, (2) fixed values assumed as inputs, (3) additional survey and CPUE data and (4) rock-lobster starting age-structure. The starting age-structures were used to mimic two contrasting hypotheses that have been proposed to explain the increase in lobsters EOCH during the early 1990s, but are currently unresolved: (1) the increase was due to an abrupt immigration of adult rock lobsters into the area EOCH, or (2) it was due to increased rock-lobster larval settlement, probably in the late 1970s/early 1980s, which led to the increase in adult rock lobsters observed during the early 1990s. Projections of either 20 or 50 years were made for urchin, abalone and rock lobster biomass under different future catch scenarios.

5.2 Sensitivity Analyses

In addition to the base case model, a number of sensitivity analyses were conducted to test various assumptions and inputs, as outlined below.

5.2.1 Steepness parameter h

The 'steepness' of the stock-recruitment curve h is defined as the fraction of the virgin recruitment obtained when the spawning-stock biomass level is 20% of the virgin spawning-stock biomass. The base-case model assumed that h = 0.7, which corresponds roughly to the median (0.74) of a distribution of h values for various fish stocks (Myers *et al*. 1995). Sensitivity analyses were performed by applying a range of h values: $h = 0.55$, $h = 0.6$, $h = 0.75$, $h = 0.8$ and $h = 0.85$.

5.2.2 Shape of the stock-recruitment relationship

Three spawner-recruitment parameters were used in the spawner-recruit function. The first two parameters, α and β are typical of a Beverton-Holt spawner-recruitment relationship and the third parameter γ produces a Beverton-Holt relationship when set at one, but can emulate a Ricker-type relationship when greater than one. In the base-case model, γ was fixed at one and sensitivity analyses were then performed using a γ value of 1.5 (Ricker-type relationship) and by estimating γ.

5.2.3 Rock lobster spawner carrying capacity

Rock-lobster spawning carrying capacity K_J^{sp} was estimated in the base-case model. Sensitivity analyses were run for values that were 50% greater and 25% less.

5.2.4 Urchin carrying capacity

The base-case urchin carrying capacity (K_u) was approximated using the maximum mean urchin density EOCH (see Chapter 4). Sensitivity tests were conducted using a 50% increase and a 50% decrease of the input K_u, as well as attempting to allow the model to estimate K_u.

5.2.5 Rock lobster natural mortality

The natural mortality of rock lobsters M^J was fixed at 0.10 in the base-case model. This corresponds to a natural survivorship (S) of 0.9, which is the value used in the stock-assessment model for *J. lalandii* (S.J. Johnston, University of Cape Town, pers. comm.). Sensitivity analyses were run using a 50% increase and 50% decrease in M^J. In addition, a scenario was run that attempted to estimate M^J.

5.2.6 Abalone natural mortality

In the base-case model, all estimable parameters from the abalone component remained at their original estimated values. The original single-species model included the lobster-urchin mortality effect on abalone indirectly, and hence the initial aim of the multispecies model was to replace this component with an explicit representation of the mortality due to inter-specific interactions. The different sources of mortality are difficult to estimate because of confoundment between different sources of mortality (natural, legal fishing, illegal fishing and interspecific effects). In the sensitivity analyses, the abalone natural mortality parameter (μ), which had been fixed in the base-case model, was now estimated.

5.2.7 Urchin intrinsic growth rate

The intrinsic annual (population) growth rate of the urchin *Parechinus angulosus* (r_u) was set at 0.5 in the base-case model, which was arbitrary but reflected the relatively fast growth rate of this species. Research on urchin growth is mostly limited to individual growth rates and very little has been published on population growth rate for any urchin species (only one study was found – Lafferty 2004). Locally, one relevant study on *P. angulosus* exits (Greenwood 1980), but spanned 16 months only and was confined to individual somatic growth rates. Sensitivity analyses were conducted using $r_u \pm 50\%$, $r_u + 100\%$ and $r_u + 200\%$, as well as a sensitivity scenario in which r_u was estimated.

5.2.8 Interaction parameters

Four interaction parameters were estimated in the base-case model: the abalone-lobster interaction parameters α_{Ab_J} and β_{Ab_J}, and the urchin-lobster interaction parameters α_{U_J} and β_{U_J}. These parameters were extremely difficult to estimate, as revealed by the wide confidence intervals shown in Chapter 4. Insufficient data prevented pinning down credible parameter values and therefore, best estimates were obtained by fitting the model to observed data. Sensitivity analyses for these parameters were run using both a 50% increase and a 50% decrease in the base-case values.

5.2.9 Additional rock lobster CPUE data

The commercial fishery for *Jasus lalandii* extended to the area EOCH in 2003, and although catch data from this region exist for 2000-2007 (excluding 2003), the catches made during 2000-2002 were classed as ‘experimental’ and were not incorporated into the base-case model. These experimental catches comprised a TAC of 10 tonnes (MT) compared to the subsequent 60-100 MT allocated to the EOCH commercial fishery, and fewer boats (bakkies) were employed in the experimental fishery than commercial fishery. A sensitivity analysis was run in which the ‘experimental’ CPUE data were included in the model (Table 5.01), although these data are not directly comparable.

5.2.10 Rock lobster starting age structure

The increase in abundance of large rock lobsters EOCH was first noticed in the early 1990s (Tarr *et al*. 1996). Two hypotheses that could explain the apparently sudden increase have been proposed: (1) a migration of adult rock lobsters into the EOCH area around 1990 and (2) increased larval settlement in the EOCH area, later resulting in an increase in juveniles and subsequently an increase in large rock lobsters by the early 1990s. A separate possibility is that a decline in top-predation allowed the increase in lobsters, and this was added to the model as a hypothesis in Chapter 7.

The base-case model used a rock-lobster starting age-structure that aimed to mimic a sudden increase in large lobsters in the early 1990s (Fig 5.01), corresponding to the first hypothesis of an adult lobster migration. Accordingly, at the start of the model the population was set to constitute a uniform proportion of individuals in age groups 0-10, allowing time for individual growth to generate a population that would mimic the arrival of adult immigrants large enough to exceed the 68mm CL threshold required for them to be able to consume urchins.

Two additional different scenarios were then used for the sensitivity analyses. The first one (Model S31) used an age structure that would have yielded a population by 1990 that would have mimicked the second hypothesis – establishment of the population by larval settlement. For large rock lobsters to have increased in the early 1990s, increased larval settlement was assumed to have happened in the late-1970s/early-1980s. Therefore, when the model began in 1985, the majority of the starting biomass was set to comprise 3-5 year olds, with few very young rock lobsters and even fewer larger rock lobsters (Fig 5.01). The second scenario (Model S32) was an intermediate between Model S31 and the base-case model with a starting biomass of mostly 4-7 year-old rock lobsters, but also including very young rock lobsters and a small proportion of rock lobsters large enough to prey on urchins (Fig 5.01).

5.3 Akaike Information Criterion

The Akaike Information Criterion (AIC) is a measure of goodness of fit of an estimated model and is calculated as: $AIC = 2p - 2\ln(L)$ where p is the number of estimated parameters and L is the likelihood (Burnham and Anderson 2002). The model with the lowest AIC is considered to be the most parsimonious representation of the data. The AIC was used to select between models.

5.4 Future Projections

Increased rock lobster abundance and the virtual disappearance of urchins during the early-to-mid 1990s, combined with a dwindling abalone parent stock as a result of illegal fishing, has led to probable abalone recruitment failure EOCH in Zones C and D (Chapter 4, Fig 4.01). Consequently, the continued presence of rock lobsters in both Zones C and D is a threat to both urchins and abalone. Future projections were conducted for urchin, abalone and rock lobster biomass under six different scenarios (Table 5.02) using the base-case model. Despite uncertainty in both future legal and illegal catch levels, these projections were forecast for either 20 or 50 years following the end of the model (2007).

Projections were obtained for the following scenarios (Table 5.02):

1. Urchin and abalone biomass with rock lobster predation
2. Urchin and abalone biomass without rock lobster predation (i.e. no rock lobsters)

3. Rock lobster biomass when rock lobster legal catch = 0 (but with continued illegal catch still assumed)
4. Rock lobster biomass at current (2007) catch level
5. Rock lobster biomass at 10 x current (2007) catch level
6. Rock lobster biomass at 10 x illegal catch (legal catch assumed to be zero)

5.5 Results and Discussion

5.5.1 Sensitivity analyses

Results of the sensitivity analyses are shown in Fig 5.02 and in a succession of tables in which the manipulated parameter is given first followed by the goodness of fit tests and lastly the response of other parameters.

Steepness parameter h

A fixed h of 0.7 was input into the base-case model, producing an overall log likelihood of -156.7 and an AIC of -301.4 (Table 5.03). A smaller h produced a slightly worse likelihood, whereas a greater h improved the likelihood but not significantly. Attempts to estimate h resulted in it hitting the upper bound (h=1) at a B^J_{y0} of 196 MT, with no significant improvement in the likelihood (Table 5.03). The effect of increasing h was to result in a lower predicted initial total rock lobster biomass (B^J_{y0}). For all the input h values, B^J_{y0} changed slightly but remained between 300 and 322 MT with no significant improvements in the likelihood suggesting that the base-case model was adequate.

Shape of the stock-recruitment relationship (γ)

The spawner-recruitment parameter γ was fixed at γ = 1 in the base-case model, which produces a Beverton-Holt spawner-recruitment relationship. A sensitivity analysis using γ = 1.5 (Table 5.04 Model S7), which produces a Ricker-type spawner-recruitment relationship, only fractionally improved the model fit (likelihood). When γ was estimated (Table 5.04, Model S8), it hit the upper bound of 1.5, and did not yield sufficient improvement in the likelihood or AIC to warrant estimating this parameter. A γ of 1.5 resulted in a more rapid increase in rock-lobster spawning biomass (Fig 5.02a), reaching a peak of over 1500 MT in 1994, compared to the base-case model(γ=1), in which spawning biomass increased at a slower rate, only peaking at about 1000 MT.

Rock lobster spawner carrying capacity

The base-case model estimated a rock-lobster spawner carrying capacity K_J^{sp} of just over 1500 MT. Sensitivity analyses were run using $K_J^{sp} - 25\%$ (~1133 MT) and $K_J^{sp} + 50\%$ (~2266 MT). A 25% decrease in the carrying capacity (Model S9) resulted in a greater starting biomass and thus a slight change in the β interaction parameters (Table 5.05). The opposite occurred when K_J^{sp} was increased by 50% (Model S10). A reduction in the carrying capacity produced a significantly worse likelihood and AIC value, whereas the increase in K_J^{sp} yielded no significant change in likelihood or AIC. Therefore, the base-case model, which estimated K_J^{sp}, was the preferred model.

Urchin carrying capacity

Prior to 1990, large rock lobsters (>68 mm CL) were scarce EOCH (Tarr *et al*. 1996; Mayfield and Branch 2000) and urchins, abalone and other grazers dominated the kelp-forest benthos (Field *et al.* 1980a). Thus, at the start of the model (1985), urchins were assumed to have been at their carrying capacity. The urchin carrying capacity (K_u) for Zone D (a lobster-invaded zone) was input into the base-case model and was approximated using a mean maximum observed urchin density of 80 urchins.m^{-2} (Mayfield and Branch 2000), a mean urchin weight of 28.5g (Appendix 1 Table A1.01) and the estimated kelp-forest area (which included a habitat multiplication factor) of 6 712 131 m^2 for Zone D (Tarr 1993, Plagányi 2004). This equated to an urchin carrying capacity of approximately 15 000 MT for Zone D. Results from sensitivity analyses showed virtually no change in the starting rock lobster biomass B^J_{y0} when K_u was either increased or decreased by 50% (Table 5.06, Models S11 and S12). However, when K_u increased by 50%, the second urchin-lobster interaction parameter β_{U_J} decreased (Table 5.06, Model S11), and when K_u decreased by 50%, β_{U_J} doubled and the abalone-lobster interaction parameter β_{Ab_J} increased (Table 5.06, Model S12). The likelihoods did not improve with any of the sensitivity analyses; rather there was a trade-off between K_u and the interaction parameters.

Rock lobster natural mortality

Three sensitivity analyses were conducted on the rock lobster natural mortality parameter (M^J). In the base-case model, M^J was fixed at 0.10 – equating to the 0.9 natural survivorship used in stock assessments of *J. lalandii* (S.J. Johnston, University of Cape Town pers. comm.). Sensitivity analyses were then conducted on M^J = 0.15

(50% increase) and M^J = 0.05 (50% decrease). The model was quite sensitive to changes in M^J (Table 5.07), with the initial rock lobster biomass B^J_{y0} increasing by approximately 50% when M^J was increased to 0.15 (Table 5.07, Model S13) and decreasing by about 50% when M^J was halved (Table 5.07 Model S14). The other estimated parameters changed slightly, but not as noticeably as the change in B^J_{y0} and the associated spawning biomass (Fig 5.02b). An increase in natural mortality would result in an increased rock-lobster productivity, which would explain the rapid increase in rock-lobster spawning biomass when M^J was increased to 0.15 (Fig 5.02b). The opposite took place if M^J was decreased to 0.05 (Fig 5.02b).

Estimating M^J resulted in a value of 0.087 (Table 5.07, Model S15), which equates to a natural survivorship of 0.92. This is not an unrealistic estimate of M^J given that rock lobsters are long-lived animals and in some cases *Jasus lalandii* natural survivorship has been estimated to be as high as 0.95 (S.J. Johnston, University of Cape Town, pers. comm.). However, the likelihood did not improve when estimating this parameter and the AIC value was less than that of the base-case model. Hence, the fixed M^J value of 0.10 used in the base-case model is considered the most appropriate choice. Parameter changes were less noticeable when M^J was estimated (Table 5.07, Model S15) and the rock-lobster spawning biomass followed a similar trend to that of the base-case model (Fig 5.02b). Overall these results suggest that the base-case assumed value of M^J is a reasonable one and that the model is not overly sensitive to the choice of lobster natural mortality, because it is the combination of M^J and spawning biomass that affects the dynamics. Model results are thus robust to uncertainty regarding the exact *M* for lobsters, and the base-case value of 0.1 is considered realistic.

Abalone natural mortality

In the abalone stock-assessment model developed by Plagányi (2004), natural mortality was assumed to be age dependent and was determined in a mortality-at-age relationship by estimating the mortality parameter μ, which was input into the base-case model as μ=0.126. As with the other abalone model parameters, μ was kept fixed at the previously estimated best-fit value for the abalone model. However when estimated (Table 5.08, S17), μ changed from 0.126 to 0.128, with very little effect on any of the other parameters and the likelihood showed an improvement of only 0.06. This test served to explore whether the single-species estimation of the relative contributions to total mortality from "natural" mortality and interspecific-related mortality effects may be in error because of the inclusion of the indirect effects of the lobster invasion. The results suggest that this is not the case, validating the use of the simplified representation in the stock assessment, and its incorporation into the more complicated multispecies model.

Urchin intrinsic growth rate

To describe intrinsic population growth rate using density data, a long time series of data is required and even then, it is necessary to assume that conditions remain relatively unchanged over this time period. This is rarely the case, as there are often year-to-year fluctuations in recruitment and survival (T. Ebert, Oregon State University, pers. comm.). Most of the literature reviewed describes individual urchin growth rates (e.g. Ebert 1968, 1975, 1982, 2007, Ebert and Russell 1993, Ebert *et al.* 1999, Ebert and Southon 2003, Greenwood 1980, Himmelman 1986, Turon *et al.* 1995, Minor and Scheibling 1997), as well as factors limiting individual growth (e.g. Ebert 1968, Ebert *et al*. 1999, Himmelman 1986, Guillou and Michel 1994, Minor and

Scheibling 1997), such as food availability, water temperature and wave exposure. Not only does individual growth rate vary among species, but also with age. Ebert and Southon (2003) believe the maximum age of many sea urchins to be underestimated, and that many urchins may be slower growing (particularly as they get older) than originally thought. An example is the Red sea urchin *Strongylocentrotus franciscanus*, which was originally thought to have a life span of 7-10 years, but is now believed to exceed 100 years (Ebert *et al*. 1999, Ebert and Southon 2003). Although the red urchin is much larger (TD >19 cm) than the endemic Cape urchin *Parechinus angulosus* (TD ~6 cm), very little is known about *P. angulosus* growth rate and survival/mortality - let alone the population growth rate. Only one study on *P. angulosus* has recorded individual growth rates and attempted to approximate mortality using cohort analyses (Greenwood 1981). Lafferty (2004) estimated a population growth rate of 0.3 for a disease-free population of the purple-urchin *Strongylocentrotus purpuratus* off the coast of California, but because of differences in species size and region, this growth-rate could not validly be applied to *P. angulosus*.

Insufficient data make it very difficult to estimate or place any confidence in the intrinsic growth rate parameter r_u. For these reasons, r_u was not estimated in the base-case model. Instead, a value of 0.5, which takes into account the likely rapid population growth rate of this relatively short-lived, fast-growing species (Greenwood 1981), was input into the model. Sensitivity analyses (Table 5.09) were carried out on a 50% decrease in r_u (Model S17), as well as on 50%, 100% and 200% increases in r_u (Models S18, S19 and S20 respectively). A slight improvement in the likelihood occurred when r_u was decreased but this was not significant. Increases in r_u also produced marginal changes in the likelihood and the interaction parameters adjusted accordingly to minor changes in the rock lobster starting biomass and carrying capacity. The likelihood showed the greatest improvement when r_u was estimated (Table 5.09, Model S21); however, when estimated, r_u hit the lower bound of 0.1 and even 0.001. Clearly there are insufficient data in the model to permit estimation of the urchin growth rate parameter. This is not an issue when simulating the rapid decline in urchin biomass observed in Zone D, but is a major constraint when trying to project future recovery if lobster predation diminishes.

Interaction parameters

Tables 5.10a-d show results from the sensitivity analyses performed on the interaction parameters. Each of the parameters was varied one at a time to keep the analysis tractable, but ideally different combinations of parameters should be explored. The abalone-lobster interaction parameter α_{Ab_J} from the base-case model was first decreased and then increased by 50%. The other parameters remained relatively constant, except for the abalone-lobster interaction parameter β_{Ab_J}, which increased with an increase in α_{Ab_J} (Table 5.10a, Model S23). However, both the likelihoods and AICs remained unchanged. This is not surprising, given the wide confidence intervals associated with these difficult-to-estimate parameters. Similar results emerged for the sensitivity analysis run on β_{Ab_J}, this time with α_{Ab_J} decreasing when β_{Ab_J} was halved (Table 5.10b, Model S24). Again, there were no changes in the likelihoods or AICs. The urchin-lobster interaction parameter α_{U_J} appeared to be more sensitive to changes than the abalone-lobster interaction parameters (Table 5.10c). When α_{U_J} was doubled, there was scarcely any change in rock lobster biomass, but when it was halved, the rock-lobster starting biomass B_{y0}^{J} increased by over 50% and α_{Ab_J} almost halved (Table 5.10c, Model S26). With this increase in B_{y0}^{J}, the rock-lobster spawning biomass increased rapidly, reaching a peak of just over 1800 MT in 1994 (Fig 5.02c). However, the likelihood did not change significantly (Table 5.10c). When α_{U_J} was increased by 50%, β_{U_J} doubled and the likelihood weakened, thus increasing the AIC (Table 5.10c, Model S27). The second urchin-lobster interaction parameter β_{U_J} appeared to be the most sensitive to changes, given that all the other parameters changed when β_{U_J} was either halved or increased by 50% (Table 5.10d, Models S28 and S29). Trends in the rock-lobster spawning biomass varied according to changes in the starting biomass that resulted from a change in β_{U_J} (Fig 5.02d). Although the AIC improved when β_{U_J} was increased, the likelihood did not show a significant improvement.

Additional rock lobster CPUE data

The sensitivity analysis that incorporated additional rock-lobster CPUE data (Table 5.11 Model S30), resulted in a minor increase and decrease in B_{y0}^{J} and K_{J}^{sp} respectively. Both the alpha interaction parameters decreased, while the beta interaction parameters remained virtually unchanged. These additional CPUE data were not incorporated into the base-case model because they were based on experimental catches, and thus were not considered reliably representative of the fishery. Despite this, the data followed the trend of a decreasing rock lobster biomass during the late 1990s/early 2000s, and thus are potentially informative and may improve the model fit.

Rock-lobster starting age-structures

Two different starting age-structures were used to mimic the two alternative hypotheses regarding the increase in rock-lobster abundance. The base-case model assumed the first hypothesis, i.e. that lobsters arrived by immigration of adults, and therefore a sensitivity test was carried out for the second hypothesis age-structure based on postulated arrival of lobsters by larval settlement (Model S31), as well as for an intermediate age-structure (Model S32).

The age-structure used in Model S31 produced a significantly worse likelihood (-135.9) compared to the base-case model (Table 5.12). An increase in both the starting biomass and in the spawner carrying-capacity was observed, as well as large changes in the interaction parameters as the model tried to fit to the data. Although the overall abalone likelihood for Zone D improved, the urchin and juvenile abalone survey likelihoods were significantly worse. The fishing-mortality (*F*) diagnostic showed that the recreational sector *F* (F^{J_rec}) hit the upper bound of 0.95 in 1995, and a 95% removal of the rock-lobster biomass available to recreational fishers is not considered realistic. This suggests an underestimation of the number of large lobsters. Additionally, the urchin population only crashed in 1999, indicating that S31 would not have yielded enough 'large' rock lobsters during the early 1990s.

Model S32, which represented an intermediate age-structure, showed an improvement in the likelihood (-154.5) and AIC (-296.9) compared with Model S31, but was still significantly worse than the base-case model (Table 5.12). Once again, the overall abalone fit improved, but the urchin and juvenile abalone survey showed a worse fit to the data. F^{J_rec} values were less than those in Model S31, but hit 0.7 in 1993, again suggesting that the recreational biomass was under-estimated. F^{J_comm} values were above 0.3 for period 2002-2007. The base model thus remains the preferred one and, by inference, this favours the hypothesis of adult immigration into the area EOCH.

5.5.2 Future projections

Urchin biomass

In the base-case model, the urchin population crashed in 1996/1997 and remained as such until the end of the model (2007). Future projections were initially run for 20 years following the end of the base-case model. Under Scenario 1 (Table 5.02), in which rock lobster predation was present and rock lobster catches remained at the 2007 level, future projections predicted that the urchin population would not recover (Fig 5.03a). Less anticipated was that even under Scenario 2, which excluded rock-lobster predation on urchins and abalone, the urchin population failed to recover within 20 years, i.e., by 2028 (Fig 5.03a). However, when future projections were run for 50 years, the urchin population showed signs of recovery by the mid-2030s and by 2058 reached carrying capacity (Fig 5.03a). Although the model predicted approximately 50 years for the urchin population to fully recover, several factors influence this outcome. (1) The prediction is based on an intrinsic population growth rate for urchins of 0.5 that takes into account the likely longevity of urchins. However, this input growth rate is uncertain, particularly as there is no information about the population growth rate during recovery; only a record of how quickly the urchin population declined. (2) The model prediction assumed a complete absence of rock lobster predation on urchins. (3) Additional factors influencing urchin population growth, such as disease, other predators, and larval dispersal from adjacent areas were not considered. Given that complete elimination of rock-lobster predation is unlikely, even if heavy depletion takes place, it is probable that urchin recovery will take longer than 50 years. However, if urchin growth rate is greater that 0.5, recovery would be more rapid. In a preliminary abalone-urchin-lobster model developed by Plagányi (2004), urchin recovery time was predicted to be less than 20 years based on an intrinsic growth rate of 0.77, but that model did not incorporate the level of detail about urchin data that was available for incorporation in my model.

Abalone biomass

The inshore abalone population crashed in 2006/2007. Future projections were modelled for 20 years following the end of the model under Scenarios 1 and 2 (Table 5.02). Although legal catches ceased by 2008 and future legal catches were set at zero, future illegal catches were assumed to continue, and were (probably conservatively) set as the mean take of the last two model years (2006 and 2007). In the presence of rock-lobster predation, there was no recovery in the abalone population (Fig 5.03b). Moreover, even in the absence of rock-lobster predation, the abalone population failed to recover after either 20 or 50 years (Fig 5.03b). Various explanations exist. Firstly, after the model end-year, illegal harvesting of abalone continued even though the adult stock was depleted. Secondly, with a severe depletion of parental stock, abalone recruitment would have been limited. Thirdly, the survival of juvenile abalone would have been dependant on a threshold-density of urchins of roughly 5000 MT, which was only reached after 2048 (Fig 5.03b). Thus, despite an 'absence of rock-lobster predation', recovery of the abalone population will be largely dependent on both an adequate adult stock and the attainment of an adequate urchin density (Mayfield and Branch 2000). Given the difficulties of parameterising the urchin population growth rate, it is thus equally problematic to accurately predict how fast the abalone population may increase. Nonetheless, the model highlights the likely long time-scale for any urchin recovery, and the even greater delays anticipated for any potential abalone recovery, which was not manifested even in the 50-year timescale.

Rock lobster biomass

Future projections for rock-lobster spawning biomass, as well as available rock-lobster commercial (≥75 mm CL) and recreational (≥80 mm CL) biomass, were made using various rock-lobster catch scenarios for the period 2008-2028 (numbered 3-6 in Table 5.02 as follows): (3) No legal catches – but illegal catch remains constant, (4) all catches remain at current (2007) levels, (5) legal catch increases to 10 times current level, and (6) no legal catches are made but illegal catch increases ten times. Projections for lobster spawning biomass from 2008 are shown in Fig 5.04a. A closure of both the commercial and recreational rock lobster fisheries (i.e. no legal catches, only illegal catches) will result in a projected increased in rock-lobster spawning biomass, later levelling off. If future catches are made at the 2007 level that will lead to an initial decrease in the rock lobster spawning biomass until 2014, after which biomass will level off. A similar trend would be observed if legal catches were to be increased by a factor of ten. The initial decline in biomass would be faster but the end point would reach a similar level. An increase in the illegal catch will have the strongest influence on spawning biomass, resulting in the most rapid and most substantial decline in the spawning biomass. This is understandable, given that the illegal rock lobster fishery was assumed to remove rock lobsters that are the same size/age as those entering into maturity.

Future projections for the rock lobster biomass available for capture by the commercial and recreational fisheries are shown in Figs 5.04b and 5.04c respectively. An absence of legal catches will result in an initial increase in both commercial and recreational available biomass, reaching a plateau at around 450 MT and 330 MT respectively. Both a current-level catch (Scenario 4) and an increased catch (Scenario 3) will result in a decrease in available commercial biomass (Fig 5.04b). A future increase in catch will be particularly harsh, levelling-off the commercial catch at around 75 MT. The effect of these scenarios on the recreational biomass will be far more extreme, with both the current catch and an increased catch resulting in a complete collapse of rock lobster biomass by 2013 (Fig 5.04c).

5.6 Summary

Progress in ecosystem models remains limited due to the amount of data that are required, inadequacies in knowledge regarding ecosystem interactions, and unreliable parameter estimation resulting from insufficient data. Although a good understanding of major benthic interactions within kelp-forest ecosystems EOCH exists, data for particular elements are still lacking and estimation of some parameters is difficult. The interaction parameters (α_{Ab_J}, β_{Ab_J}, α_{U_J}, β_{U_J}) and the urchin intrinsic growth rate (r_u) were particularly problematic, and sensitivity analyses revealed that these parameters, notably α_{U_J} and β_{U_J}, were especially sensitive to changes. Despite the abundance of the Cape urchin *Parechinus angulosus* along the South African temperate coastline, only one study has focused on its (individual) growth rate (Greenwood 1980) and none on population (intrinsic) growth rate. Additionally, no data were available reflecting the likely population increases over time, and therefore urchin intrinsic growth rate could not be estimated in the base-case model and was consequently input into the model. Sensitivity tests revealed a non-significant improvement in the overall likelihood when r_u was decreased. However, when estimated, r_u continuously hit the lower bound. Additional data on intrinsic population growth rate of urchins are vital for a confident estimation of this parameter.

The sensitivity analyses revealed that natural mortality values for both abalone and rock lobsters, which were input into the base-case model, were reasonable. The estimation of urchin carrying capacity, calculated using a mean maximum observed urchin density, also proved robust. The estimated rock lobster starting biomass from the base-case model appeared best, given that a lower value would result in an insufficient biomass to sustain known recreational harvest rates, and a higher value would cause premature urchin depletion.

Sensitivity analyses revealed that an increased rock-lobster larval settlement could not explain the observed increased abundance of adult rock lobsters during the early 1990s. It appeared more likely that the increased abundance was due to an abrupt arrival of large rock lobsters – i.e. immigration of adults. However, it remains unknown whether this was caused by an inshore migration or a south-east migration, although the latter seems unlikely given the evidence of Atkinson and Branch (2001) that long-shore movements of adult males is limited, and the former is supported by similarities in size composition and sex ratios between offshore and inshore lobster stocks (Cockcroft *et al*. 2008).

Robustness of the model permitted future scenarios to be examined, and future projections showed that continued rock lobster harvesting would likely remove all recreational-sized lobsters and restrict commercial-sized lobsters to less than 100 MT – which equates to a density of 0.05 adult rock lobsters.m^{-2}. If the urchin population was at carrying capacity, this lobster density would not lead to urchin depletion according to calculations by Mayfield and Branch (2000). However, given a virtual absence of urchins, it is probable that this density will be sufficient to prevent urchins from becoming re-established in Zone D. A complete removal of large rock lobsters would be required if urchins are to re-appear. Even if this attainable, given an urchin intrinsic growth rate of 0.5, urchin recovery could take up to 50 years. The recovery of abalone is likely to take even longer as a result of their dependence on urchins, and their recovery would require the elimination of illegal fishing in addition to urchin recovery.

Chapter 6

Modelling a hypothetical invasion of rock lobsters

6.1 Introduction

The collapse of marine ecosystems is largely attributed to the severe overfishing that occurred during the 20th century (Roberts 1995, Turner *et al*. 1999, Steneck *et al*. 2004, Frank *et al*. 2005, Osterblom *et al*. 2007), combined with more recent stressors such as anthropogenic climate change, water pollution, habitat degradation and invasive species (Jackson *et al*. 2001). For ecosystem and fisheries management to succeed, it is vital to understand how these stressors affect associated ecosystems and how to promote their recovery (Scheffer *et al*. 2005). In a particularly gloomy prognosis, Frank *et al*. (2005) question the reversibility of ecosystem shifts, highlighting collapsed systems that continue to show no signs of recovery.

Like many other marine systems, the South African south-west coast has experienced intense harvesting of top-predators and benthic invertebrates (Attwood and Farquhar 1999, Hauck and Sweijd 1999, Griffiths 2000, Hauck 2009). In addition, significant increases and decreases in sea surface temperature (SST) have occurred since the 1980s in the offshore and inshore waters respectively (Roy *et al*. 2007, Rouault 2009), and a number of species have shifted eastwards, including kelps (G.M. Branch, unpublished data), rock lobsters (Cockcroft *et al*. 2008), pelagic fish (van der Lingen *et al.* 2001, 2002, Fairweather *et al.* 2006b) and seabirds (Underhill *et al*. 2006, Crawford *et al.* 2007, 2008a, 2008b, 2008d, Pichegru *et al*. 2007).

The south-west coast experienced a dramatic 'lobster invasion' during the early 1990s (Tarr *et al*. 1996, Mayfield and Branch 2000) and based on lobster densities, the area East of Cape Hangklip (EOCH) is divided into two regions that have been respectively labelled 'invaded' and 'non-invaded'. The lobster-invaded region stretches roughly from Cape Hangklip to Hermanus and includes abalone fishing Zones C and D and rock-lobster fishing Areas 12 and 13 (Fig 6.01). The non-invaded region incorporates abalone Zones A and B, and rock lobster Area 14. Zone B is essentially the entire Danger Point Peninsula and Area 14 is the western side of the peninsula.

As outlined in Chapter 2, before the lobster invasion, all Zones (A-D) were characterized by encrusting coralline-covered reefs populated with high densities of herbivores – particularly the urchin *Parechinus angulosus*, the abalone *Haliotis midae* and large winkles. Foliar algae were sporadic and rock lobsters rare if not absent. Illegal fishing of abalone during the 1990s and 2000s has substantially dented the abalone population EOCH, particularly in Zones C and D where increased rock lobsters have indirectly exacerbated this effect (Plagányi and Butterworth in press). After the lobster invasion, Zones C and D were transformed into macroalgal-dominated systems (see Chapter 3), while Zones A and B, where rock lobsters remain rare, are relatively unchanged and the abalone population is substantially better off than in the invaded areas. However, should a further eastward invasion of rock lobsters occur, the consequences for the urchin and abalone populations could be severe.

To mimic the current situation EOCH, the base-case model developed in Chapter 4 incorporated rock lobsters into Zone D (invaded), but not into Zone B (non-invaded). This chapter focuses on Zone B and simulates the consequences of a hypothetical rock-lobster invasion into this zone to answer the following questions.

1. Following an introduction of rock lobsters (at different densities and different starting age-structures), what would be the population trajectory of urchins, and in the event of their collapse, how long would it take?

2. What rock-lobster biomass could Zone B support without collapse of the urchin population?
3. What would be the effects of a lobster invasion on juvenile (0-1 year old) abalone?

6.2 Model Description and Data

The base-case model for Zone D that was developed in Chapter 4 formed the basis for the Zone B model. Using field data collected from non-invaded areas (Chapter 3), as well as outputs from the base-case model, three scenarios were simulated in which rock-lobster biomasses were ‘introduced’ into Zone B. These were termed ‘small’, ‘medium’ and ‘large’ invasions and respectively comprised starting rock-lobster biomasses of 50 MT (~0.03 lobsters.m^{-2}), 100 MT (~0.06 lobsters.m^{-2}) and 500 MT (~0.29 lobsters.m^{-2}). All three invasions were exercised using two different starting age-structures from 2008 (when I began forecasting trajectories): (A) an even distribution of ages across the population (5% in each age class 0 to 18 years, plus 2.5% in ages 19 and 20), approximating the age-structure observed in the non-invaded area (L.K. Blamey, pers. obs.); (B) a young rock-lobster population (10% in each of the ages 0-8 and 2.5% in ages 9 and 10), which yielded an age-structure closely approximating that recorded in Zone D when the invasion was first detected, inferring that the invasion was by way of an adult movement into the area rather than by settlement of larvae.

Rock lobster and urchin starting values used to model the Zone B component of the ecosystem are given in Table 6.01, and Chapter 4 contains the details of the model and other lobster, urchin and abalone data that are employed here.

6.3 Model Assumptions

Model year

1. Rock lobsters were added to Zone B in 2008
2. Consistent with the abalone model and the rock-lobster model for Zone D, the model year ran from October year $y-1$ through to September of year y.
3. The rock lobster model year comprised 4 seasons of equal length.

Lobster Demographics

4. Rock-lobster sex ratio was assumed to be 50:50
5. Males and females are of similar size up to the age of about 10 years. Only after that (when lobsters reach the 68-mm CL size at which they are able to consume urchins), do males begin to grow faster and get larger than females (Johnston and Butterworth 2001). A mean length- and weight-at-age was thus assumed for both sexes (Appendix 2 Table A2.05).
6. Age-length matrices used were based on the average length-at-age for the years 1980-2008.
7. 50% maturity is reached at 10yrs and 100% maturity at 11yrs (derived from Johnston and Butterworth 2001).

Lobster recruitment

8. Recruitment was assumed to be local only, contributing directly into the Zone B population despite acknowledging that rock-lobster larvae are capable of dispersing over large distances (Pollock and Melville-Smith 1993).

Lobster Harvesting

9. No rock lobsters are harvested from Zone B

Lobsters-urchin-abalone interactions

10. Only lobsters ≥ 12 years eat urchins, and lobsters of this age are capable of feeding on all sizes of urchins (Mayfield and Branch 2000, Mayfield *et al.* 2001).
11. Lobsters ≥ 11years show 50 % selectivity for abalone at age 0, 100% selectivity for abalone that have reached age 1 (derived from Van Zyl *et al*. 2003) and 0% selectivity for abalone > age 1.
12. The pristine urchin density estimate was the maximum urchin density recorded in the area EOCH.
13. Juvenile abalone survival is a function of urchin density and below a certain urchin threshold (30 urchins.m^{-2} Mayfield and Branch 2000), abalone survival decreases with urchin density.
14. Juvenile abalone survival rate has a lower bound of 1% per annum.
15. The estimated interaction parameters from Zone D (see Table 4.07, Chapter 4) are applicable to Zone B.

6.4 Results

In the model, rock lobsters were 'introduced' into Zone B in 2008 using three levels of 'invasion' biomass: small (50 MT), medium (100 MT) and large (500 MT) and under two different starting age-structures specified above. Rock lobster biomass trajectories for the 50-year period 2008-2058 are shown in Fig 6.02a-b. An even distribution of ages across the starting population (starting age-structure A) yielded an initial decline in rock lobster biomass for about 10 years, followed by an increase, with the final biomass reaching ~1000 MT (Fig 6.02a). The initial decline was most likely due to dynamic changes in the age structure, which in turn would have affected the biomass estimates. Starting age-structure B, which mimicked an invasion of large rock lobsters (as was recorded in Zone D), resulted in a slow increase in rock-lobster biomass for small and medium invasions of 50 and 100 MT respectively (Fig 6.02b). The large invasion (500 MT) resulted in a rapid increase in biomass during the first 10 years, followed by a decline, levelling out at about 1000 MT (Fig 6.02b), which equates to roughly 0.55 lobsters.m^{-2} (~50% carrying capacity). This rapid increase and subsequent decline of biomass occurred because the sexually mature lobsters would have contributed to recruitment almost immediately, resulting in a population increase, followed by a decline driven by density-dependent effects.

Urchin biomass in Zone B was assumed to have been at carrying capacity from 1985-2007 before rock lobsters were added to the model from 2008. Using starting age-structure A, rock-lobster biomasses of 50 MT and 100 MT resulted in oscillating minor declines in urchin biomass between 2008 and 2028, accelerating to a disappearance of urchins by the 2050s (Fig 6.02c). A lobster starting biomass of 500 MT caused a more obvious initial oscillation and a faster disappearance of urchins by 2040 (Fig 6.02c). Employing a lobster starting age-structure that mimicked the Zone D invasion (age-structure B) resulted in a significantly quicker disappearance of urchins, with the speed of disappearance again correlated with the starting biomass of lobsters (Fig 6.02d).

With respect to juvenile abalone, the model forecasted that in the absence of rock lobsters, juvenile abalone in Zone B would decline by about 30% over 50 years (Fig 6.02e,f) as a consequence of illegal fishing diminishing reproductive output and the abrupt nature of the decline can be attributed to the fact that there is a threshold of urchin density, below which juvenile abalone collapse (Fig 4.06b). The decline of juvenile abalone would be more rapid and more severe with the introduction of lobsters, particularly with starting age-structure B. A small-to-medium rock-lobster invasion would eliminate juvenile abalone within 30-50 years. A large invasion would result in a depletion of juvenile abalone in approximately 15-30 years.

6.5 Discussion

Research along the Tasmanian east coast has shown that in no-take MPAs, where the rock lobster *Jasus edwardsii* has increased as a consequence of protection, predation has reduced populations of the urchins *Heliocidaris erythrogramma* and *Centrostephanus rogersii* and the abalone *Haliotis rubra*, with serious ramifications for the ecosystem (Barrett *et al.* 2009a). This is similar to the situation EOCH although the mechanism of the interaction with juvenile abalone is different: juveniles of *H. midae* are indirectly affected by the rock lobsters preying on, and ultimately eliminating, urchins that provide protection and nourishment for juvenile abalone (Day and Branch 2002a). This indirect relationship, combined with the illegal fishing of abalone, has had dramatic consequences for both the abalone fishery and the ecosystem as a whole, as documented for Zones C and D in Chapters 2 and 3.

An invasion of rock lobsters into Zone B is predicted to have critical effects on the urchin population and subsequently the abalone population (Fig 6.02). Answering questions (1) and (2) posed in the Introduction, the model indicated that following a rock-lobster invasion, urchins would disappear within 8-50 years depending on the size of the invasion, and even the smallest rock-lobster biomass examined (50 MT) resulted in the eventual disappearance of urchins. Answering question (3), an influx of lobsters would in all cases tested lead to the elimination of juvenile abalone. In the absence of a lobster invasion, juvenile abalone would continue to decline because of the depletion of the brood-stock by poaching, but would not disappear within the 50-year modelling period. For both urchins and juvenile abalone, the outcome of introducing lobsters would be intensified if the invasion were to involve a greater biomass of rock lobsters. Although not modelled, lobsters would also likely deplete other herbivores. Disappearance or substantial reductions of herbivores in the currently non-invaded Zone B would likely result in an ecosystem state similar to that of the currently invaded Zones C and D. These conclusions depend to some extent on the model-fitted lobster-urchin-abalone interaction formulations, but even if these are not precise, the conclusions drawn are likely to be robust, particularly in terms of the effect of a lobster invasion in Zone B, which was more reliably modelled than the recovery scenario, as it is based on historical observations.

If the community composition in Zones A and B were to be transformed into one like that existing in Zones C and D, the recovery of abalone populations in this region, which forms the heart of the abalone industry, would be almost impossible because: (1) The lobster-urchin-abalone effect is most obvious in the shallows (0-5m) where any reduction in lobsters will be retarded by the fact that commercial rock-lobster fishing operates in waters deeper than 5m. (2) If rock lobsters remain at a density above 0.25m^{-2} (Mayfield and Branch 2000), urchins on which juvenile abalone depend will be unable to maintain a population (Day and Branch 2000a, 2000b, 2002a). (3) In the absence of herbivores, macroalgae will increase and siltation rates will rise, as has been observed in Zones C and D (Day and Branch 2002a; Chapter 3 and L.K. Blamey pers. obs.). (4) Increased siltation and macroalgal growth are likely to smother and outcompete encrusting corallines, upon which abalone recruitment depends (Day and Branch 2000a). (5) Intense illegal fishing of abalone combined with the invasion of lobsters will deplete the abalone stock to levels at which recruitment failure is likely to occur. (6) Should rock lobsters decline, model simulations for Zone D predicted that even under a best-case recovery scenario (i.e. lobsters immediately eliminated, zero future catches of abalone, and no impediments such as changed substratum), urchin recovery could take up to 50 years and abalone recovery even longer (see Chapter 5). Recovery of both urchins and abalone would be even slower than predicted by the model if these species are subject to an Allee effect, whereby fertilization collapses below a threshold adult density (Allee *et al*. 1949, Stephens *et al*. 1999). Shepherd and Partington (1995) and Babcock and Keesing (1999) have estimated that for *Haliotis laevigata* an Allee effect will come into operation at densities of $0.15\text{-}0.3\text{m}^{-2}$. Butterworth (2009) has suggested that the critical value is probably lower than this. My model results estimate near-zero remaining densities of abalone in the Zone D inshore region (see FIAS depletion estimate in Appendix 5 Table A5.01), highlighting that the Zone D stock may already be below the threshold for an Allee effect.

6.5 Summary

The invasion of rock lobsters EOCH into Zones C and D, combined with the illegal harvesting of abalone, has had substantial impacts on both the ecosystem and fisheries. Herbivores have virtually disappeared and abalone recruitment failure is in effect. Just east of the invaded area, in Zones A and B, rock lobsters are either rare or absent. Urchins and other herbivores are abundant and the abalone population is slightly better off (although repercussions of illegal fishing are evident). A continued eastward invasion of rock lobsters into these Zones would without doubt transform the ecosystem and eliminate any last prospects for the recovery of the commercial abalone fishery in the region. Recovery would require suitable habitat and the existence of adult stocks sufficient to supply recruitment to areas where stocks have been depleted to the point of recruitment collapse. At present, the stocks in Zones A and B probably constitute the most important adult stocks capable of supplying recruitment.

Chapter 7

Impacts of depleting top predators on the predatory effects of rock lobsters on benthic communities

7.1 Introduction

The cascading effects of overfishing top-predators have been demonstrated for a variety of marine ecosystems (Strong 1992, Sala *et al*. 1998, Pace *et al*. 1999, Tegner and Dayton 2000, Jackson *et al*. 2001, Shears and Babcock 2003, Worm and Myers 2003, Bellwood *et al*. 2004, Frank *et al*. 2005, Scheffer *et al*. 2005, Myers *et al*. 2007, Osterblom *et al*. 2007, Baum and Worm 2009, Eriksson *et al*. 2009, Ling *et al*. 2009b). This often results in a system that is more vulnerable to disruptions in structure and function, ecological extinctions and to other natural and human disturbances (e.g. disease, nutrient loading, habitat loss, climate change etc) (Turner *et al*. 1999, Jackson *et al*. 2001, Ling *et al*. 2009b).

Along the south-eastern section of the South African coast, a regime-shift has taken place in the kelp-forest ecosystem East of Cape Hangklip (EOCH) following an invasion of the West Coast rock lobster *Jasus lalandii* in the early 1990s (Tarr *et al*. 1996, Mayfield and Branch 2000). What was formerly dominated by herbivores and encrusting corallines has been transformed into a lobster- and algal-dominated system (Chapter 3), with substantial repercussions for local fisheries, particularly for the abalone *Haliotis midae*.

Predators of *J. lalandii* include predatory reef fish, small sharks, the Cape Fur Seal *Arctocephalus pusillus*, the Bank Cormorant *Phalacrocorax neglectus* and the Cape Clawless Otter *Aonyx capensis*. At pristine densities, seals and reef-dwelling fish were probably the most important predators of rock lobsters. However, uncontrolled exploitation of seals during the 18th, 19th and part of the 20th centuries caused a marked decline in seal populations (Shaughnessy 1984). Reef fish have also been over-exploited (Attwood and Farquhar 1999). Using three CPUE snapshots from the 20th century (1897-1906, late 1920s to early 1930s and 1985 to 2007), Griffiths

(2000) revealed drastic declines in CPUE for commercial linefishing during the 20th century, the larger part of which would have occurred well before the 1980s. Most other predators have not suffered the same exploitation levels. Small sharks (e.g. the Spotted Gully Shark *Triakis megalopterus*) have not been targeted by fisheries or experienced declines of any consequence (C. Attwood, University of Cape Town, pers. comm.). Bank Cormorants historically occurred predominantly on the west coast where the majority of their diet consists of rock lobsters (Hockey *et al*. 2005). Only recently have colonies increased along the south-west coast, presumably as a result of the shift in the centre of abundance of rock lobsters (Crawford 2008d). This shift in rock lobsters also resulted in a change of diet of the Cape Clawless Otter EOCH (Kemp 2000). Prior to 1990, otters there fed primarily on fish but by 2000 rock lobsters comprised almost 70% of their diet (Kemp 2000). However, because otters are not abundant, they are unlikely to have a detectable effect on the rock lobster population EOCH. By contrast, predatory reef fish and seals at ‘pristine’ densities would very likely have had substantial effects on rock lobsters. Depletions of these predators must have substantially reduced predation pressure on rock lobsters.

The aim of this chapter is to explore the effects of ‘adding’ lobster predators into the model in Zone D (a currently lobster-invaded zone), with a focus on the role of reef-dwelling fish as predators. A generic ‘redfish’ predator was created based on dominant fish species occurring EOCH that prey on rock lobsters. Using two scenarios, (a) a fish population based on current fish densities and biomasses and (b) a fish population based on historical fish densities and biomasses, the following questions were explored: (1) Is it possible that declines in linefish played a role in the increase in rock-lobster abundance EOCH associated with the rock-lobster invasion? (2) If fish populations had remained at densities considered pristine (equivalent to those in the late 1890s and early 1900s), could they have prevented the rock-lobster invasion in the early 1990s? (3) Would urchin and abalone populations consequently have remained at high densities rather than collapsing as they did in the mid-1990s?

7.2 Fish Species

Predatory fish found on South African temperate reefs that are known to feed on *Jasus lalandii* include Roman *Chrysoblephus laticeps* (Nepgen 1982, Buxton 1984, Buxton 1993), Red Stumpnose *Chrysoblephus gibbiceps* (Nepgen 1982), Dageraad *Chrysoblephus cristiceps* (Buxton 1987, 1993), Hottentot *Pachymetopon blochii* (Nepgen 1977, Pulfrich and Griffiths 1988) and, to a lesser extent, Galjoen *Coracinus capensis* (Bennett and Griffiths 1986, C.G. Attwood, University of Cape Town, pers. comm.). For purposes of this study, Roman, Red Stumpnose, and Dageraad were considered most important and provided the foundation for a generic 'redfish' that would prey on rock lobsters.

7.3 Model Description

Fish were added to the multispecies model described in Chapter 4 using two scenarios: (1) current fish biomass and (2) historical fish biomass.

Scenario 1: Current model

Fish were incorporated into the multispecies model for the years 1980-2007 and were modelled using a surplus production model. Catch and effort data were available only for the years 1985-2007 and so a mean catch rate for the period 1985-1989 was assumed for 1980-1984. An initial fish biomass of 48 tonnes (MT) (starting in 1980) was calculated using density estimates (Table 7.01), and the annual consumption of rock lobsters by fish was calculated using Roman and Red Stumpnose dietary data and a consumption/biomass ratio of 4.86 for redfish (Table 7.01).

Scenario 2: Historical model

Using the same time frame (1980-2007), but for historical fish data, I assumed an initial fish biomass of 724 MT (again starting in 1980) equivalent to what might have been the pristine level a century or so ago. This was achieved by setting the starting biomass equal to fish carrying capacity, which was estimated in the current model. Using this starting biomass as well as an annual mean catch rate, calculated using catch and effort data for the years 1897-1905 (Gilchrist 1898, 1899, 1900, 1901, 1902, 1903, 1904, 1906, 1907), the historical fish population was modelled and its annual consumption of rock lobsters calculated.

7.4 Data

7.4.1 Commercial linefish data

Since 1985, owners of commercial lineboats have been required to submit their daily catch and effort to Marine and Coastal Management (MCM). These data were available for the period 1985-2007 from the National Marine Linefish System (NMLS). For this study I extracted catch and effort data for Roman, Red Stumpnose, Dageraad and 'other red fish'[*] (henceforth all referred to as redfish) for the area between Cape Point and Dyer Island (near Danger Point). However, only catch data for the invaded area EOCH were incorporated into the model.

Data used in the model-fitting process included non-standardized commercial CPUE (kg.boat^{-1}.year^{-1}) (Fig 7.02), which was calculated using the NMLS catch and

---

[*] 'other red fish' include all other red reef-fish similar to and possibly including Roman, Red Stumpnose and Dageraad.

effort data. To standardize, the annual effort was taken to be only those boats that caught redfish during a given year and not all boats catching linefish (C.G. Attwood, University of Cape Town, pers. comm.).

Reliance on the available catch and effort data spanning 1985-2007 ignores the fact that major declines in these linefish species occurred prior to the 1980s (Griffiths 2000), but restricting the fish trajectories to the available data does have the advantage of grounding the model on empirical data and keeping simulations as realistic as possible.

7.4.2 Historical linefish data

Catch and effort data for the early commercial line fishery, as well as mean weights of the species caught, were documented at the turn of the 19th century in a series of governmental reports by the then Government Marine Biologist of the Cape Colony (Gilchrist 1898, 1899, 1900, 1901, 1902, 1903, 1904, 1906, 1907). While an obvious decline in CPUE between the early 1900s and the more recent 1980s-2000s has taken place (Griffiths 2000), early data were considered insufficiently comparable to incorporate both sets of data together in the model, due to technological creep that occurred during the 20th century, which would have inflated the more recent CPUE values (C.G. Attwood, University of Cape Town, pers. comm.). Consequently, the current and historical data were employed in separate runs of the model. A mean weight of 1.36 kg for redfish for the years 1887-1905 was used for the historical component of the fish model (Table 7.01).

7.4.3 Redfish density estimates

The only available density estimates for redfish were for Roman, the most abundant of the redfish, which were counted by SCUBA divers in an underwater visual census carried out inside and adjacent to two MPAs: the Castle Rock MPA situated in False Bay (Kerwath *et al*. 2008) and the Goukamma MPA (Götz 2005) situated along the south coast (Fig 7.01). Roman density data do not exist for the EOCH area and the densities adjacent to the Castle Rock MPA were considered to be most similar to those in the Zone D area (C.G. Attwood, University of Cape Town, pers. comm.).

7.4.4 Dietary data

Two dietary analyses exist for Roman (Nepgen 1982, Buxton 1984) and one for Red Stumpnose (Nepgen 1982). For my study, I employed only the data from Nepgen (1982) because his study was carried out in False Bay, immediately adjacent to my study area, whereas the study by Buxton (1984) was done in Algoa Bay (Port Elizabeth), and may therefore be less representative of redfish diets in my study area. Of the Roman and Red Stumpnose stomachs sampled by Nepgen (1982), a respective 5% and 4% contained rock-lobster remains. In my model I have assumed that 5% of the redfish diet comprises rock lobsters. This assumption is probably representative of both higher lobster densities such as those recorded EOCH after the invasion (which would likely have been associated with proportionally greater consumption rates) and the lower densities that would have ensued following depletion by fish (reducing proportional consumption).

Roman and Red Stumpnose stomachs contained proportions of the urchin *Parechinus angulosus* similar to the proportions of rock lobster in their diets (Nepgen 1982). Therefore I have assumed that 5% of redfish diet would also contain urchins.

Using the total annual biomass of prey consumed by the fish population and the percentage of urchins making up this total biomass, I calculated that at pristine densities, fish could consume 176 MT of urchins each year. This equates to roughly 1.1% of the urchin population at carrying capacity and is therefore unlikely to have any effect on the population. For this reason I did not include a fish-urchin interaction in the model.

7.5 Model Assumptions

Base-case model

1. The base-case model developed in Chapter 4 was used as a foundation for the addition of fish.
2. All lobster, urchin and abalone parameters were fixed at their base-case estimated levels.
3. The rock-lobster natural mortality M^J was adjusted from the value of 0.1 used in the base-case model to 0.085, to compensate for the additional mortality due to fish, which is modelled explicitly in these model scenarios.

Model year

4. The fish model was started in 1980 and the starting biomass calculated using data from a fished area in False Bay (Table 7.01).
5. The lobster model year was divided into 4 seasons, with the fisheries catch being taken during the second season – i.e. in the second quarter, and the numbers left after the 4th quarter of year $y-1$ are the numbers that contribute to season 1 of the next model year y. Lobsters ‘caught’ by fish were removed quarterly.

Fish catch and effort

6. Catch and effort data used in the current model comprised all recorded species of redfish caught by the commercial line fishery along the south-west coast.
7. Commercial catches for the Zone D area were taken to be 50% of those recorded for the south-west coast from Cape Point to Dyer Island because of their respective areas.
8. Recreational catch and effort data were not included because redfish are not usually their target species (C. Attwood, University of Cape Town, pers. comm.).
9. There were no data for the period 1980-1984 and so a mean catch for the years 1985-1989 (14 MT per annum) was used.
10. In the historical model, a conservative mean catch of 20 MT was used for the years 1897-1905 (Gilchrist 1898, 1899, 1900, 1901, 1902, 1903, 1904, 1906, 1907).

Fish data

11. Data for the fish population are largely based on data for Roman *Chrysoblephus laticeps*, but generalized to ‘redfish’.
12. Roman protogyny was not taken into account.
13. The fish intrinsic growth rate r_P was fixed at 0.3 in both current and historical models.
14. The pristine (historical) fish starting-biomass was equal to the carrying capacity estimated in the current fish model.

15. The mean weight of an individual fish decreased from 1.36 to 0.775 kg over the last 100 years (Table 7.01).

Fish predation

16. Fish predation on lobsters was modelled assuming a constant daily ration model.
17. Rock lobsters comprised 5% of fish diet.
18. All redfish were able to consume lobsters
19. The Q/B (consumption/biomass) ratio of 4.86 (Table 7.01) was fixed across the century.

Fish selectivities

20. Conservatively, fish were assumed to consume lobsters that are between 25 mm CL (~ 6yrs) and 65 mm CL (~ 11 years).

7.6 Equations

7.6.1 Fish population dynamics

The fish population was modelled using a surplus production (Schaefer) model, which assumed that lobster density had no effect on the fish population because they make up a small constituent of the fish diet:

$$P_{y+1} = P_y + r_P P_y (1 - P_y / K_P) - C_y^P \qquad (7.1)$$

where

P_y is the biomass of fish in year y

r_P is the fish population intrinsic growth rate parameter

K_P is the fish carrying capacity, and

C_y^P is the total catch of fish (MT) in year y

Initial starting population

The fish population EOCH was assumed to be heavily fished in 1980 and therefore the initial starting biomass was calculated using a mean redfish (Roman) density taken from a fished area in False Bay (outside the Castle Rock MPA) (Kerwath *et al*. 2008). An estimate of this starting population using data in Table 7.01 was calculated as follows:

$$P_{1980} = (P_{density} * Area^D * W_P) \tag{7.2}$$

where

P_{1980} is the initial starting population biomass (MT)

$P_{density}$ is the mean number of Roman per m^2 recorded in a fished area (Kerwath *et al.* 2008)

$Area^D$ is the area covered by kelp forest in Zone D (Tarr 1993)

W_P is the mean weight of Roman from a fished area (Götz 2005).

Scaling up density estimates will likely over-estimate fish biomass for a given area because habitat will not be suitable throughout the area; to counteract this, I assumed that the starting-biomass I calculated was for all redfish and not just for Roman, despite using Roman densities.

Annual food consumption

The annual food consumption of fish was calculated using the consumption/biomass ratio (*Q/B*) for Roman (Palomares and Pauly 1998):

$$\log Q/B = 7.964 - 0.204\log W_\infty - 1.965T' + 0.083A + 0.532H + 0.398D \qquad (7.3)$$

where

W_∞ = asymptotic weight (g) derived from the von Bertalanffy Growth Formula

T' is the mean annual temperature of a water body expressed as 1000/Kelvin (Kelvin = °C + 273.15)

$A = h^2/s$, where *A* is the aspect ratio, *h* is the height and *s* is the surface area of the caudal fin.

H = 1 if the fish is a herbivore, otherwise H = 0 (as in this case)

D = 1 if the fish is a detritivore, otherwise D = 0 (as in this case)

The various data (and sources) required for equation 7.3 are given in Table 7.02.

Biomass of prey eaten each year

The redfish population was considered as an additional 'fishing fleet' that targeted rock lobsters. Chapter 4 outlines other details of the rock-lobster population model.

The total biomass of prey consumed by the fish population in year y (P_y^{prey}) was calculated by assuming a constant daily ration model:

$$P_y^{prey} = P_y * Q/B \tag{7.4}$$

where

P_y is the annual fish biomass

Q/B is the consumption to biomass ratio for Roman.

It then follows that:

$$P_y^J = \frac{\xi}{100} * P_y^{prey}$$

where

P_y^J is the biomass of lobsters consumed by fish

ξ is the percentage of lobsters making up the fish diet

The exploitable or 'available' component of rock lobster abundance that can be 'caught' by fish is expressed in terms of exploitable biomass:

$$B_y^{\exp\_J,P} = \sum_{a=1}^{z} w_a^J S_a^{J-P} J_{y,a} \tag{7.5}$$

where

$B_y^{\exp\_J,P}$ is the exploitable biomass available for consumption by fish

w_a^J is the weight of a rock lobster at age a in years

S_a^{J-P} is the fish's selectivity-at-age for lobsters

$J_{y,a}$ is the number of rock lobsters at age a in year y

z is the oldest lobster considered i.e. the plus group (containing all lobsters aged z and older).

The minimum and maximum age of rock lobsters consumed by fish is assumed to be 5 and 11 years respectively (G.M. Branch, University of Cape Town, pers. comm.) and so $S_a^{J\_P} = 0$ for $a < 5$ and $a > 11$.

The proportion of rock lobsters consumed annually ($F_y^{J\_P}$) by fish is given by:

$$F_y^{J\_P} = P_y^J / B_y^{\exp\_J,P} \tag{7.6}$$

It then follows that rock lobsters 'caught' at age *a* by fish ($P_{y,a}^{J\_prey}$) is:

$$P_{y,a}^{J\_prey} = S_a^P F_y^P J_{y,a} e^{\frac{-M^J}{4}} \tag{7.7}$$

The rock lobster population was modelled in quarterly time steps (see Chapter 4) and therefore lobsters that were consumed by fish were subtracted quarterly from the lobster population:

$$J_{y+1,a+1}^1 = (J_{y,a}^4 - \frac{P_{y+1,a}^{J\_prey}}{4})e^{-M^J/4} \tag{7.8}$$

$$J_{y+1,a+1}^2 = (J_{y+1,a+1}^1 - C_{y+1,a}^J - \frac{P_{y+1,a}^{J\_prey}}{4})e^{-M^J/4} \tag{7.9}$$

$$J_{y+1,a+1}^3 = (J_{y+1,a+1}^2 - \frac{P_{y+1,a}^{J\_prey}}{4})e^{-M^J/4} \tag{7.10}$$

$$J_{y+1,a+1}^4 = (J_{y+1,a+1}^3 - \frac{P_{y+1,a}^{J\_prey}}{4})e^{-M^J/4} \tag{7.11}$$

where

$J_{y,a}^{q}$ is the number of rock lobsters in age class a during quarter q of year y

M^{J} is the rock lobster annual natural mortality

$C_{y,a}^{J}$ is the total fishery catch of rock lobsters from age class a during year y, which is taken only in season 2.

7.6.2 Likelihood Function

The model was fitted to all available data to estimate the model parameters. This was achieved by employing the estimates generating the smallest negative of the log likelihood function. Various data contribute to the overall likelihood, and are described in Chapter 4, along with the relevant likelihood functions. New data added as part of the fish model include redfish CPUE data for the period 1985-2007. Equations used to fit these data to the model are given below and were developed based on those in Plagányi (2004).

Abundance data

$$\varepsilon_{y}^{s} = \ln\left(I_{y}^{s}\right) - \ln\left(\hat{I}_{y}^{s}\right) \tag{7.12}$$

where I_{y}^{s} is the abundance index for year y and sector of data s and

$\hat{I}_{y}^{s} = q^{s} P_{y}$ which is the corresponding model estimated value, where P_{y} is the model value for fish biomass (given by equation 7.1).

The abundance data contribute to the negative of the log likelihood as follows:

$$-\ln L = \sum_{s} \left[\sum_{y} \ln \sigma_y^s + \left(\varepsilon_y^s\right)^2 / 2\left(\sigma_y^s\right)^2 \right] \qquad (7.13)$$

Variance unspecified (CPUE abundance data)

The standard deviation $\hat{\sigma}^s$ of the residuals for the logarithm of abundance series s was estimated in the fitting procedure by its maximum likelihood value:

$$\hat{\sigma}^s = \sqrt{\frac{1}{n_s} \sum_{y} \left(\ln I_y^s - \ln \hat{I}_y^s\right)^2} \qquad (7.14)$$

where n_s is the number of data points for the abundance series corresponding to sector s.

The catchability co-efficient $\hat{q}^s$ for the abundance index of sector s was estimated by its maximum likelihood value:

$$\ln \hat{q}^s = \frac{1}{n_s} \sum_{y} \left(\ln I_y^s - \ln P_y\right) \qquad (7.15)$$

7.7 Parameters

In the current fish component of the multispecies model, the starting biomass P_{1980} was calculated, the fish intrinsic growth rate r_P was fixed at 0.3 (which is expected for fish of this type) and the carrying capacity K_P was estimated. For the historical fish model, all parameters were fixed and the starting biomass was assumed equal to K_P. Sensitivity analyses were performed on the intrinsic fish growth rate (r_P) as well as on different historical fish starting-biomasses (K_P).

7.8 Results

Below follow results for both the model for the current status of fish as well as the model that used historical data and estimates for a pristine fish population were then substituted into the current model to create a historical model. Using these two model scenarios, the three questions posed in the Introduction about the capacity of a pristine fish population to influence lobster predation and community composition could be addressed.

7.8.1 Current fish model

Based on an initial estimated starting biomass of 48 MT for redfish and a fish intrinsic growth rate of 0.3, the current model estimated a fish carrying capacity K_P of 724 MT. Narrow confidence intervals (715-732 MT) were attached to this estimate. This is likely a consequence of not accounting for all sources of uncertainty, but nonetheless the estimate of K_P is considered robust for use in the simulations performed. A biomass of 724 MT equates to roughly 0.12 fish.m^{-2} (i.e. 1 fish per 8 m^2). This estimate is realistic if considered in terms of all redfish.

Fig 7.02a shows the progressive decline in the actual commercial catch for the period 1980-2007. Catches were particularly low post-2000, when they were recorded at being <20% of the catches made in the 1980s and early 1990s. This sudden drop in catch was most likely due to the abrupt cut in commercial quotas that followed analyses unequivocally demonstrating that most linefish were depleted to 5-10% of pristine levels (Griffiths 2000). Given a starting biomass of 48 MT, the model predicted that fish biomass EOCH would have declined at a steady rate up until 2000, after which it would have increased (Fig 7.02a) due to the drop in commercial catches during the 2000s, and by 2007 fish biomass would have been back at around 50 MT.

Even this figure would have constituted a substantial depletion relative to 'pristine' values for the turn of the 19th century.

The observed CPUE (kg.boat^{-1}.year^{-1}) showed a slight downward trend between the mid-1980s and the mid-1990s (Fig 7.02b), but appeared to increase and then fluctuate from 2000 onwards. The model provided a reasonable fit to the initial decline in fish CPUE, but failed to fit to the fluctuating data thereafter (Fig 7.02b, Table 7.03). This is not unexpected given the simplistic representation of fish dynamics and the numerous problems associated with the CPUE series used. However, the modelled increase in fish over the recent period is consistent with the substantial decline in catches (and presumed consequent recovery of stocks), providing support for the use of the model fish trend in exploratory simulations.

7.8.2 Ecosystem effects of a top-predator

The two model scenarios using (1) current fish biomass and (2) historical fish biomass (Fig 7.03a) could be used to explore the direct predatory effects of fish on lobsters (Fig 7.03b), and indirect effects on urchin and abalone (Fig 7.03c-d) relative to the base-case model trajectories (developed in Chapter 4) that were modelled without the inclusion of fish. Addition of the current (heavily depleted) fish biomass had little effect on the rock-lobster biomass relative to that forecast by the base-case model (Fig 7.03b). This was largely because the current fish biomass consumed only 12 MT of rock lobsters in the start year, which equated to 3% of the lobster biomass, and thereafter 4-13 MT lobsters.yr^{-1} (Fig 7.04a). Although lobster natural mortality from sources other than fish was reduced from $M^J = 0.1$ to $M^J = 0.085$ to allow for competition among predators and thus offset the mortality due to fish predation, the initial lobster biomass showed signs of a slightly more rapid population growth, as a result of increased productivity, and then an increase in biomass toward the end of the model projection period (2007). Consequently, urchin biomass (Fig 7.03c) and abalone biomass (Fig 7.03d) similarly differed little between the base-case and 'current fish' models.

The historical model scenario assumed a pristine fish biomass, which was equated with the carrying capacity of redfish (K_P), at the start of the model year. This biomass remained relatively untouched over the 28 modelled years 1980-2008 (Fig 7.03a) due to the small proportion of fish being harvested by the early linefishery. At this pristine level of fish biomass, for which I assumed the same consumption/biomass ratio and proportion of lobsters eaten as in the current model, lobsters would virtually have disappeared by the mid-1990s (Fig 7.03b), given that fish consumed 176 MT of lobsters at the lobster start year (1985) (52% of the lobster biomass). Subsequent to this, fish would have been potentially able to continue to consume between 158-170 MT of lobsters per year (Fig 7.04a), dependent on the availability of lobsters. Consequences for both urchins and abalone would have been dramatic, with urchins remaining close to carrying capacity (Fig 7.03c) and the decline in inshore abalone biomass during the 1990s being far less severe and never culminating in total collapse (Fig 7.03d). The implication of this is that in the absence of a pristine redfish population, the 'lobster-effect' was far more detrimental to the abalone population than illegal fishing.

7.8.3 Sensitivity analyses

Sensitivity analyses were performed on the intrinsic fish growth rate (r_P) as well as on different historical fish starting-biomasses (K_P).

Fish intrinsic growth rate

In the current model, the fish intrinsic growth rate r_P was set at 0.3. Sensitivity analyses were then conducted for $r_P = 0.25$ and $r_P = 0.35$ (Table 7.03). Using the Akaike Information Criterion goodness of fit test ($AIC = -2\ln L + 2p$), the fish base-model (r_P=0.3) proved best with a K_P of 724 MT and an AIC of -12.46, followed by the S2 model (r_P=0.35) with a K_P of 229 MT and an AIC of -10.46. A growth rate of 0.25 (S1 model) resulted in a poor fit with a K_P of 71 MT and an AIC of 19.16 (Table 7.03). On the basis of these sensitivity analyses, I concluded that the preferred model was the fish-base model in which $r_P = 0.3$.

Historical model starting biomass

The historical model assumed a fish starting-biomass equivalent to the carrying capacity K_P estimated in the current fish model. To test whether a smaller or larger 'pristine' fish biomass would have equally negatively impacted the rock lobster population, I performed sensitivity using $K_P - 50\%$ and $K_P + 50\%$. Population trajectories for lobsters, urchins and abalone, using various levels of K_P, are shown in Fig 7.05. A fish starting-biomass set at K_P or at $K_P + 50\%$ would have prevented rock lobsters from establishing themselves and they would eventually have disappeared by the mid-1990s (Fig 7.05a). As a result, urchins would have remained unaffected (Fig 7.05b) and the decline in the abalone inshore biomass would have been much less (Fig 7.05c).

When a fish starting-biomass of $K_P - 50\%$ was used, the rock lobster biomass was predicted to have increased to just over 200 MT, but then gradually declined, leading to zero biomass by the late-1990s (Fig 7.05a). Consequently, the model forecasted that the urchin biomass would have dropped by roughly 3000 MT during the time lobsters were increasing, followed by a recovery after the disappearance of rock lobsters (Fig 7.05b). Abalone biomass remained the same for all three values of historical fish biomass (Fig 7.05c), probably because the reductions of urchin biomass recorded for $K_P - 50\%$ would not have dropped them below the level at which urchin availability would have been limiting for juvenile abalone (Mayfield and Branch 2000).

At current fish levels or in the absence of fish, lobsters would become established at a spawning biomass of around 600 MT, urchins would have collapsed by 1996, and abalone by 2006.

7.9 Discussion

The ecosystem effects of historical exploitation of top predators in the region EOCH are largely unknown and ecosystem models are an important means of exploring the direct and indirect impacts, particularly given the fact that experimental tests are not possible.

Research has shown that changes in predator abundance can have substantial ramifications on ecosystem structure, functioning and resilience (Paine 1969, Roberts 1995, Duffy 2002, Frank *et al*. 2005, Ling *et al*. 2009b), affecting not only the target species, but also having indirect ripple effects on the rest of the ecosystem (e.g. Steneck 1998, Williams 1998, Jackson *et al*. 2001, Scheffer *et al*. 2005). Top-down effects of predators have been frequently demonstrated in kelp-forest ecosystems (Estes and Palmisano 1974, Estes *et al*. 1998, Steneck *et al*. 2002, Halpern *et al*. 2006), subtidal temperate reefs (Shears and Babcock 2002, 2003, Barrett *et al*. 2009a), and intertidal rocky shores (Paine 1974, 1980, Castilla 1999, Menge 2000). However, it is only during the past decade that top-down control is becoming increasingly apparent in open-ocean systems as the overfishing of top-predators reaches critical levels (Worm and Myers 2003, Frank *et al*. 2005, Baum and Worm 2009, Eriksson *et al*. 2009). Simultaneous with the decline in top-predators is on-going human-induced climate-change, implying that we are exerting extreme modifications on both top-down and bottom-up forces (Scheffer *et al*. 2005, Ling *et al*. 2009b) resulting in ecosystem shifts that are not easily reversible (Frank *et al*. 2005). A recent example of this has occurred off the east Tasmanian coast, where overfishing of predators (including another rock lobster, *Jasus edwardsii*), coupled with a warming of temperate coastal waters has allowed the long-spined sea urchin *Centrostephanus rogersii* to extend its range, causing catastrophic overgrazing of Tasmanian kelp forests and a subsequent loss of ecosystem functions (Ling *et al*. 2009b).

Along the South African Cape coast, the overfishing of linefish during the 20th century has resulted in a heavily depleted linefish population. Concurrently, a cooling of inshore waters occurred along the south coast, particularly east of Cape Agulhas (Roy *et al*. 2007, Rouault *et al*. 2009). This coincided with the rock-lobster ‘invasion’ EOCH, but is unlikely to have caused it as the cooling lay further east than the region that was invaded. The exhaustion of linefish is also unlikely to have caused the rock-lobster invasion, but the model indicates that an absence of predatory fish may have been a critical factor in allowing the establishment or persistence of a dense lobster population in the invaded area EOCH. Had fish populations been at ‘pristine’ levels, it is likely that any lobster-invasion would not have sustained itself.

Confirmatory evidence of the capacity of large ‘redfish’ to consume rock lobsters comes from a mesocosm experiment in which Atkinson (2001) introduced *J. lalandii* (70-95 mm CL) into an aquarium (thought to represent natural kelp-forest conditions) containing large individuals of Roman *Chrysoblephus laticeps*, Red Stumpnose *C. gibbiceps*, Poenskop *Cymatoceps nasutus*, White Steenbras *Lithognathus lithognathus*, Hottentot *Pachymetopon blochii* etc. Two important outcomes relate to the predictions of my model. First, if the lobsters were free to move, they immediately sought out and remained continually in shelters, where their survival was relatively high (at least 52% over 44 days) (Atkinson 2001). This behaviour, would, however, have restricted foraging by the lobsters and indirectly constrained their predatory activities. This conclusion is strongly supported by the fact that acoustic tagging of lobsters in the Castle Rock MPA in False Bay revealed that lobsters foraged only at night and remained concealed in crevices during the day, whereas those EOCH, where fish are depleted, were also active during the day (Cockcroft *et al*. 2005). This was thought to be due to increased predatory pressure within the MPA. More importantly, if the lobsters were tethered in the open where they could not secure shelter, they were almost immediately attacked and consumed by the fish, with zero survivors remaining after 3 hours (Atkinson 2001).

Although the model results presented in this chapter are based on the rock-lobster starting age structure employed in Chapter 4 and on a poorly estimated lobster stating-biomass (see Chapters 4 and 5), both sensitivity analyses and empirical data (Atkinson 2001, Cockcroft *et al*. 2005) suggest that at larger sizes and densities than now exist, redfish would have had the predatory capability to consume and influence lobster populations, including those of large lobsters, or at least confine them to crevices and reduce their predatory effects.

The fish model developed in this chapter adds to the multispecies model developed in Chapter 4 and provides a better understanding of the ecosystem changes EOCH documented in Chapters 2 and 3. Specifically, it explores ideas that can no longer be tested experimentally because over-exploitation has changed the ecosystem by depleting top-predators. The overall conclusions were:

(1) The major decline in linefish occurred long before the 1980s (Griffiths 2000), which was supported by model trends in fish biomass and CPUE.

(2) The current fish biomass, which was based on redfish density estimates taken from an exploited region in False Bay, would not have been large enough to have had a significant impact on the lobster population. Therefore, it appears unlikely that changes in linefish abundance over the period 1980 onwards triggered the current ecosystem change. However, the fact that current fish biomass is low may have allowed the change to take place.

(3) If linefish populations were still to be at pristine levels, my model outputs suggest that the invasion of rock lobsters would have been controlled by linefish and consequently, the urchin and abalone populations would not have collapsed.

(4) The lobster-effect had a greater influence on the abalone population than illegal fishing, but in combination they severely depleted the abalone stock.

(5) Current redfish populations were estimated to be <10% of the carrying capacity (pristine level). Even if the pristine biomass of fish was over-estimated, a biomass half that value would still have prevented rock lobsters from establishing themselves.

Wider perspectives on ecosystem processes EOCH

My multispecies model focused solely on the addition of fish as a predator of rock lobsters, but it would be profitable to incorporate other species into future elaborations, especially seals and encrusting corallines.

Extensive exploitation of the Cape Fur seal *Arctocephalus pusillus* during the late 18th century resulted in very low population levels, including the extinction of seals from at least 23 island breeding colonies along the west coast (Shaughnessy 1984). Despite seals receiving initial protection in 1893, commercial exploitation continued until 1990 (David *et al*. 2003) and although numbers have increased, there is great uncertainty about the current population level relative to the pre-exploitation level (Butterworth *et al*. 1995). Seals are mainly piscivorous, but also feed on the West Coast rock lobster *Jasus lalandii*. David (1987) estimated that their annual consumption of rock lobsters in Namibia and South Africa is 31 500 MT and 600 MT on the west and south coasts respectively. Although he considers this an over-estimate, the data do suggest that at high population levels, seals would have had a negative impact on rock-lobster populations. Making predictions about this is, however, complicated by the fact that the direct negative effects of seals may be offset or negated by potential indirect positive effects of seals consuming other prey such as fish that are themselves predators of rock lobsters.

Ecosystem interactions EOCH are further complicated by the roles of encrusting corallines and erect algae, including kelps and understory algae. Day and Branch (2000a) found that abalone recruits (<3 mm) occur exclusively on encrusting corallines, which seem vital for larval settlement. Urchins benefit encrusting corallines by clearing the substrate of sediment and benthic herbivores collectively prevent overgrowth of encrusting corallines by erect algae (Day and Branch 2002a, Branch 2008). Increased rock lobster predation on herbivores therefore has indirect negative effects on encrusting corallines and consequently on abalone recruitment. Results from my benthic surveys (Chapter 3) showed that encrusting corallines were less abundant in lobster-invaded areas than in the non-invaded areas. In addition to this, large amounts of silt were observed on the invaded reefs (L.K. Blamey, pers. obs.), similar to the increase in siltation that Day and Branch (2002a) recorded after experimental removal of urchins.

Species interactions involving kelps and understory algae are slightly more complicated, given that urchins and abalone are largely trappers of drift algae rather than being active grazers, although under certain circumstances they may switch their behaviour and become grazers. This behaviour has been suggested or demonstrated for other urchins (Mattison *et al*. 1977, Reed and Foster 1984, Dayton 1985a, Harrold and Reed 1985, Konar 2001, Rodríguez 2003).

Fig 7.06 summarizes the ecosystem processes East of Cape Hangklip. Top-down control by predators in this system is both direct and indirect. At pristine densities, top predators such as fish and seals are likely to have had a direct negative predatory effect on rock lobsters and therefore an indirect positive effect on urchins and abalone. However, through a combination of overfishing (removal of top predators) and an eastward shift in rock lobsters, rock lobsters have become established at sufficient densities to exert (1) a bottom-up effect on Bank Cormorants, which have increased EOCH following the increase in rock lobsters (Crawford 2008d), (2) a direct predatory effect on urchins and other herbivores, (3) an indirect positive effect on macroalgae as documented in Chapters 2 and 3, and (4) an indirect negative effect on juvenile abalone. Urchins facilitate juvenile abalone by providing nourishment and protection (Day and Branch 2000a, 2000b, 2002a). In addition, they facilitate encrusting corallines by preventing sediment build up and hence prevent smothering. Encrusting corallines facilitate the settlement of abalone recruits (Day and Branch 2000a), but compete with erect algae for space and are vulnerable to smothering. A combination of illegal fishing and the indirect negative effect of rock lobsters on juvenile abalone has had a severe negative impact on the abalone population, resulting in a dwindling parent stock and possible recruitment failure.

Conclusions

Although ecosystem models are rarely used in tactical decision-making and hence are mostly strategic (Plagányi 2007), they are useful in exploring hypotheses related to ecosystem functioning and associated changes. In the case of the ecosystem EOCH, my multispecies models have substantially improved understanding of ecosystem shifts and associated interactions. Specifically, the models uphold the conclusion derived from temporal and spatial comparisons in Chapters 2 and 3 that invasion by lobsters was the major factor leading to an ecosystem regime shift. The model also indicates that the 'lobster effect' on abalone exceeds that of illegal fishing. The greatest insight gained from modelling is the fact that overfishing fish that are predators of lobsters was at the very least a contributory factor to the expansion of lobsters into the invaded area. In addition to altering the ecosystem structure and functioning, the synergistic effects of top-predator removal and a changing climate have almost certainly reduced capacity of the ecosystem EOCH to return to its previous state.

Chapter 8

Synthesis

Synthesis

Predators are known to exert a powerful influence on community composition, including indirect effects on species that interact with their prey (e.g. Paine 1969, 1974, Menge 2000, Estes *et al*. 1998, 2004, Shears and Babcock 2003). More specifically, the West Coast Rock lobster *Jasus lalandii* is capable of transforming benthic communities, particularly when it achieves high densities (Barkai and Branch 1988a, 1988b, Barkai and McQuaid 1988, Mayfield and Branch 2000). In Chapter 1 of this thesis, I described the background to a geographic shift of *J. lalandii* that occurred East of Cape Hangklip (EOCH) along the south-west coast of South Africa during the early 1990s (Tarr *et al*. 1996, Mayfield and Branch 2000), and became known as a lobster 'invasion'. Reasons for the invasion are unknown, but evidence suggests it was linked to a change in climate. Given the predatory effects of *J. lalandii* (Barkai and Branch 1988a, 1988b, Barkai and McQuaid 1988, Mayfield *et al*. 2000a, 2000b, 2001, Van Zyl *et al*. 2003) and particularly its consumption of the Cape urchin *Parechinus angulosus*, with which juveniles of the abalone *Haliotis midae* are associated (Day and Branch 2000a, 2000b, 2002a), the lobster invasion is likely to have had considerable implications for both the ecosystem and local fisheries.

In Chapter 2 I presented temporal analyses for two sites EOCH, Cape Hangklip and Betty's Bay, showing that prior to 1990, few rock lobsters were recorded there, but from the mid 1990s onwards rock lobsters became abundant. Before the lobster invasion, the benthic communities at these sites were significantly different from those recorded after the invasion. Three major changes following the lobster invasion were identified: (1) a decline or even a disappearance of most herbivores, including urchins (a direct effect of intensified predation), (2) a proliferation of macroalgae (an indirect effect of depletion of herbivores) and (3) increases in a range of sessile taxa (for unknown reasons).

In Chapter 3 I undertook a more detailed analysis examining spatial differences in rock lobsters and benthic communities. Surveys were conducted at six sites EOCH (Cape Hangklip, Betty's Bay, Mudge Point, Romans Bay, Kruismans Bay and Quoin Point; Fig 3.02), at 3 depth intervals at each site (< 5m, 6-12m and 13-20m). The first three of these sites were classified *a priori* as 'invaded' and the last three as 'non-invaded', based on rock-lobster densities recorded prior to my study. My own surveys verified this classification of sites, with invaded areas having significantly greater densities of *J. lalandii* than the non-invaded areas, and also showed that benthic communities at invaded sites were significantly different from those at non-invaded sites – at the level of both species and functional groups. Invaded sites were characterized by a larger cover of macroalgae and sessile species, whereas non-invaded sites were characterized by greater abundances of herbivores and encrusting corallines. The most obvious differences in community structure were found in the <5m and 6-12m depth zones. At the non-invaded sites where top-down predation by *J. lalandii* would have been less intense, faunal species diversity was greater than at invaded sites and faunal species dominance reduced. Floral species diversity was on average greater at invaded sites and increased with depth.

The main ecological concepts emerging from this study are: (1) Top-down predation by *J. lalandii* has directly impacted herbivore abundance and has consequently led to (2) indirect effects, whereby a reduction in herbivores has allowed macroalgal proliferation, in turn increasing primary productivity. Similar effects by rock lobsters have been reported elsewhere (Babcock *et al.* 1999, Shears and Babcock 2002, Barrett *et al.* 2009a, Ling *et al.* 2009b). (3) The ecosystem EOCH is further complicated by indirect non-trophic ripple effects. Given the relationship between urchins and juvenile abalone (Day and Branch 2000a, 2000b, 2002a), the decline in urchins has had severe consequences for the abalone population. This effect is further enhanced by a decline in encrusting corallines, which are required for abalone larval settlement (Day and Branch 2000a), due to increased siltation related to the disappearance of urchins (Day 1998) and an increase in macroalgal cover. (4) Species diversity differed between invaded and non-invaded areas with a greater floral diversity and reduced faunal diversity in areas with intense top-down predation by lobsters, and the reverse in areas where lobsters remain scarce.

The empirical data outlined in Chapters 2 and 3 can only be used to imply causes and effects. Manipulative experiments are a logical next step to address these implied relationships, but the ecosystem has undergone changes that are so large-scale that experiments on a relevant scale will be difficult. More importantly, some of the ecosystem changes, such as those caused by overfishing linefish, have had historical consequences extending back over a century and cannot be experimentally reversed. Theoretically, a ‘no-take’ Marine Protected Area might achieve this, but cannot be done at the whim of a PhD student, and would take decades of rigorous implementation at a sufficiently large scale to attain anything like a pristine state. In cases like this, ecosystem models are extremely valuable in probing “what-if” questions and are increasingly being employed in a move towards an ecosystem approach to fisheries management (Plagányi 2007). Although whole-ecosystem models are the most widely employed ecosystem modelling approach, the EOCH ecosystem was better suited to using a Minimally Realistic Model (MRM) to explore specific interactions for reasons outlined in Chapter 4.

In Chapter 4 I developed a lobster-urchin-abalone MRM. To mimic the EOCH ecosystem, the base-case model included rock lobsters in the invaded Zone D and excluded them from the non-invaded Zone B. An existing abalone stock-assessment model (Plagányi and Butterworth in press) formed the foundation for this multispecies model, with the addition of rock lobsters and urchins. Abalone and rock lobsters were modelled using age-structured production models and urchins were modelled using a surplus production model. The base-case model was used to estimate six parameters: a rock-lobster starting biomass, a rock-lobster carrying capacity and four species interaction parameters. The lobster-abalone interaction parameters proved most difficult to estimate. The model was unable to estimate the urchin intrinsic growth rate and the absence of empirical data led to uncertainty in this input parameter.

Sensitivity analyses conducted in Chapter 5 showed that the base-case model proved best for the following estimated/input parameters: lobster carrying capacity, steepness parameter *h*, urchin carrying capacity, lobster natural mortality, and the abalone natural mortality parameter. The model was most sensitive to changes in the interaction parameters, particularly those between urchin and rock lobster. Further sensitivity analyses suggested that the lobster invasion was more likely to have been caused by an influx of large lobsters (>68 mm CL) in the early 1990s (i.e. an immigration of large lobsters) rather than by increased larval settlement in the early 1980s that might eventually have led to a population of large lobsters.

Given the virtual disappearance of urchins and a heavily depleted abalone stock in Zone D, future projections suggested that a complete removal of rock lobsters would be necessary for the urchin and abalone populations to recover, even under the assumption that changes to the substratum would not impede such a recovery. Even with a complete removal of rock lobsters, urchin population recovery could take up to 50 years and abalone even longer.

As a further development of the model, in Chapter 6 I included a hypothetical invasion of rock lobsters into Zone B – a currently non-invaded region. Model output suggested that introduction of even a small biomass of lobsters would cause a collapse of the urchin population and, associated with this, juvenile abalone were predicted to decline and the abalone population to disappear. Larger biomasses of 'invading' lobsters sped up these collapses. Although these outcomes are intuitive, they are important for two reasons. First, they helped validate the model in that it yielded effects comparable to those observed empirically for the invaded areas. Second, they indicate that invasion of the currently non-invaded section of coast EOCH would lead to a situation in which recovery of abalone would then be almost impossible, as the remaining stocks that are currently above the threshold for Allee effects would be reduced to levels at which fertilisation would precipitously decline. Removal of the last stocks capable of reproduction would eliminate the possibility of replenishing stocks in invaded areas by larval supplies from adjacent non-invaded areas, although this is unlikely because abalone recruitment is very localised (Prince 2005, Prince *et al*. 2008, Miller *et al*. 2008, Saunders *et al*. 2009).

In Chapter 7 I expanded the model to incorporate a top predator to address a question that is tractable only by modelling: whether historical depletion of predatory linefish contributed to the lobster invasion. A generic 'redfish' that preyed on rock lobsters was introduced into Zone D to test various hypotheses. Fish were modelled using a surplus production model based on data from redfish species found along the south-west coast. An intrinsic growth rate for fish was input into the model as 0.3 and sensitivity analyses suggested this was appropriate, given other fixed parameters. Fish carrying capacity for Zone D was estimated to be 724 MT. The overall conclusions were: (1) the major decline in linefish occurred long before the 1980s (Griffiths 2000), which was supported by model trends in fish biomass and CPUE. (2) Current fish biomass is not large enough to significantly impact the lobster population. Therefore, it appears unlikely that changes in linefish triggered the current ecosystem change, but rather that the reduced fish biomass permitted persistence of the invasion.. (3) If linefish populations had remained at pristine levels, the model predicted that any invasion of rock lobsters would have been controlled by them and, consequently, urchin and abalone populations would not have crashed. (4) The lobster-effect had more influence on the abalone than did illegal fishing, but in combination they decimated the abalone stock in my model.

One of the major challenges faced in this study was the absence of key data. For example, statistical analyses proved difficult in the analyses of change due to the nature of past data that had been collected (small sample size, lack of replication in some cases, coarse taxonomic resolution etc). Data are required to improve the ecosystem model. They include:

1) Urchin intrinsic growth rate

   Long-term monitoring of *Parechinus angulosus* populations would provide information on potential population growth rate. However, even this is problematic as this requires that conditions remain relatively unchanged. In reality this is unlikely, and fluctuations in recruitment and survival are likely to be the norm (T. Ebert, Oregon State University, pers. comm.). Nonetheless, the intrinsic growth rate parameter represents the average over a long time period and it would be useful to have idea more precise estimate of a plausible range for this parameter. Such data are not available for *P. angulosus*, and a literature search yielded no results detailing the long-term monitoring of increasing urchin populations either locally or internationally and only one study estimating intrinsic growth - for a larger species, the purple urchin *Strongylocentrotus purpuratus* off California (Lafferty 2004).

2) Interaction parameters

   Aquaria experiments would be useful in determining the capture rates (α) of urchins and juvenile abalone by rock lobsters, as well as predator handling time (β) (see equations 4.30 and 4.33 in Chapter 4). These data would help to better estimate interaction parameters and thus improve the representation of lobster-prey interactions.

3) Additional indices of abundance

   Only limited commercial and fisheries-independent CPUE data exist for rock lobsters EOCH because the commercial fishery is a recent development there. Future catch and effort data will improve lobster parameter estimation. Unfortunately the Fisheries Independent Monitoring Survey (FIMS) in this area was discontinued after 2005: its resurrection would be advantageous.

4) Additional fish data

   Aquaria experiments and dietary analyses could provide information on (1) the minimum and maximum size of lobsters eaten by fish, (2) the minimum size of fish capable of feeding on lobsters and (3) the proportion of the fish diet that comprises lobsters.

The costs (in terms of resources) of collecting additional such data need to be weighed, taking into account the potential benefit contribution of these additional data.

Although there is substantial observational evidence to suggest that rock lobsters are the major driving force behind the ecosystem shift EOCH, experimental evidence is lacking. While recognizing the difficulty of extrapolating from small-scale field experiments to large-scale phenomena, experimental tests of the effect of rock lobsters through the use of exclusion cages would strengthen the conclusions. By either including or excluding rock lobsters, urchins and grazing winkles, the following questions could be asked: (1) In the absence of *J. lalandii*, will herbivores reduce macroalgal cover and promote encrusting corallines, returning the ecosystem to its former state? (2) In the presence of *J. lalandii* will herbivores be eliminated, leaving an algal-dominated system? (3) In the absence of lobsters, can urchins alone control macroalgal growth?

Future work on the ecosystem model could include the addition of more species, particularly the Cape fur seal *Arctocephalus pusillus*, encrusting corallines and erect algae. Possible models/interactions include:

1) Seal predation on rock lobsters – a population dynamics model for seals that is both age- and sex-structured has already been developed (Butterworth *et al*. 1995). Although there are additional rock-lobster predators, seals and fish were considered the most influential and should therefore form the focus of a more detailed multispecies model. However, limitations of historical data and data standardization remain a problem.
2) Substratum coverage of encrusting corallines relative to urchin density.

3) Survival of abalone recruits in relation to different types of corallines and the threshold density of corallines, below which recruits decline.

To move towards an ecosystem approach to fisheries management, it is imperative that we understand the structure and functioning of ecosystems and their associated fisheries. Ecosystem models are becoming increasingly useful alongside empirical studies in gaining such insight. There are currently few Minimally Realistic Model (MRM) approaches developed worldwide (Butterworth *et al.* 1995, Punt and Butterworth 1995, Bogstad *et al.* 1997) and hence this study makes a valuable contribution to this approach. It provides a more rigorous approach to modelling multispecies interactions in that it is conditioned to all available data and hence can produce more robust results that ultimately may be useful in an assessment/tactical context. The EOCH ecosystem houses four resources that have either been or are currently exploited: reef fish (Attwood and Farquhar 1999, Griffiths 2000), the West Coast rock lobster *Jasus lalandii*, the abalone *Haliotis midae* and the kelp *Ecklonia maxima* (Troell *et al.* 2006), all of which form part of the complex kelp-forest ecosystem in this region and contribute to the national economy. Using both empirical and modelling approaches, this study provided insight into (1) an ecosystem shift that occurred following an 'invasion' of rock lobsters, (2) the complexity of ecosystem interactions in the EOCH region, and (3) the causes and implications of human- and environmentally-induced shifts in community structure, all of which highlight the imperative need for an ecosystem approach to fisheries. Ideally such an approach should encompass physical, biological, social and economic factors. My study represents a first step in this direction, having focused on the biological interactions, and thereby enhances understanding and complements more traditional single-species assessment models.

Appendices

Appendix 1

Appendix Table A1.01: A list of all the species recorded, including their taxonomic and functional groups as well as their mean biomass. Mean biomass was recorded as a wet weight (g) per 0.0025 m^2 (1% cover of 0.25 m^2 quadrat) or per individual and used to convert percentage cover or counts into biomass.

Taxonomic group	Functional group	Species	% cover or individual	Mean biomass (g)
Chlorophyta	**Turf**	*Caulerpa bartoniae*	% cover	1.08
Chlorophyta	**Turf**	*Caulerpa holmesiana*	% cover	4.72
Chlorophyta	**Foliose**	*Cladophora mirabilis*	% cover	6.88
Chlorophyta	**Turf**	*Codium lucasii capense*	% cover	15.72
Chlorophyta	**Foliose**	*Codium stephensiae*	% cover	9.6
Chlorophyta	**Foliose**	*Ulva*	% cover	7.47
Phaeophyta	**Foliose**	*Anthophycus longifolius*	% cover	4.85
Phaeophyta	**Foliose**	*Axillariella constricta*	% cover	4.85
Phaeophyta	**Turf**	*Bifurcariopsis capensis*	% cover	7.84
Phaeophyta	**Foliose**	*Carpomitra costata*	% cover	1.4
Phaeophyta	**Foliose**	*Desmarestia firma*	% cover	2.65
Phaeophyta	**Foliose**	*Dictyota naevosa*	% cover	3.29
Phaeophyta	**Primary**	*Ecklonia maxima*	individual	1240
Phaeophyta	**Primary**	Juvenile Kelp	individual	17.56
Phaeophyta	**Primary**	Kelp holdfast	individual	205.7
Phaeophyta	**Secondary**	*Laminaria pallida*	individual	1025
Phaeophyta	**Turf**	*Stypocaulon funiculare*	% cover	6
Phaeophyta	**Turf**	*Stypopodium zonale*	% cover	6.58
Phaeophyta	**Turf**	*Zonaria harveyana*	% cover	3.5
Phaeophyta	**Turf**	*Zonaria subarticulata*	% cover	6.58
Rhodophyta	**Turf**	*Acrosorium ciliolatum*	% cover	2.8
Rhodophyta	**Foliose**	*Aeodes orbitosa*	% cover	2.17
Rhodophyta	**Turf**	*Amphiroa ephedraea*	% cover	11.36
Rhodophyta	**Turf**	*Arthrocardia corymbosa*	% cover	3.97
Rhodophyta	**Turf**	*Arthrocardia filicula*	% cover	2.8
Rhodophyta	**Turf**	*Arthrocardia flabellata*	% cover	8
Rhodophyta	**Turf**	*Ballia callitricha*	% cover	6.13
Rhodophyta	**Foliose**	*Bartoniella crenata*	% cover	4
Rhodophyta	**Foliose**	*Botryocarpa prolifera*	% cover	6.3
Rhodophyta	**Foliose**	*Botryoglossum platycarpum*	% cover	6.3
Rhodophyta	**Foliose**	*Callophycus densus*	% cover	3.7
Rhodophyta	**Turf**	*Carpoblepharis flaccida*	% cover	7.6
Rhodophyta	**Turf**	*Champia compressa*	% cover	3.58
Rhodophyta	**Turf**	*Cheilosporum sagittatum*	% cover	1.86
Rhodophyta	**Turf**	*Corallina officinalis*	% cover	3.97
Rhodophyta	**Foliose**	*Delesseriaceae vel. aff.*	% cover	5.61
Rhodophyta	**Foliose**	*Delisea flaccida*	% cover	3.29
Rhodophyta	**Foliose**	*Epymenia capensis*	% cover	3.17
Rhodophyta	**Foliose**	*Gelidium capensis*	% cover	3.47
Rhodophyta	**Foliose**	*Gigartina insignis*	% cover	4.46
Rhodophyta	**Foliose**	*Grateloupia doryphora*	% cover	3.47
Rhodophyta	**Turf**	*Heringia mirabilis*	% cover	4.6

Appendix Table A1.01 continued: A list of all the species recorded, including their taxonomic and functional groups as well as their mean biomass. Mean biomass was recorded as a wet weight (g) per 0.0025 m^2 (1% cover of 0.25 m^2 quadrat) or per individual and used to convert percentage cover or counts into biomass.

Taxonomic group	Functional group	Species	% cover or individual	Mean biomass (g)
Rhodophyta	**Turf**	*Heterosiphonia dubia*	% cover	4.6
Rhodophyta	**Foliose**	*Hymenena venosa*	% cover	2.9
Rhodophyta	**Turf**	*Hypnea ecklonii*	% cover	9.6
Rhodophyta	**Turf**	*Jania verrucosa*	% cover	5.5
Rhodophyta	**Foliose**	*Neinburgia serrata*	% cover	2.34
Rhodophyta	**Foliose**	*Nemastoma lanceolatum*	% cover	3.15
Rhodophyta	**Foliose**	*Nothogenia erinacea*	% cover	4.46
Rhodophyta	**Foliose**	*Pachymenia carnosa*	% cover	10.92
Rhodophyta	**Foliose**	*Pachymenia cornea*	% cover	5.53
Rhodophyta	**Turf**	*Peyssonnelia capensis*	% cover	3
Rhodophyta	**Foliose**	*Phyllymenia belangeri*	% cover	11.6
Rhodophyta	**Turf**	*Plocamium beckerii*	% cover	2.8
Rhodophyta	**Foliose**	*Plocamium corallorhiza*	% cover	5.03
Rhodophyta	**Turf**	*Plocamium glomeratum*	% cover	2.71
Rhodophyta	**Turf**	*Plocamium maxillosum*	% cover	3
Rhodophyta	**Turf**	*Plocamium rigidum*	% cover	2.27
Rhodophyta	**Turf**	*Plocamium surhii*	% cover	3.17
Rhodophyta	**Turf**	*Polyopes contrictus*	% cover	1.91
Rhodophyta	**Turf**	*Pterosiphonia cloiophylla*	% cover	8.79
Rhodophyta	**Turf**	*Rhodophyllis reptans*	% cover	3.2
Rhodophyta	**Foliose**	*Rhodymenia natalensis*	% cover	3.6
Rhodophyta	**Foliose**	*Scinaia salicornioides*	% cover	12
Rhodophyta	**Foliose**	*Thamnophyllis discigera*	% cover	3.6
Rhodophyta	**Turf**	*Trematocarpus flabellatus*	% cover	4.6
Rhodophyta	**Turf**	*Trematocarpus fragilis*	% cover	4
Encrusting algae	**Encrusting algae**	*Heydrichia woelkerlingii*	% cover	33.2
Encrusting algae	**Encrusting algae**	*Hildenbrandia rubra*	% cover	2.7
Encrusting algae	**Encrusting algae**	*Leptophytum foveatum*	% cover	1.6
Encrusting algae	**Encrusting algae**	White encrusting	% cover	1.6
Porifera	**Sessile species**	Sponge	% cover	36.05
Actiniaria	**Sessile species**	*Actinia mandelae*	individual	6.2
Actiniaria	**Sessile species**	*Anthopleura stephensoni*	individual	7.5
Actiniaria	**Sessile species**	*Anthothoe stimpsoni*	individual	0.18
Actiniaria	**Sessile species**	*Aulactinia reynaudi*	individual	26
Actiniaria	**Sessile species**	*Bunodosoma capensis*	individual	13
Actiniaria	**Sessile species**	*Corynactis annulata*	individual	2.5
Actiniaria	**Sessile species**	*Pseudactinia flagellifera*	individual	26
Alcyonacea	**Sessile species**	*Alcyonium distinctum*	individual	2.7
Alcyonacea	**Sessile species**	*Alcyonium fauri*	individual	2.7
Alcyonacea	**Sessile species**	*Capnella thyrsoidea*	individual	2.2

Appendix Table A1.01 continued: A list of all the species recorded, including their taxonomic and functional groups as well as their mean biomass. Mean biomass was recorded as a wet weight (g) per 0.0025 m^2 (1% cover of 0.25 m^2 quadrat) or per individual and used to convert percentage cover or counts into biomass.

Taxonomic group	Functional group	Species	% cover or individual	Mean biomass (g)
Gorgonacea	**Sessile species**	*Acabaria rubra*	individual	3.2
Gorgonacea	**Sessile species**	*Eunicella papillosa*	individual	4.45
Gorgonacea	**Sessile species**	*Leptogorgia palma*	individual	76
Scleractinia	**Sessile species**	*Balanophyllia bonaespei*	individual	1.45
Hydrozoa	**Sessile species**	Hydroid	individual	3.54
Hydrozoa	**Sessile species**	*Amphisbetia operculata*	individual	1
Hydrozoa	**Sessile species**	*Lytocarpus filamentosus*	individual	5.6
Hydrozoa	**Sessile species**	*Lytocarpus philippinus*	individual	5.6
Hydrozoa	**Sessile species**	*Sertularella arbuscula*	individual	2.75
Polychaeta	**Sessile species**	Fan worm	individual	4.7
Polychaeta	**Sessile species**	Tube worm	% cover	4.7
Cirripedia	**Sessile species**	*Austromegabalanus cylindricus*	individual	5.6
Cirripedia	**Sessile species**	*Balanus amphitrite*	individual	0.38
Cirripedia	**Sessile species**	*Balanus venustus*	individual	0.38
Cirripedia	**Sessile species**	*Notomegabalanus algicola*	individual	2.35
Macrura	**Predator**	*Jasus lalandii*	individual	321.38
Brachyura	**Scavenger**	*Platydromia spongiosa*	individual	0.5
Brachyura	**Scavenger**	*Dromidia hirsutissima*	individual	0.5
Brachyura	**Scavenger**	*Pseudodromia latens*	individual	0.8
Brachyura	**Scavenger**	*Plagusia chabrus juv*	individual	0.3
Anomura	**Scavenger**	*Paguristes gamianus*	individual	3.79
Anomura	**Scavenger**	unknown hermit	individual	0.3
Bryozoa	**Sessile species**	*Bugula dentata*	% cover	8
Bryozoa	**Sessile species**	*Bugula neritina*	% cover	30
Bryozoa	**Sessile species**	*Bicellariella ciliata*	% cover	8
Bryozoa	**Sessile species**	*Menipea crispa*	% cover	17.8
Bryozoa	**Sessile species**	*Cellepora cylindriformis*	% cover	28.4
Bryozoa	**Sessile species**	*Elzerina blainvillii*	% cover	7.85
Bryozoa	**Sessile species**	*Electra verticillata*	% cover	0.5
Bryozoa	**Sessile species**	*Margaretta triplex*	% cover	9.8
Bryozoa	**Sessile species**	*Chaperia* spp.	% cover	38.56
Bryozoa	**Sessile species**	*Gigantopora polymorpha*	% cover	24.67
Bryozoa	**Sessile species**	*Laminopora bimunita*	% cover	38.56
Bryozoa	**Sessile species**	*Schizoretepora tesselata*	% cover	26.4
Bryozoa	**Sessile species**	*Tubulipora pulcherrima*	% cover	36.9
Brachiopoda	**Sessile species**	*Kraussina rubra*	individual	0.55

Appendix Table A1.01 continued: A list of all the species recorded, including their taxonomic and functional groups as well as their mean biomass. Mean biomass was recorded as a wet weight (g) per 0.0025 m^2 (1% cover of 0.25 m^2 quadrat) or per individual and used to convert percentage cover or counts into biomass.

Taxonomic group	Functional group	Species	% cover or individual	Mean biomass (g)
Bivalvia	**Sessile species**	*Aulacomya ater*	individual	0.29
Bivalvia	**Sessile species**	*Musculus cuneatus*	individual	0.3
Bivalvia	**Sessile species**	*Modiolus ligneus*	individual	0.9
Bivalvia	**Sessile species**	*Chlamys tincta*	individual	0.21
Bivalvia	**Sessile species**	*Corbula rugifera*	individual	0.05
Bivalvia	**Sessile species**	*Pecten sulcicostatus*	individual	0.2
Bivalvia	**Sessile species**	*Limaria rotundata*	individual	0.62
Bivalvia	**Sessile species**	*Parvicardium turtoni*	individual	0.32
Bivalvia	**Sessile species**	*Pandora dissimilis*	individual	0.8
Polyplacophora	**Herbivore**	*Chaetopleura pertusa*	individual	1.1
Polyplacophora	**Herbivore**	*Chiton tulipa*	individual	1.5
Gastropoda	**Scavenger**	*Afrocominella elongata*	individual	8.5
Gastropoda	**Scavenger**	*Ranella australasia gemmifera*	individual	36.1
Gastropoda	**Scavenger**	*Burnupena cincta*	individual	14.05
Gastropoda	**Scavenger**	*Burnupena denseliriata*	individual	0.1
Gastropoda	**Scavenger**	*Burnupena lagenaria*	individual	8.5
Gastropoda	**Scavenger**	*Burnupena papyracea*	individual	4.55
Gastropoda	**Scavenger**	*Burnupena pubescens*	individual	8.03
Gastropoda	**Scavenger**	*Latirus rousi*	individual	0.9
Gastropoda	**Scavenger**	*Mitra picta*	individual	1.1
Gastropoda	**Scavenger**	*Nucella squamosa*	individual	7.9
Gastropoda	**Scavenger**	*Peristernia forskali*	individual	0.9
Gastropoda	**Scavenger**	*Fusinus ocelliferus*	individual	1.5
Gastropoda	**Herbivore**	*Haliotis midae*	individual	45
Gastropoda	**Herbivore**	*Cymbula miniata*	individual	4.85
Gastropoda	**Herbivore**	*Scutellastra barbara*	individual	20.08
Gastropoda	**Herbivore**	*Scutellastra longicosta*	individual	8.25
Gastropoda	**Herbivore**	*Scutellastra tabularis*	individual	122.5
Gastropoda	**Herbivore**	*Calliostoma ornatum*	individual	0.3
Gastropoda	**Herbivore**	*Gibbula capensis*	individual	0.3
Gastropoda	**Herbivore**	*Gibbula multicolor*	individual	0.27
Gastropoda	**Herbivore**	*Oxystele sinensis*	individual	31.05
Gastropoda	**Herbivore**	*Oxystele variegata*	individual	1.55
Gastropoda	**Herbivore**	*Turbo cidaris*	individual	33.9
Gastropoda	**Herbivore**	*Turbo sarmaticus*	individual	37.15
Gastropoda	**Herbivore**	*Tricolia capensis*	individual	0.22
Gastropoda	**Scavenger**	*Turritella carinifera*	individual	0.6
Gastropoda	**Scavenger**	*Clionella rosaria*	individual	1.2
Gastropoda	**Sessile species**	*Clionella sinuata*	individual	1.4
Gastropoda	**Scavenger**	*Volvarina zonata*	individual	0.45
Gastropoda	**Scavenger**	*Marginella nebulosa*	individual	8.5
Gastropoda	**Scavenger**	*Marginella sp juv*	individual	0.33
Gastropoda	**Herbivore**	*Cypraea algoensis*	individual	2.3

Appendix Table A1.01 continued: A list of all the species recorded, including their taxonomic and functional groups as well as their mean biomass. Mean biomass was recorded as a wet weight (g) per 0.0025 m^2 (1% cover of 0.25 m^2 quadrat) or per individual and used to convert percentage cover or counts into biomass.

Taxonomic group	Functional group	Species	% cover or individual	Mean biomass (g)
Opisthobranchia	**Scavenger**	Nudibranch	individual	2.4
Opisthobranchia	**Scavenger**	*Phyllodesmium horridus*	individual	2.4
Opisthobranchia	**Scavenger**	*Hypselodoris capensis*	individual	2.4
Asteroidea	**Scavenger**	*Marthasterias glacialis*	individual	269.56
Asteroidea	**Sessile species**	*Callopatiria granifera*	individual	19.95
Asteroidea	**Herbivore**	*Patiriella dyscrita*	individual	4
Asteroidea	**Sessile species**	*Henricia ornata*	individual	10.8
Ophiuroidea	**Sessile species**	*Astrocladus euryale*	individual	269.6
Ophiuroidea	**Sessile species**	*Ophiactis carnea*	individual	0.25
Ophiuroidea	**Sessile species**	*Ophioderma wahlbergi*	individual	16
Ophiuroidea	**Sessile species**	*Ophiothrix fragilis*	individual	1.6
Echinoidea	**Herbivore**	*Parechinus angulosus juv*	individual	0.83
Echinoidea	**Herbivore**	*Parechinus angulosus*	individual	28.5
Crinoidea	**Sessile species**	*Comanthus wahlbergi*	individual	2.63
Crinoidea	**Sessile species**	*Tropiometra carinata*	individual	7.9
Holothuroidea	**Sessile species**	*Holothuroidea*	individual	12
Ascidiacea	**Sessile species**	*Pyura stolonifera*	individual	126.12
Ascidiacea	**Sessile species**	*Styela angularis*	individual	2.4
Ascidiacea	**Sessile species**	*Podoclavella* sp.	individual	2.63
Ascidiacea	**Sessile species**	*Sigillina digitata*	individual	12
Ascidiacea	**Sessile species**	Compound ascidian	% cover	37.4
Ascidiacea	**Sessile species**	Solitary ascidian	individual	1.2

Appendix 2:

Tables A2.01-A2.05 contain data that were used to develop the Base-case model described in Chapter 4.

Appendix Table A2.01: Commercial abalone catches (MT) and estimated recreational abalone catches (MT) for Zones B and D for the period 1951-2007. See Plagányi (2004) for details.

	Zone B		Zone D	
Year	**Commercial**	**Recreational**	**Commercial**	**Recreational**
1951	66	0.6	67	1.3
1952	132	1.1	133	2.7
1953	198	1.7	200	4.0
1954	381	2.2	384	5.3
1955	139	2.8	140	6.6
1956	114	3.3	115	7.9
1957	153	3.8	154	9.2
1958	148	4.4	149	10.5
1959	128	4.9	129	11.8
1960	321	5.4	323	13.1
1961	378	6.0	381	14.4
1962	549	6.5	553	15.7
1963	442	6.9	445	16.9
1964	507	7.4	511	18.1
1965	732	7.8	738	19.2
1966	675	8.2	680	20.4
1967	545	8.4	550	21.4
1968	424	8.8	427	22.5
1969	336	9.1	339	23.7
1970	296	9.6	298	24.9
1971	206	11.1	207	28.8
1972	223	12.8	226	32.8
1973	227	14.4	229	36.9
1974	220	16.1	222	41.0
1975	229	17.8	232	45.0
1976	222	19.5	225	49.1
1977	176	21.1	197	53.2
1978	258	22.8	227	57.2
1979	206	24.4	234	61.3
1980	202	26.1	223	65.3
1981	221	27.7	188	69.2
1982	209	29.3	214	73.2
1983	187	30.9	75	77.2
1984	194.9	32.5	106.5	81.3
1985	162.4	34.2	156.8	85.4
1986	229.4	35.9	50.3	89.4
1987	166.2	37.5	45.2	93.5
1988	138.7	39.1	49.2	97.7
1989	137.3	40.8	52.1	101.8
1990	142.4	44.4	46.3	110.7
1991	138	51.9	49.8	129.1
1992	147.5	55.8	56.3	138.6
1993	152.7	53.8	53.7	130.3
1994	150	105.6	92.5	207.2
1995	152.3	34.3	90.2	163.1
1996	146.8	97.6	90.9	136.1
1997	145.9	100.3	93.2	142.5
1998	148.3	33.1	108.3	90.2
1999	146.7	41.1	104.7	38.0
2000	144.1	37.2	105.2	64.0
2001	135.2	30.9	67.3	35.2
2002	103.3	21.2	47.8	37.9
2003	53.4	26.2	29.9	38.4
2004	151.9	0.0	11	0.0
2005	145	0.0	10	0.0
2006	145	0.0	8	0.0
2007	75	0.0	0	0.0

Appendix Table A2.02: Mean number of urchins and juvenile abalone from the Tarr *et al.* (1996) survey at Betty's Bay for the period 1989-1996.

Year	**urchin numbers.m^{-2}**	**juvenile abalone numbers.m^{-2}**
1989	52.57	8.8
1990	53.44	8.23
1991	44.15	15.84
1992	43.89	12.73
1993	42.11	15.17
1994	15.97	10.01
1995	1	1
1996	1	1

Appendix Table A2.03: West Coast rock lobster (*Jasus lalandii)* catches (MT) for Area 12 (Zone F) for the model period 1985-2007.

	Rock lobster catch (MT)		
Year	**Commercial**	**Recreational**	**Illegal**
1985	0	0	0
1986	0	0	0
1987	0	0	0
1988	0	0	0
1989	0	0	0
1990	0	0	0
1991	0	0	0
1992	0	7.5	0
1993	0	35	0
1994	0	37.5	0
1995	0	37.5	0
1996	0	25.6	0
1997	0	25.6	0
1998	0	25.6	0
1999	0	25.6	0
2000	10	25.6	9
2001	10	25.6	9
2002	9	25.6	9
2003	0	19.5	9
2004	65	20.5	9
2005	66	32.5	9
2006	58	19.5	9
2007	91	20.5	9

Appendix Table A2.04: Commercial CPUE (kg/bakkie/day) and FIMS (lobsters/hoopnet) data for the West Coast rock lobster fishery - Area 12 (Zone F).

Year	Commercial CPUE	
2004	186.47	
2005	170.58	
2006	196.64	
2007	161.28	
2008	123.87	
Year	**FIMS CPUE**	**CV**
2002	9.45	0.238
2003	10.4	0.214
2004	5.61	0.206
2005	11.71	0.177

Appendix Table A2.05: West Coast rock lobster (*Jasus lalandii*) mean length- and mass-at-age. Length-at-age data were taken from Johnston and Butterworth (2001) and mass was calculated using the formula from Heydorn (1969).

Rock lobster length-weight relations		
Age	**Carapace Length (mm)**	**Mass (g)**
1	3.019	0.018
2	4.166	0.047
3	6.424	0.169
4	10.656	0.746
5	17.91	3.425
6	26.138	10.387
7	35.957	26.491
8	46.166	55.176
9	55.465	94.563
10	62.646	135.138
11	67.582	168.909
12	71.041	195.923
13	73.696	218.901
14	76.008	240.829
15	78.074	262.104
16	79.974	283.155
17	81.742	304.046
18	83.398	324.733
19	84.955	345.113
20	86.422	365.128

Appendix 3:

Abalone age-structured production model

The abalone age-structured production model of Plagányi (2004, Appendix 6.1) is reproduced here verbatim, with permission, for ease of reference by the reader. It provides the framework upon which my multispecies model is developed. It must be noted that this is not the current model used in the abalone stock-assessment – the most recent model can be found in Plagányi and Butterworth (in press).

The base-case inshore/offshore population model used for estimating resource dynamics parameters and projecting biomass trends

The model applied is basically an age-structured production model (ASPM) with a spatial extension to allow inshore and offshore components of the resource to be modelled separately with exchange between the two. In each of Zones A, B and D, the resource is modelled using two compartments – an inshore and offshore compartment. Zone C is split further into two subareas, one "poached" (CP) and one "nonpoached" (CNP), and hence the model for this Zone has four compartments. The description which follows is for the Zone C base-case model, but also applies to Zones A, B and D.

1. Dynamics

For each subarea, the dynamics of the **inshore** component are given by:

$$N^I_{y+1,0} = r_I \cdot R(B^{sp}_{y+1}) \tag{A3.1}$$

$$N^I_{y+1,a+1} = \left(N^I_{y,a} e^{-\frac{M_a}{4}} - C^I_{y,a}\right) e^{-\frac{3M_a}{4}} \qquad 0 \le a \le 4 \tag{A3.2}$$

$$N^I_{y+1,a+1} = \left((1-\rho)\cdot N^I_{y,a} e^{-\frac{M_a}{4}} - C^I_{y,a}\right) e^{-\frac{3M_a}{4}} \qquad 5 \le a \le z\text{-}2 \tag{A3.3}$$

$$N^I_{y+1,z} = ((1-\rho)\cdot N^I_{y,z} e^{-\frac{M_z}{4}} - C^I_{y,z})e^{-\frac{3M_z}{4}} + ((1-\rho)\cdot N^I_{y,z-1} e^{-\frac{M_{z-1}}{4}} - C^I_{y,z-1})e^{-\frac{3M_{z-1}}{4}} \tag{A4.4}$$

where	$N^I_{y,a}$	is the *inshore* number of abalone of age a at the start of Model year y,
	ρ	is the proportion of inshore animals of age a ($5 \le a \le z$) that moves offshore at the start of Model year y,
	$C^I_{y,a}$	is the total number of abalone of age a taken by recreational fishers and by poachers in Model year y, as well as the *inshore* number of abalone taken by the commercial fishery,
	$R(B^{sp})$	is the assumed recruitment vs spawning biomass relationship (see below),
	r_I	is the proportion of the recruits that settles inshore,

M_a is the (time-invariant) natural mortality rate on abalone of age a, and
z is the largest age considered (i.e. corresponding to a "plus group").

Similarly, for each subarea, the dynamics of the **offshore** component are given by:

$$N^O_{y+1,0} = r_O \cdot R(B^{sp}_{y+1}) \tag{A3.5}$$

$$N^O_{y+1,a+1} = \left(N^O_{y,a} e^{-\frac{M_a}{4}} - C^O_{y,a}\right) e^{-\frac{3M_a}{4}} \qquad 0 \le a \le 4 \tag{A3.6}$$

$$N^O_{y+1,a+1} = \left((N^O_{y,a} + \rho \cdot N^I_{y,a}) e^{-\frac{M_a}{4}} - C^O_{y,a}\right) e^{-\frac{3M_a}{4}} \qquad 5 \le a \le z\text{-}2 \tag{A3.7}$$

$$N^O_{y+1,z} = ((N^O_{y,z} + \rho \cdot N^I_{y,z}) e^{-\frac{M_z}{4}} - C^O_{y,z})\, e^{-\frac{3M_z}{4}} + ((N^O_{y,z-1} + \rho \cdot N^I_{y,z-1}) e^{-\frac{M_{z-1}}{4}} - C^O_{y,z-1})\, e^{-\frac{3M_{z-1}}{4}} \tag{A3.8}$$

where $N^O_{y,a}$ is the *offshore* number of abalone of age a at the start of Model year y,
r_O is the proportion of the recruits which settle offshore (= 1-r_I), and
$C^O_{y,a}$ is the *offshore* number of abalone of age a taken by the commercial fishery.

The commercial abalone fishery season currently extends from October to June but several historic changes in the commencement and closure dates for the commercial fishing season are on record (see Chapter 3 in Plagányi 2004). For reasons of internal consistency in the assessment process, a standard Model or fishing year y is thus taken to run from October of year y-1 to September of year y. The population model used here assumes pulse fishing (Pope's approximation – Pope 1984), rather than the more customary Baranov catch equations which assume continuous fishing through the year. Pope's approximation has been used in order to simplify computations. As long as mortality rates are not too high, the differences between the Baranov and Pope formulations will be minimal. The approximation of the fishery as a pulse catch at the start of each calendar year is here considered to be of sufficient accuracy given that most of the catch is made over the October-March period, and because the annual catches from this long lived resource are not that large a fraction of the overall biomass. This last reason also constitutes the justification for treating inshore-to-offshore movement as a pulse at the start of the Model year. The equations reflect the fact that catches are subtracted at the end of the first quarter of the Model year (i.e. in the middle of the October-March period of high catches). As the fishery-independent surveys (FIAS) are conducted only towards the end of the second quarter of the Model year, comparisons with the abundance indices obtained from FIAS are made at time $y + \frac{1}{2}$ in terms of the model whereas comparisons with the CPUE data are made at time $y + \frac{1}{4}$ in the model.

Because different sectors of the fishery exhibit different selectivity patterns with age, the following five sectors are explicitly differentiated in the model: the commercial fishery sector (mostly offshore); the recreational sector (mostly inshore); the poaching/illegal sector (mostly inshore), the fishery-independent survey (inshore and offshore) and the "old survey" (inshore and offshore). Note that the small-scale commercial sector of the fishery is not modelled separately in the current analysis but allocations to this sector have simply been added to the commercial catches for 2001 and 2002.

The equations given below are applied separately to each of the inshore and offshore components of the two subareas.

The total number of abalone of age *a* caught each year ($C_{y,a}$) is given by:

$$C_{y,a} = \sum_{s} C^{s}_{y,a} \tag{A3.9}$$

where *s* indicates the sector of the fishery (e.g. commercial, recreational, poaching).

The annual catch by mass (C^{s}_{y}) for sector *s* is given by:

$$C^{s}_{y} = \sum_{a=4}^{z} w_{y,a+\frac{1}{4}} C^{s}_{y,a} \tag{A3.10}$$

where $w_{y,a+\frac{1}{4}}$ is the mass of an abalone of age *a* at the end of the first quarter of Model year *y* (note however that only the plus group mass $w_{y,z}$ is year-dependent in the model formulation pursued and that the plus group mass is modelled separately for the inshore and offshore components). The summation is taken from age *a* = 4 as no abalone of a size corresponding to ages below 4 are taken by any of the fishing sectors.

A von Bertalanffy growth equation is used to relate shell length λ (mm) to age in years (*t*), and is based on tagging data from Betty's Bay (Tarr 1995):

$$\lambda(t) = \lambda_{\infty}[1 - e^{-\kappa(t-t_0)}] \tag{A3.11}$$

The relationship between *shell length* (mm) and abalone whole wet mass (g) is based on data from the Betty's Bay and Danger Point areas and is determined using the following power relationship that was revised from the original during the course of this study:

$$w_{y,a} = w(y, t = a) = c \cdot (\lambda)^{d} \tag{A3.12}$$

Note that mass-at-age is year-independent for abalone of age $a < z$ and that $w_{y,a+\frac{1}{4}} = w(y, t = a + \frac{1}{4})$ is computed for use in calculating the sector-specific exploitable biomasses after the first quarter of each year (see below). However, the mass-at-age for the plus group varies over time, depending on the average age of the inshore and offshore plus group components in year *y*, $\bar{z}^{I}_{y}$ and $\bar{z}^{O}_{y}$ respectively, which are calculated as:

$$\bar{z}^{I}_{y} = \frac{\left(\bar{z}^{I}_{y-1} + 1\right)\left((1-\rho)N^{I}_{y,z} - C^{I}_{y,z}\right)e^{-M_{z}} + z \cdot \left((1-\rho)N^{I}_{y,z-1} - C^{I}_{y,z-1}\right)e^{-M_{z-1}}}{N^{I}_{y,z}} \tag{A3.13}$$

$$\bar{z}^O_y = \frac{\left(\left(\bar{z}^O_{y-1}+1\right)\left(N^O_{y,z} - C^O{}_{y,z}\right) + \left(\bar{z}^I_{y-1}+1\right)\rho\, N^I_{y,z}\right)e^{-M_z} + z\cdot(N^O_{y,z-1} + \rho\, N^I_{y,z-1} - C^O_{y,z-1})e^{-M_{z-1}}}{N^O_{y,z}} \tag{A3.14}$$

The above is an approximation only (as it ignores, e.g., the fact that catches are subtracted not at the start of the year but at the end of the first quarter of each year) but is considered sufficiently accurate for present purposes.

The recreational catch by mass in year *y* is given by:

$$C^s_y = \sum_{a=8}^{z-1} w_{a+1/4} N^I_{y,a}(1-\rho)e^{-M_a/4} S^s_a F^s_y + w^I_{y,\bar{z}_y+1/4} N^I_{y,z}(1-\rho)e^{-M_z/4} S^s_z F^s_y \tag{A3.15}$$

and the poaching catch by mass in year *y* by:

$$\begin{aligned} C^s_y = {} & w_{4+1/4} N^I_{y,4}\, e^{-M/4} S^s_4 F^s_y + \sum_{a=5}^{z-1} w_{a+1/4}\, N^I_{y,a}(1-\rho)e^{-M/4} S^s_a F^s_y \\ & + w^I_{y,\bar{z}_y+1/4}(1-\rho)N^I_{y,z}\, e^{-M/4} S^s_z F^s_y \end{aligned} \tag{A3.16}$$

where S^s_a is the fishing selectivity-at-age for sector *s* (this pattern is assumed not to change over time), $w^I_{y,\bar{z}_y+1/4}$ is the mean mass of the inshore plus group with average age $\bar{z}_y + 1/4$ after the first quarter of Model year *y*, and F^s_y is the fishing "mortality" (strictly here that proportion of the numbers present after the first quarter of the Model year which are caught) at a reference age, set for these computations to be *a* = 11 for all sectors. Based on data from A. Mackenzie (Marine & Coastal Management, pers. comm.), the minimum age of animals assumed caught by the poaching sector is 4 years, so that for this sector $S^s_a = 0$ for $a < 4$. Note also (cf. equation A4.16) that there is no inshore-offshore movement of animals aged four and younger. The commercial and recreational sectors are both assumed not to catch animals below the legal size limit, so that for these sectors $S^s_a = 0$ for $a < 8$.

In the case of the recreational sector (which reports in terms of numbers rather than mass), estimates of the annual catch by mass are computed using equation (A3.15) but it is necessary to first compute the fishing "mortality" F^s_y, using the following relation for the numbers caught in year *y*:

$$N^s_y = \sum_{a=8}^{z} N^I_{y,a}(1-\rho)e^{-M_a/4} S^s_a F^s_y \tag{A3.17}$$

The relative proportions of the Zone C recreational catch (i.t.o. numbers) taken from the two subareas CP and CNP are assumed to be proportional to the relative lengths of the coastline (CP:CNP = 1:2).

The amount of poached abalone is estimated in terms of numbers and hence the following relation is used to compute the fishing "mortality" F_y^s for the poaching sector in year y:

$$N_y^s = \sum_{a=5}^{z} N_{y,a}^I (1-\rho) e^{-M_a/4} S_a^s F_y^s + N_{y,4}^I e^{-M_a/4} S_4^s F_y^s \tag{A3.18}$$

Equations (A3.15) to (A3.18) assume that poaching and recreational activities occur exclusively in the inshore region. In the case of the commercial sector, the 0-2 m depth range is thought to be the only habitat that is almost never fished by commercial divers encroaching inshore because the shallow depth prevents boats from operating easily in these waters. Inshore encroachment by commercial divers is seen as being particularly common in areas that do not have residential houses along the beachfront. Thus, whereas this is thought to be a relatively minor problem in subarea CNP, inshore encroachment by commercial fishers is considered to have been a problem throughout the history of the fishery in subarea CP.

Thus, whereas the commercial catch by mass in year y in subarea CP is given by:

$$C_y^s = \sum_{a=8}^{z-1} w_{a+1/4} \left(N_{y,a}^I + N_{y,a}^O \right) e^{-M_a/4} S_a^s F_y^s + \left(w_{y,\bar{z}_y+1/4}^I N_{y,z}^I + w_{y,\bar{z}_y+1/4}^O N_{y,z}^O \right) e^{-M_z/4} S_z^s F_y^s \tag{A3.19}$$

in subarea CNP, the commercial catch by mass in year y is given by equation (A3.19) above for years prior to 1967, and by equation (A3.20) for years 1967 onwards:

$$C_y^s = \sum_{a=8}^{z-1} w_{a+1/4} \left(N_{y,a}^O + \rho\, N_{y,a}^I \right) e^{-M_a/4} S_a^s F_y^s + \left(w_{y,\bar{z}_y+1/4}^O N_{y,z}^O + \rho\, w_{y,\bar{z}_y+1/4}^I N_{y,z}^I \right) e^{-M_z/4} S_z^s F_y^s \tag{A3.20}$$

where $w_{y,\bar{z}_y+1/4}^O$ is the mean mass of the offshore plus group with average age $\bar{z}_y + 1/4$ after the first quarter of Model year y.

The exploitable ("available") components of abundance for the recreational and poaching sectors are both expressed in terms of population numbers and are computed using equation (A3.21) below for the recreational sector and equation (A3.22) for the poaching sector:

$$B_y^{exp,s} = \sum_{a=8}^{z} S_a^s (1-\rho) N_{y,a}^I e^{-M_a/4} \tag{A3.21}$$

$$B_y^{exp,s} = \sum_{a=5}^{z} S_a^s (1-\rho) N_{y,a}^I e^{-M_a/4} + S_4^s N_{y,4}^I e^{-M_4/4} \tag{A3.22}$$

On the other hand, the exploitable components of abundance for the commercial sector operating in subareas CP (all years) and CNP (years prior to 1967) are computed as:

$$B_y^{exp,s} = \sum_{a=8}^{z-1} S_a^s w_{a+1/4} \left(N_{y,a}^I + N_{y,a}^O \right) e^{-M/4} + S_z^s \left(w_{y,\bar{z}_y+1/4}^I N_{y,z}^I + w_{y,\bar{z}_y+1/4}^O N_{y,z}^O \right) e^{-M/4} \tag{A3.23}$$

and in the case of subarea CNP, exploitable biomass for years from 1967 onwards is computed as:

$$B_y^{exp,s} = \sum_{a=8}^{z-1} S_a^s w_{a+\frac{1}{4}} \left(N_{y,a}^O + \rho N_{y,a}^I \right) e^{-M_a/4} + S_z^s \left(w^O_{y,\bar{z}_y+\frac{1}{4}} N^O_{y,z} + \rho \; w^I_{y,\bar{z}_y+\frac{1}{4}} N^I_{y,z} \right) e^{-M_z/4} \quad \text{(A3.24)}$$

In the case of FIAS, which for these purposes can be considered as another fishery sector *s,* "available" population numbers are given by:

$$N_y^{exp,s} = \sum_{a=5}^{z} S_a^s \left((1-\rho) N_{y.a}^I e^{-M_a/4} - C_{y,a}^I \right) e^{-M_a/4} \quad \text{(A3.25)}$$

The summation is from age $a = 5$ as only animals larger than 100 mm shell length are recorded so as to reduce uncertainty in the estimates due to the non-emergent/cryptic behaviour of juveniles. This corresponds to a minimum sampling age of approximately 5 years, so that for this sector $S_a^s = 0$ for $a < 5$.

The proportion of the resource harvested each year (F_y^s) by sector *s* is given by:

$$F_y^s = C_y^s \; / \, B_y^{exp,s} \quad \text{(A3.26)}$$

so that numbers-at-age removed each year by the poaching and recreational sectors can be computed from:

$$C_{y,a}^s = S_a^s F_y^s (1-\rho) N_{y,a}^I e^{-\frac{M_a}{4}} \quad \text{for } a \geq 5 \quad \text{(A3.27)}$$

and

$$C_{y,a}^s = S_a^s F_y^s N_{y,a}^I e^{-\frac{M_a}{4}} \quad \text{for } a = 4 \text{ (poaching catches)} \quad \text{(A3.28)}$$

In the case of the commercial sector, the numbers-at-age removed each year from subarea CP is given by:

$$C_{y,a}^s = S_a^s F_y^s \left(N_{y,a}^I + N_{y,a}^O \right) e^{-M_a/4} \quad \text{(A3.29)}$$

The commercial numbers-at-age removed from subarea CNP for each of the years prior to 1967 is given by equation (A3.29) above, and then by equation (A3.30) below as from 1967:

$$C_{y,a}^s = S_a^s F_y^s \left(N_{y,a}^O + \rho \cdot N_{y,a}^I \right) e^{-M_a/4} \quad \text{(A3.30)}$$

The annual Zone C catch by the illegal sector C_y^{poach} is modelled by estimating the numbers poached in the year with the greatest level of poaching and then extrapolating this figure to other years using the poaching trend scenarios given in Plagányi (2004, Table 4.4). Three poaching trend scenarios (i.t.o. numbers poached) are considered and are based on poaching confiscation data and a correction factor used to account for changes in policing efficiency (see Chapter 4 in Plagányi 2004). A separate model parameter p_{poach} sets a fixed ratio between the proportions of the resource poached each year from CNP and CP by relating to the exploitation rate for poachers rather than the catch by this sector.

2. Spawning biomass - recruitment relationship

The spawning biomass for each subarea in year y is given by:

$$B_y^{sp} = \sum_{a=1}^{z-1} f_a w_a \left(N_{y,a}^I + N_{y,a}^O\right) + f_z \left(w_{y,\bar{z}_y}^I N_{y,z}^I + w_{y,\bar{z}_y}^O N_{y,z}^O\right) \qquad \text{(A3.31)}$$

where f_a is the proportion of abalone of age a that is mature. Note that this formulation assumes independence of subareas in terms of recruitment, *viz*. the recruitment in one subarea depends only on the spawning biomass in that subarea and not on the biomass in adjoining subareas.

The number of recruits in each of the two subareas at the start of Model year y is related to the spawner stock size by a stock-recruitment relationship. A Beverton-Holt form (Beverton and Holt 1957) is assumed, i.e. :

$$R\left(B_y^{sp}\right) = \frac{\alpha\, B_y^{sp}}{\beta + B_y^{sp}} \qquad \text{(A3.32)}$$

Note from equations (A3.1) and (A3.5) that the relative proportion of recruits settling inshore versus offshore in each subarea is determined by parameter r_I.

In order to work with estimable parameters that are more meaningful biologically, the stock-recruit relationship is re-parameterised in terms of the pre-exploitation equilibrium spawning biomass, B_0^{sp}, and the "steepness" of the stock-recruit relationship, where "steepness" is the fraction of pristine recruitment that results when spawning biomass drops to 20% of its pristine level, i.e.

$$hR_0 = R\left(0.2B_0^{sp}\right) \qquad \text{(A3.33)}$$

from which it follows that:

$$h = 0.2\left[\beta + B_0^{sp}\right] / \left[\beta + 0.2B_0^{sp}\right] \qquad \text{(A3.34)}$$

and hence:

$$\alpha = \frac{4hR_0}{5h-1} \qquad \text{(A3.35)}$$

and: $$\beta = \frac{B_0^{sp}(1-h)}{5h-1} \qquad \text{(A3.36)}$$

3. Starting values for biomass trajectories

The resource is assumed to be at the deterministic equilibrium (corresponding to an absence of harvesting) at the start of 1951, the initial year considered here. Given a value for the pre-exploitation spawning biomass B_0^{sp} of abalone, together with the assumption of an initial equilibrium age structure, it follows that on a subarea basis:

$$B_0^{sp} = R_0 \cdot \left[\sum_{a=1}^{z-1} f_a w_a \exp\left(-\sum_{a'=0}^{a-1} M_{a'}\right) + f_z w_{0,\bar{z}_0} \frac{\exp\left(-\sum_{a'=0}^{z-1} M_{a'}\right)}{1-\exp(-M_z)} \right] \tag{A3.37}$$

which can be solved for *R₀*. Note that here $w_{0,\bar{z}_0}$ means the equilibrium value of this quantity prior to exploitation, computed using the equilibrium plus group mean age $\bar{z}_0$, where:

$$\bar{z}_0 = z + \frac{e^{-M_{z-1}}}{1-e^{-M_z}} \tag{A3.38}$$

The initial **inshore** numbers at age for the projections, corresponding to the deterministic equilibrium, are:

$$\begin{aligned}
N_{0,0}^I &= r_I R_0 \\
N_{0,a+1}^I &= N_{0,a}^I e^{-M_a} && 0 \le a \le 4 \\
N_{0,a+1}^I &= N_{0,a}^I (1-\rho) e^{-M_a} && 5 \le a \le z-2 \\
N_{0,z}^I &= \frac{N_{z-1}^I (1-\rho) e^{-M_{z-1}}}{1-(1-\rho)e^{-M_z}}
\end{aligned} \tag{A3.39}$$

Similarly, the initial **offshore** numbers at age, corresponding to the deterministic equilibrium, are:

$$\begin{aligned}
N_{0,0}^O &= (1-r_I) R_0 \\
N_{0,a+1}^O &= N_{0,a}^O e^{-M_a} && 0 \le a \le 4 \\
N_{0,a+1}^O &= N_{0,a}^O e^{-M_a} + N_{0,a}^I \rho e^{-M_a} && 5 \le a \le z-2 \\
N_{0,z}^O &= \frac{N_{z-1}^O e^{-M_{z-1}} + \rho\left(N_{0,z}^I e^{-M_z} + N_{0,z-1}^I e^{-M_{z-1}}\right)}{1-e^{-M_z}} && a = z
\end{aligned} \tag{A3.40}$$

It follows from the steady-state solutions to these equations that the inshore and offshore equilibrium plus group mean ages are as follows:

$$\begin{aligned}
\bar{z}_0^I &= z + \frac{(1-\rho)e^{-M_{z-1}}}{1-(1-\rho)e^{-M_z}} \\
\bar{z}_0^O &= z + \frac{e^{-M_{z-1}}}{1-e^{-M_z}} + \frac{\rho\, e^{-M_{z-1}}}{\left(1-e^{-M_z}\right)\left(1-(1-\rho)e^{-M_z}\right)} \cdot \frac{N_{0,z}^I}{N_{0,z}^O}
\end{aligned} \tag{A3.41}$$

Numbers-at-age for subsequent years are then computed by means of equations (A3.1)-(A3.36).

4. Parameter Values

Input parameters:

The following fixed parameter values are used in the model. The three von Bertalanffy parameters are from Tarr (1995) and the two mass-length relationship parameters were computed in this study:

λ_∞ = 172.76 mm

κ = 0.186 yr^{-1}

t_0 = 0 yr (and is assumed to correspond to October because Tarr (1995) tagged animals *in situ* in October and November)

c = 0.000098 $\text{gm/mm}^{3.155}$

d = 3.1549

with the computations assuming a plus group at age z = 15 yrs.

The proportion of abalone of age a that are mature is approximated by $f_4 = 0.25$, $f_5 = 0.5$, $f_6 = 0.75$ and $f_a = 1$ for $a \geq 7$ (Tarr 1995).

Moreover, the base-case assumes that h = 0.7. The base-case value of the steepness parameter h corresponds roughly to the median (h = 0.74) of a distribution of h values for stock-recruit functions fitted to the fisheries stock recruitment database developed by R.A. Myers and colleagues (Myers *et al*. 1995), as advised by J. Ianelli (pers. comm.).

Estimable parameters:

The sector-specific fishing selectivities S_a^s (including those for FIAS) are assumed to follow the functional form:

$$S_a^s = \frac{P \cdot e^{-\mu a}}{1 + e^{-\delta(a - \tilde{a})}} \tag{A3.42}$$

where μ, δ and $\tilde{a}$ are three estimable parameters that control the shape of the function and P is simply a scalar fixed at a value such that S_{11}^s = 1.00. In essence, μ controls the slope of the right hand limb of the function, δ controls the steepness of the ascending left hand limb, and $\tilde{a}$ shifts the function to the left or right, all in relation to age a.

The assumption that commercial selectivity parameters are the same for the inshore and offshore compartments might seem severe, given the greatly different age profiles of abalone in the inshore and offshore areas. Note however that only a small component of the commercial fishing takes place in the inshore region (the numbers of commercially exploitable size in that region being small), so that even if the assumption is in error, the impact on results should not be substantial.

Under the assumption that the sampling methodology is the same inshore and offshore, the same selectivity parameters are used for the inshore and offshore FIAS sectors. A separate selectivity function is used to compute model-predicted catch-at-age when fitting to the "old survey" data and it is again assumed that the same parameters apply to the inshore and offshore regions.

5. The likelihood function

Below follows the likelihood function which is maximised in the parameter estimation process. The model is fitted to CPUE and FIAS abundance and catch-at-age data from all sectors (commercial, recreational, poaching, old survey, inshore FIAS and deep (offshore) FIAS) and the contributions by each of these to the negative of the log-likelihood (*-ln L*) calculated as described below.

Abundance data:

The likelihood contribution is calculated assuming that the observed abundance index is log-normally distributed about its expected value:

$$I_y^s = \hat{I}_y^s e^{\varepsilon_y^s} \qquad \text{or} \qquad \varepsilon_y^s = \ln(I_y^s) - \ln(\hat{I}_y^s) \tag{A3.43}$$

where I_y^s is the abundance index for year y and sector s,

$\hat{I}_y^s = q^s \, B_y^{exp,s}$ is the corresponding model estimated value, where $B_y^{exp,s}$ is the model value for exploitable resource biomass corresponding to sector s, given by equations (A4.21- A4.24) (if the index refers to numbers, $B_y^{exp,s}$ is replaced by $N_y^{exp,s}$ - see equation (A4.25)).

q^s is the constant of proportionality for abundance series corresponding to sector s, and

ε_y^s from $N\left(0, \left(\sigma_y^s\right)^2\right)$.

The contribution of the abundance data to the negative of the log-likelihood function (after removal of constants) is given then by:

$$-\ln L = \sum_s \left[\sum_y \ln \sigma_y^s + \left(\varepsilon_y^s\right)^2 / 2\left(\sigma_y^s\right)^2 \right] \tag{A3.44}$$

Variance unspecified: (CPUE abundance series)

In this case the standard deviation of the residuals for the logarithms of abundance series *s* is assumed to be independent of *y*, and is estimated in the fitting procedure by its maximum likelihood value:

$$\hat{\sigma}^s = \sqrt{\frac{1}{n_s} \sum_y \left(\ln I_y^s - \ln \hat{I}_y^s\right)^2} \tag{A3.45}$$

where n_s is the number of data points for the abundance series corresponding to sector *s*.

The catchability coefficient q^s for the abundance index of sector *s* is estimated by its maximum likelihood value:

$$\ln \hat{q}^s = \frac{1}{n_s} \sum_y \left(\ln I_y^s - \ln \hat{B}_y^{exp,s}\right) \tag{A3.46}$$

Variance specified: (FIAS data)

The catchability coefficient q^s for such a sector's abundance index is estimated by its maximum likelihood value which, for the case of a log-normal error distribution, is given by:

$$\ln \hat{q}^s = \frac{\sum_y 1 \big/ \left(\sigma_y^s\right)^2 \left(\ln I_y^s - \ln \hat{B}_y^{exp,s}\right)}{\sum_y 1 \big/ \left(\sigma_y^s\right)^2} \tag{A3.47}$$

where $\left(\sigma_y^s\right)^2 = \ln\left(1 + \left(CV_y\right)^2\right)$ and the coefficient of variation (CV_y) of the resource abundance estimate for year *y* is input.

Catches-at-age:

The likelihood contribution is calculated assuming a log-normal error distribution and by making an adjustment (suggested by A. Punt, pers. comm.) to weight in relation to the observed proportions so that undue importance is not attached to poorly represented age classes:

$$-\ln L = \sum_s \sum_y \sum_a \left[\ln\left(\sigma_c^s \Big/ \sqrt{p_{y,a}^s}\right) + p_{y,a}^s \left(\ln(\delta + p_{y,a}^s) - \ln(\delta + \hat{p}_{y,a}^s)\right)^2 \Big/ 2\left(\sigma_c^s\right)^2 \right] \quad \text{(A3.48)}$$

where $p_{y,a}^s = C_{y,a}^s \Big/ \sum_{a'} C_{y,a'}^s$ is the observed proportion of abalone caught/sampled by sector s in year y that are of age a,

$\delta = 0.05$ is a constant included because not all of the $p_{y,a}^s$ values are nonzero,

σ_c^s is the standard deviation associated with the catch-at-age data for sector s, estimated in the fitting procedure by:

$$\sigma_c^s = \sqrt{\sum_y \sum_a p_{y,a}^s \left(\ln(\delta + p_{y,a}^s) - \ln(\delta + \hat{p}_{y,a}^s)\right)^2 \Big/ \sum_y \sum_a 1} \quad \text{(A3.49)}$$

and $\hat{p}_{y,a}^s = \hat{C}_{y,a}^s \Big/ \sum_{a'} \hat{C}_{y,a'}^s$ is the model-predicted proportion of abalone caught/sampled by sector s in year y that are of age a.

For subarea CNP, the earliest catch-at-age data are from 1980 and hence correspond to the period during which all commercial catches are assumed taken from the offshore region, so that $\hat{C}_{y,a}^s$ is given by:

$$\hat{C}_{y,a}^s = \left(N_{y,a}^O + \rho N_{y,a}^I\right) e^{-\frac{M_a}{4}} S_a^s F_y^s \quad \text{(A3.50)}$$

whereas for subarea CP, $\hat{C}_{y,a}^s$ is determined as follows:

$$\hat{C}_{y,a}^s = \left(N_{y,a}^I + N_{y,a}^O\right) e^{-\frac{M_a}{4}} S_a^s F_y^s \quad \text{(A3.51)}$$

The model-predicted recreational catch-at-age data is based on abalone assumed caught from both the CNP and CP subareas, such that for this sector:

$$\hat{C}_{y,a}^s = \left((1-\rho_{CNP}) N_{y,a}^{I_{CNP}} + (1-\rho_{CP}) N_{y,a}^{I_{CP}}\right) e^{-\frac{M_a}{4}} S_a^s F_y^s \quad \text{(A3.52)}$$

except in the case of the single year’s (1997) recreational catch-at-age data from subarea CP, for which $\hat{C}_{y,a}^s$ is computed as:

$$\hat{C}_{y,a}^s = (1-\rho) N_{y,a}^{I_{CP}} e^{-\frac{M_a}{4}} S_a^s F_y^s \quad \text{(A3.53)}$$

The poached catch is taken primarily from the inshore region of subarea CP and hence equation (A3.53) above is used to calculate $\hat{C}_{y,a}^s$ for the poaching sector.

The FIAS, "old survey" and industry survey catches-at-age are similarly incorporated into the negative of the log-likelihood, except that comparisons with observed proportions are made at mid-year rather than after the first quarter of each Model year. Data from the inshore FIAS stations is assumed to correspond to the inshore model region whereas data from the deep FIAS stations is assumed to correspond to the offshore model region. The 0-5 m and 5-15 m "old survey" data are assumed to respectively correspond to the inshore and offshore model regions. Thus, for each subarea, the inshore FIAS and inshore "old survey" model-predicted numbers of abalone of age *a* sampled are computed as:

$$\begin{aligned} \hat{C}^s_{y,a} &= \left(N^I_{y.a}e^{-\frac{M_a}{4}} - C^I_{y,a}\right)e^{-\frac{M_a}{4}} S^s_a F^s_y & a < 5 \\ \hat{C}^s_{y,a} &= \left((1-\rho)N^I_{y.a}e^{-\frac{M_a}{4}} - C^I_{y,a}\right)e^{-\frac{M_a}{4}} S^s_a F^s_y & a \geq 5 \end{aligned} \qquad \text{(A3.54)}$$

and $\hat{C}^s_{y,a}$ for the deep FIAS and offshore "old survey" are given by:

$$\begin{aligned} \hat{C}^s_{y,a} &= \left(N^O_{y.a}e^{-\frac{M_a}{4}} - C^O_{y,a}\right)e^{-\frac{M_a}{4}} S^s_a F^s_y & a < 5 \\ \hat{C}^s_{y,a} &= \left(\left(N^O_{y.a} + \rho\, N^I_{y,a}\right)e^{-\frac{M_a}{4}} - C^O_{y,a}\right)e^{-\frac{M_a}{4}} S^s_a F^s_y & a \geq 5 \end{aligned} \qquad \text{(A3.55)}$$

Data from the 2002 industry “total population size composition” survey are assumed representative of the entire Zone C area and hence $\hat{C}^s_{y,a}$ for the industry survey is computed by summing over mid-year inshore and offshore regions for both CNP and CP.

The summation of the above quantities over age *a* is taken from the minimum age (or minus group where applicable) to the plus group for each catch-at-age series as summarised in Table 3.6 (Plagányi 2004). This was necessary because of small sample sizes outside these age ranges.

Inspection of the various –ln *L* contributions has revealed that the catch-at-age –ln *L* contributions are substantially larger than those for CPUE and the FIAS series, in part because they include many more data points as a result of summation over age as well as year. This is questionable as the $p^s_{y,a}$ values for a given *y* and *s* are not likely to be independent of each other (as implicitly assumed by equation (A3.48)), because the cohort-slicing method used to provide the catch-at-age information from length composition data likely introduces positive correlation. The catch-at-age –ln *L* contributions are thus downweighted by a multiplicative factor of 0.1, thereby downscaling these contributions to a similar order of magnitude as the CPUE and FIAS contributions.

6. Literature cited in Appendix 3

Beverton, R.J.H. and S.J. Holt. 1957. *On the dynamics of exploited fish populations*. Fisheries Investment Series 2, Vol. **19**, U.K. Ministry of Agriculture and Fisheries, London. 533 pp.

Myers, R. A., Bridson, J. and N.J. Barrowman. 1995. Summary of worldwide stock and recruitment data. *Canadian Technical Report of Fisheries and Aquatic Sciences* **2024**: 327.

Pope, J.G. 1984. Notes of the scientific problems of TAC management. Papers presented at the Expert Consultation on the regulation of fishing effort. Rome, 17–26 January 1983. FAO Fisheries Report No. 289 Supplement 2, FAO, Rome.

Appendix 4:

Holling (1959) described three types of functional responses (Appendix Fig A4.01) – Type I is a linear response in which predator consumption increases linearly with prey density, eventually reaching a plateau at predator satiation; Type II is an asymptotic response in which consumption rate increases at a decelerating rate and gradually levels off at a maximum rate when predators become satiated; and Type III is a sigmoid response in which consumption rate accelerates at first and then decelerates as predators reach satiation.

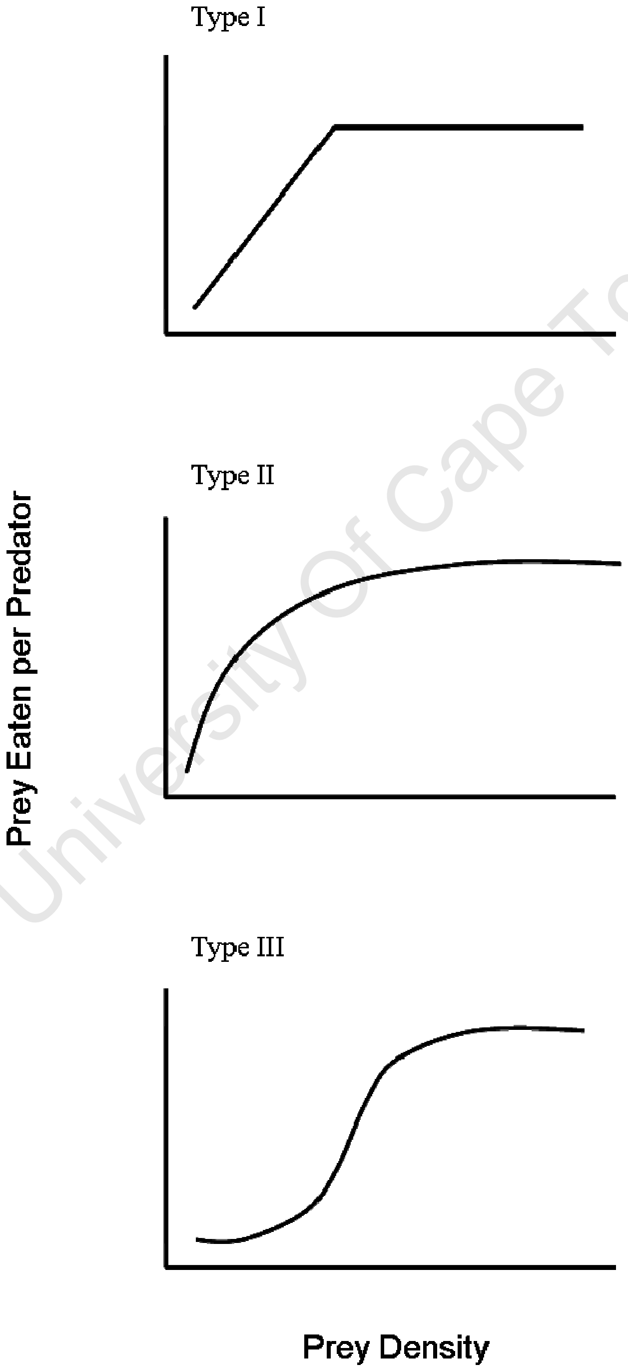


Fig A4.01: Type I, II and III Holling functional responses.

Appendix 5:

Full parameter estimation

The full set of base-case model parameter estimates is given in Appendix Table A5.01. In addition, results are shown from a model version with all parameters freed such that the abalone parameters for Zones B and D were estimated simultaneously with the six new parameters ($B^{J}_{y_0}$, α_{Ab_J}, β_{Ab_J}, α_{U_J}, β_{U_J} and K^{sp}_{J}). The model had trouble converging with the changes to the abalone parameters shown in Appendix Table A5.01. The latter model version results in an improved fit to the data. The main improvement is to the Zone D fit to the FIAS data (Appendix Table A5.01) and this results in a lower depletion estimate for Zone D. However, the version with all parameters estimated simultaneously is problematic from a number of other perspectives: a) the rock-lobster starting biomass was reduced considerably (139 MT); b) the lobster fishing mortality estimates are unrealistically large, for both the recreational fishery (F = 0.6) and commercial fishery (F = 0.5), and c) the lobster spawning biomass trend doesn't appear very realistic (Appendix Fig A5.01).

As explained previously, one of the difficulties in modelling this system is the potential confounding between three sources of mortality: natural mortality, poaching and mortality due to the lobster invasion. This is resolved to some extent in the underlying stock assessment model by fitting simultaneously to Zones A, B, C and D, and through the use of a full population survey contrasting Zones C and B (Plagányi and Butterworth in press). For this reason, the mortality and poaching estimates thus estimated are held constant in the extended multispecies model developed here, and the focus is instead on explicitly representing the lobster invasion. This is facilitated by fixing the other sources of mortality in the base-case model version, thereby assisting in quantifying the complex and uncertain inter-specific interactions in the model. When all the model parameters are freed and re-estimated, some trade-offs between parameters result, with changes to the natural mortality and poaching estimates (Appendix Table A5.01). This should be further explored in future work, but was not adopted as the base-case model here for the reasons outlined above.

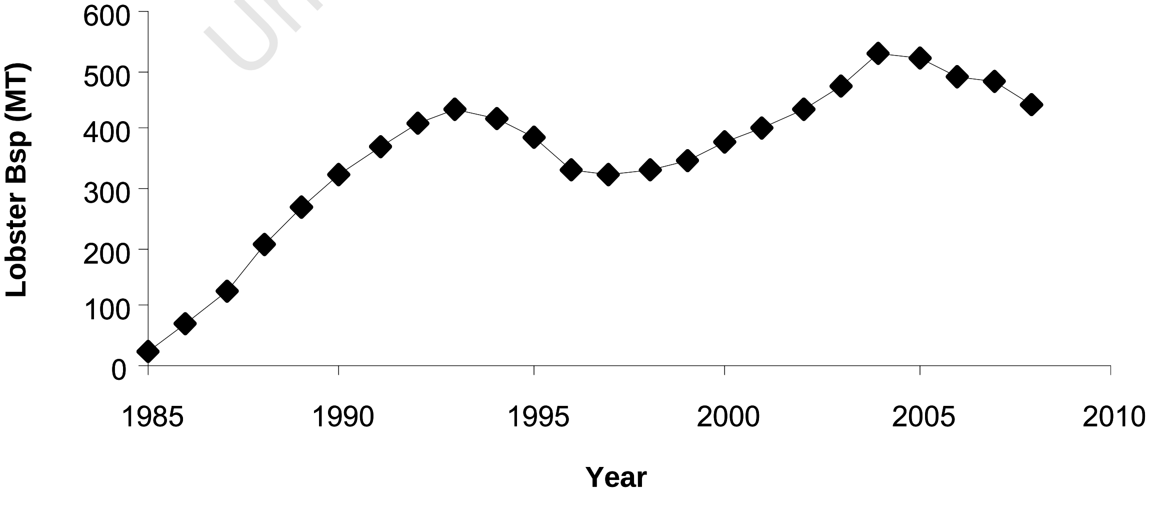


Fig A5.01: Trend in rock lobster spawning biomass (MT) for the model period 1985-2007 when all parameters are estimated.

Appendix Table A5.01: Comparison between the Base-case model (abalone parameters fixed) and the model in which abalone parameters were estimated (except r^I, and the selectivities (a, μ, δ) for IS, which were kept fixed). 'Common' refers to parameters that are common for both Zones. Estimates are given for the following abalone parameters: pre-exploitation spawning biomass $B(0)^{sp}$ (or K), the inshore/offshore migration ρ, the recruitment proportion r^I, the poaching maximum CP_{max} (i.t.o. numbers and biomass), the mortality parameter μ, sector selectivity parameters (a, μ, δ) for commercial (CS), recreational (RS), poaching (PS), FIAS (FS), old survey (OS) and industry survey (IS) sectors; the lobster starting biomass B_0^J; the lobster carrying capacity K^J; the abalone-lobster interaction parameters α_{Ab_J}, β_{Ab_J} and the urchin-lobster interaction parameters α_{U_J}, β_{U_J}. Values of the negative log likelihood (-*ln* L) are also shown.

Model	Base model			All parameters		
No. parameters estimated	6			27		
Zone	B	D	Common	B	D	Common
$B(0)^{sp}$ (MT)	5843	9647		5722	8272	
ρ	0.00053			0.00017		
r^I	0.9	0.9		0.9	0.9	
Cpmax (no.)	730399	576207		553703	391496	
Cpmax (MT)	335	417		285	313	
Mpar (μ)			0.126254			0.114245
a(CS)			8.999			8.999
a(RS)			8.998			8.998
a(PS)			4.903			4.987
a(FS)			6.509			7.766
a(OS)			4.678			5.182
a(IS)			5.811			5.811
μ *(CS)*			0.000			0.000
μ *(RS)*			0.001			0.001
μ *(PS)*			0.000			0.000
μ *(FS)*			0.002			0.002
μ *(OS)*			0.000			0.000
μ *(IS)*			0.002			0.002
δ *(CS)*			896.5			984.6
δ *(RS)*			134.9			264.7
δ *(PS)*			306.2			305.6
δ *(FS)*			0.9			0.6
δ *(OS)*			0.6			0.5
δ *(IS)*			0.6			0.6
B_0^J (MT)		314.0			139.0	
K^J (MT)		1510.6			1976.7	
α_{Ab_J}		0.00703			0.00980	
β_{Ab_J}		5.76799			5.85996	
α_{U_J}		0.00192			0.00400	
β_{U_J}		0.00023			0.00017	
	B	D	Common	B	D	Common
-*ln* L CPUE	-49.910	-30.866		-51.856	-32.071	
-*ln* L FIAS	-8.185	3.559		-7.230	-1.929	
-*ln* L age CS	-18.223	-10.045		-18.375	-9.498	
-*ln* L age RS	-7.041	-6.407		-7.942	-7.986	
-*ln* L age PS	-1.634	0.202		-4.961	0.103	
-*ln* L age FIAS	-8.387	-1.378		-9.690	-0.979	
-*ln* L age OS inshore	-1.071	-1.127		-0.999	-0.642	
-*ln* Lage OS offsh.	-1.389	-2.034		-1.751	-1.544	
-*ln* L age IS insh+offsh.	-0.990	0.000		-1.013	0.000	
-*ln* L CPUE lobster		-9.65231			-9.60707	
-*ln* L FIMS		-1.893			-1.713	
-*ln* L abalone survey		-1.867			-2.668	
-*ln* L urchin survey		1.622			-0.782	
-*ln* L zone subtotal	-96.831	-59.885		-103.817	-69.315	
-*ln* L TOTAL & AIC		**-156.716**			**-173.132**	
σ CPUE	0.097	0.197		0.091	0.188	
σ age CS	0.074	0.108		0.073	0.112	
σ age RS	0.067	0.084		0.058	0.067	
σ age PS	0.161	0.199		0.106	0.196	
σ age FIAS	0.082	0.161		0.071	0.171	
σ OS insh.	0.063	0.062		0.067	0.097	
σ OS offsh.	0.054	0.031		0.041	0.045	
σ IS	0.037	0.000		0.036	0.000	
σ CPUE lobster		0.0972508			0.0981347	
q CPUE	0.0006147	0.0002470		0.0006897	0.0003011	
q CPUE lobster		0.6269820			0.8989630	
q FIMS		0.0000023			0.0000026	
q abalone survey		0.0000018			0.0000031	
q urchin survey		0.0000001			0.0000002	
Depletion statistics						
B^{sp}(2007)/K (Insh. + Offsh)	0.30	0.18		0.27	0.11	
B^{sp}(2007)/K (Insh.)	0.23	0.00		0.25	0.03	
B^{sp}(2007)/K (Offsh.)	0.38	0.41		0.36	0.36	
FIAS N_{2007}/N_{1951}	0.27	0.000		0.34	0.001	
B^J (2007)/B^J (1985)		0.60			0.65	

Literature cited

Allee, W.C., Emerson, A.E. and O. Park. 1949. Principles of animal ecology. W.B. Saunders, Philadelphia, PA.

Anderson, M.J., Gorley, R.N. and K.R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-E: Plymouth, UK, 214 pp.

Anderson, R.J., Carrick, P., Levitt, G.J. and A. Share. 1997. Holdfast of adult kelp *Ecklonia maxima* provide refuges from grazing for recruitment of juvenile kelps. *Marine Ecology progress Series* **159**: 265-273.

Anderson, R.J., Rothman, M.D., Share, A. and H. Drummond. 2006. Harvesting of the kelp *Ecklonia maxima* in South Africa affects its three obligate, red algal epiphytes. *Journal of Applied Phycology* **18**: 343-349.

Andrew, N.L. 1993. Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in temperate Australia. *Ecology* **74**: 292-302.

Andrew, N.L. and A.J. Underwood. 1993. Density-dependent foraging in the sea urchin *Centrostephanus rodgersii* on shallow subtidal reefs in New South Wales, Australia. *Marine Ecology Progress Series* **99**: 89-98.

Andrew, N.L. and A.L. O'Neill. 2000. Large-scale patterns in habitat structure on subtidal rocky reefs in New South Wales. *Marine and Freshwater Research* **51**:255-263.

Andrew, N.L. and M. Byrne. 2001. The ecology of *Centrostephanus rogersii*. In: *Edible sea urchins: biology and ecology*. Lawrence, J.M. (Ed), Elsevier: pp. 149-160.

Annala, J.H. and B.L. Bycroft. 1993. Movements of rock lobsters (*Jasus edwardsii*) tagged in Fiordland, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **27**: 183-190.

Atkinson, L.J. 2001. *Large and small-scale movement patterns of the West Coast rock lobster Jasus lalandii*. M.Sc. Thesis, University of Cape Town. 100 pp.

Atkinson, L. J. and G.M. Branch. 2003. Longshore movements of adult male *Jasus lalandii*: evidence from long-term tag recaptures. *African Journal of Marine Science* **25**: 387-390.

Attwood, C. and M. Farquhar. 1999. Collapse of linefish stocks between Cape Hangklip and Walker Bay, South Africa. *South African Journal of Marine Science* **21**: 415-432.

Babcock, R.C. and J. Keesing. 1999. Fertilization biology of the abalone *Haliotis laevigata*: laboratory and field studies. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1668-1678.

Babcock, R.C., Kelly, S., Shears, N.T., Walker, J.W. and T.J. Willis. 1999. Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series* **189**: 125-134.

Barkai, A. and G.M. Branch. 1988a. Contrasts between the benthic communities of subtidal hard substrata at Marcus and Malgas Islands: A case study of alternative stable states? *South African Journal of Marine Science* **7**: 117-137.

Barkai, A. and G.M. Branch. 1988b. The influence of predation and substratal complexity on recruitment to settlement plates: a test of the theory of alternative states. *Journal of Experimental Marine Biology and Ecology* **124**: 215-237.

Barkai, A. and G.M. Branch. 1988c. Energy requirements for a dense population of rock lobsters *Jasus lalandii*: novel importance of unorthodox food sources. *Marine Ecology Progress Series* **50**: 83-96.

Barkai, A. and C. McQuaid. 1988. Predator-prey role reversal in a marine benthic ecosystem. *Science* **242**: 62-64.

Barkai, A., Davis, C.L. and S. Tugwell. 1996. Prey selection by the South African cape rock lobster *Jasus lalandii*: ecological and physiological approaches. *Bulletin of Marine Science* **58**: 1-8.

Barrett, N.S., Buxton, C.D. and G.J. Edgar. 2009a. Changes in invertebrate and macroalgal populations in Tasmanian marine reserves in the decade following protection. *Journal of Experimental Marine Biology and Ecology* **370**: 104-119.

Barrett, N.S., Buxton, C.D. and C. Gardner. 2009b. Rock lobster movement patterns and population structure within a Tasmanian Marine Protected Area inform fishery and conservation management. *Marine and Freshwater Research* **60**: 417-425.

Baum, J.K. and B. Worm. 2009. Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*. doi: 10.1111/j.1365-2656.2009.01531.x

Bellwood, D.R., Hughes, T.P., Folke, C. and M. Nyström. 2004. Confronting the coral reef crisis. *Nature* **429**: 827-833.

Bennett, B.A. and C.L. Griffiths. 1986. Aspects of the biology of Galjoen *Coracinus capensis* (Cuvier) off the south-western Cape, South Africa. *South African Journal of Marine Science* **4**: 153-162.

Beverton, R.J.H. and S.J. Holt. 1957. *On the dynamics of exploited fish populations*. Fisheries Investment Series 2, Vol 19, U.K. Ministry of Agriculture and Fisheries, London.

Branch, G.M. 1975. Mechanisms reducing intraspecific competition in *Patella* spp.: migration, differentiation and territorial behaviour. *Journal of Animal Ecology* **44**: 575-606.

Branch, G.M. 2007. Trophic interactions in subtidal rocky reefs on the west coast of South Africa. In: *Food Webs and the Dynamics of Marine Reefs*. Branch, G.M. and T.R. McClanahan (Eds.). Oxford University Press, Inc., New York: pp 50-78.

Branch, G.M. and C.L. Griffiths. 1988. The Benguela ecosystem Part V. The coastal zone. *Oceanography and Marine Biology Annual Review* **26**: 395-486.

Breen, P.A. and K.H. Mann. 1976. Changing lobster abundance and the destruction of kelp beds by sea urchins. *Marine Biology* **34**: 137-142.

Breitburg, D.L. 1984. Residual effects of grazing: inhibition of competitor recruitment by encrusting coralline algae. *Ecology* **65**: 1163-1143.

Bogstad, B., Hauge, K.H., and Ø. Ulltang. 1997. MULT-SPEC – A multispecies model for fish and marine mammals in the Barents sea. *Journal of Northwest Atlantic Fisheries Science* **22**: 317-341.

Bolton, J.J. 1986. Marine phytogeography of the Benguela upwelling region on the west coast of southern Africa: a temperature dependent approach. *Botanica Marina* **29**: 251-156.

Bulleri, F., Bertocci, I. and F. Micheli. 2002. Interplay of encrusting coralline algae and sea urchins in maintaining alternative habitats. *Marine Ecology Progress Series* **243**: 101-109.

Burnham, K.P. and D.R. Anderson. 2002. *Model selection and multi-model inference: a practical information-theoretic approach*. Springer, New York. 353 pp.

Bustamante, R.H. and G.M. Branch. 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. *Journal of Experimental Marine Biology and Ecology* **196**: 1-28.

Butterworth, D.S. 2008. Some lessons from implementing management procedures. In: *Fisheries for Global Welfare and Environment*. Tsukamoto, K., Kawamura, T., Takeuchi, T., Beard, T.D. Jr., Kaiser, M.J. (Eds). 5th World Fisheries Congress 2008, TERRAPUB, Tokyo: pp. 381-397.

Butterworth, D.S. 2009. Comments regarding the Allee effect and the South African abalone resource NRF-MCM Stock Assessment Workshop. International scientific review of assessments of the South African hake and abalone resources. MARAM IWS/DEC09/AP/12. 1 p.

Butterworth, D.S. and J. Harwood (Eds). 1991. Report on the Benguela ecology programme workshop on seal-fishery biological interactions. *Reports of the Benguela Ecology Programme of South Africa* **22**: 65 pp.

Butterworth, D.S. and É.E. Plagányi. 2004. A brief introduction to some approaches to multispecies/ecosystem modelling in the context of their possible application in the management of South African fisheries. *African Journal of Marine Science* **26**: 53-61.

Butterworth, D.S., Punt, A.E., Oosthuizen, W.H. and P.A. Wickens. 1995. The effects of future consumption by the Cape Fur seal on catches and catch rates of the Cape hakes. 3. Modelling the dynamics of the Cape Fur seal *Arctocephalus pusillus pusillus*. *South African Journal of Marine Science* **16**: 161-183.

Buxton, C.D. 1984. Feeding biology of the Roman *Chrysoblephus laticeps* (Pisces: Sparidae). *South African Journal of Marine Science* **2**: 33-42.

Buxton, C.D. 1987. *Life history changes of two reef fish species in exploited and unexploited marine environments in South Africa*. Ph.D. Thesis, Rhodes University, 215 pp.

Buxton, C.D. 1993. Life-history changes in exploited reef fishes on the east coast of South Africa. *Environmental Biology of Fishes* **36**:47-63.

Byrnes, J., Stachowicz, J.J., Hultgren, K.M., Hughes, A.R., Olyarnik, S.V. and C.S. Thornbert. 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. *Ecology Letters* **9**: 61-71.

Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* **56**: 345-364.

Carpenter, R.C. 1988. Mass mortality of *Diadema antillarum* 1. Long-term effects on sea urchin population-dynamics and coral reef algal communities. *Marine Biology* **104**: 67-77.

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. and C. Moreno. 1982. Sea urchins and *Macrocystis pyrifera*: experimental test on their ecological relations in southern Chile. In: *International echinoderm conference, Tampa Bay*. Lawrence, J.M. (Ed) A.A. Balkema, Rotterdam: pp. 257-263.

Choat, J.H. and D.R. Schiel. 1982. Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *Journal of Experimental Marine Biology and Ecology* **60**: 129-162.

Christensen, V. and D. Pauly. 1992. ECOPATH II – a software for balancing steady-state models and calculating network characteristics. *Ecological Modelling* **61**: 169-185.

Clark, R.P., Edwards, M.S. and M.S. Foster. 2004. Effects of shade from multiple kelp canopies on an understory algal assemblage. *Marine Ecology Progress Series* **267**: 107-119.

Clarke, K.R. and R.N. Gorley. 2006. PRIMER v6: User manual/tutorial. PRIMER-E: Plymouth, UK, 190 pp.

Cochrane, K.L., Augustyn, C.J., Cockcroft, A.C., David, J.H.M., Griffiths, M.H., Groeneveld, J.C., Lipinski, M.R., Smale, M.J., Smith, C.D. and R.J.Q. Tarr. 2004. An ecosystem approach to fisheries in the southern Benguela context. *African Journal of Marine Science* **26**: 9-35.

Cockcroft, A.C. and A.J. Mackenzie. 1997. The recreational fishery for West Coast rock lobster *Jasus lalandii* in South Africa. *South African Journal of Marine Science* **18**: 75-84.

Cockcroft, A.C. and A.I.L. Payne. 1999. A cautious fisheries management policy in South Africa: the fisheries for rock lobster. *Marine Policy* **23**: 587-600.

Cockcroft, A.C., Griffiths, M.H. and R.J.Q. Tarr. 1999. Marine recreational fisheries in South Africa: status and challenges. In: *Evaluating the Benefits of Recreational Fisheries* Pitcher, T.J. (Ed). The Fisheries Centre, University of British Columbia, Canada: pp. 64-70

Cockcroft, A.C., Kerwath, S. and C. Wilke. 2005. Effectiveness of a radio-acoustic positioning system tracking West Coast rock lobster *Jasus lalandii* – a preliminary investigation. 6th International Crustacean Conference, Glasgow Scotland, 18-22 July 2005. Book of Abstracts, p.237.

Cockcroft, A.C., van Zyl, D and L. Hutchings. 2008. Large-scale changes in the spatial distribution of South African West Coast rock lobsters: an overview. *African Journal of Marine Science* **30**: 149-159.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302-1310.

Connell, S.D. 2003. The monopolization of understorey habitat by subtidal encrusting coralline algae: a test of the combined effects of canopy-mediated light and sedimentation. *Marine Biology* **142**: 1065-1071.

Cowen, R.K. 1983. The effects of sheephead (*Semicossyphus pulcher*) predation on red sea urchin (*Strongylocentrotus franciscanus*) populations: an experimental analysis. *Oecologia* **58**: 249-255.

Cox C., Hunt J.H., Lyons W.G., and G.E. Davis. 1997. Nocturnal foraging of the Caribbean spiny lobster (*Panulirus argus*) on offshore reefs of Florida, USA. *Marine and Freshwater Research* **48**: 671-679.

Crawford, R.J.M., Dundee, B.L., Dyer, B.M., Klages, N.T.W., Meÿer, M.A. and L. Upfold. 2007. Trends in numbers of Cape gannets (*Morus capensis*), 1956/57–2005/06, with a consideration of the influence of food and other factors. *ICES Journal of Marine Science* **64**: 169-177.

Crawford, R.J.M., Cockcroft, A.C., Dyer, B.M. and L. Upfold. 2008a. Divergent trends in bank cormorants *Phalacrocorax neglectus* breeding in South Africa's Western Cape consistent with a distributional shift of rock lobsters *Jasus lalandii*. *African Journal of Marine Science* **30**: 161-166.

Crawford, R.J.M., Underhill, L.G., Coetzee, J.C., Fairweather, T., Shannon, L.J. and A.C. Wolfaardt. 2008b. Influences of the abundance and distribution of prey on African Penguins *Spheniscus demersus* off western South Africa. *African Journal of Marine Science* **30**: 167-175.

Crawford, R.J.M., Sabarros, P.S., Fairweather, T., Underhill, L.G. and A.C. Wolfaardt. 2008c. Implications for seabirds off South Africa of a longterm change in the distribution of sardine. *African Journal of Marine Science* **30**: 177-184.

Crawford, R.J.M., Tree, A.J., Whittington, P.A., Visagie, J., Upfold, L., Roxburg, K.J., Martin, A.P. and B.M. Dyer. 2008d. Recent distributional changes of seabirds in South Africa: is climate having an impact. *African Journal of Marine Science* **30**: 189-193.

Crowder, L.B., Hazen, E.L., Avissar, N., Bjorkland, R., Latanich, C. and M.B. Ogburn. 2008. The impacts of fisheries on marine ecosystems and the transition to ecosystem-based management. *Annual Review of Ecology, Evolution and Systematics* **39**: 259-278.

Cury P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J. and H.M. Verheye. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in ‘‘wasp-waist’’ ecosystems. *ICES Journal of Marine Science* **57**: 603–618.

David, J.H.M. 1987. Diet of the South African fur seal (1974-1985) and an assessment of competition with fisheries in southern Africa. *South African Journal of Marine Science* **5**: 693-713.

David, J.H.M., Cury, P., Crawford, R.J.M, Randall, R.M., Underhill, L.G. and M.A. Meyer. 2003. Assessing conservation priorities in the Benguela ecosystem, South Africa: analysing predation by seals on threatened seabirds. *Biological Conservation* **114**: 289-292.

Day, E.G. 1998. *Ecological interactions between abalone (Haliotis midae) juveniles and sea urchins (Parechinus angulosus), off the south-west coast of South Africa*. Ph.D. Thesis, University of Cape Town. 183 pp.

Day, E.G. and G.M. Branch. 2000a. Relationships between recruits of abalone *Haliotis midae*, encrusting corallines and the sea urchin *Parechinus angulosus*. *South African Journal of Marine Science* **22**: 137-144.

Day, E.G. and G.M. Branch. 2000b. Evidence for a positive relationship between juvenile abalone *Haliotis midae* and the sea urchin *Parechinus angulosus* in the south-western Cape, South Africa. *South African Journal of Marine Science* **22**: 145-156.

Day, E.G. and G.M. Branch. 2002a. Effects of sea urchins (*Parechinus angulosus*) on recruits and juveniles of abalone (*Haliotis midae*). *Ecological Monographs* **72**: 133-149.

Day, E.G. and G.M. Branch. 2002b. Influences of the sea urchin *Parechinus angulosus* (Leske) on the feeding behaviour and activity rhythms of juveniles of the South African abalone *Haliotis midae* Linn. *Journal of Experimental Marine Biology and Ecology* **276**: 1-17.

Dayton, P.K. 1985a. Ecology of kelp communities. *Annual Review of Ecology and Systematics* **16**: 215-245.

Dayton, P.K. 1985b. The structure and regulation of some South American kelp communities. *Ecological Monographs* **55**: 447-468.

Dayton, P.K., Tegner, M.J., Parnell, P.E. and Edwards, P.B. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecological Monographs* **62**: 421-445.

Dayton, P.K., Tegner, M.J., Edwards, P.B. and K.L. Riser. 1998. Sliding baselines, ghosts and reduced expectations in kelp forest communities. *Ecological Applications* **8**: 309-322.

De B. Beyers, C.J, and P.C. Goosen. 1987. Variations in fecundity and size at sexual maturity of female rock lobster *Jasus lalandii* in the Benguela ecosystem. *South African Journal of Marine Science* **5**: 513-521.

DEAT [Department of Environmental Affairs and Tourism]. 2005a. Policy for the allocation and management of commercial fishing rights in the West Coast rock lobster limited commercial (nearshore) fishery: 2005. Marine and Coastal Management, Department of Environmental Affairs and Tourism, South Africa. 14 pp.

DEAT [Department of Environmental Affairs and Tourism]. 2005b. Policy for the allocation and management of commercial fishing rights in the West Coast rock lobster offshore fishery: 2005. Marine and Coastal Management, Department of Environmental Affairs and Tourism, South Africa. 16 pp.

Dichmont, C.M., Butterworth, D.S. and K.L. Cochrane. 2000. Towards adaptive management of the South African Abalone *Haliotis midae* fishery. *South African Journal of Marine Science* **22**: 33–42.

Duffy, J.E. 2002. Biodiversity and ecosystem function: the consumer connection. *Oikos* **99**: 201-219.

Duggins, D.O. and M.N. Dethier. 1985. Experimental studies of herbivory and algal competition in a low intertidal habitat. *Oecologia* **67**: 183-191.

Ebert, T.A. 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology* **49**: 1075-1091.

Ebert, T.A. 1975. Growth and mortality of post-larval Echinoids. *American Zoologist* **15**: 755-775.

Ebert, T.A. 1982. Longevity, life history and relative body wall size in sea urchins. *Ecological monographs* **52**: 353-394.

Ebert, T.A. 2007. Growth and survival of postsettlement sea urchins. In: *Edible sea urchins: biology and ecology*. Lawrence, J.M. (Ed), Elsevier: pp. 79-102.

Ebert, T.A. and M.P. Russell. 1993. Growth and mortality of subtidal red sea urchins (*Strongylocentrotus franciscanus*) at San Nicolas Island, California, USA: problems with models. *Marine Biology* **117**: 79-89.

Ebert, T.A. and J.R. Southon. 2003. Red sea urchins (*Strongylocentrotus franciscanus*) can live over 100 years: confirmation with A-bomb^{14} carbon. *Fishery Bulletin* **101**: 915-922.

Ebert, T.A., Dixon, J.D., Schroeter, S.C., Kalvass, P.E., Richmond, N.T., Bradbury, W.A. and D.A. Woodby. 1999. Growth and mortality of red sea urchins (*Strongylocentrotus franciscanus*) across a latitudinal gradient. *Marine Ecology Progress Series* **190**: 189-209.

Edgar, G.J. 1990. Predator-prey interactions in seagrass beds. 1. The influence of macrofaunal abundance and size-structure on the diet and growth of the western rock lobster *Panulirus cygnus* George. *Journal of Experimental Marine Biology and Ecology* **139**: 1-22.

Edwards, M.S. 1998. Effects of long-term kelp canopy exclusion on the abundance of the annual alga *Desmarestia ligulata* (Light F). *Journal of Experimental Marine Biology and Ecology* **228**: 309-326.

Emanuel, B.P., Bustamante, R.H., Branch, G.M., Eekhout, S. and F.J. Odendaal. 1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. In: *Benguela Trophic Functioning*. Payne, A.I.L, Brink, K.H., Mann, K.H. and R. Hilborn (Eds). *South African Journal of Marine Science* **12**: 341-354.

Eriksson, B.K., Ljunggren, L., Sandström, A., Johansson, G., Mattila, J., Rubach, A., Råberg, S. and M. Snickars. 2009. Declines in predatory fish promote bloom-forming macroalgae. *Ecological Applications* **19**: 1975-1988.

Estes, J.A. 2007. Kelp forest food webs in the Aleutian Archipelago. In: *Food Webs and the Dynamics of Marine Reefs*. Branch, G.M. and T.R. McClanahan (Eds.). Oxford University Press, Inc., New York: pp. 29-49.

Estes, J.A. and J.F. Palmisano. 1974. Sea Otters: Their role in structuring nearshore communities. *Science* **185**: 1058-1060.

Estes, J.A. and D.O. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs* **65**: 75-100.

Estes, J.A., Duggins, D.O. and G.B. Rathbun. 1989. The ecology of extinctions in kelp forest communities. *Conservation Biology* **3**: 252-264.

Estes, J.A., Tinker, M.T., Williams, T.M. and D.F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**:473-476.

Estes, J.A., Danner, E.M., Doak, D.F., Konar, B., Springer, A.M., Steinberg, P.D., Tinker, M.T. and T.M. Williams. 2004. Complex trophic interactions in kelp forest ecosystems. *Bulletin of Marine Science* **74**: 621-638.

Fairweather T.P., Hara, M., van der Lingen C.D., Raakjær, J. Shannon, L.J., Louw, G.G., Degnbol, P. and R.J.M. Crawford. 2006a. A knowledge base for management of the capital-intensive fishery for small pelagic fishery off South Africa. *African Journal of Marine Science* **28**: 645–660.

Fairweather T.P., van der Lingen C.D., Booth A.J., Drapeau L., and J.J. van der Westhuizen. 2006b. Indicators of sustainable fishing for South African sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*. *African Journal of Marine Science* **28**: 661–680.

FAO [Food and Agriculture Organization]. 2007. The state of world fisheries and aquaculture. Food and Agriculture Organization of the United Nations, Fisheries Department, Rome. 162 pp.

Fariña, J.M., Palma, A.T., and F.P. Ojeda. 2007. Subtidal kelp-associated communities off the temperate Chilean coast. In: *Food Webs and the Dynamics of Marine Reefs*. Branch, G.M. and T.R. McClanahan (Eds.). Oxford University Press, Inc., New York: pp. 79-102.

Farrell, D. 2010. *Investigation of community composition on abalone (Haliotis midae) shells at two sites in the Western Cape, South Africa*. M.Sc. Thesis, University of Cape Town.

Field, J.G., Jarman, N.G., Dieckmann, G.S., Griffiths, C.L., Velimirov, B. and P. Zoutendyk. 1977. Sun, waves, seaweed and lobsters: the dynamics of a West Coast kelp bed. *South African Journal of Marine Science* **73**: 7-10.

Field, J.G., Griffiths, C.L., Griffiths, R.J., Jarman, N., Zoutendyk, P., Velimirov, B. and A. Bowes. 1980a. Variation in structure and biomass of kelp communities along the south-west Cape coast. *Transactions of the Royal Society of South Africa* **44**: 145-203.

Field, J.G., Griffiths, C.L., Linley, E.A., Carter, R.A. and P. Zoutendyk. 1980b. Upwelling in a nearshore marine ecosystem and its biological implications. *Estuarine and Coastal Marine Science* **11**: 133-150.

Fletcher, W.J. 1987. Interactions among subtidal Australian sea urchins, gastropods and algae: effects of experimental removals. *Ecological Monographs* **57**: 89-109.

Frank, K.T., Petrie, B., Choi, J.S. and W.C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* **308**: 1621-1623.

Frank, K.T., Petrie, B. and N.L. Shackell. 2007. The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology and Evolution* **22**: 236-242.

Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C. and S. Wanless. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology* **75**: 1259-1268.

Fricke, A.H. 1979. Kelp grazing by the common sea urchin *Parechinus angulosus* Leske in False Bay, Cape. *South African Journal of Zoology* **14**: 143-148.

Gardner, C., Frusher, S., Haddon, M. And C. Buxton. 2003. Movements of the southern rock lobster *Jasus edwardsii* in Tasmania, Australia. *Bulletin of Marine Science* **73**: 653-671.

Gascoigne, J. and R.N. Lipcius. 2004. Allee effects in marine systems. *Marine Ecology Progress Series* **269**: 49-59.

Geromont, H.F. and D.S. Butterworth. 1999. A fleet-disaggregated age-structured production model for application to Atlantic bluefin tuna. *Int. Commn Cons. Atl. Tuna., Coll. Vol. Sci. Pap*. 47: 403-415 (SCRS/98/77).

Gilchrist, J.D.F. 1898. *Report of the Marine Biologist, Department of Agriculture, Cape of Good Hope, for the year 1897*. Cape Town, Government printer: 148 pp + 1 chart.

Gilchrist, J.D.F. 1899. *Report of the Marine Biologist, Department of Agriculture, Cape of Good Hope, for the year 1898*. Cape Town, Government printer: 362 pp + 21 charts.

Gilchrist, J.D.F. 1900. *Report of the Marine Biologist, Department of Agriculture, Cape of Good Hope, for the year 1899*. Cape Town, Government printer: 124 pp.

Gilchrist, J.D.F. 1901. *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1900*. Cape Town, Government printer: 180 pp + 3 charts.

Gilchrist, J.D.F. 1902. *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1901*. Cape Town, Government printer: 104 pp + 2 charts.

Gilchrist, J.D.F. 1903. *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1902*. Cape Town, Government printer: 283 pp + 3 charts.

Gilchrist, J.D.F. 1904. *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1903*. Cape Town, Government printer: 194 pp.

Gilchrist, J.D.F. 1906. *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1904*. Cape Town, Government printer: 40 pp.

Gilchrist, J.D.F. 1907. *Report of the Government Biologist, Department of Agriculture, Cape of Good Hope, for the year 1906*. Cape Town, Government printer: 44 pp.

Gillett, N.P., Zwiers, F.W., Weaver, A.J. and P.A. Stott. 2003. Detection of human influence on sea-level pressure. *Nature* **422**: 292-294.

Gislason, H., Sinclair, M., Sainsbury, K. and R. O'Boyle. 2000. Symposium overview: incorporating ecosystem objectives within fisheries management. *ICES Journal of Marine Science* **57**: 468-475.

Glazer, J.P. and S.L. Brouwer. 2005. Analysis of the Fisheries Independent Monitoring Survey (FIMS) CPUE data. Marine and Coastal Management, South Africa, West Coast Rock Lobster Working Group Report. RLWS/DEC05/DAT/6/1/2/1. 10 pp.

Glynn, P.W. 1976. Some physical and biological determinants of coral community structure in the eastern Pacific. *Ecological Monographs* **46**: 431-456.

Goñi, R., Quetglas, A. and O. Reñones. 2001. Diet of the spiny lobster *Palinurus elephas* (Decapoda: Palinuridea) from the Columbretes Islands Marine Reserve (north-western Mediterranean). *Journal of the Marine Biological Association of the UK* **81**: 347-348.

Götz, A. 2005. *Assessment of the effect of Goukamma Marine Protected Area on community structure and fishery dynamics*. Ph.D. Thesis, Rhodes University, 232 pp.

Götz, A., Kerwath, S.E., Attwood, C. G. and W.H.H. Sauer. 2009a. Effects of fishing on a temperate reef community in South Africa 1: Icthyofauna. *African Journal of Marine Science* **31**: 241-251.

Götz, A., Kerwath, S.E., Attwood, C. G. and W.H.H. Sauer. 2009b. Effects of fishing on a temperate reef community in South Africa 2: Benthic invertebrates and algae. *African Journal of Marine Science* **31**: 253-262.

Graham, M., Halpern, B., and M. Carr. 2007. Diversity and dynamics of Californian subtidal kelp forests. In: *Food Webs and the Dynamics of Marine Reefs*. Branch, G.M. and T.R. McClanahan (Eds.). Oxford University Press, Inc., New York: pp. 103-134.

Greenwood, P.J. 1980. Growth, respiration and tentative energy budgets for two populations of the sea urchin *Parechinus angulosus* (Leske). *Estuarine and Coastal Marine Science* **10**: 347-367.

Griffiths, M.H. 2000. Long-term trends in catch and effort of commercial linefish off South Africa's Cape Province: snapshots of the 20th century. *South African Journal of Marine Science* **22**: 81-110.

Grime, J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* **242**: 344-347.

Guillou, M. and C. Michel. 1994. The influence of environmental factors on the growth of *Sphaerechinus granularis* (Lamarck) (Echinodermata: Echinoidea). *Journal of Experimental Marine Biology and Ecology* **178**: 97-111.

Hagen, N.T. 1983. Destructive grazing of kelp beds by sea urchins in Vestfjorden, Northern Norway. *Sarsia* **68**: 177-190.

Hagen, N.T. 1995. Recurrent destructive grazing of successionally immature kelp forests by green sea urchins in Vestfjorden, Northern Norway. *Marine Ecology Progress Series* **123**: 95-106.

Hairston, N.G., Smith, F.E. and L.B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**: 421–424.

Haley, C. 2008. *Dietary analysis of the West Coast rock lobster (Jasus lalandii) east of Cape Hangklip: effects of size, abundance and food availability*. Honours Thesis, University of Cape Town. 27 pp.

Halpern, B.S., Cottenie, K. and B.R. Broitman. 2006. Strong top-down control in southern California kelp forest ecosystems. *Science* **312**: 1230-1232.

Harrold, C. and D.C. Reed. 1985. Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* **66**: 1160-1169.

Hauck, M. 2009. Crime, environment and power: revisiting the abalone fishery. South African Journal of Criminal Justice, **22**: 229-245.

Hauck, M. and N.A. Sweijd. 1999. A case study of abalone poaching in South Africa and its impact on fisheries management. *ICES Journal of Marine Science* **56**: 1024-1032.

Hay, M.E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* **65**: 446-454.

Heydorn, A.E.F. 1969. Notes on the biology of *Panulirus homarus* and on length/weight relationships of *Jasus lalandii*. *Investigational Report Division of Sea Fisheries of South Africa* **69**: 1-27.

Hily, C., Potin, P. and J. Floc′h. 1992. Structure of subtidal algal assemblages on soft-bottom sediments: fauna/flora interactions and role of disturbances in the Bay of Brest, France. *Marine Ecology Progress Series* **85**: 115-130.

Himmelman, J.H. 1986. Population biology of green sea urchins on rocky barrens. *Marine Ecology Progress Series* **33**: 295-306.

Himmelman, J. H., Cardinal, A. and E. Bourget. 1983. Community development following removal of urchins, *Strongylocentrotus droebachiensis*, from the rocky subtidal zone of the St. Lawrence Estuary, eastern Canada. *Oecologia* **59**: 27-39.

Hockey, P.A.R and A.L. Bosman. 1986. Man as an intertidal predator in Transkei: Disturbance, community convergence and management of a natural food resource. *Oikos* **46**: 3-14.

Hockey P.A.R., Dean W.R.J., and P.G. Ryan (Eds). 2005. *Roberts Birds of Southern Africa* (7th edition). John Voelcker Bird Book Fund, Cape Town.

Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly. *Canadian Entomologist* **91**: 293-320

Horn, H.S. 1975. Markovian properties of forest succession: In: *The ecology and evolution of communities*. Cody, M.L. and J.M. Diamond (Eds). Belknap, Cambridge, Massachusetts, USA: pp. 196-211.

Huston, M.A. 1985a. Patterns of species diversity on coral reefs. *Annual Review of Ecology and Systematics* **16**: 149-177.

Huston, M.A. 1985b. Patterns of species diversity in relation to depth at Discovery Bay, Jamaica. *Bulletin of Marine Science* **37**: 928-935.

Huston, M.A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge, UK. 681 pp.

Irving, A.D, Connell, S.D. and T.S. Elsdon. 2004. Effects of kelp canopies on bleaching and photosynthetic activity of encrusting coralline algae. *Journal of Experimental Marine Biology and Ecology* **310**: 1-12

Irving, A.D, Connell, S.D., Johnston, E.L., Pile, A.J. and B.M. Gillanders. 2005. The response of encrusting coralline algae to canopy loss: an independent test of predictions on an Antarctic coast. *Marine Biology* **147**: 1075-1083.

Jackleman, J. 1996. *Structure and dynamics of the algal understorey in a kelp community at Cape Hangklip, Western Cape, South Africa*. M.Sc. Thesis, University of Cape Town. 160 pp.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**: 629-638.

Johnson, C.R. and K.H. Mann. 1986. The crustose coralline alga, *Phymatolithon foslie*, inhibits the overgrowth of seaweeds without relying on herbivores. *Journal of Experimental Marine Biology and Ecology* **96**: 127-146.

Johnson, C.R. and K.H. Mann. 1988. Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. *Ecological Monographs* **58**: 129-154.

Johnson, C.R., Ling, S.D., Ross, J., Shepherd, S. and K. Miller. 2005. Establishment of the long-spined sea urchin (*Centrostephanus rogersii*) in Tasmania: first assessment of potential threats to fisheries. Project No. 2001/044, Final Report, Fisheries Research and Development Corporation. University of Tasmania, Hobart.

Johnston, S.J. 2002. A first look at East of Hangklip (EoH) west coast rock lobster biomass estimates and projections. Marine and Coastal Management, South Africa, West Coast Rock Lobster Working Group Report, WG/08/02/WCL. 3 pp.

Johnston, S.J. and D.S. Butterworth. 2001. An age-structured production model for the South African West Coast rock lobster resource. Marine and Coastal Management, South Africa, West Coast Rock Lobster Working Group Report, BEN/NOV/01/WCRL/1d.

Johnston, S.J. and D.S. Butterworth. 2005. Evolution of operational management procedures for the South African West Coast rock lobster (*Jasus lalandii*) fishery. *New Zealand Journal of Freshwater and Marine Research* **39**: 687-702.

Jury, M. 1991. The weather of False Bay. *Transactions of the Royal Society of South Africa* **47**: 401-417.

Keats, D.W., Wilton, P. and G. Maneveldt. 1994. Ecological significance of deep-layer sloughing in the eulittoral zone coralline alga, *Spongites yendoi* (Foslie) Chamberlain (Corallinaceae, Rhodophyta) in South Africa. *Journal of Experimental Marine Biology and Ecology* **175**: 145-154.

Keats, D.W., Knight, M.A. and C.M. Pueschel. 1997. Anti-fouling effects of epithallial shedding in three crustose coralline algae (Rhodophyta, Corallinales) on a coral reef. *Journal of Experimental Marine Biology and Ecology* **213**: 281-293.

Kelly, S. 2001. Temporal variation in the movement of the spiny lobster *Jasus edwardsii*. *Marine and Freshwater Research* **52**: 323-331.

Kemp, L. 2000. *A shift in the diet of the Cape Clawless Otter, Aonyx capensis, at Betty's Bay, South Africa: response to a change in rock lobster abundance?* Honours Thesis, University of Cape Town. 19 pp.

Kennelly, S.J. 1989. Effects of kelp canopies on understory species due to shade and scour. *Marine Ecology Progress Series* **50**: 215-224.

Kennelly, S.J. and A.J. Underwood. 1993. Geographic consistencies of effects of experimental physical disturbance on understorey species in sublittoral kelp forests in central New South Wales. *Journal of Experimental Marine Biology and Ecology* **168**: 35-58.

Kerwath, S.E., Götz, A., Attwood, C.G. and W.H.H. Sauer. 2008. The effect of marine protected areas on an exploited population of sex-changing temperate reef fish: an individual-based model. *African Journal of Marine Science* **30**: 337-350.

Konar, B. 2001. Seasonal changes in subarctic sea urchin populations from different habitats. *Polar Biology* **24**: 745-763.

Köster, F.W. and C. Möllmann. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod. *ICES Journal of Marine Science* **57**: 310-323.

Lafferty, K.D. 2004. Fishing for lobsters indirectly increases epidemics in sea urchins. *Ecological Applications* **14**: 1566-1573.

Lang, C. and K.H. Mann. 1976. Changes in sea urchin populations after the destruction of kelp beds. *Marine Biology* **36**: 321-326.

Lawrence, J. M. 1975. On the relationships between marine plants and sea urchins. *Oceanography and Marine Biology Annual Review* **13**: 213-286.

Levitt, G.J., Anderson, R.J., Boothroyd, C.J.T. and F.A. Kemp. 2002. The effects of kelp harvesting on its regrowth and the understorey benthic community at Danger Point, South Africa, and a new method of harvesting kelp fronds. *South African Journal of Marine Science* **24**:71–85.

Littler, M.M., Littler, D.S. and P.R. Taylor. 1995. Selective herbivore increases biomass of its prey: a chiton-coralline reef-building association. *Ecology* **76**: 1666-1681.

Ling, S.D. 2008. Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia* **156**: 883-894.

Ling, S.D. and C.R. Johnson. 2009. Population dynamics of an ecologically important range-extender: kelp-beds versus sea urchin barrens. *Marine Ecology Progress Series* **374**: 113-125.

Ling, S.D., Johnson, C.R., Frusher, S. and C.K. King. 2008. Reproductive potential of a marine ecosystem engineer at the edge of a newly expanded range. *Global Change Biology* **14**: 1-9.

Ling, S.D., Johnson, C.R., Ridgway, K., Hobday, A.J. and M. Haddon. 2009a. Climate-driven range extension of a sea urchin: inferring future trends by analysis of recent population dynamics. *Global Change Biology* **15**: 719-731.

Ling, S.D., Johnson, C.R., Frusher, S. and K. Ridgway. 2009b. Overfishing reduces resilience of kelp beds to climate-driven catastrophic phase shift. *Proceedings of the National Academy of Sciences* **106**: 22341-22345.

Loewenthal, D., Mayfield, S. and G.M. Branch. 2000. Improving the catch efficiency of the West Coast rock lobster, *Jasus lalandii*. *Marine and Freshwater Research* **51**: 613-617.

Lotka, A. J. 1925. *Elements of physical biology*. Baltimore: Williams & Wilkins Co.

Loya, Y. 1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Marine Biology* **13**: 100-123.

Lutjeharms, J.R.E and A.E.F Heydorn 1981. The rock-lobster *Jasus tristani* on Vema Seamount: Drifting buoys suggest a possible recruiting mechanism. *Deep-Sea Research* **28**: 631-636.

Mann, K.H. 1977. Destruction of kelp-beds by sea urchins: a cyclical phenomenon or irreversible degradation? *Helgoländer wiss. Meeresunters* **30**: 455-467.

Mann, K.H. and P.A. Breen. 1972. The relation between lobster abundance, sea urchins and, kelp beds. *Journal of the Fisheries Research Board of Canada* **29**: 603-609.

Mattison, J.E., Trent, J.D., Shanks, A.L., Akin, T.B. and J.S. Pearse. 1977. Movement and feeding activity of red sea urchin (*Strongylocentrotus franciscanus*) adjacent to a kelp forest. *Marine Biology* **39**: 25-30.

Mayfield, S. 1998. *Dietary assessment of the diets of West Coast rock lobster (Jasus lalandii): relationships between growth rate, diet and benthic community* *composition, with implications for the survival of juvenile abalone (Haliotis midae)*. Ph.D. Thesis, University of Cape Town. 213 pp.

Mayfield, S. and G.M. Branch. 2000. Interrelations among rock lobsters, sea urchins and juvenile abalone: implications for community management. *Canadian Journal of Fisheries and Aquatic Science* **57**: 2175-2185.

Mayfield, S., Atkinson, L.J., Branch, G.M. and A.C. Cockcroft. 2000a. Diet of the West Coast rock lobster *Jasus lalandii*: Influence of lobster size, sex, capture depth, latitude and moult stage. *South African Journal of Marine Science* **22**: 57-69.

Mayfield, S., Branch, G.M. and A.C. Cockcroft. 2000b. Relationships among diet, growth rate, and food availability for the South African rock lobster, *Jasus lalandii* (Decapoda, Palinuridea). *Crustaceana* **73**: 815-834.

Mayfield, S., De Beer, E. and G.M. Branch. 2001. Prey preference and the consumption of sea urchins and juvenile abalone by captive rock lobsters (*Jasus lalandii*). *Marine and Freshwater Research* **52**: 773-780.

Mayfield, S., Branch, G.M. and A.C. Cockcroft. 2005. Role and efficiency of marine protected areas for the South African rock lobster, *Jasus lalandii*. *Marine and Freshwater Research* **56**: 913-924.

McKoy, J.L. 1983. Movements of rock lobsters, *Jasus edwardsii* (Decapoda: Palinuridae), tagged near Steward Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **17**: 357-366.

Melville, A.J. and S. D. Connell. 2001. Experimental effects of kelp canopies on subtidal coralline algae. *Austral Ecology* **26**: 102-108.

Menge, B.A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* **250**: 257-289.

Menge, B.A. and J.P. Sutherland. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *The American Naturalist* **110**: 351-369.

Menge, B.A. and J. Lubchenco. 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecological Monographs* **51**: 429-450.

Miller, K.J., Maynard, B.T. and C.N. Mundy. 2008. Genetic diversity and gene flow in collapsed and healthy abalone fisheries. *Molecular Ecology* **18**: 200-211.

Minor, M.A. and R.E. Scheibling. 1997. Effects of food ration and feeding regime on growth and reproduction of the sea urchin *Strongylocentrotus droebachiensis*. *Marine Biology* **129**: 159-167.

Morrison, D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* **69**: 1367-1382.

Morse, D.E., Hooker, N., Duncan, H. and L. Jensen. 1979. g-aminobutyric acid, a neurotransmitter, induces planktonic abalone larvae to settle and begin metamorphosis. *Science* **204**: 407-410.

Myers, R.A., Barrowman, N.J., Hutchings, J.A. and A.A. Rosenberg. 1995. Population dynamics of exploited fish stocks at low population levels. *Science* **269**: 1106-1108.

Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P., and C.H. Peterson. 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science 315*: 1846-1850.

Nepgen, C.S. De V. 1977. The biology of the Hottentot *Pachymetopon blochii* (Val.) and the Silverfish *Argyrozona argyrozona* (Val.) along the Cape south-west coast. *Investigational Report of the Sea Fisheries Institute of South Africa* **105**: 1-35.

Nepgen, C.S. De V. 1982. Diet of predatory and reef fish in False Bay and possible effects of pelagic purse-seining on their food supply. *Fisheries Bulletin of South Africa* **16**: 75-93.

O'Connor, N.E. and J.F. Bruno. 2007. Predatory fish loss affects the structure and functioning of a model marine food web. *Oikos* **116**: 2027-2038.

Ojeda, F.P. and B. Santelices. 1984. Ecological dominance of *Lessonia nigrescens* (Phaeophyta) in central Chile. *Marine Ecology Progress Series* **19**: 83-91.

Osterblom, H., Hansson, S., Hjerne, O., Larsson, U., Wulff, F., Elmgren, R. and C. Folke. 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* **10**:877–889.

Pace, M.L., Cole, J.J., Carpenter, S.R. and J.F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* **14**: 483-488.

Paine, R.T. 1966. Food web complexity and species diversity. *The 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. 1974. Intertidal community structure. *Oecologia* **15**: 93-120.

Paine, R.T. 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**: 667-685.

Paine, R.T. 1984. Ecological determinism in the competition for space. *Ecology* **65**: 1339-1348.

Palomares, M.L.D. and D. Pauly. 1998. Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. *Marine and Freshwater Research* **49**: 447-453.

Pauly, D. 1998. Large Marine ecosystems: analysis and management. *South African Journal of Marine Science* **19**: 487-499.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. and F. Torres. 1998. Fishing down marine food webs. *Science* **279**: 860-863.

Pauly, D., Christensen, V., and C. Walters. 2000a. ECOPATH, ECOSIM and ECOSPACE as tools for evaluating ecosystem impact of fisheries. *ICES Journal of Marine Science* **57**: 697-706.

Pauly, D., Christensen, V., Froese, R. and M. Palomares. 2000b. Fishing down aquatic food webs. *American Scientist* **88**: 46-51.

Pichegru, L., Ryan, P.G., van der Lingen, C.D., Coetzee, J., Ropert-Coudert, Y. And D. Grémillet. 2007. Foraging behaviour and energetics of Cape gannets *Morus capensis* feeding on live prey and fishery discards in the Benguela upwelling system. *Marine Ecology Progress Series* **350**: 127-136.

Plagányi, É.E. 2004. *Walking the bridge from single- to multi-species approaches in Southern African fisheries management*. Ph.D. Thesis, University of Cape Town. 460 pp.

Plagányi, É.E. 2007. Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper. No. 477. Rome, FAO. 108 pp.

Plagányi, É.E. and D.S. Butterworth. 2004. A critical look at the potential of ECOPATH with ECOSIM to assist in practical fisheries management. *African Journal of Marine Science* **26**: 261-287.

Plagányi, É.E. and D.S. Butterworth. In press. A spatial- and age-structured assessment model to estimate illegal fishing and ecosystem change impacting the management of South African abalone (*Haliotis midae*). *African Journal of Marine Science*.

Plagányi, É.E., Butterworth, D.S. and A. Brandão. 2001. Toward assessing the South African abalone *Haliotis midae* stock using an age-structured production model. *Journal of Shellfish Research* **20**: 813-827.

Plagányi, É.E., Brandão, A., Butterworth, D.S., de Moor, C.L., Glazer, J., Johnston, S.J. and R.A. Rademeyer. 2009. Stock assessment in South Africa - building on a consistent yet flexible approach. *Proceedings of the Fifth World Fisheries Congress*. 2 pp.

Pollock, D.E. 1979. Predator-prey relationships between the rock lobster *Jasus lalandii* and the mussel *Aulacomya ater* at Robben Island on the Cape west coast of Africa. *Marine Biology* **52**: 347-356.

Pollock, D.E. 1986. Review of the fishery for and biology of the Cape rock lobster *Jasus lalandii* with notes on larval recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* **43**: 2107-2117.

Pollock, D.E. 1989. Spiny lobsters. In: *Oceans of Life off Southern Africa*. Payne, A.I.L and R.J.M Crawford (Eds) Cape Town, Vlaeberg: pp. 70-80.

Pollock, D.E. 1990. Palaeoceanography and speciation in the spiny lobster genus *Jasus*. *Bulletin of Marine Science* **46**: 387-405.

Pollock, D.E. 1992. Palaeoceanography and speciation in the spiny lobster genus *Panulirus* in the Indo-Pacific. *Bulletin of Marine Science* **51**: 135-146.

Pollock, D.E. and C.J. De B. Beyers. 1981. Environment, distribution and growth rates of West Coast rock lobster *Jasus lalandii* (H. Milne Edwards). *Transactions of the Royal Society of South Africa* **44**: 379-400.

Pollock, D.E. and L.V. Shannon. 1987. Response of rock-lobster populations in the Benguela ecosystem to environmental change – a hypothesis. *South African Journal of Marine Science* **5**: 887-899.

Pollock, D.E. and R. Melville-Smith. 1993. Decapod life histories and reproductive dynamics in relation to oceanography off southern African. *South African Journal of Marine Science* **13**: 205-212.

Pollock, D.E., Augustyn, C.J. and P.C. Goosen. 1982. The rock lobster *Jasus lalandii* and its environmental biology on the Saldanha-Columbine fishing ground off the Cape west coast, 1978-1981. *Investigational Report of the Sea Fisheries Institute of South Africa* **125**: 1-30.

Pollock, D.E., Cockcroft, A.C. and P.C. Goosen. 1997. A note on reduced rock lobster growth rates and related environmental anomalies in the southern Benguela, 1988-1995. *South African Journal of Marine Science* **18**: 287-293.

Polovina, J.J. 1984. Model of a coral reef ecosystem. 1. The ECOPATH model and its application to French frigate shoals. *Coral Reefs* **3**: 1-11.

Pope, J.G. 1984. The performance of short cut methods for catch forecasts. ICES document CM 1984/D: 3. 12 pp.

Prince, J. 2005. Combating the tyranny of scale for Haliotids: micro-management for microstocks. *Bulletin of Marine Science* **76**: 557-577.

Prince, J., Peeters, H., Gorfine, H. and R.W. Day. 2008. The novel use of harvest policies and rapid visual assessment to manage spatially complex abalone resources (Genus Haliotis). *Fisheries Research* **94**: 330-338.

Pulfrich, A. and C.L. Griffiths. 1988. Growth, sexual maturity and reproduction in the Hottentot *Pachymetopon blochii* (Val.). *South African Journal of Marine Science* **7**:25-36.

Punt, A.E. and D.S. Butterworth. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals (*Arctocephalus pusillus pusillus*) and Cape hakes

(*Merluccius capensis* and *M. paradoxus*). *South African Journal of Marine Science* **16**: 255-285.

Quinn, J.F., Wing, S.R. and L.W. Botsford. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the Red sea urchin, *Strongylocentrotus franciscanus*. *American Zoologist* **33**: 357 – 550.

Rademeyer, R.A., Plagányi, É.E. and D.S. Butterworth. 2007. Tips and tricks in designing management procedures. *ICES Journal of Marine Science* **64**: 618-625.

Reaugh, K. 2001. *Trophic cascade effects of increased predator populations in South African kelp forests: a 13 year comparative study*. Honours Thesis, University of Cape Town. 58 pp.

Reed, D.C. and M.S. Foster. 1984. The effects of canopy shadings on algal recruitment and growth in a giant kelp forest. *Ecology* **65**: 937-948.

Reynolds, C.S., Padisák, J. and U. Sommer. 1993. Intermediate disturbance in the ecology of phytoplankton and the maintenance of species-diversity – a synthesis. *Hydrobiologia* **249**: 183-188.

Rice, J. 1995. Food web theory, marine food webs, and what climate change may do to northern marine fish populations. In: *Climate Change and Northern Fish Populations*. Beamish, R.J. (Ed). *Canadian Special Publication of Fisheries and Aquatic Sciences* **121**: 516–568.

Richardson, A.J. and D.S. Schoeman. 2004. Climate impact on plankton ecosystems in the northeast Atlantic. *Science* **305**: 1609-1612.

Ridgway, K. R. 2007. Long-term trend and decadal variability of the southward penetration of the East Australian Current. *Geophysical Research Letters* **34**: L13616, doi:10.1029/2007GL030393.

Roberts, C.M. 1995. Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology* **9**: 988-995.

Robles, C. 1987. Predator foraging characteristics and prey population structure on a sheltered shore. *Ecology* **68**: 1502-1514.

Robles, C., Sweetnam, D. and J. Eminike. 1990. Lobster predation on mussels: shore-level differences in prey vulnerability and predator preference. *Ecology* **71**: 1564-1577.

Rodríguez, S.R. 2003. Consumption of drift kelp by intertidal populations of the sea urchin *Tetrapygus niger* on the central Chilean coast: possible consequences at different ecological levels. *Marine Ecology Progress Series* **251**: 141-151.

Rouault, M., Penven, P. and B. Pohl. 2009. Warming in the Agulhas Current system since the 1980s. *Geophysical Research Letters* **36**: L12602, doi:10.1029/2009GL037987.

Roy, C., van der Lingen, C.D., Coetzee, J.C. and J.R.E. Lutjeharms. 2007. Abrupt environmental shift associated with changes in the distribution of Cape anchovy *Engraulis encrasicolus* spawners in the southern Benguela. *African Journal of Marine Science* **29**: 309-319.

Sala, E. and M. Zabala. 1996. Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Marine Ecology Progress Series* **140**: 71-81.

Sala, E., Boudouresque, C.F. and M. Harmelin-Vivien. 1998. Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos* **82**: 425-439.

Santelices, B. and F.P. Ojeda. 1984. Population dynamics of coastal forests of *Macrocystis pyrifera* in Peurto Tora, Isla Navarino, Southern Chile. *Marine Ecology Progress Series* **14**: 175-183.

Saunders, T.M., Connell, S.D. and S. Mayfield. 2009. Differences in abalone growth and morphology between locations with high and low food availability: morphologically fixed or plastic traits? *Marine Biology* **156**: 1255-1263.

Scheffer, M., Carpenter, S. and B. de Young. 2005. Cascading effects of over-fishing marine ecosystems. *Trends in Ecology and Evolution* **20**: 579-581.

Seidel, D. J., Fu, Q., Randel, W.J. and T. J. Reichler. 2008. Widening of the tropical belt in a changing climate. *Nature Geoscience* **1**: 21– 24.

Shannon, L.V. 1985. The Benguela Ecosystem. Part I. Evolution of the Benguela, physical features and processes. *Oceanography and Marine Biology Annual Review* **23**: 105-182.

Shannon, L.V., Crawford, R.J.M., Pollock, D.E., Hutchings, L., Boyd, A.J., Taunton-Clark, J., Badenhorst, A., Melville-Smith, R., Augustyn, C.J., Cochrane, K.L., Hampton, I., Nelson, G., Japp, D.W. and R.J.Q. Tarr. 1992. The 1980s – A decade of change in the Benguela ecosystem. In: *Benguela Trophic Functioning*. Payne, A.I.L, Brink, K.H., Mann, K.H. and R. Hilborn (Eds). *South African Journal of Marine Science* **12**: 271-296.

Shannon, L.J., Cochrane, K.L., Moloney, C.L. and P. Fréon. 2004. Ecosystem approach to fisheries management in the southern Benguela: a workshop overview. In: *Ecosystem Approaches to Fisheries in the Southern Benguela*. Shannon, L.J., Cochrane, K.L. and S.C. Pillar (Eds). *African Journal of Marine Science* **26**: 1-8.

Shaughnessy, P.D. 1984. Historical population levels of seals and seabirds on islands off southern Africa, with special reference to Seal Island, False Bay. *Investigational Report of the Sea Fisheries Institute of South Africa* **127**: 61 pp.

Shea, K., Roxburgh, S.H., E.S.J. Rauschert. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* **7**: 491-508.

Shears, N.T. and R.C. Babcock. 2002. Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia* **132**: 131-142.

Shears, N.T. and R.C. Babcock. 2003. Continuing trophic cascade effects after 25 years of no-take marine reserve protection. *Marine Ecology Progress Series* **246**: 1-16.

Shepherd, S.A. and D. Partington. 1995. Studies on southern Australian abalone (*Genus Haliotis*). XVI. Recruitment, habitat and stock relations. *Marine and Freshwater Research* **46**: 669-680.

Simenstad, C.A., Estes, J.A. and K.W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. *Science* **200**: 403-411.

Sousa, W.P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* **60**: 1225-1239.

Steneck, R.S. 1982. A limpet-coralline alga association: adaptations and defences between a selective herbivore and its prey. *Ecology* **63**: 507-522.

Steneck, R.S. 1986. The ecology of coralline algal crusts: consequent patterns and adaptive strategies. *Annual Review of Ecology and Systematics* **17**: 273-303.

Steneck, R. S. 1997. Fisheries-induced biological changes to the structure and function of the Gulf of Maine Ecosystem. Plenary Paper. In: *Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop*. Wallace, G. T., and E.F. Braasch (Eds). RARGOM Report, 97 - 1. Regional Association for Research on the Gulf of Maine. Hanover, NH: pp. 151 - 165.

Steneck, R.S. 1998. Human influences on coastal ecosystems: does overfishing create trophic cascades? *Trends in Ecology and Evolution* **13**: 429-430.

Steneck, R.S. and M .N. Dethier. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos* **69**: 476-498.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. and M.J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* **29**: 436-459.

Steneck, R.S., Vavrinec, J. and A.V. Leland. 2004. Accelerating trophic-level dysfunction in kelp forest ecosystems of the western north Atlantic. *Ecosystems* **7**: 323-332.

Stephens, P.A., Sutherland, W.J. and R.P. Freckleton. 1999. What is the Allee effect? *Oikos* **87**: 185-190.

Strong, D.R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* **73**: 747-754.

Swain, D.P. and A.F. Sinclair. 2000. Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 1321-1325.

Tarr, R.J.Q. 1993. *Stock assessment, and aspects of the biology of the South African Abalone, Haliotis midae*. M.Sc. Thesis, University of Cape Town. 156 pp.

Tarr, R.J.Q. 1995. Growth and movement of the South African abalone (*Haliotis midae*): a reassessment. Marine and Freshwater Research **46**: 583-590.

Tarr, R.J.Q., Williams, P.V.G and A.J. Mackenzie. 1996. Abalone, sea urchins and rock lobster: a possible ecological shift that may affect traditional fisheries. *South African Journal of Marine Science* **17**: 319-323.

Tarr, R.J.Q. 2000. The South African abalone (*Haliotis midae*) fishery: a decade of challenges and change. *In* Workshop on rebuilding abalone stocks in British Columbia. Campbell, A. (Ed). *Canadian Special Publication of Fisheries and Aquatic Sciences* **130**: 32-40.

Tegner, M.J. and P.K. Dayton. 1981. Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Marine Ecology Progress Series* **5**: 255-268.

Tegner, M.J. and P.K. Dayton. 1991. Sea urchins, El Niños and the long term stability of Southern California kelp forest communities. *Marine Ecology Progress Series* **77**: 49-63.

Tegner, M.J. and P.K. Dayton. 2000. Ecosystem effects of fishing in kelp forest communities. *ICES Journal of Marine Science* **57**: 579-589.

Tegner, M.J. and L.A. Levin. 1983. Spiny lobsters and sea urchins: analysis of a predator-prey interaction. *Journal of Experimental Marine Biology and Ecology* **73**: 125-150.

Thompson, D.W.J. and S. Solomon. 2002. Interpretation of recent Southern Hemisphere climate change. *Science* **296**: 895-899.

Toohey, B.D., Kendrick, G.A. and E.S. Harvey. 2007. Disturbance and reef topography maintain high local diversity in *Ecklonia radiata* kelp forests. *Oikos* **116**: 1618-1630.

Troell, M., Robertson-Andersson, D., Anderson, R.J., Bolton, J.J., Maneveldt, G., Halling, C. and T. Probyn. 2006. Abalone farming in South Africa: An overview with perspectives on kelp resources, abalone feed, potential for on-farm seaweed production and socio-economic importance. *Aquaculture* **257**: 266-281.

Turner, S. J., Thrush, S. F., Hewitt, J. E., Cummings, V. J. and G. Funnell. 1999. Fishing impacts and the degradation or loss of habitat structure. *Fisheries Management and Ecology* **6**: 401–420.

Turon, X., Giribet, G., López, S. and C. Palacín. 1995. Growth and population structure of *Paracentrotus lividus* (Echinodermata: Echinoidea) in two contrasting habitats. *Marine Ecology Progress Series* **122**: 193-204.

Turpie, J.K., Beckley, L.E. and S.M. Katua. 2000. Biogeography and the selection of priority areas for conservation of South African coastal fishes. *Biological Conservation* **92**: 59-72.

Quinn, J.F., Wing, S.R. and L.W. Botsford. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the Red Sea urchin, *Strongylocentrotus franciscanus*. *American Zoologist* **33**: 537-550.

Underhill, L.G., Crawford, R.J.M., Wolfaardt, A.C., Whittington, P.A., Dyer, B.M., Leshoro, T.M., Ruthenberg, M., Upfold, L and J. Visagie. 2006. Regionally coherent trends in colonies of African Penguins *Spheniscus demersus* in the Western Cape, South Africa, 1987-2005. *African Journal of Marine Science* **28**: 697-704.

Vadas, R.L. 1977. Preferential feeding: an optimization strategy in sea urchins. *Ecological Monographs* **47**: 337-371.

van der Lingen, C.D., L. Hutchings, D. Merkle, J.J. van der Westhuizen and J. Nelson. 2001. Comparative spawning habitats of anchovy (*Engraulis capensis*) and sardine (*Sardinops sagax*) in the Southern Benguela upwelling ecosystem. In: *Spatial Processes and Management of Marine Populations*. Kruse, G.H., Bez, N., Booth, T., Dorn, M., Hills, S., Lipcius, R.N., Pelletier, D., Roy, C., Smith, S.J. and D.Witherell (Eds.). University of Alaska Sea Grant, AK-SG-01-02, Fairbanks: pp. 185-209.

van der Lingen C.D., J.C. Coetzee and L. Hutchings. 2002. Temporal shifts in the spatial distribution of anchovy spawners and their eggs in the Southern Benguela: Implications for recruitment. In: *Report of a GLOBECSPACC/IDYLE/ENVIFISH workshop on Spatial Approaches to the Dynamics of Coastal Pelagic Resources and their Environment in Upwelling Areas*. van der Lingen, C.D., Roy, C., Fréon, P., Barange, M., Castro, L., Gutierrez, M., Nykjaer, L. and F. Shillington (Eds.). GLOBEC Report 16: 46-48.

van der Lingen CD, Coetzee JC, Demarcq H, Drapeau L, Fairweather TP, Hutchings L. 2005. An eastward shift in the distribution of southern Benguela sardine. *GLOBEC International Newsletter* **11**: 17–22.

Van Erkom Schurink, C. and C.L. Griffiths. 1990. Marine mussels of southern Africa – their distribution patterns, standing stocks, exploitation and culture. *Journal of Shellfish Research* **9**: 75-85.

Van Zyl, R.F., Mayfield, S. and G.M. Branch. 2003. Aquarium experiments comparing the feeding behaviour of rock lobster *Jasus lalandii* on abalone and sea urchins at two sites on the west coast of South Africa. *African Journal of Marine Science* **25**: 377-382.

Vance, R.R. 1979. Effects of grazing by the sea urchin, *Centrostephanus coronatus*, on prey community composition. *Ecology* **60**: 537-546.

Vanderklift, M.A. and G.A. Kendrick. 2005. Contrasting influence of sea urchins on attached and drift macroalgae. *Marine Ecology Progress Series* **299**: 101-110.

Velimirov, B., Field J.G., Griffiths, C.L. and P. Zoutendyk. 1977. The ecology of kelp bed communities in the Benguela upwelling system. *Helgoländer wiss. Meeresunters* **30**: 495-518.

Velimirov, B., and C.L. Griffiths. 1979. Wave induced kelp movement and its importance for community structure. *Botanica Marina* **22**: 169-172.

Visch, J and I. Hudson. 2000. Nonparametrics on MINITAB: a students introduction to MINITAB. [Online]. Available: http://www.math.canterbury.ac.nz/php/resources/compdocs/minitab.pdf [14 October 2009].

Volterra, V. 1926. *Variations and fluctuations of the numbers of individuals in animal species living together*. Mem. R. Accad. Naz. dei Lincei (translated in Chapman, R. 1931 Animal Ecology, McGraw-Hill).

Walters, C.J., Pauly, D. and V Christensen. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balanced assessments. *Reviews in Fish Biology and Fisheries* **7**: 139-172.

Walters, C.J., Pauly, D. and V Christensen. 2000. ECOSPACE: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems* **2**: 539-554.

Ware, D.M. and R.E. Thompson. 2005. Bottom-up ecosystem dynamics determine fish production in the northeast Pacific. *Science* **308**: 1280-1284.

Watanabe, J.M. and C. Harrold. 1991. Destructive grazing by sea urchins *Strongylocentrotus* spp. in a central California kelp forest: potential roles of recruitment, depth and predation. *Marine Ecology Progress Series* **71**: 125-141.

Wieters, E.A. 2005. Upwelling control of positive interactions over mesoscales: a new link between bottom-up and top-down processes on rocky shores. *Marine Ecology Progress Series* **301**: 43-54.

Williams, N. 1998. Over-fishing disrupts entire ecosystems. *Science* **279**: 809.

Williams, T.M., Estes, J.A., Doak, D.F. and A.M. Springer. 2004. Killer appetites: assessing the role of predators in ecological communities. *Ecology* **85**: 3373-3384.

Wootton, J.T. 1995. Effects of birds on sea urchins and algae: a lower-intertidal trophic cascade. *Ecoscience* **2**: 321-328.

Worm, B. and R.A. Myers. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. *Ecology* **84**: 162-173.

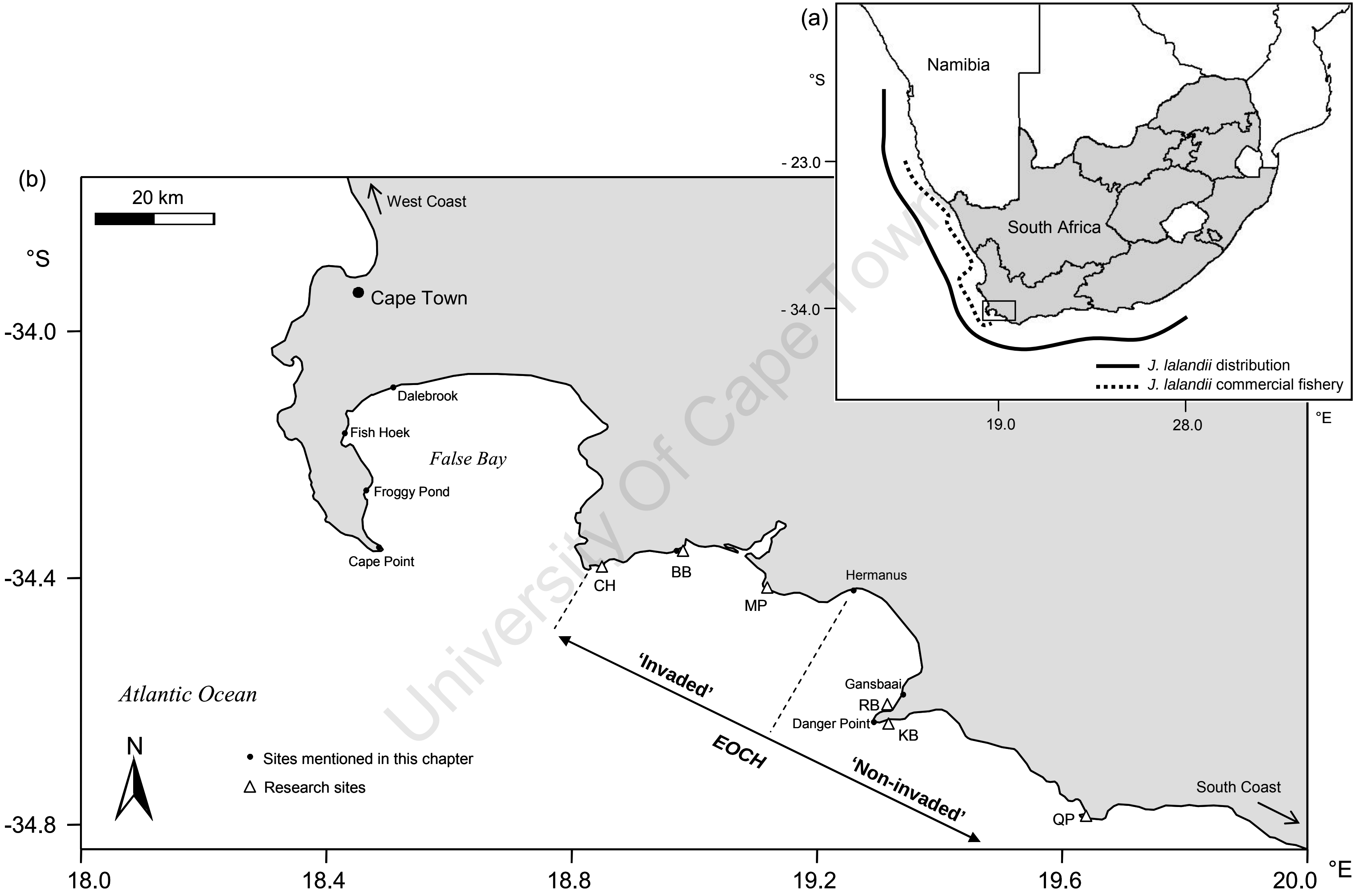


Fig 1.01: Map showing (a) *Jasus lalandii* distribution and commercial fishing grounds and (b) the south-west coast of South Africa including the area East of Cape Hangklip (EOCH). CH = Cape Hangklip, BB = Betty's Bay, MP = Mudge Point, RB = Romans Bay, KB = Kruismans Bay and QP = Quoin Point.

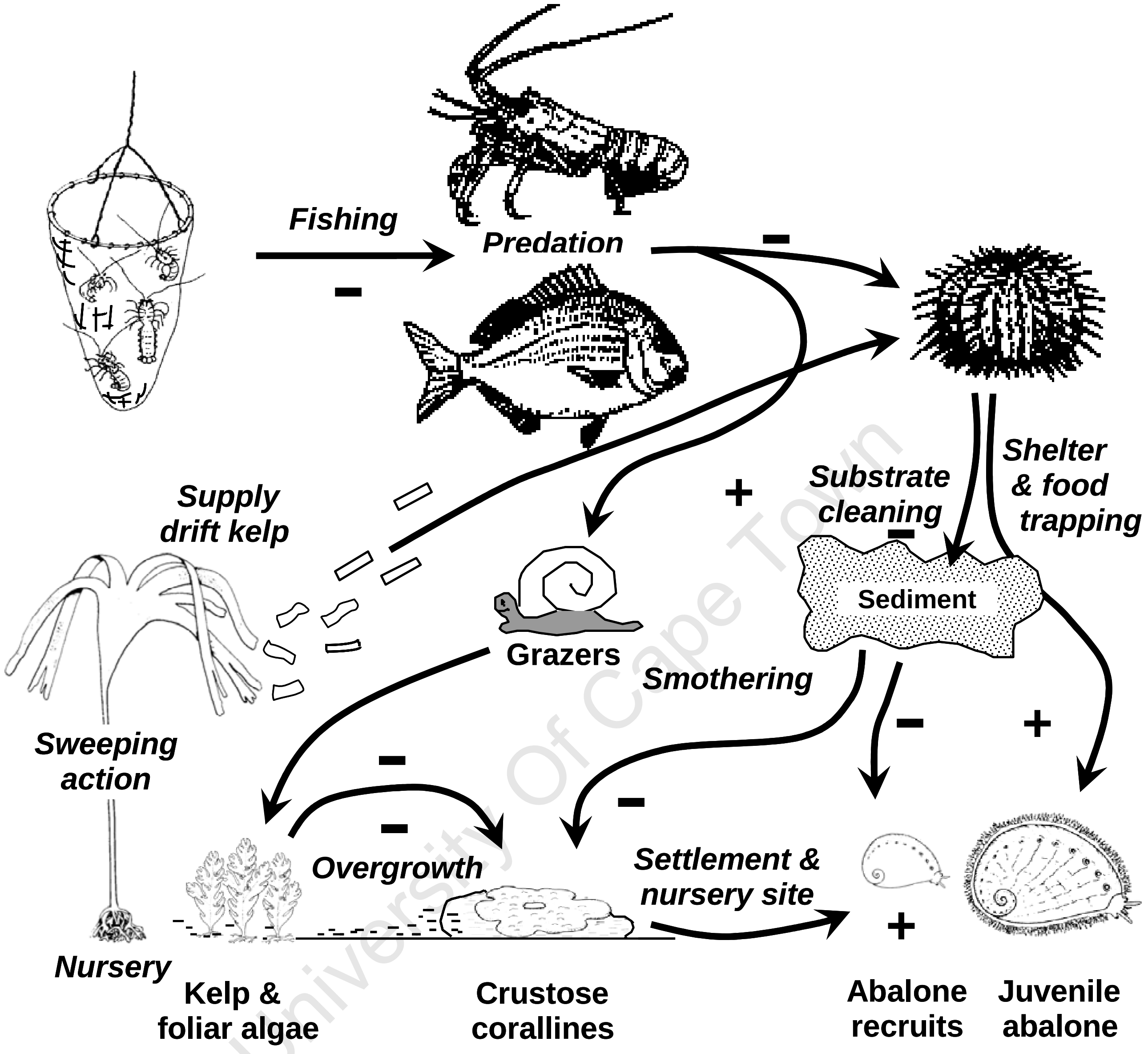


Fig 1.02: Interactions within a kelp forest East of Cape Hangklip. Arrows point to the species positively (+) or negatively (-) affected by the interactions. (Derived from Day and Branch 2002a).

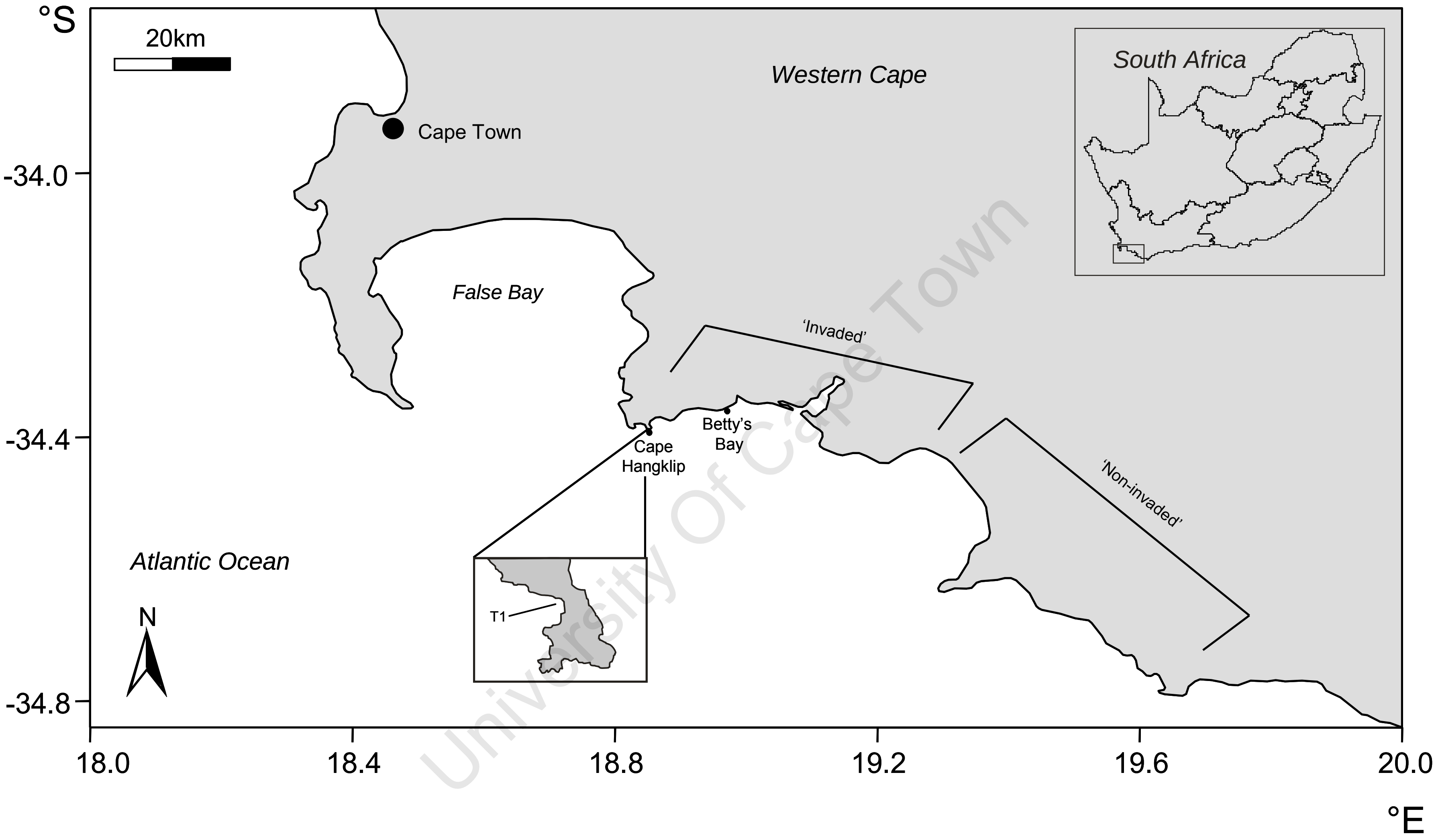
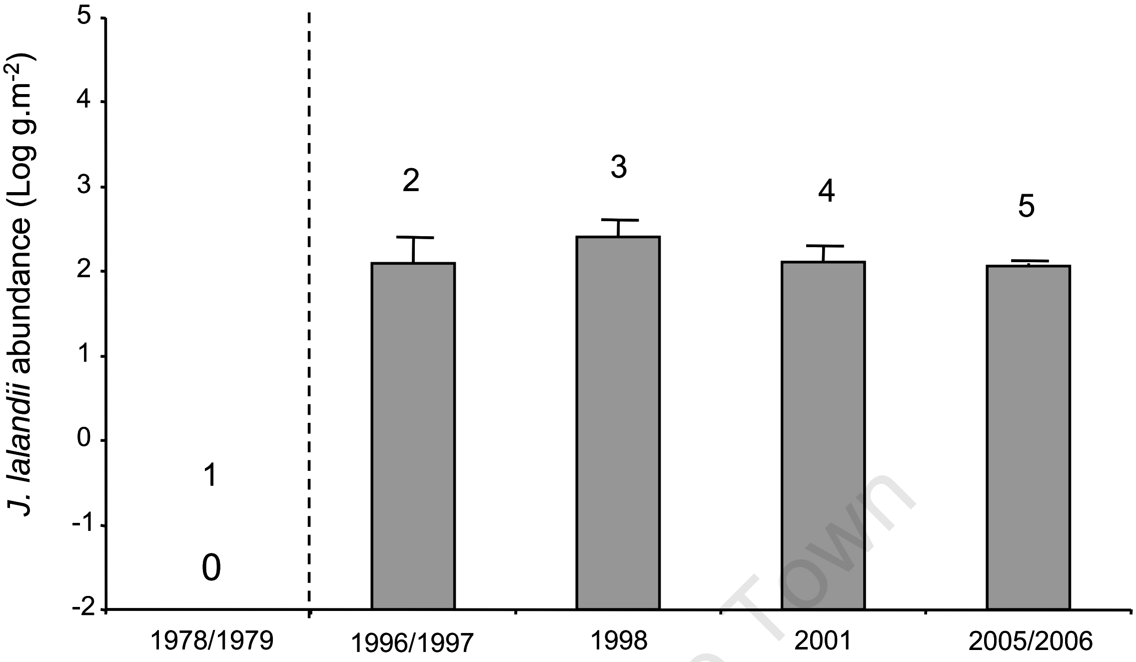


Fig 2.01: Map showing the two study sites along the south-west coast of South Africa, East of Cape Hangklip (EOCH), where pre-invasion and post-invasion comparisons were made.

(a) Betty’s Bay



(b) Cape Hangklip

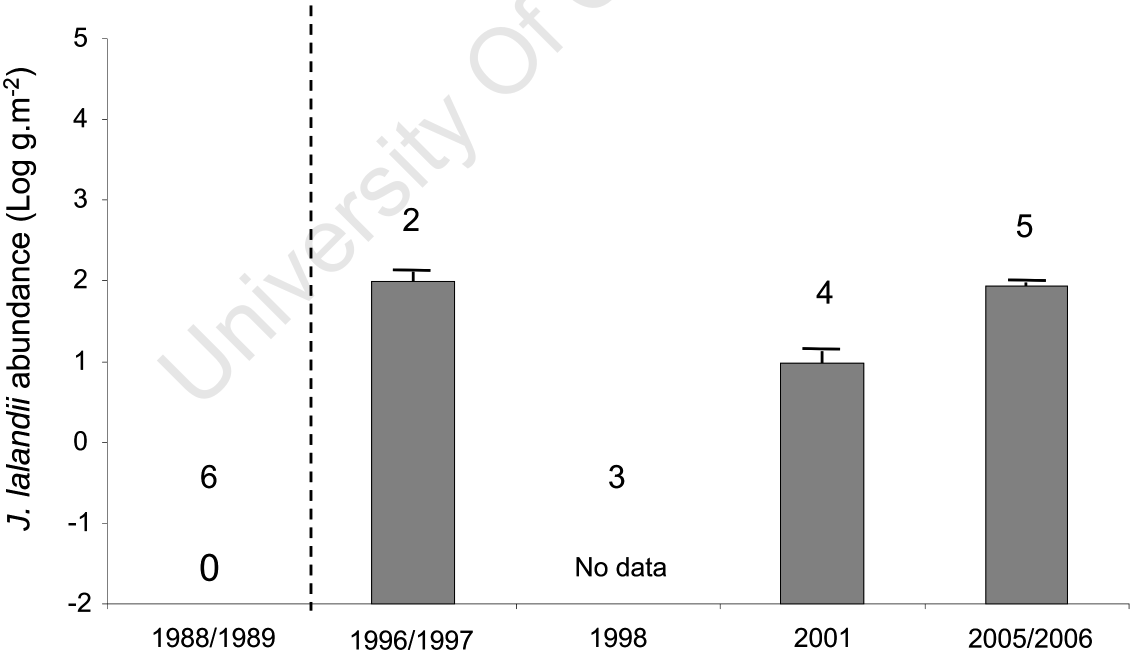


Fig 2.02: Temporal changes in West Coast rock lobster *Jasus lalandii* mean abundance (log g.m^{-2}) (+SE) at (a) Betty’s Bay and (b) Cape Hangklip before and after rock lobster ‘invasions’ (separated by broken lines). Sources of historical data are indicated in the methods. 1. Field *et al*. 1980a, 2. Mayfield 1998, 3. MCM unpublished data, 4. Reaugh 2001, 5. present surveys.

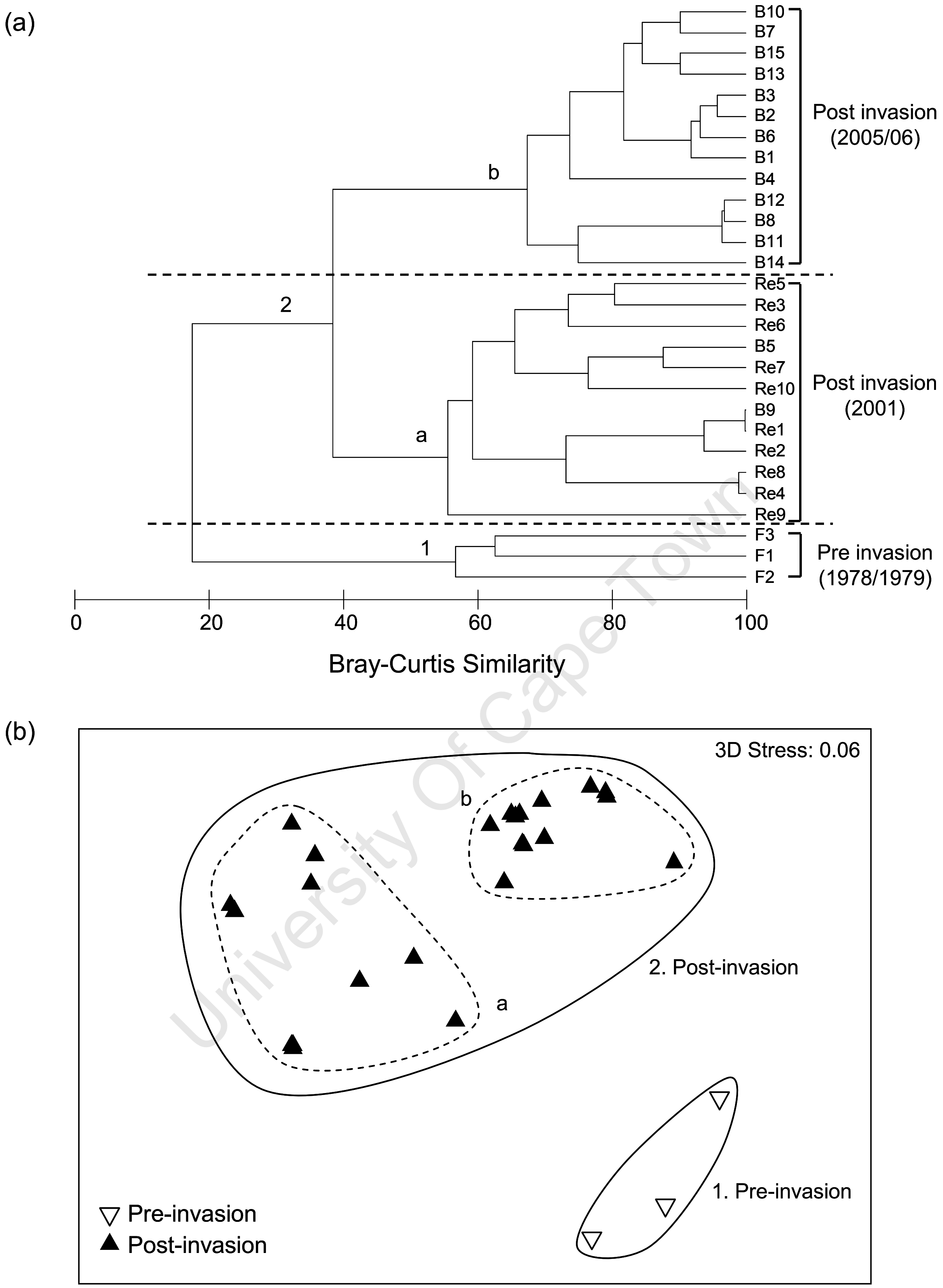


Fig 2.03: (a) Dendrogram showing hierarchical cluster analysis and (b) MDS plot based on standardized fourth-root transformed biomass data (functional groups) from Betty's Bay (<5 m depth) before and after the rock-lobster 'invasion'. F = Field *et al.* (1980a); Re = Reaugh (2001); B = Blamey (present work, 2005/2006 data); numbers indicate individual quadrats.

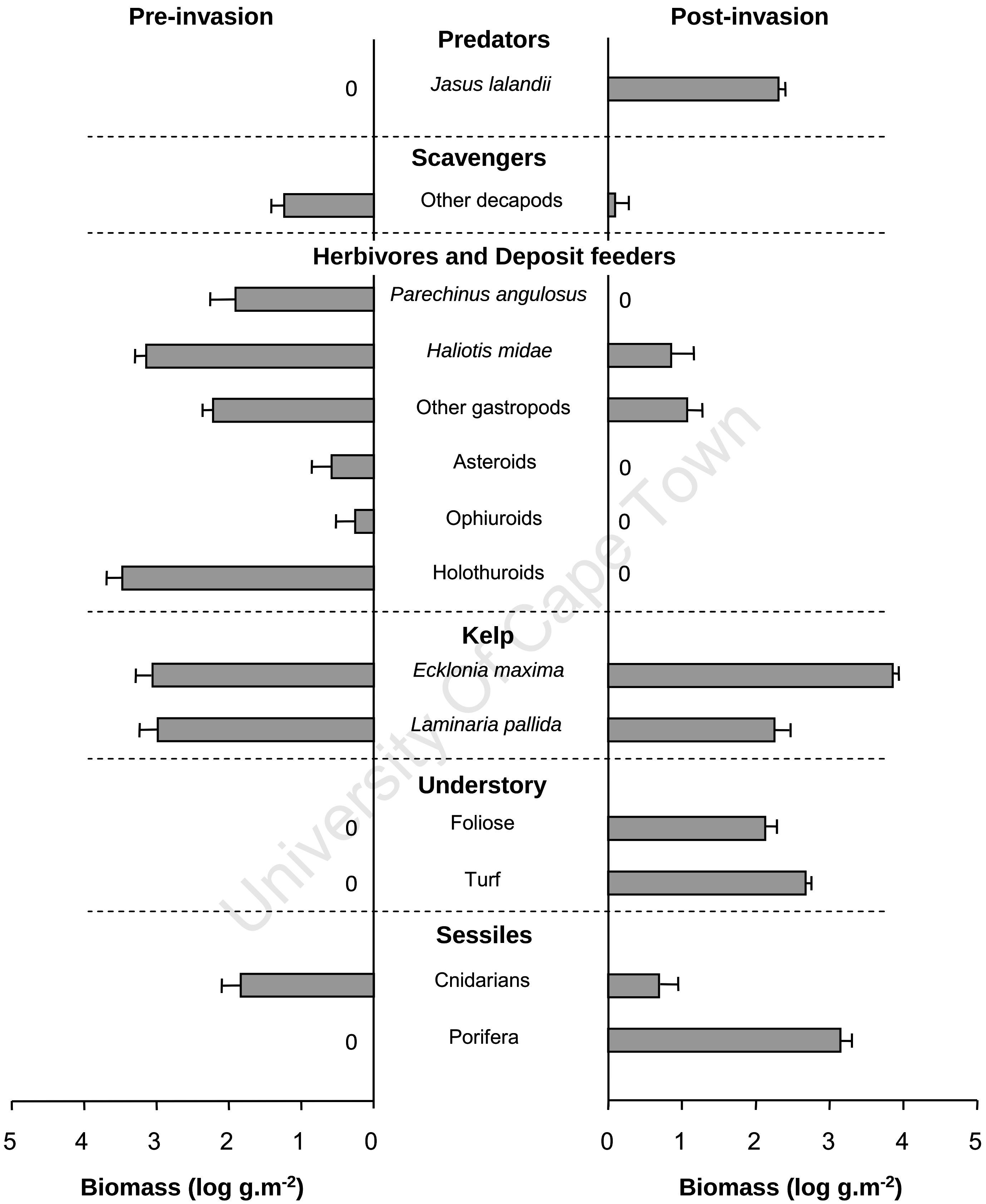


Fig 2.04: Average biomass (log g.m^{-2} +SE) of species contributing most to the dissimilarity between pre-invaded (n=3; 1978/1979) and post-invaded (n = 25; 2001 and 2005/2006) Betty's Bay at <5 m depth, as indicated by SIMPER analysis.

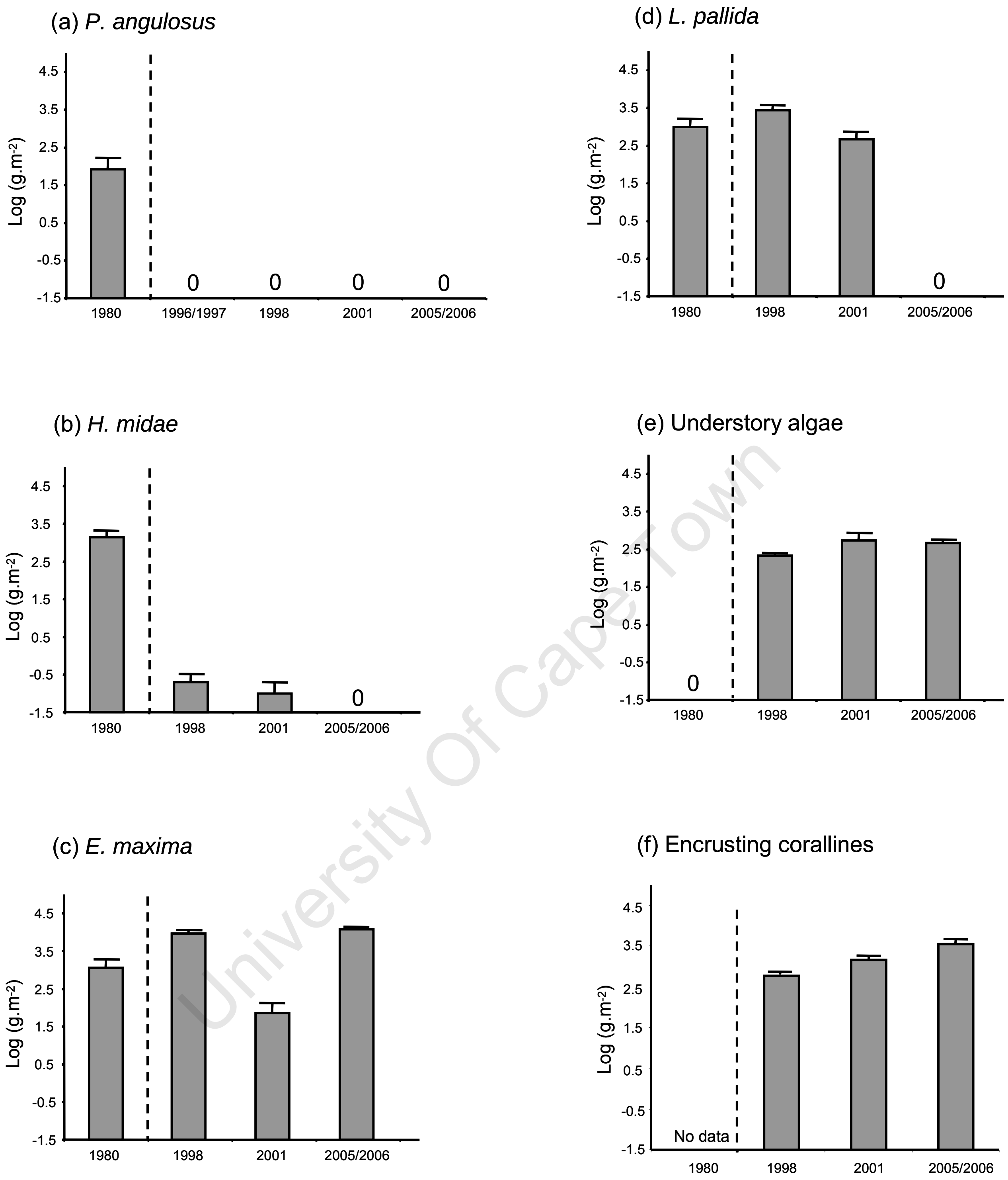


Fig 2.05: Temporal changes in abundance (log g.m^{-2}) of (a) *Parechinus angulosus*, (b) *Haliotis midae*, (c) *Ecklonia maxima* (d) *Laminaria pallida*, (e) understory algae and (f) encrusting corallines, at Betty's Bay. Broken line separates rock lobster 'pre-invasion' from 'post-invasion'.

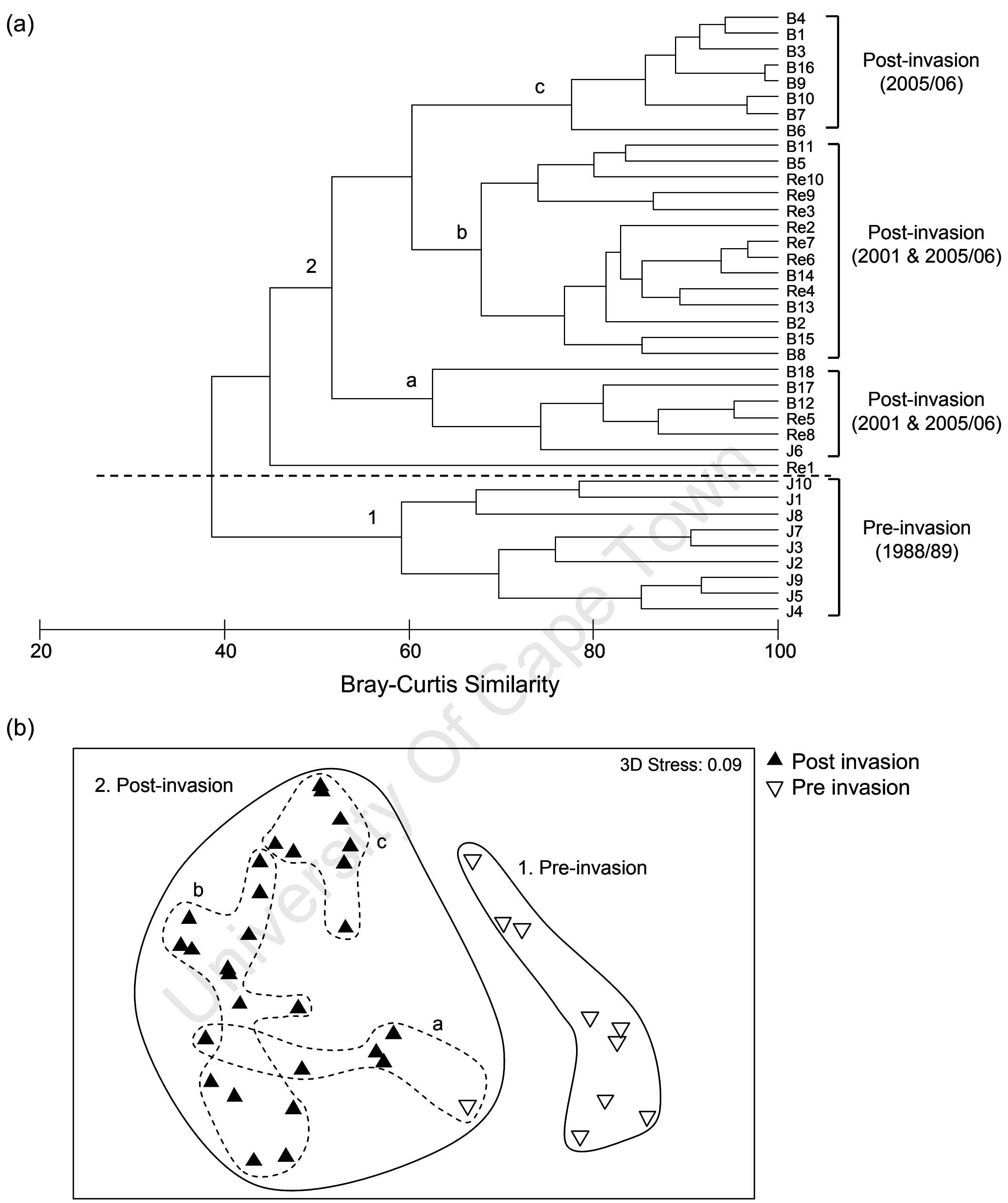


Fig 2.06: (a) Dendrogram showing hierarchical cluster analysis and (b) MDS plot based on standardized fourth-root transformed biomass data (functional groups) from Cape Hangklip (<5m depth) before and after the rock-lobster 'invasion'. J = Jackleman (1996); B = Blamey (present work, 2005/2006); Re = Reaugh (2001); numbers represent individual quadrats.

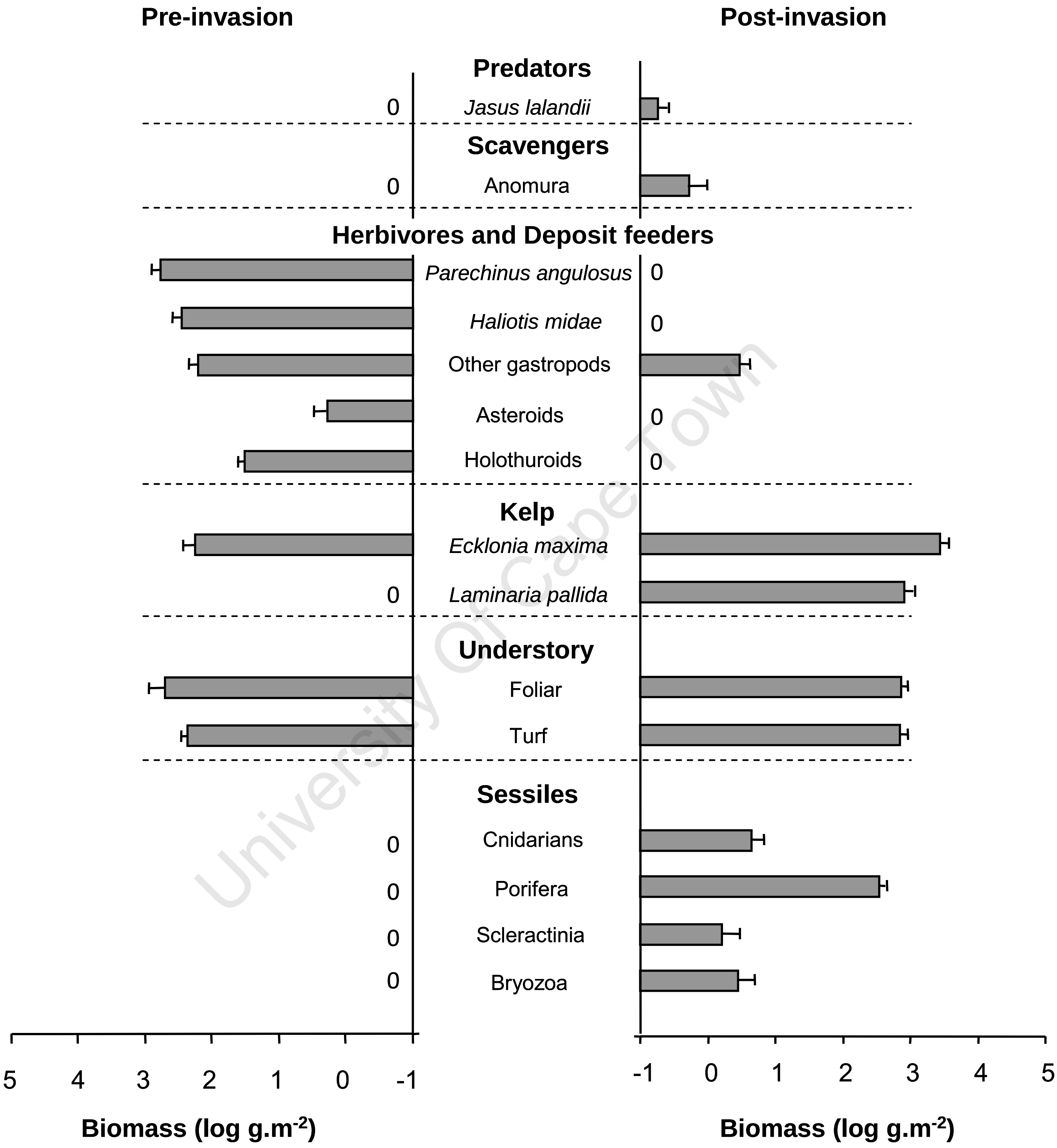


Fig 2.07: Average biomass (log $g.m^{-2}$ +SE) of species contributing most to the dissimilarity between pre-invaded (n=10; 1988/1989) and post-invaded (n = 28; 2001 and 2005/2006) conditions at Cape Hangklip at <5 m depth, as indicated by SIMPER analysis.

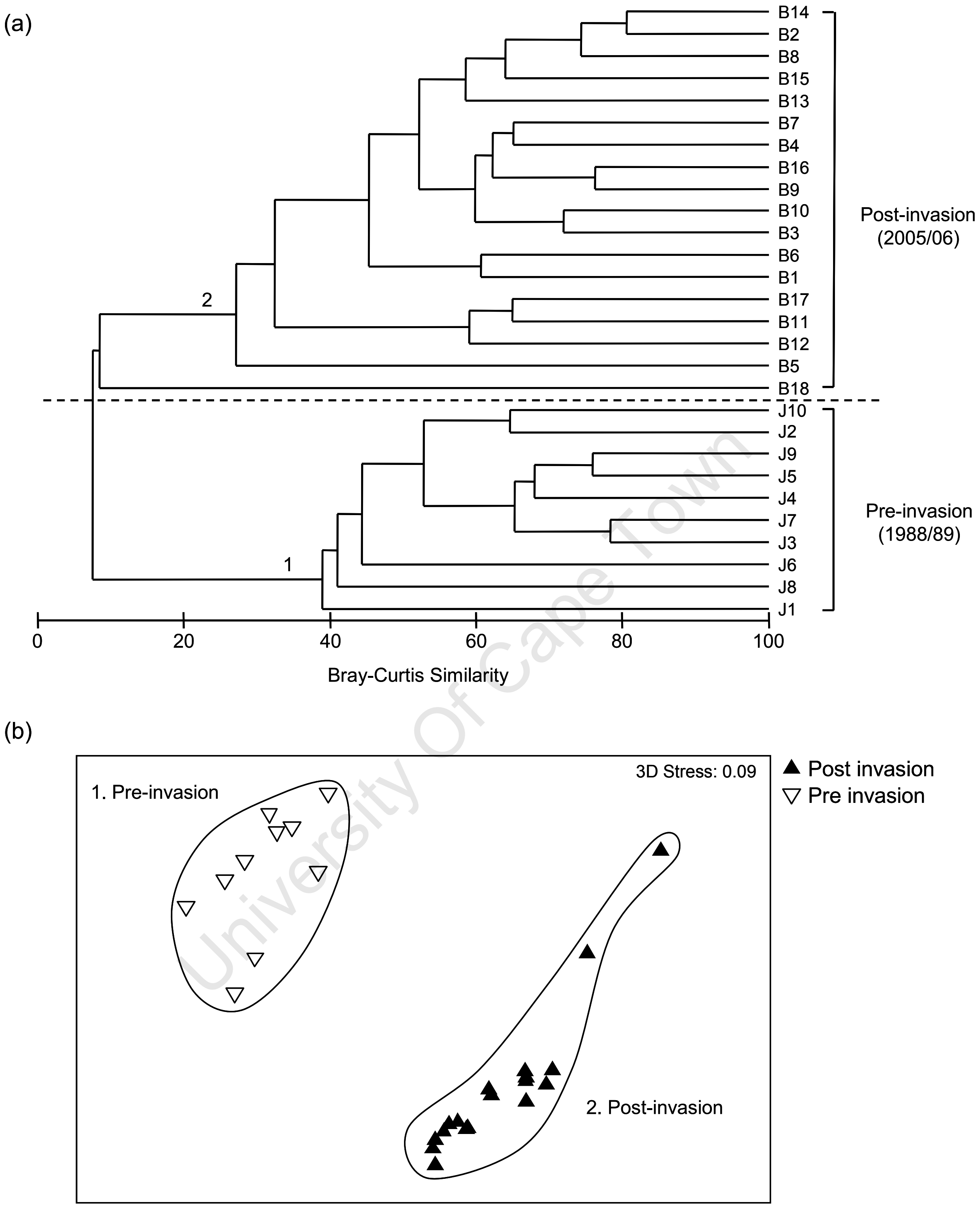


Fig 2.08: (a) Dendrogram showing hierarchical cluster analysis and (b) MDS plot based on standardized fourth-root transformed biomass data (floral species and faunal functional group data) from Cape Hangklip before and after the rock-lobster 'invasion'. J = Jackleman (1996); B = Blamey (present work, 2005/2006), numbers represent individual quadrats.

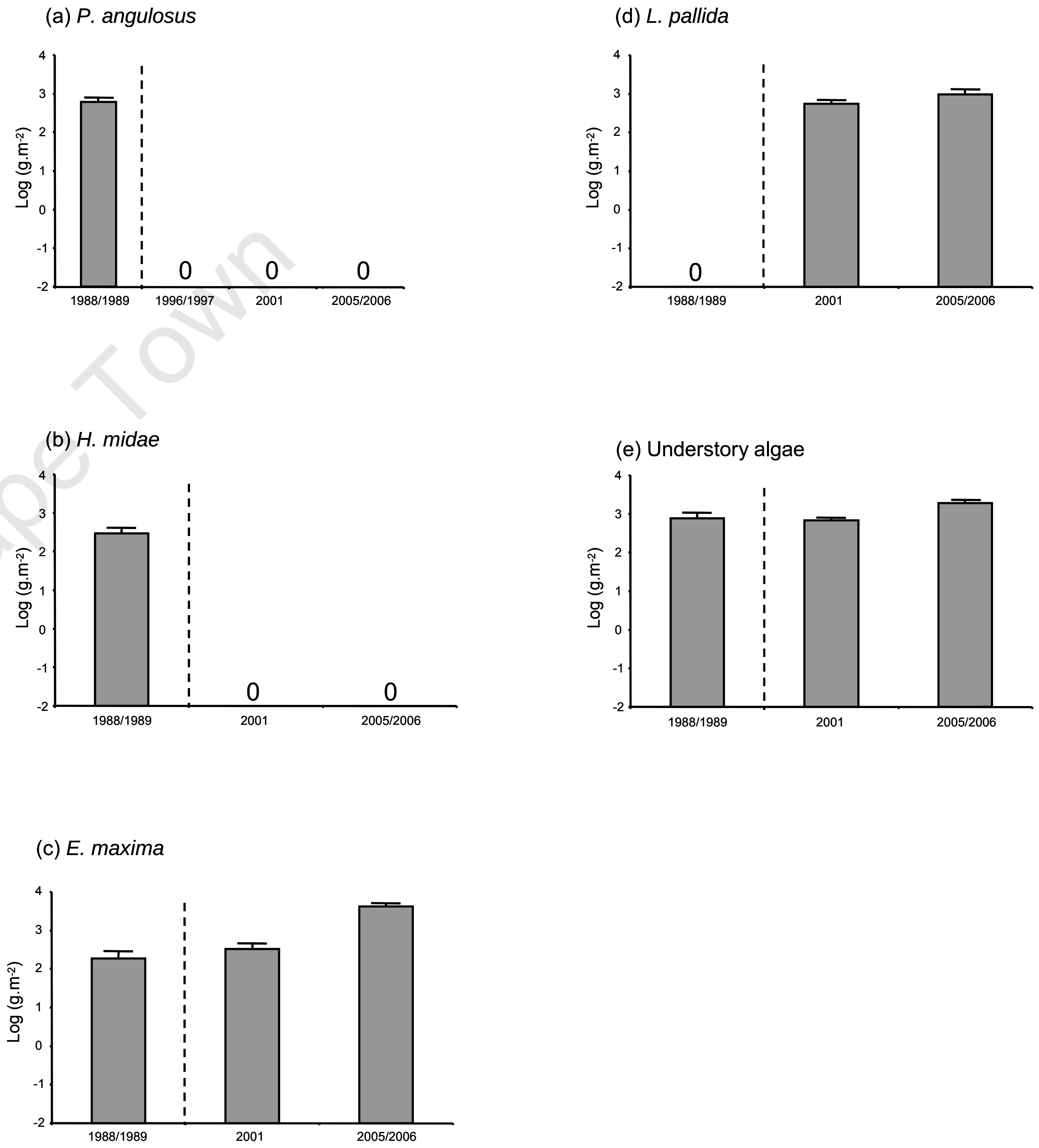


Fig 2.09: Temporal changes in abundance (log g.m^{-2}) of (a) *Parechinus angulosus*, (b) *Haliotis midae*, (c) *Ecklonia maxima* (d) *Laminaria pallida* and (e) understory algae, at Cape Hangklip. Broken line separates rock lobster ‘pre-invasion’ from ‘post-invasion’.

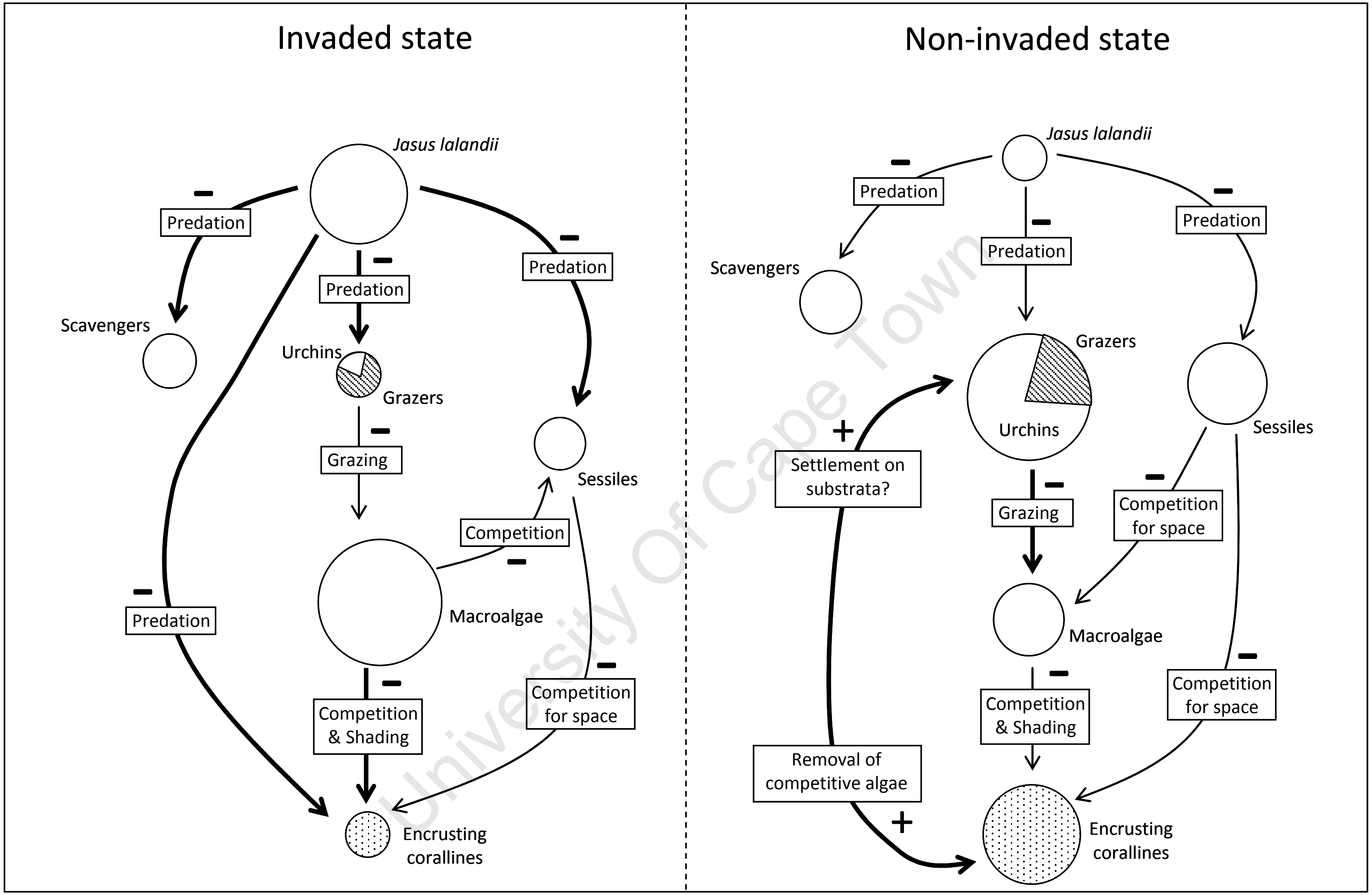


Fig 3.01: *A priori* flow model summarizing hypothesized states and interactions of the ecosystems in areas ‘invaded’ and ‘non-invaded’ by rock lobster. The bold arrows imply strong effects. Positive (+) and negative (-) effects are indicated in boxes. The sizes of circles indicate relative biomass of different functional groups.

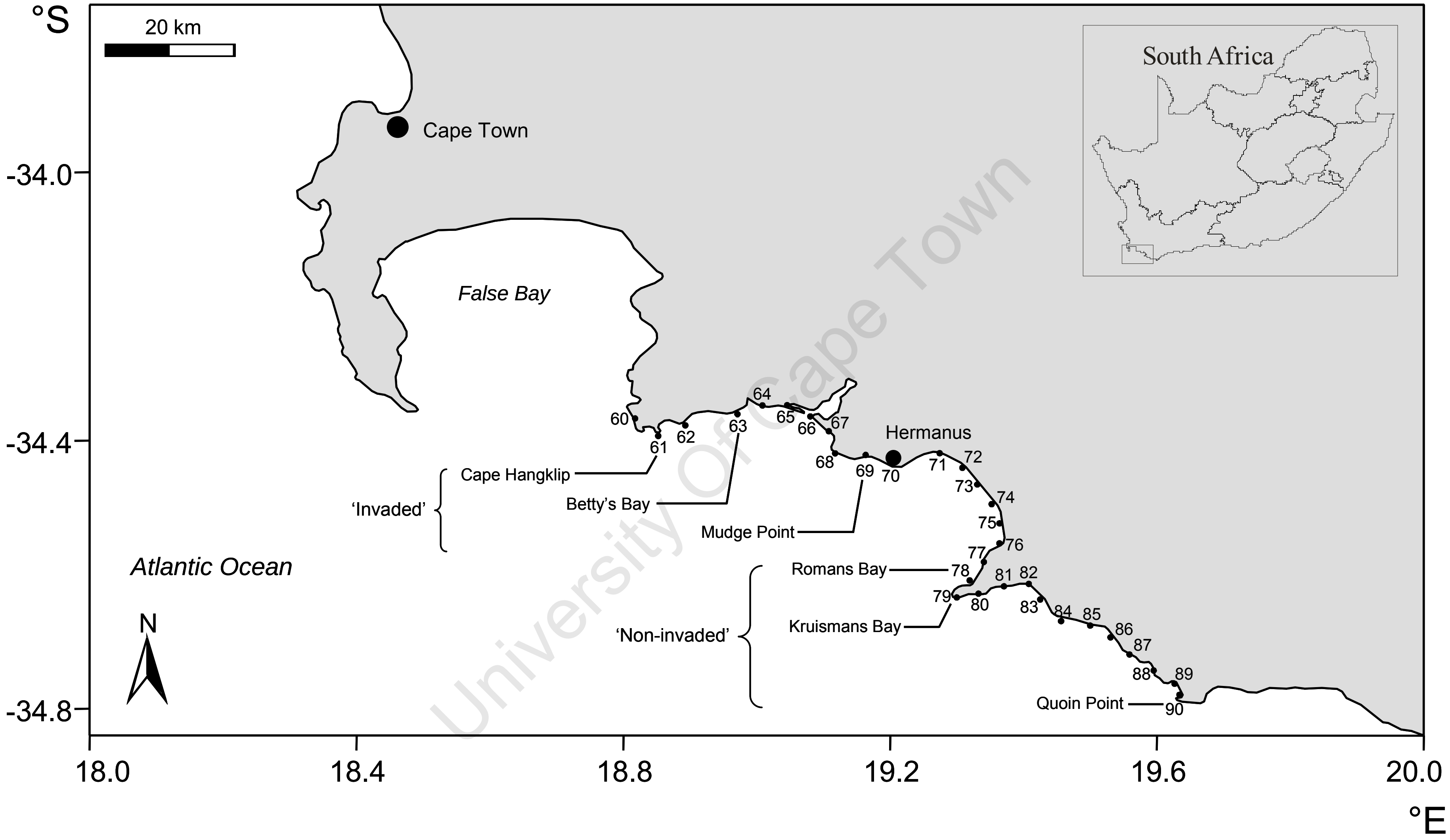


Fig 3.02: Map showing the six (named) study sites along the south-west coast of South Africa, east of Cape Hangklip (EOCH), and (numbered) Fishery Independent Monitoring Survey (FIMS) stations.

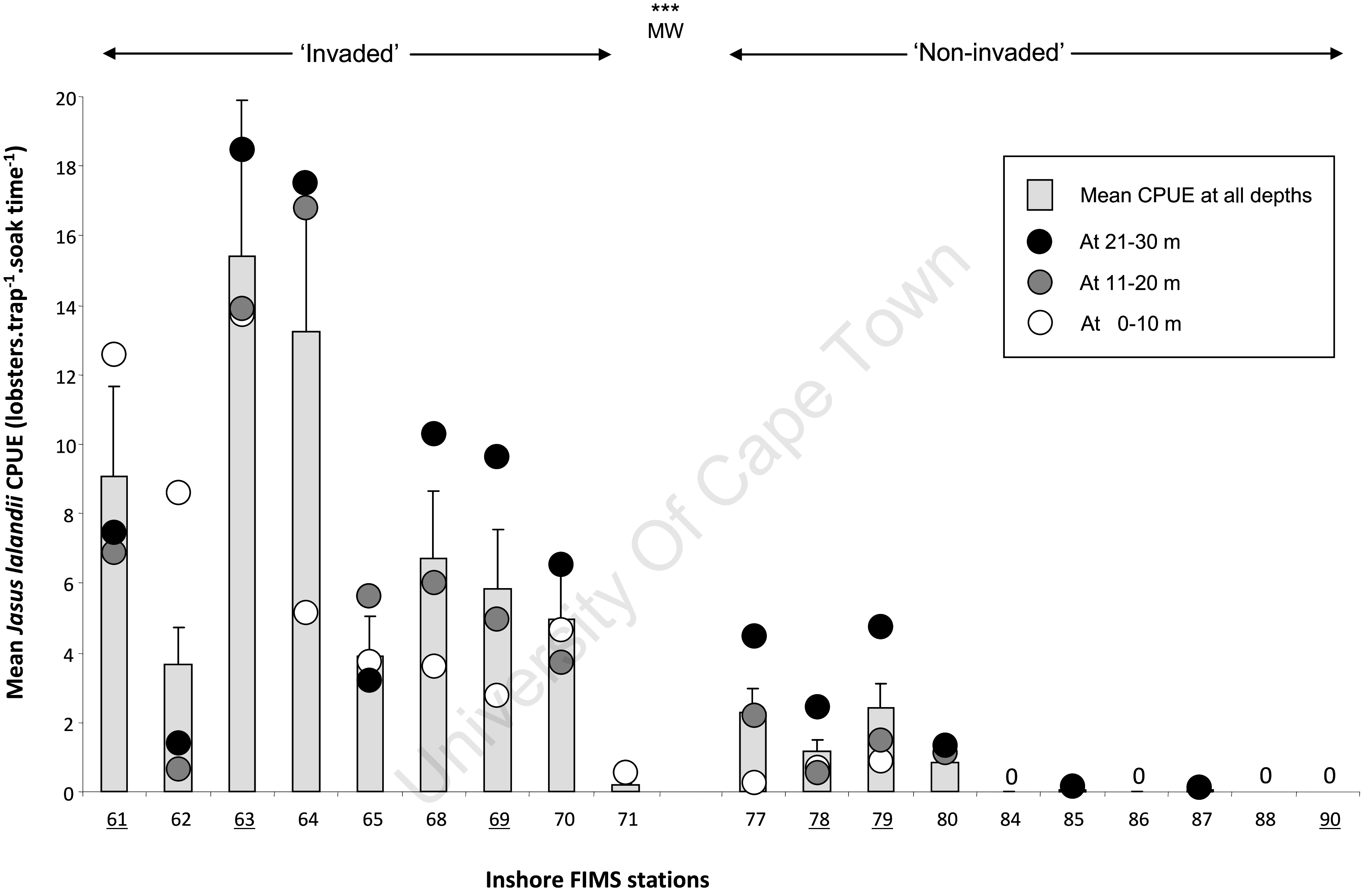


Fig 3.03: The mean *Jasus lalandii* CPUE (lobsters.trap^{-1}.soak period^{-1}) (+SE) for Fisheries Independent Monitoring Surveys (FIMS) averaged for 2002-2005 in the area EOCH. Underlined stations are where I took benthic samples: 61 = Hangklip, 63 = Betty's Bay, 69 = Mudge Point, 78 = Romans Bay, 79 = Kruismans Bay, 90 = Quoin Point. *** $p < 0.001$ for Mann-Whitney U-test (MW) between invaded and non-invaded areas.

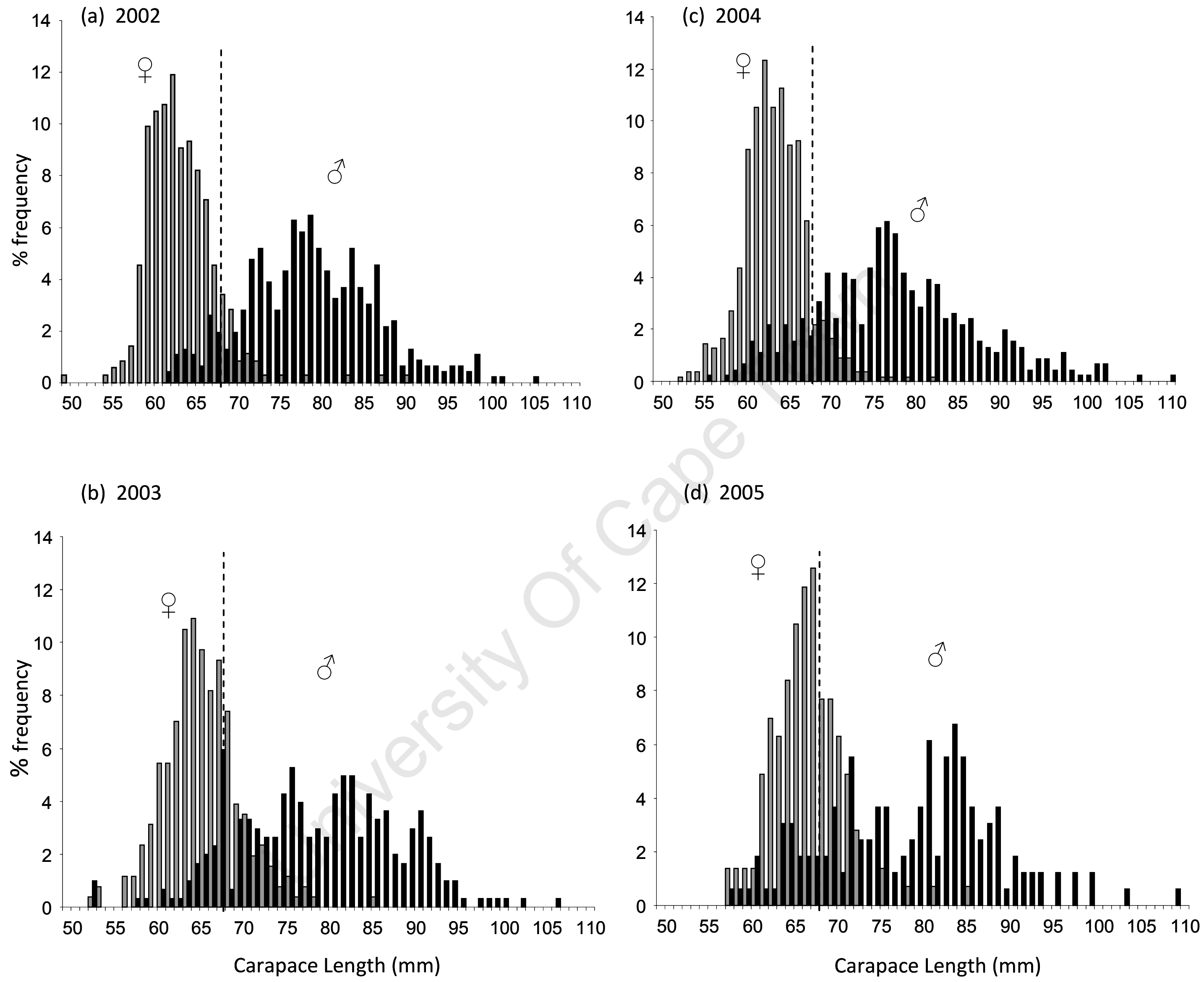


Fig 3.04: Size-frequency data for female and male *Jasus lalandii* for (a) 2002, (b) 2003, (c) 2004, (d) 2005. Dashed line indicates size (69 mm CL) at which *J. lalandii* is able to feed on the urchin *Parechinus angulosus*.

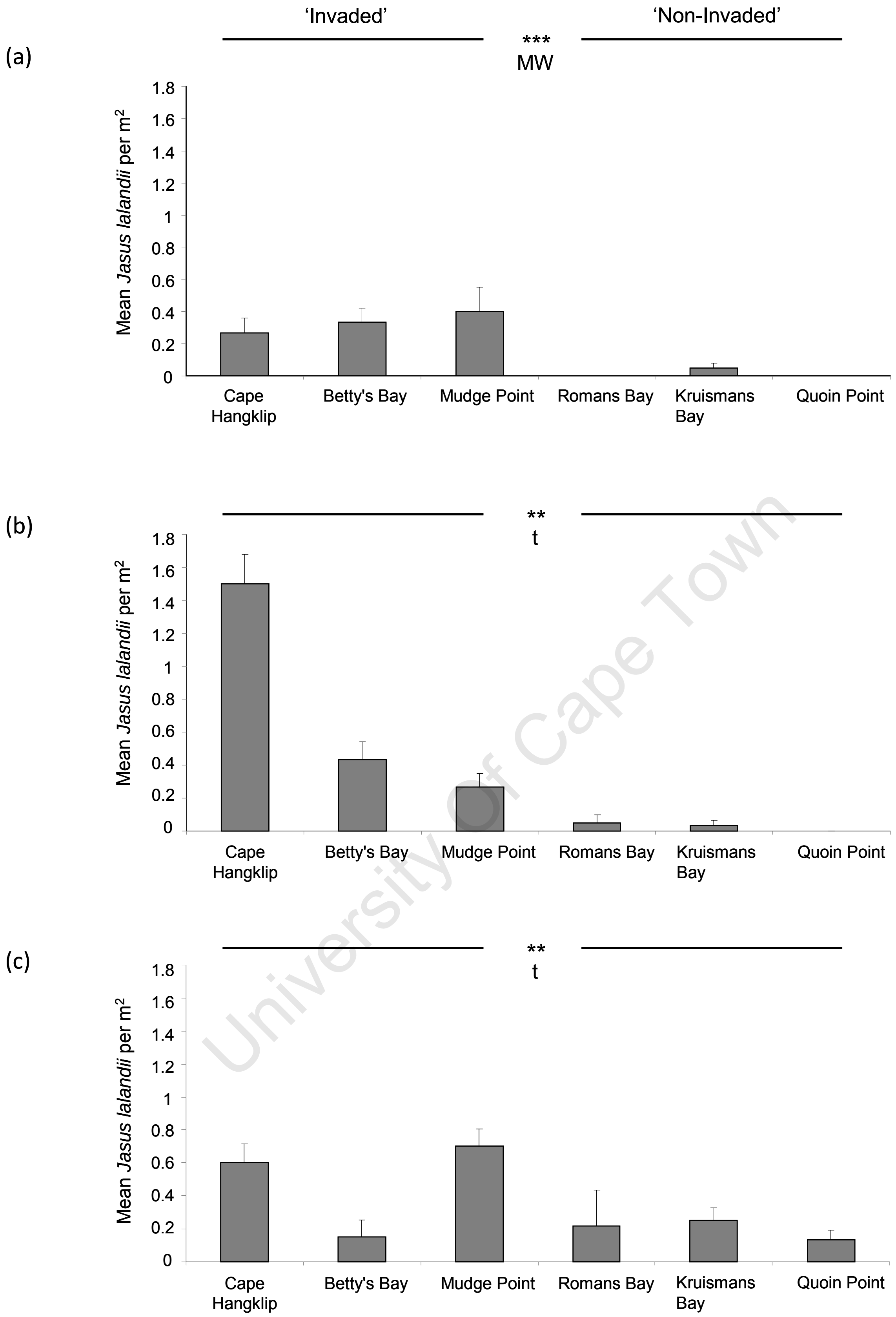


Fig 3.05: Mean number of *Jasus lalandii* per m^2 (+SE) at three different depth ranges: (a) < 5 m; (b) 6-12 m; (c) 13-20 m at six sites along the south-west coast EOCH. Significant differences between 'invaded' and 'non-invaded' areas are indicated as follows: * $p < 0.05$, ** $P < 0.01$ and *** $p < 0.001$ for either non-parametric Mann-Whitney U-tests (MW) or t-tests (t).

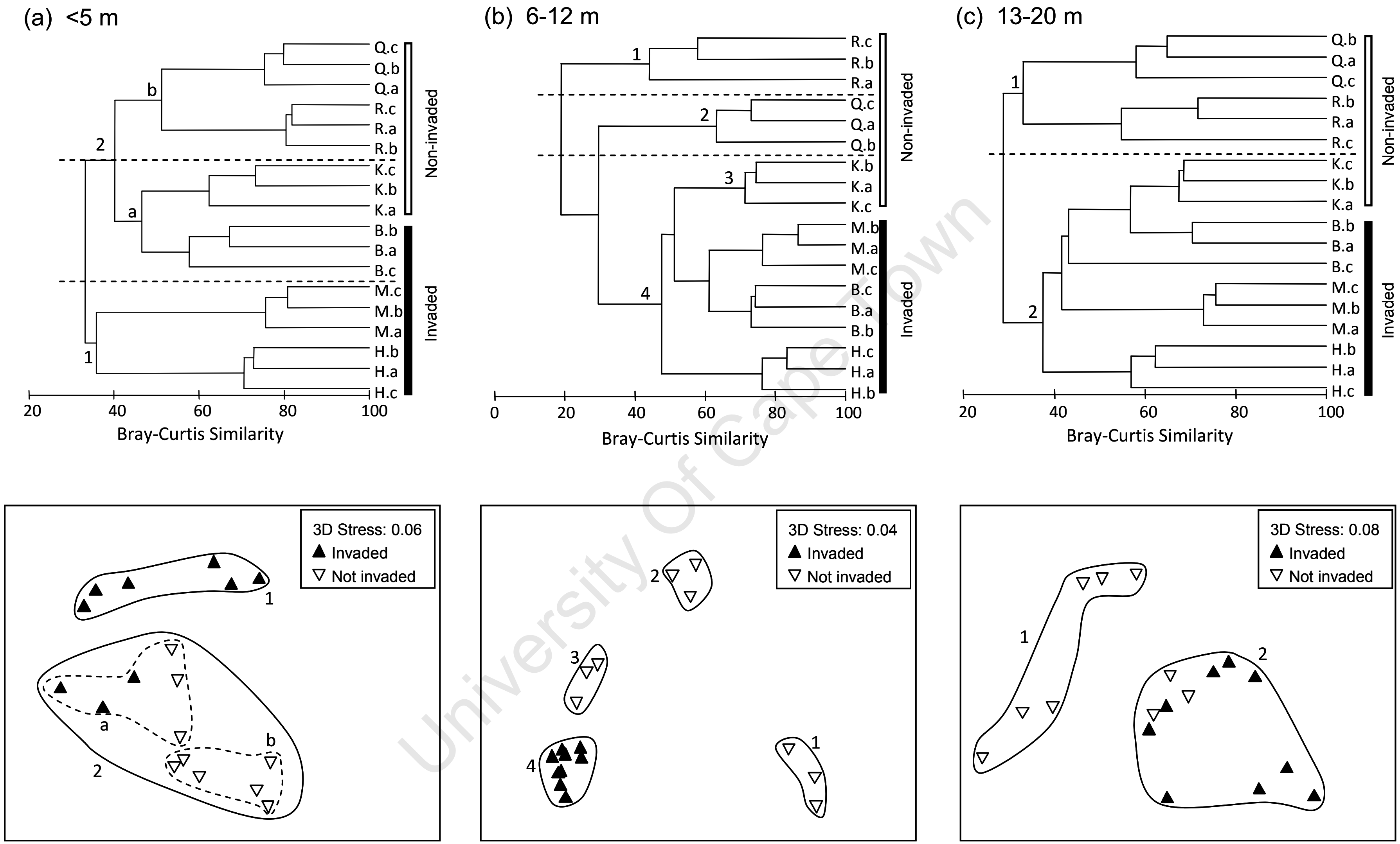


Fig 3.06: Dendrogram showing hierarchical cluster analysis and MDS plot based on standardized fourth-root transformed biomass data (species level, averaged for each transect) for (a) <5 m, (b) 6-12 m and (c) 13-20 m depth range for six sites. H = Cape Hangklip, B = Betty's Bay, M = Mudge Point, R = Romans Bay, K = Kruismans Bay and Q = Quoin Point; the suffixes a, b and c indicate the three replicate transects per site.

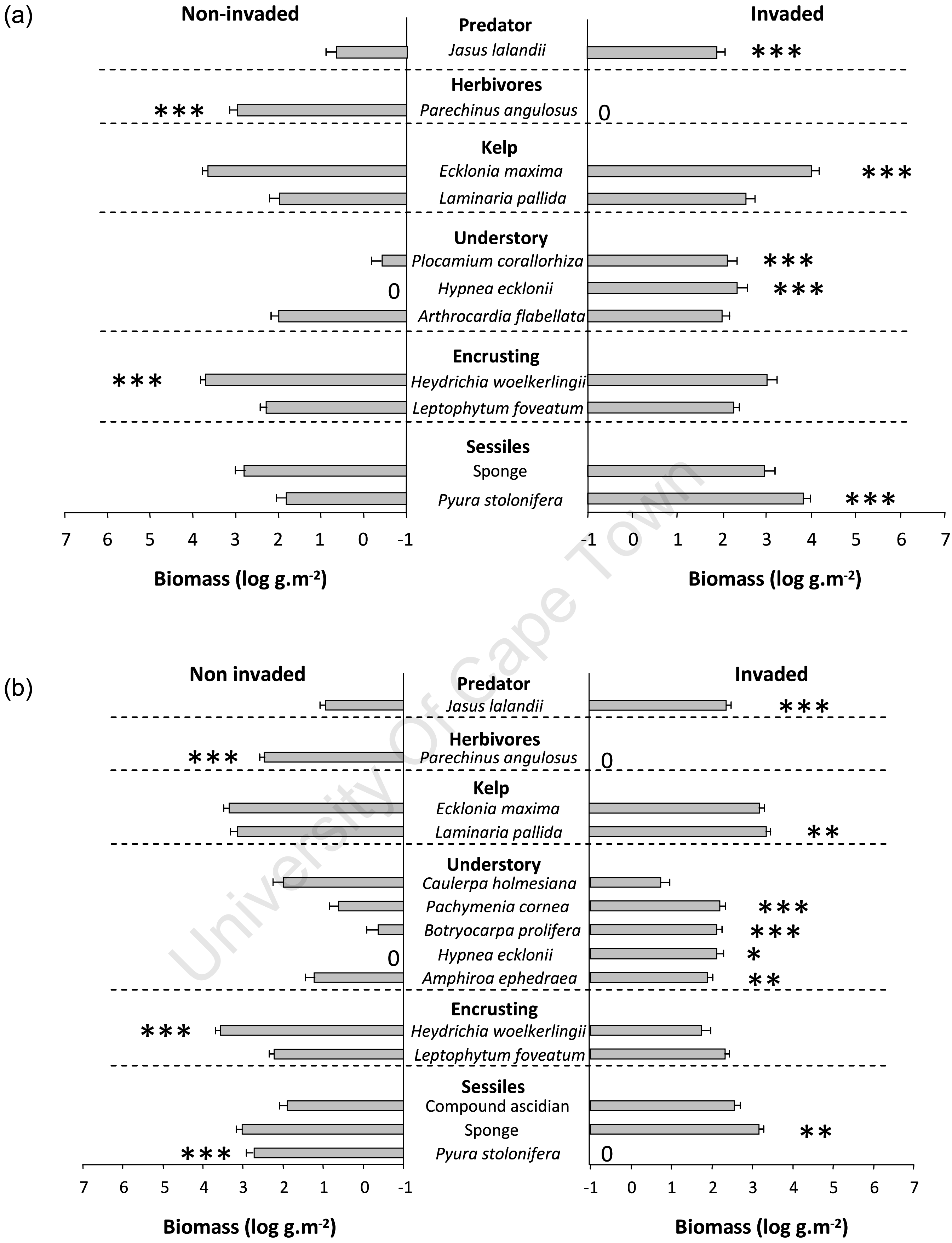


Fig 3.07a-b: Average biomass (log g.m^{-2} +SE) of species contributing most to the dissimilarity between invaded and non-invaded areas at a depth range of (a) <5 m and (b) 6-12 m, as identified by SIMPER analysis. Mann-Whitney U-tests: * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$.

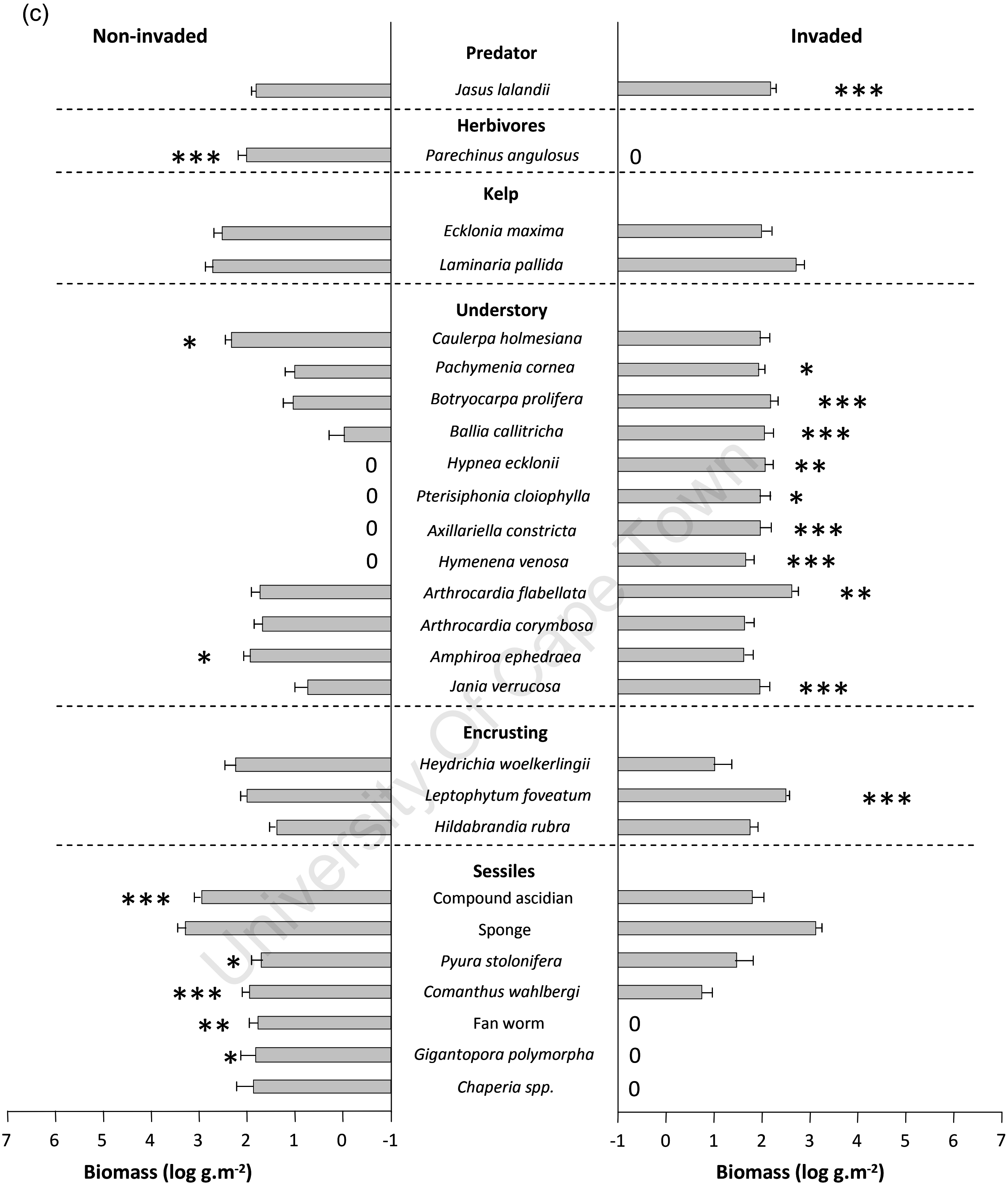


Fig 3.07c: Average biomass (log g.m^{-2} +SE) of species contributing most to the dissimilarity between invaded and non-invaded areas at a depth range of 13-20 m, as identified by SIMPER analysis. Mann-Whitney U-tests: * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$.

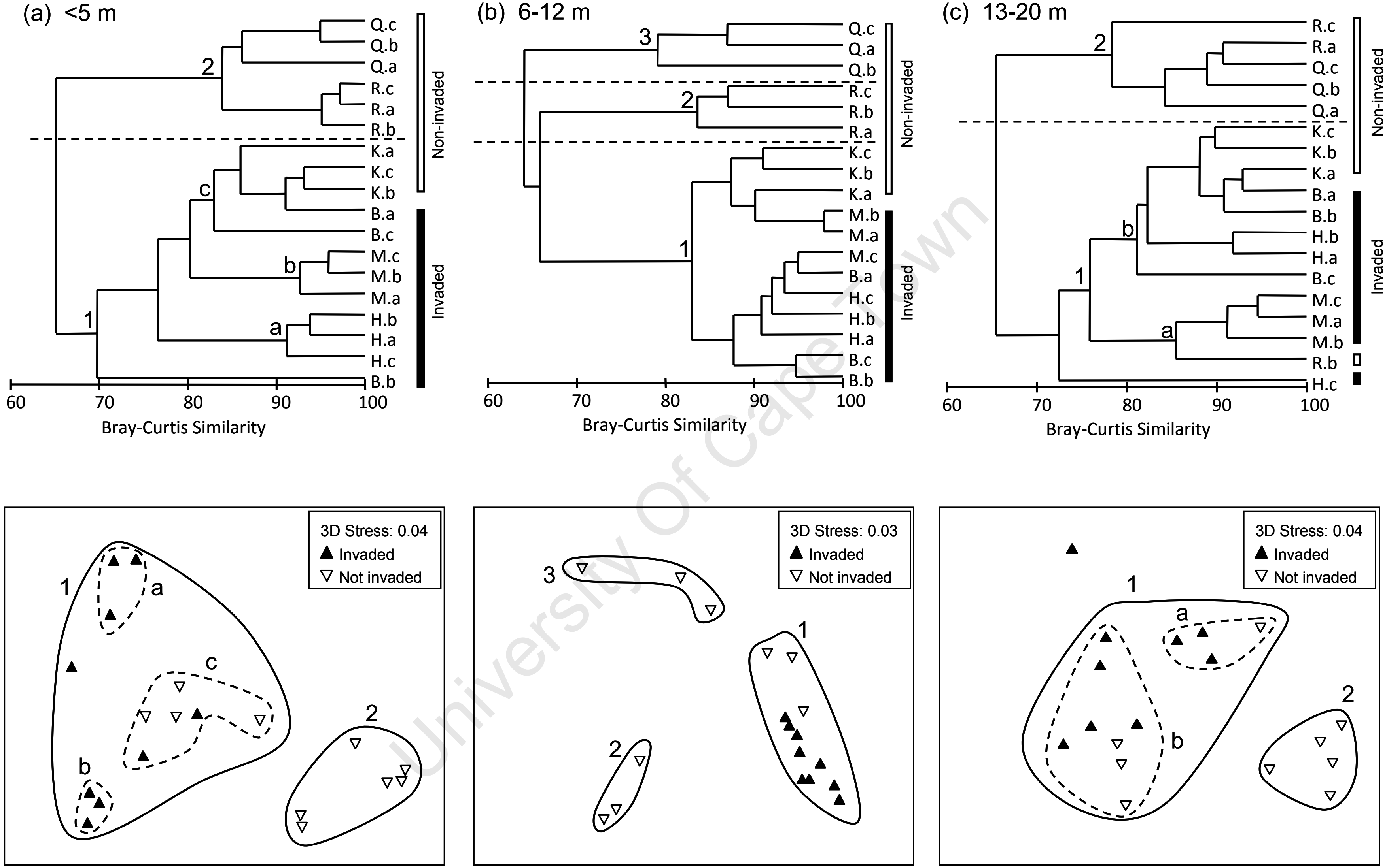


Fig 3.08: Dendrogram showing hierarchical cluster analysis and MDS plot based on standardized fourth-root transformed biomass data (functional group level, averaged for each transect) for the (a) <5 m, (b) 6-12 m and (c) 13-20 m depth ranges at six sites. See caption to Fig. 3.06 for site names.

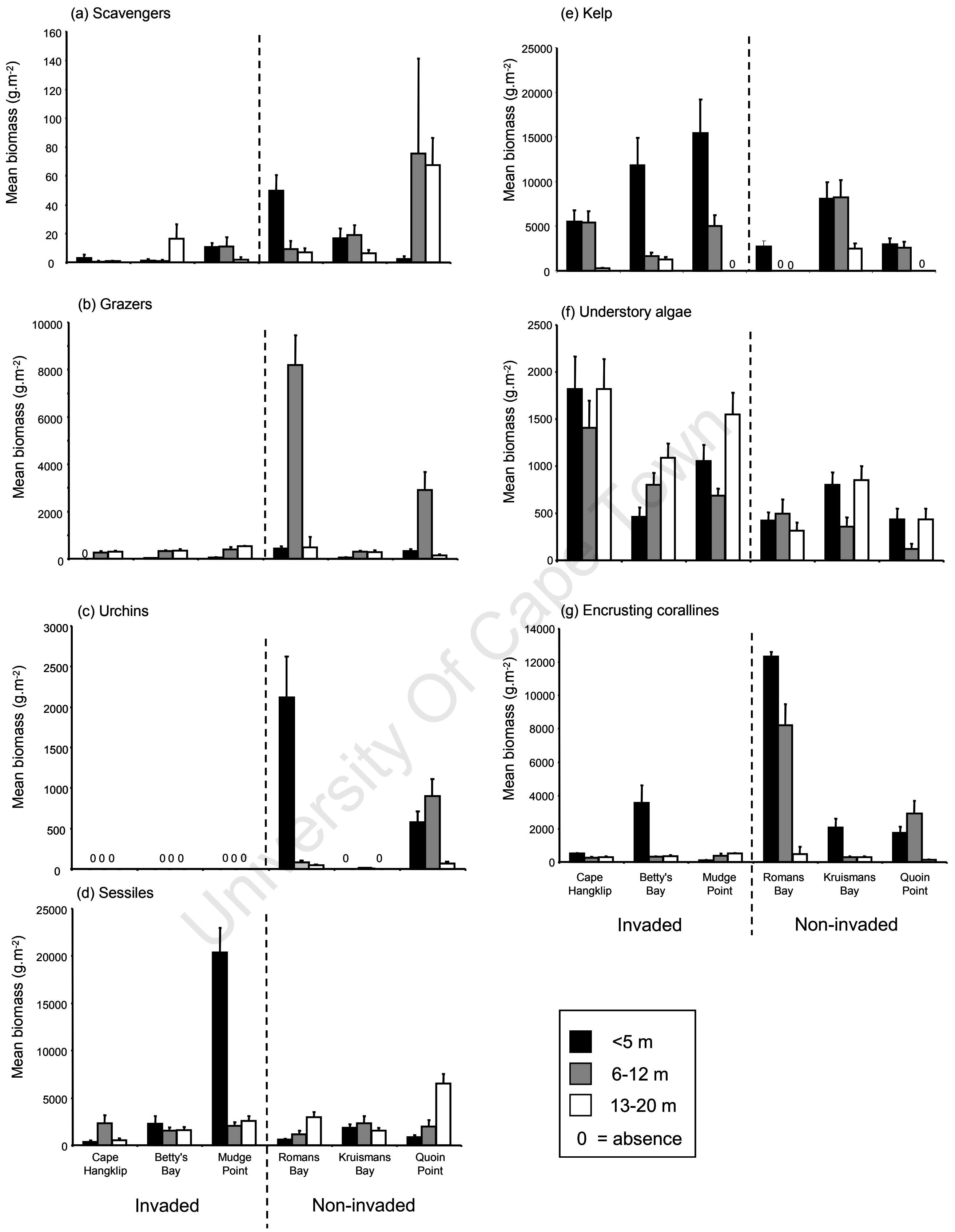


Fig 3.09: Mean biomasses (+SE) of functional groups at six sites along the south-west coast EOCH in three depth zones. Broken lines separate 'invaded' sites (left) from 'non-invaded' sites (right).

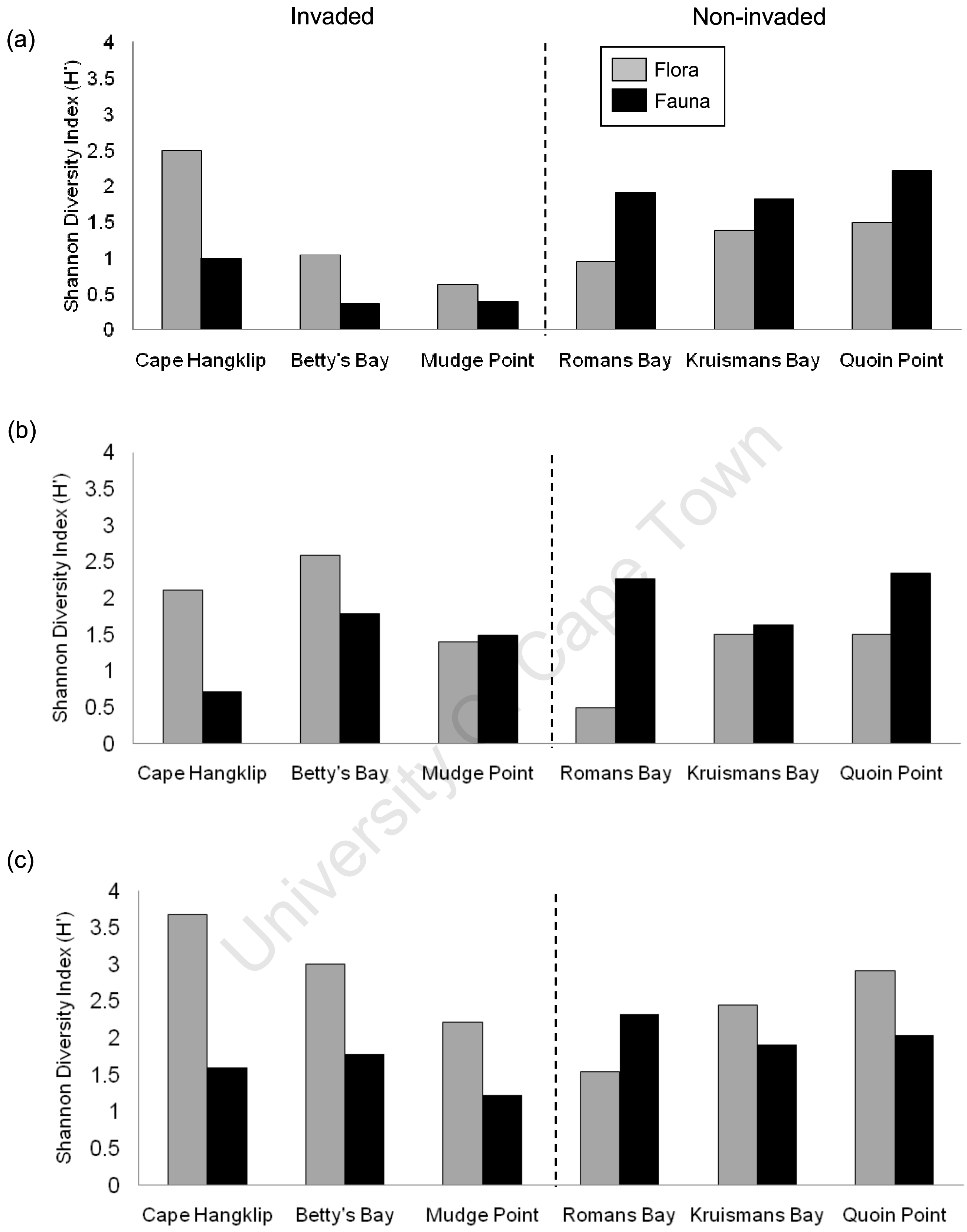


Fig 3.10: Species diversity (based on the Shannon Diversity Index (H′)) for the six sites EOCH in (a) <5m, (b) 6-12m and (c) 13-20m depth zones.

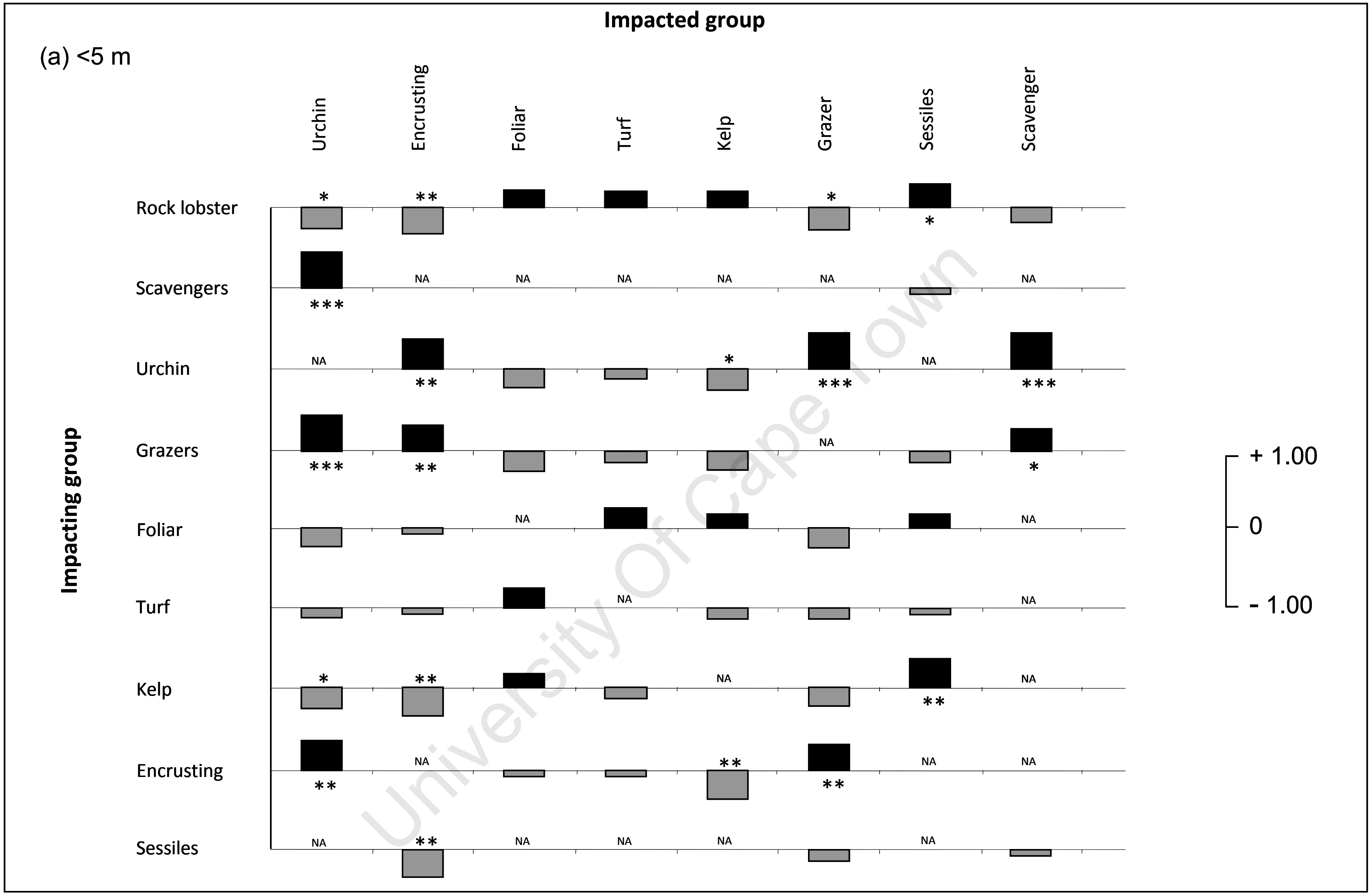


Fig 3.11a: Relationships between selected groups at a depth range of <5m. Bars indicate the correlation (scaled between 0 and ±1) between selected groups. Positive correlations are shown above the zero line for each group, and negative correlations below. Impacted groups are listed on the horizontal axis and the impacting groups on the vertical axis. Significant correlations are indicated at various levels: * = $p < 0.05$, ** = $p < 0.01$ and *** = $p < 0.001$; NA = not applicable. The scale on the right shows the maximum positive and negative values for each impacting group.

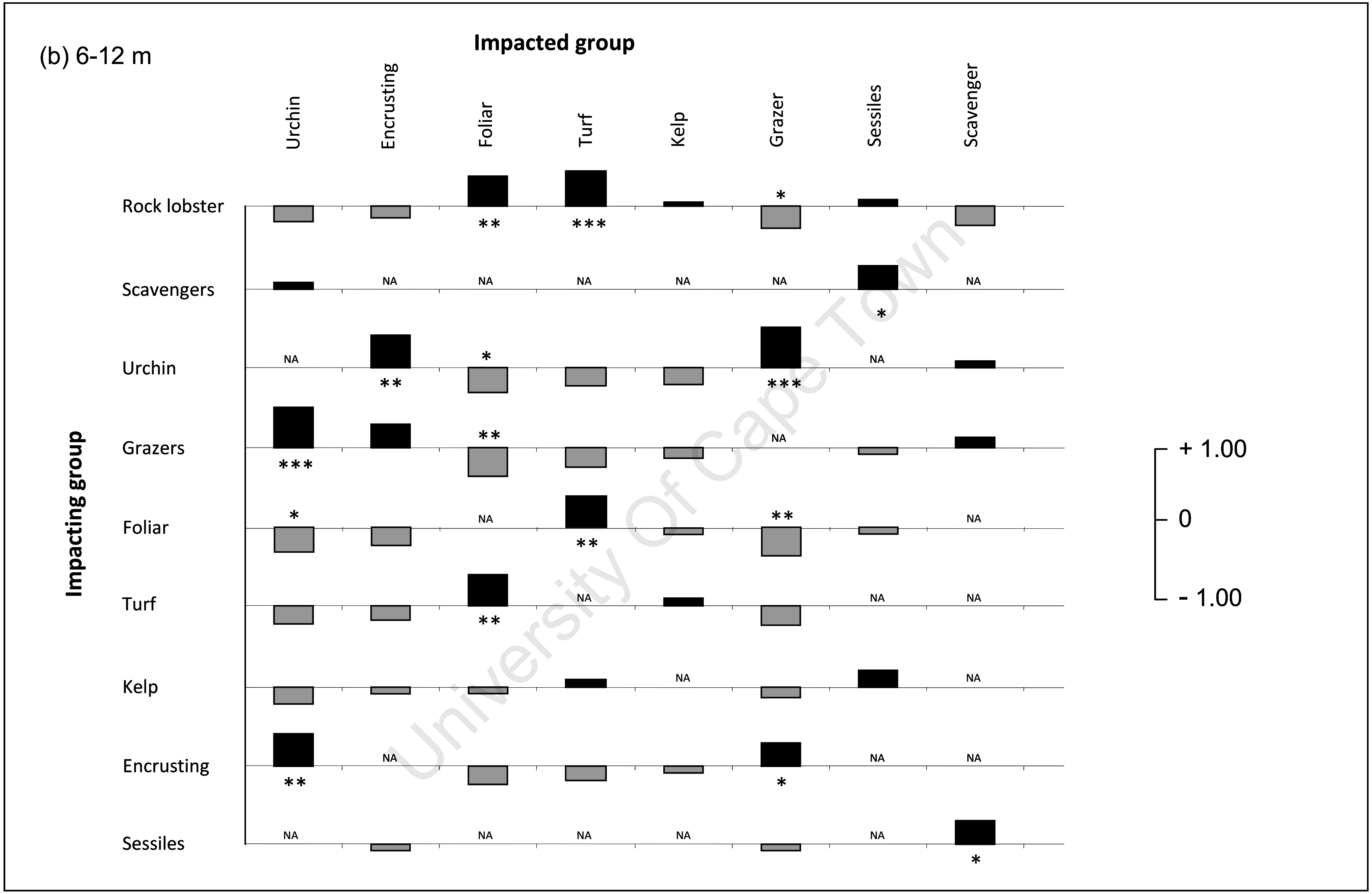


Fig 3.11b: Relationships between selected groups at a depth range of 6-12m. For further details see caption to Fig 3.11a.

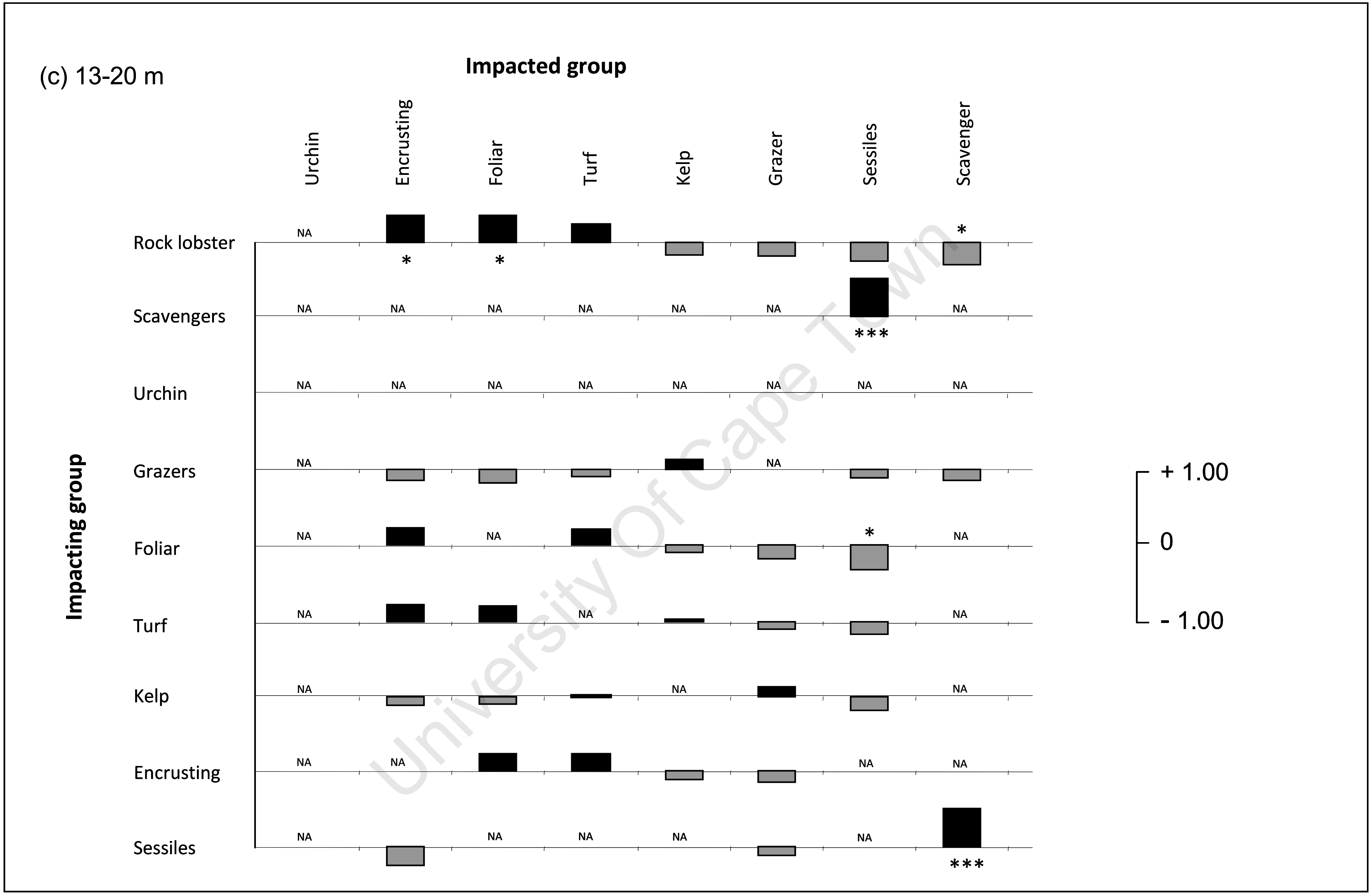


Fig 3.11c: Relationships between selected groups at a depth range of 13-20m. For further details see caption to Fig 3.11a.

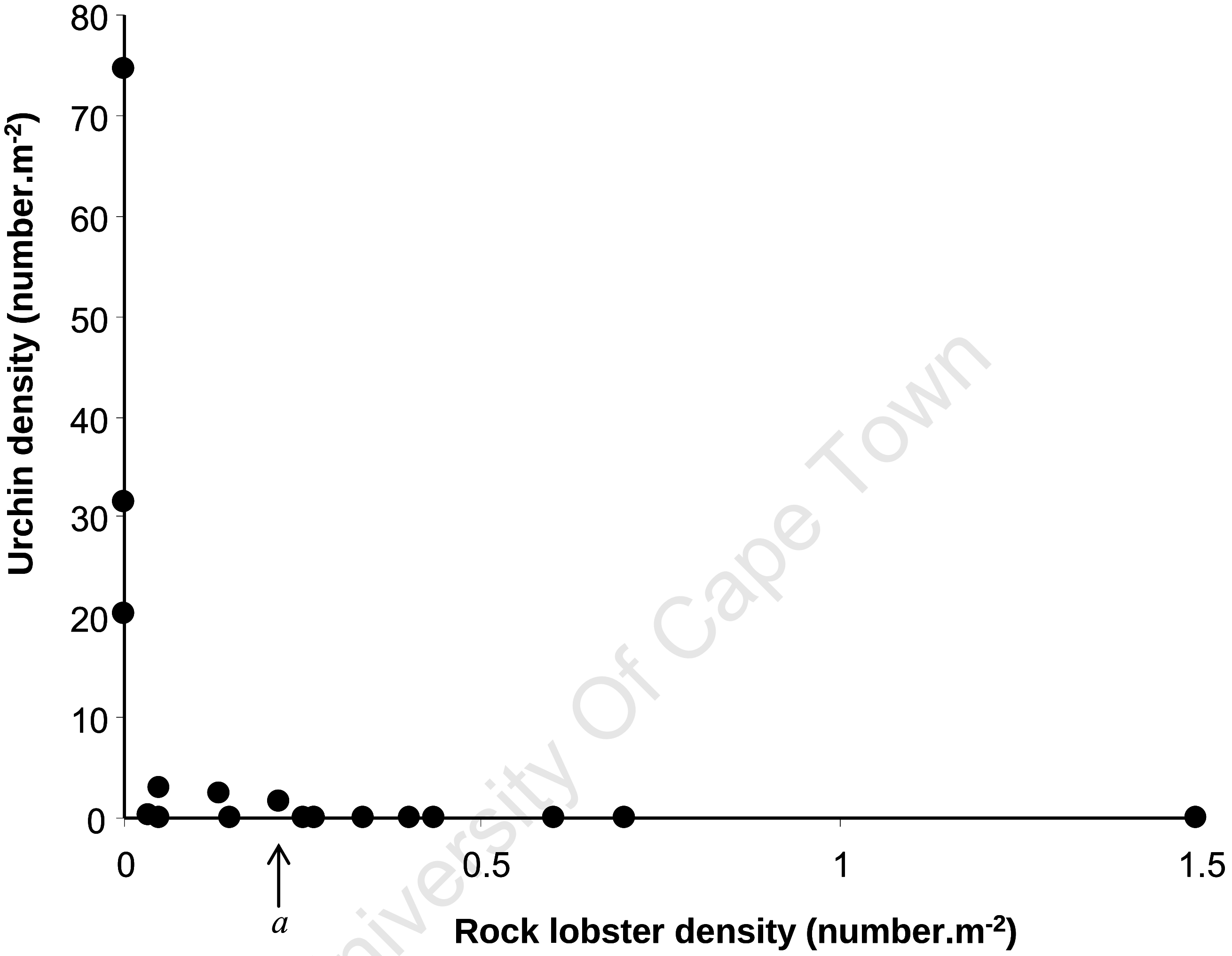
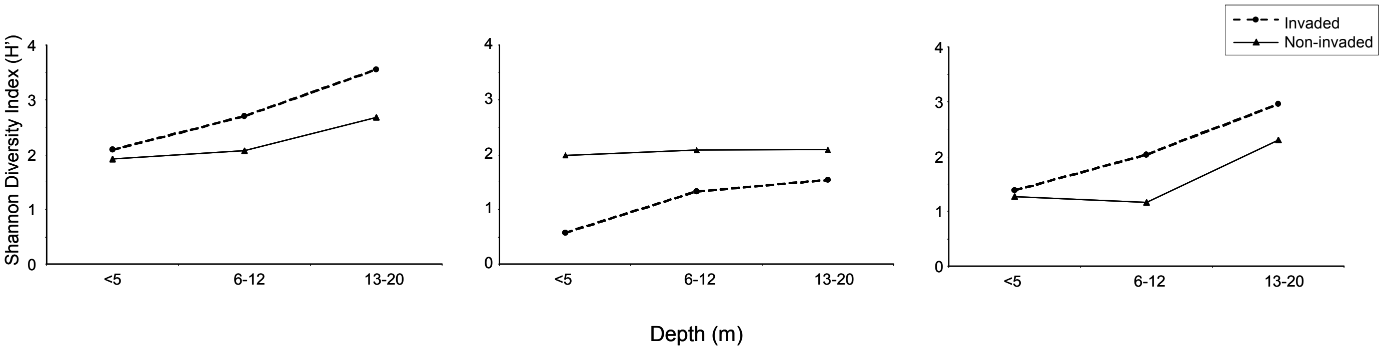


Fig 3.12: Relationship between the density of urchins and rock lobsters (numbers.m^{-2}). Point *a* indicates the rock lobster density (0.22 rock lobsters.m^{-2}) above which there are no urchins.

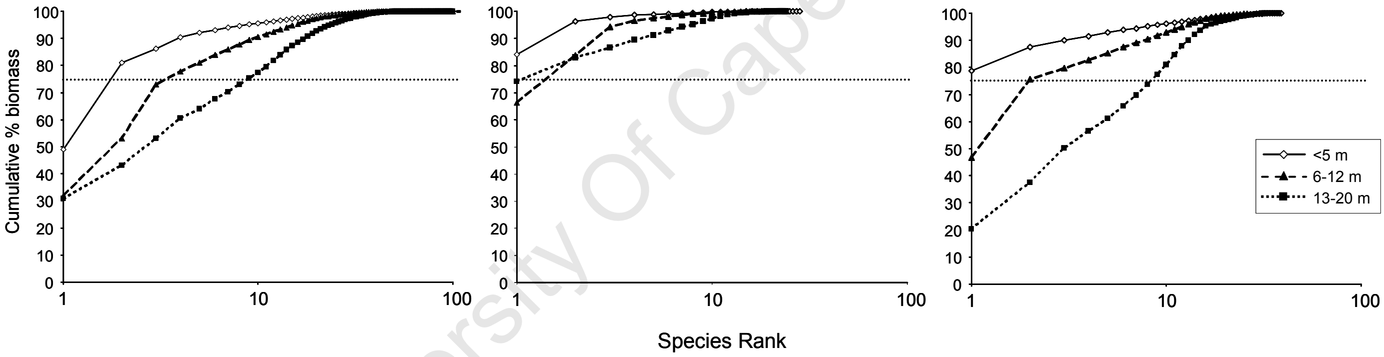
Diversity


(a) Total

(b) Fauna

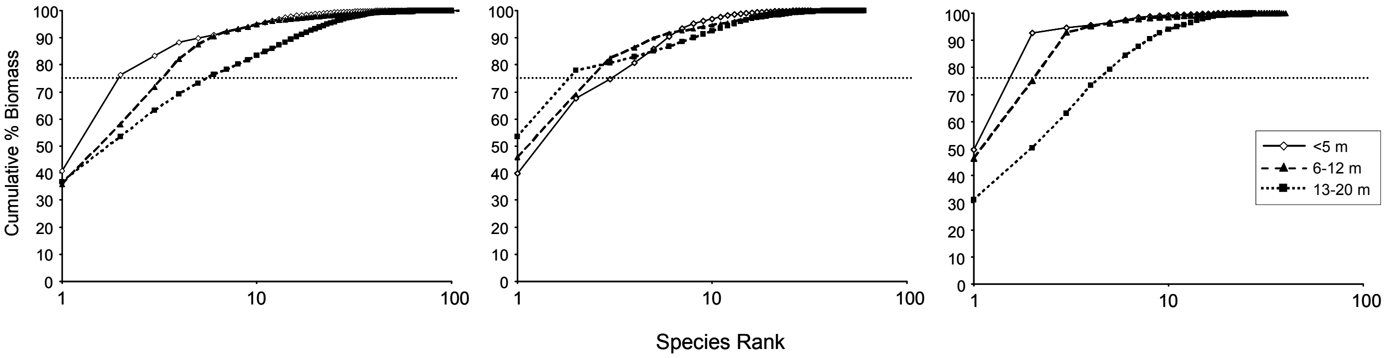
(c) Flora

Dominance


(d) Total (Invaded)

(e) Fauna (Invaded)

(f) Flora (Invaded)


(g) Total (Non-invaded)

(h) Fauna (Non-invaded)

(i) Flora (Non-invaded)

Fig 3.13: Total, faunal and floral diversity patterns and dominance curves relative to depth and invasion status. Dotted horizontal lines indicate 75% of the total biomass.

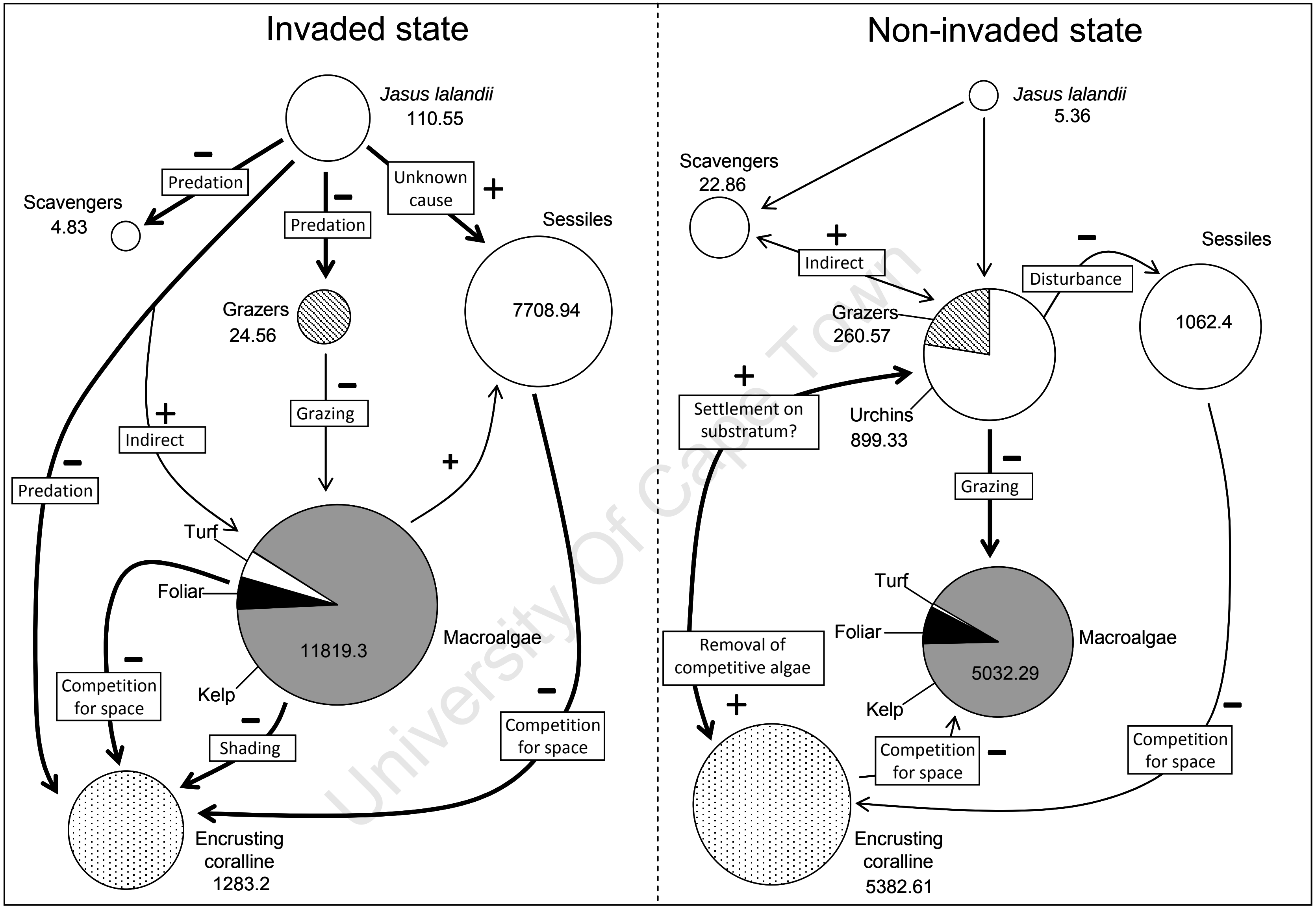


Fig 3.14a: Interaction webs for invaded and non-invaded states in the <5 m depth zone. The bold arrows imply a greater effect and the non-bold arrows a lesser effect. Positive (+) and negative (-) effects are indicated in boxes. Mean biomasses are indicated in $g.m^{-2}$ and by the areas of the circles, which are proportional to biomass on a log scale.

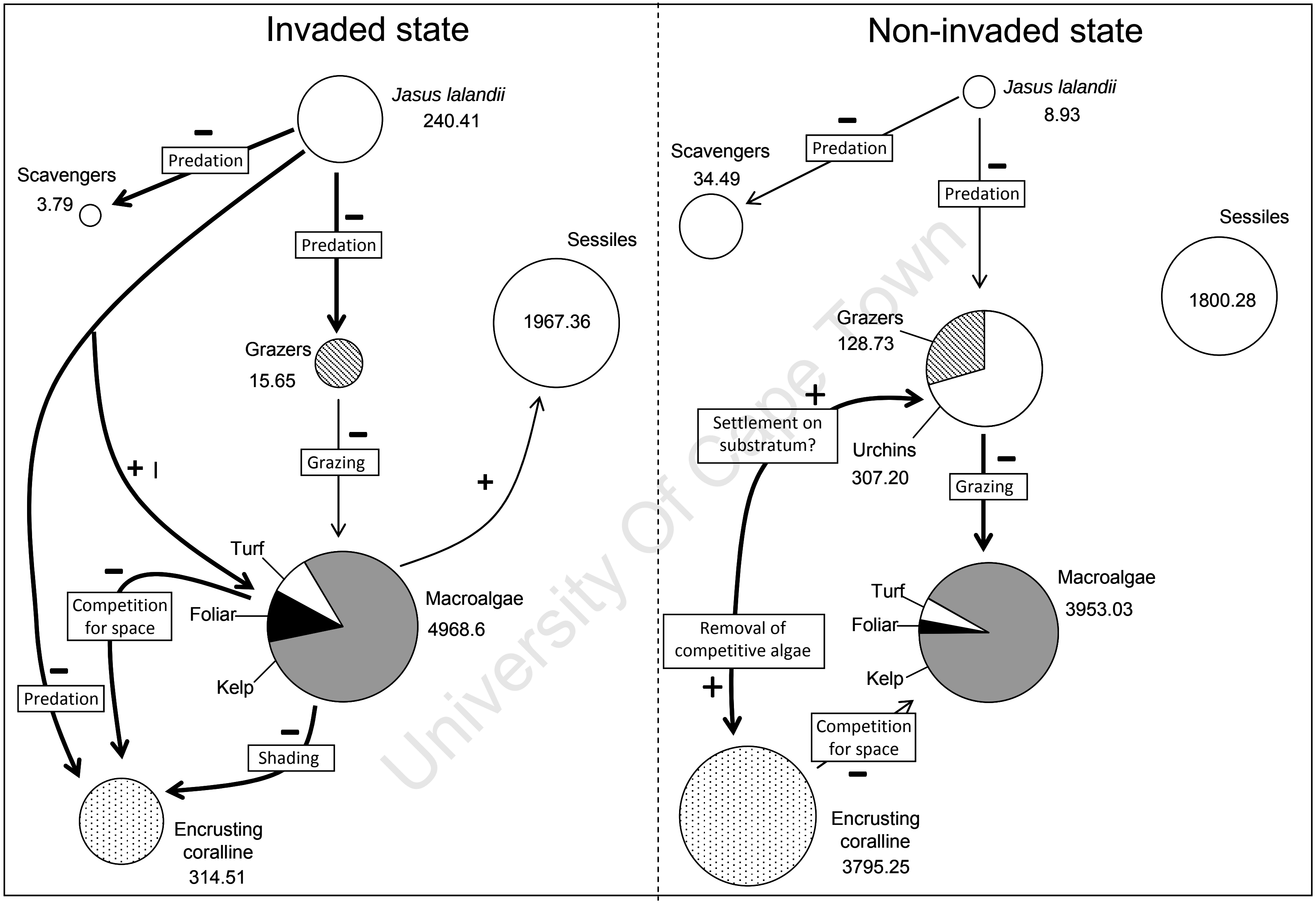


Fig 3.14b: Interaction webs for invaded and non-invaded states in the 6-12 m depth zone. See Fig. 3.12a for further details.

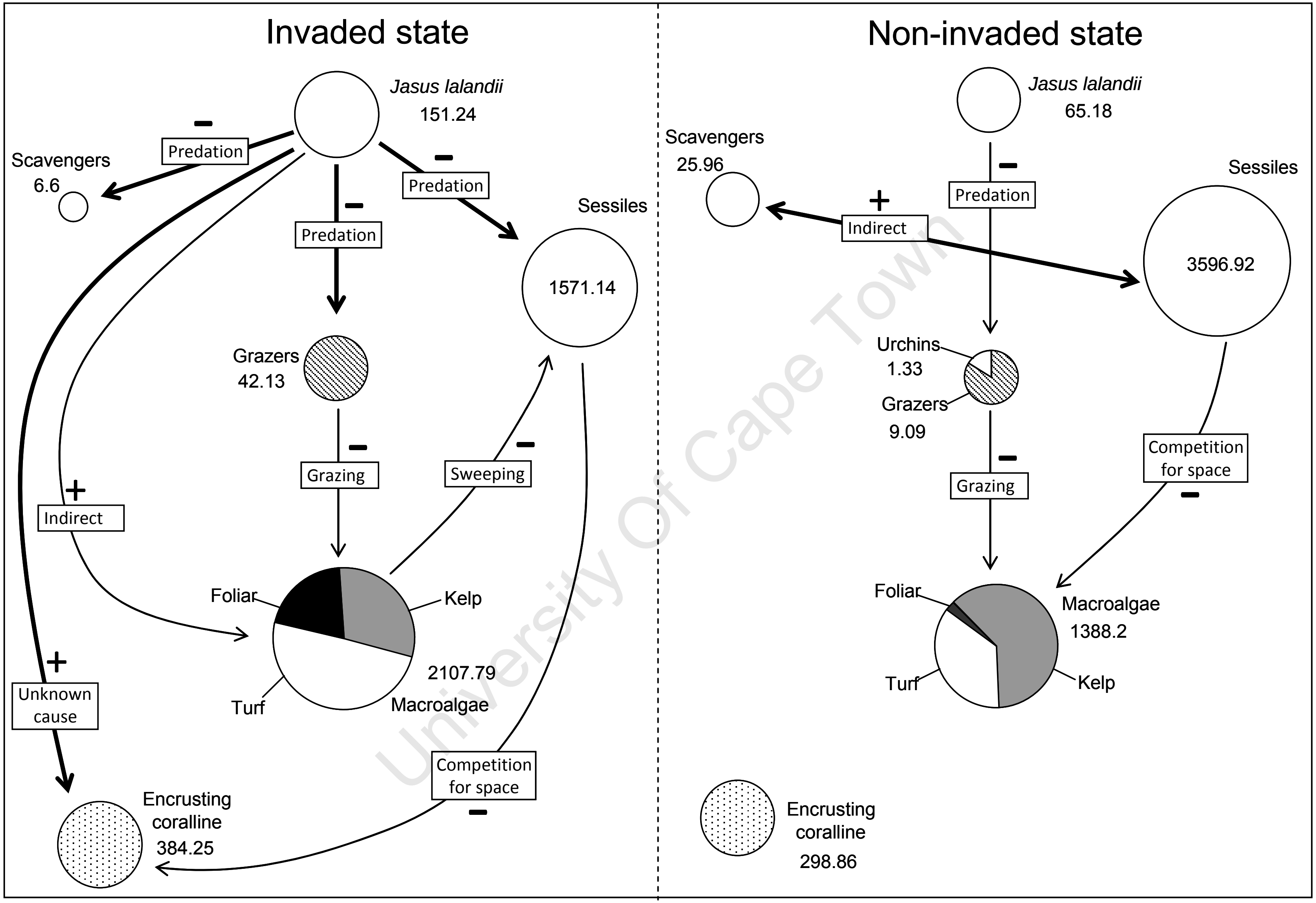


Fig 3.14c: Interaction webs for invaded and non-invaded states in the 13-20 m depth zone. See Fig. 3.12a for further details.

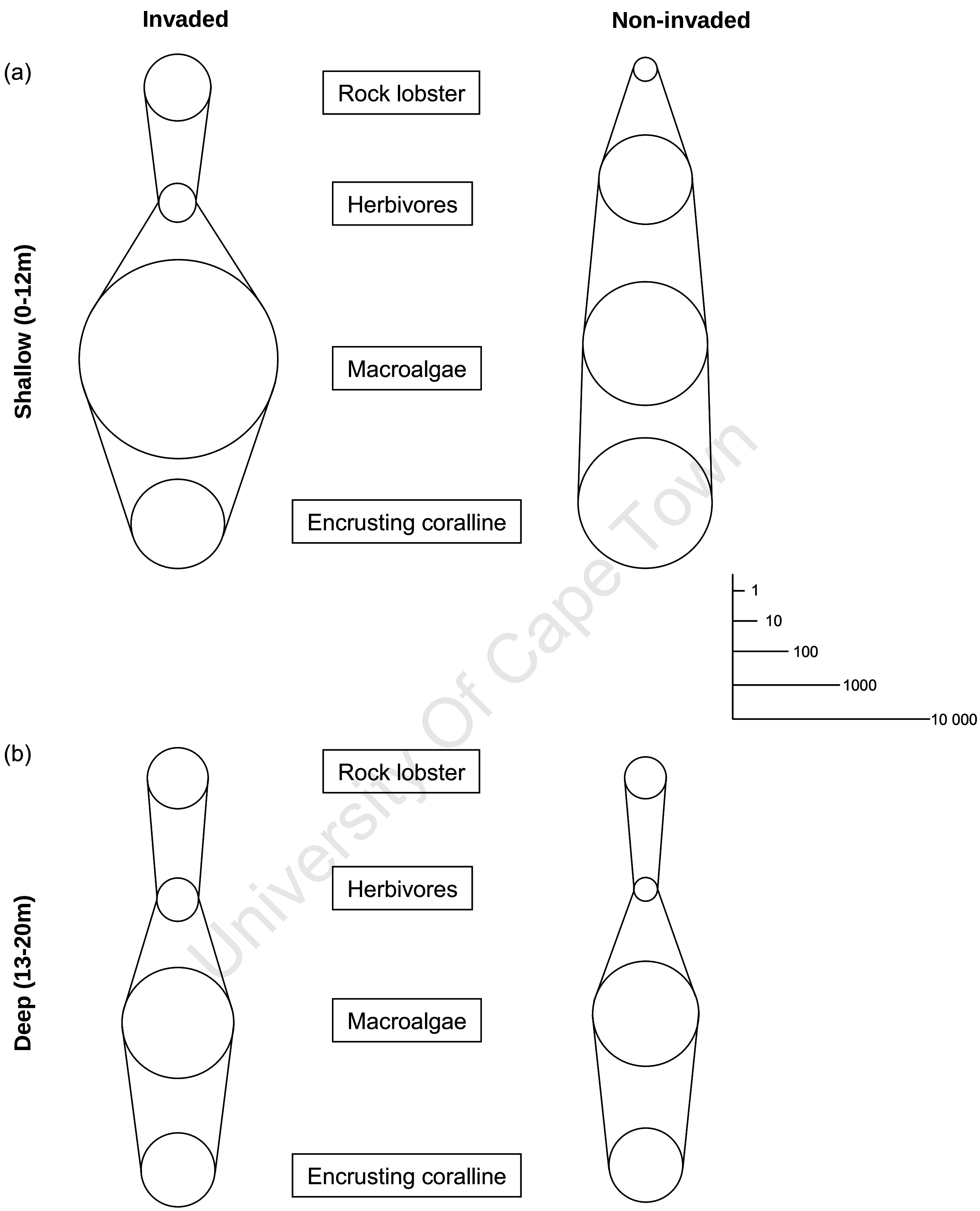


Fig 3.15: Summary of the (a) shallow and (b) deep ecosystems in both invaded and non-invaded areas EOCH. The scale bar represents the diameter (mean biomass $g.m^{-2}$) of the circles.

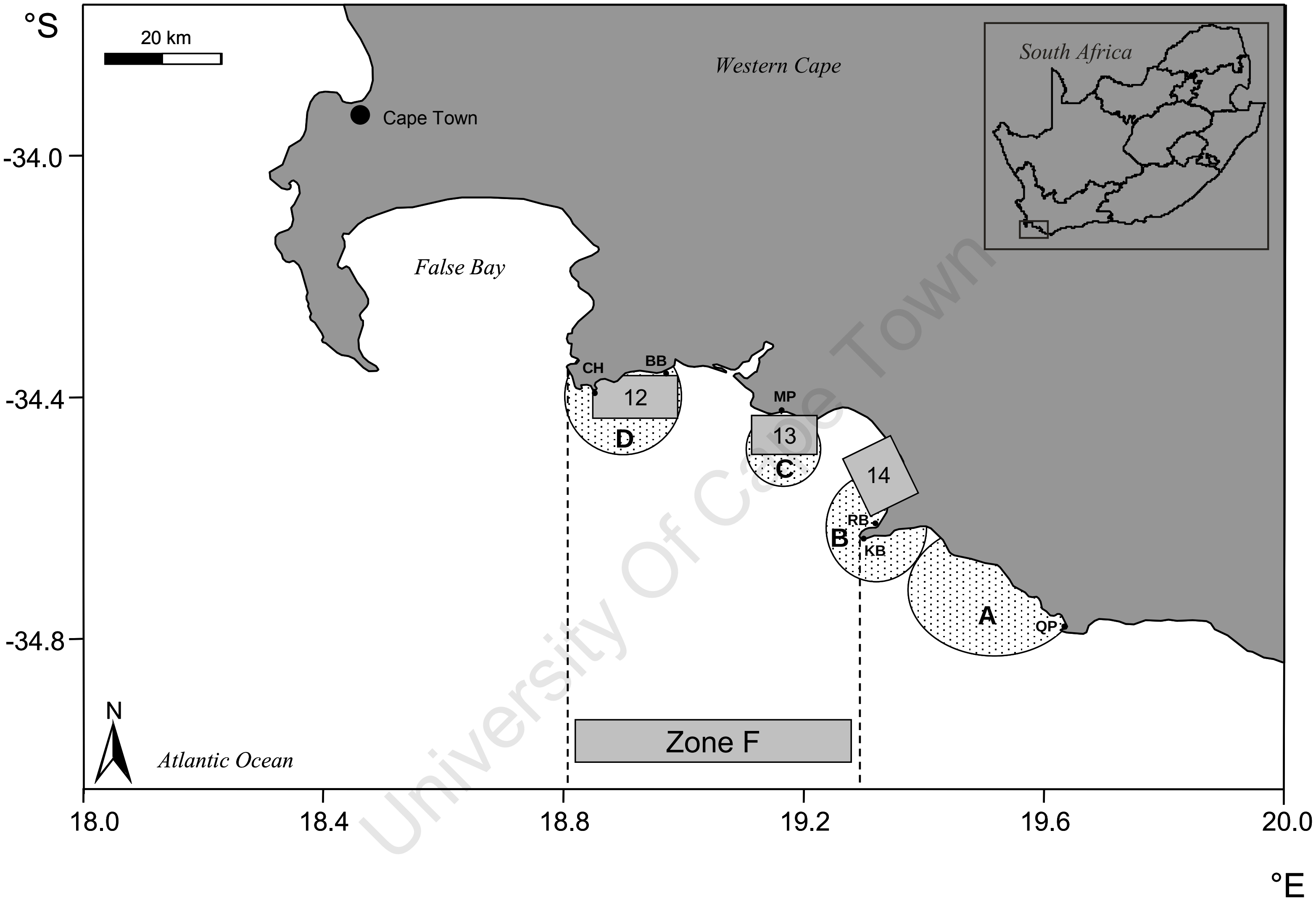


Fig 4.01: Map of the south-west coast showing the fishing zones east of Cape Hangklip. Zones A-D are the commercial abalone fishing zones and Zone F is the west coast rock lobster fishing zone. Zone F is sub-divided into three areas: Area 12 Kleinmond, Area 13 Hermanus and Area 14 Gansbaai. CH = Cape Hangklip, BB = Betty's Bay, MP = Mudge Point, RB = Romans Bay, KB = Kruismans Bay and QP = Quoin Point.

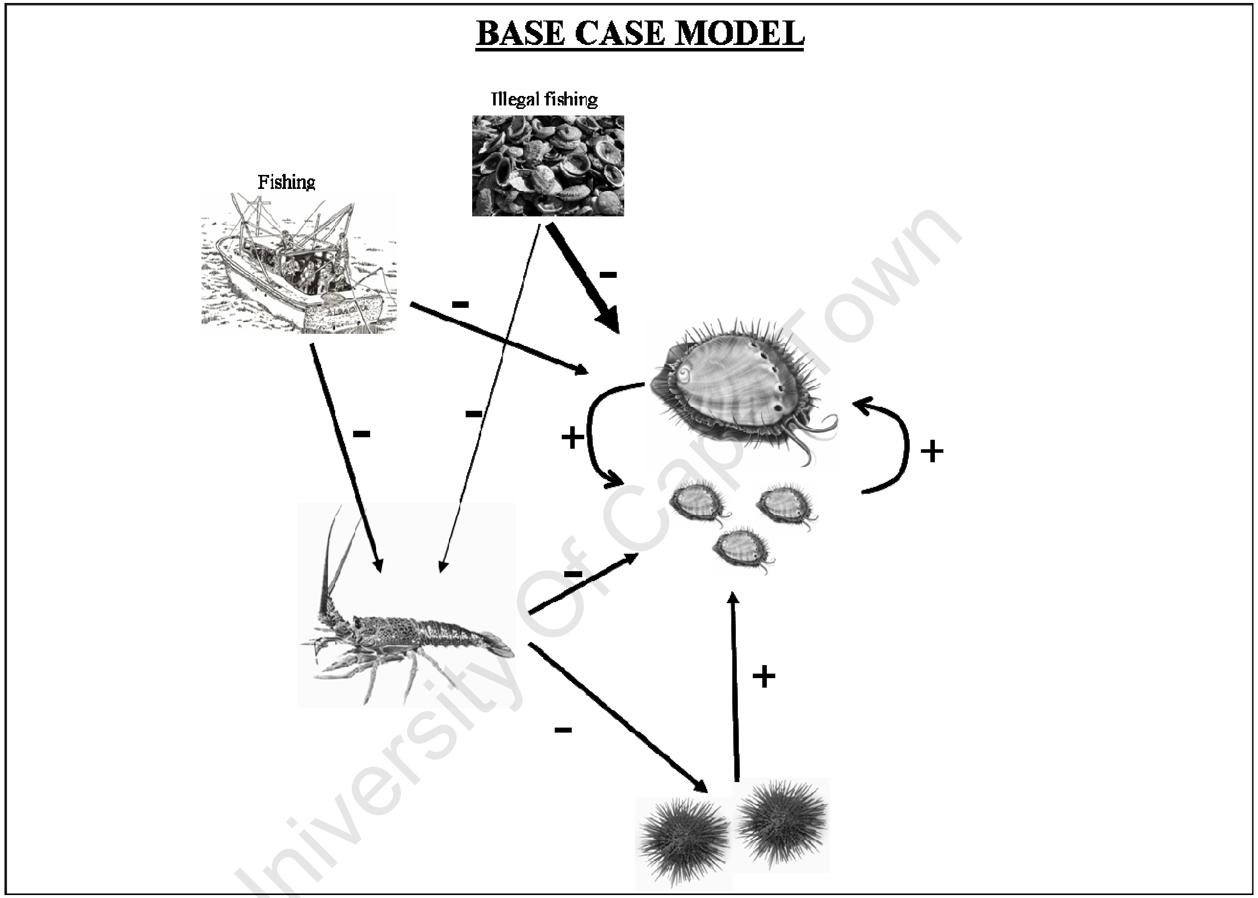


Fig 4.02: The base case multispecies model showing positive and negative associations in the model between rock lobster, abalone and urchins as well as the harvesting of rock lobsters and abalone.

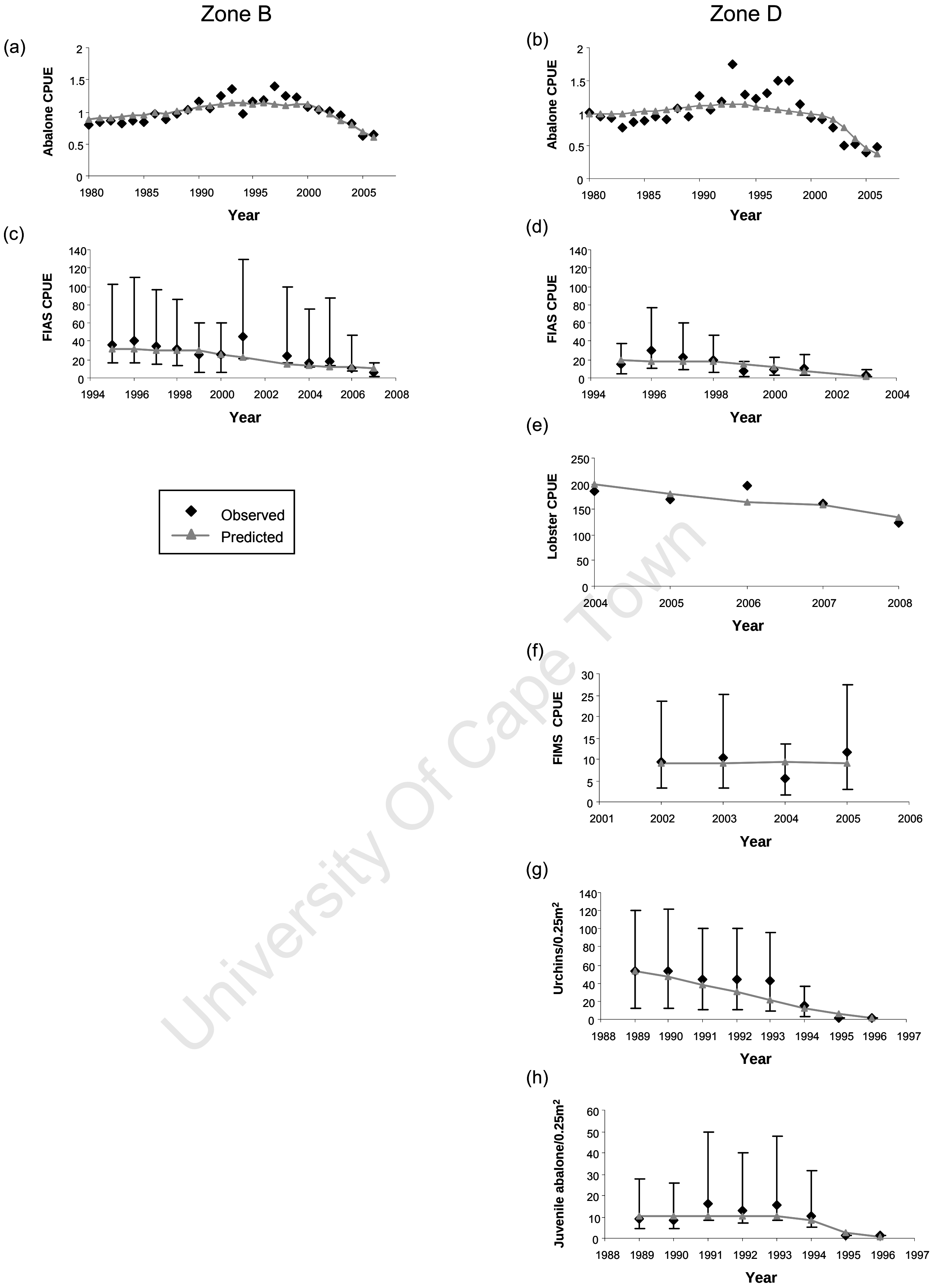


Fig 4.03: Model fits: Observed vs predicted CPUE for (a-b) the abalone commercial fishery (standardized kg.min^{-1}) and (c-d) the Fishery Independent Abalone Survey - FIAS (no. abalone per 60 m^{2}) from Zones B and D, and the observed vs predicted CPUE for the (e) rock-lobster commercial fishery (kg.bakkie^{-1}.day^{-1}), (f) Fishery Independent Monitoring Survey - FIMS (number.trap^{-1}), (g) urchin survey and (h) juvenile abalone survey for Zone D. 90% confidence intervals are shown for the observed FIAS, FIMS, juvenile abalone and urchin data.

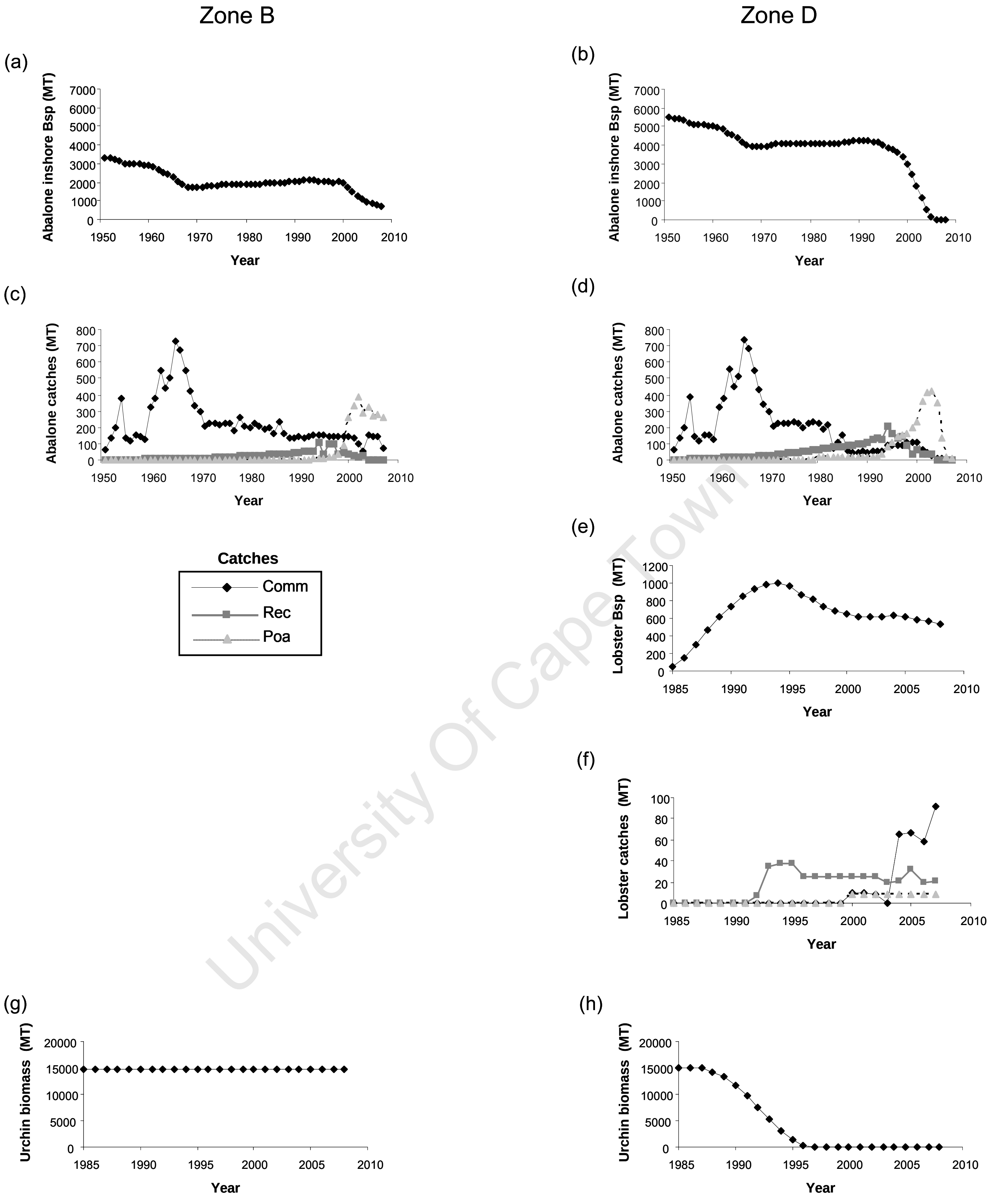


Fig 4.04: Population trajectories: Abalone inshore spawning biomass (a-b) and catch trends (c-d) for Zones B and D; rock lobster spawning biomass (e) and catch trends (f) for Zone D; and urchin biomass (g-h) for Zones B and D. Comm = commercial fishing, Rec = recreational fishing and Poa = illegal fishing.

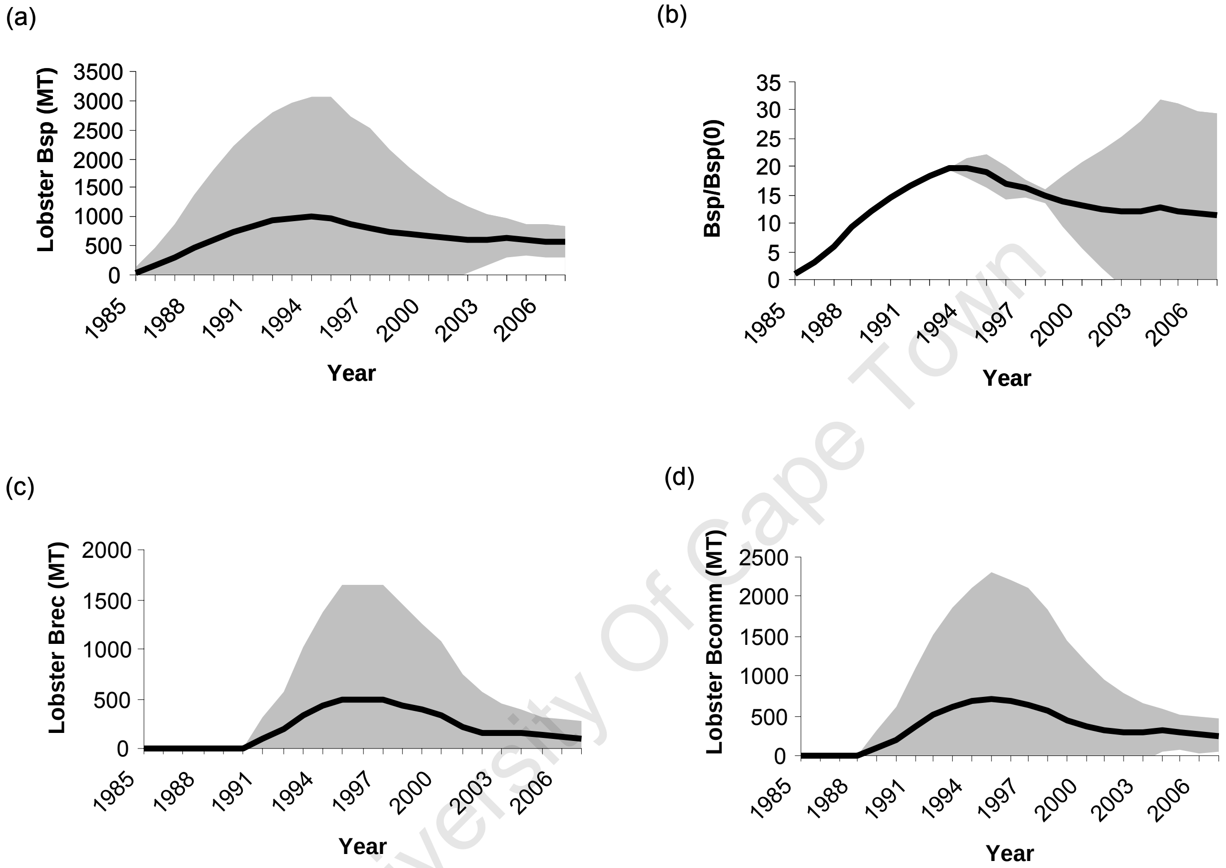


Fig 4.05: (a) Rock-lobster spawning biomass, (b) rock-lobster spawning biomass depletion (i.e. spawning biomass Bsp relative to the start-year spawning biomass Bsp(0)), (c) the available rock-lobster recreational biomass and (d) the available rock-lobster commercial biomass for model period 1985-2007. Solid lines represent the model values and shaded areas represent the 90% confidence intervals.

Zone D

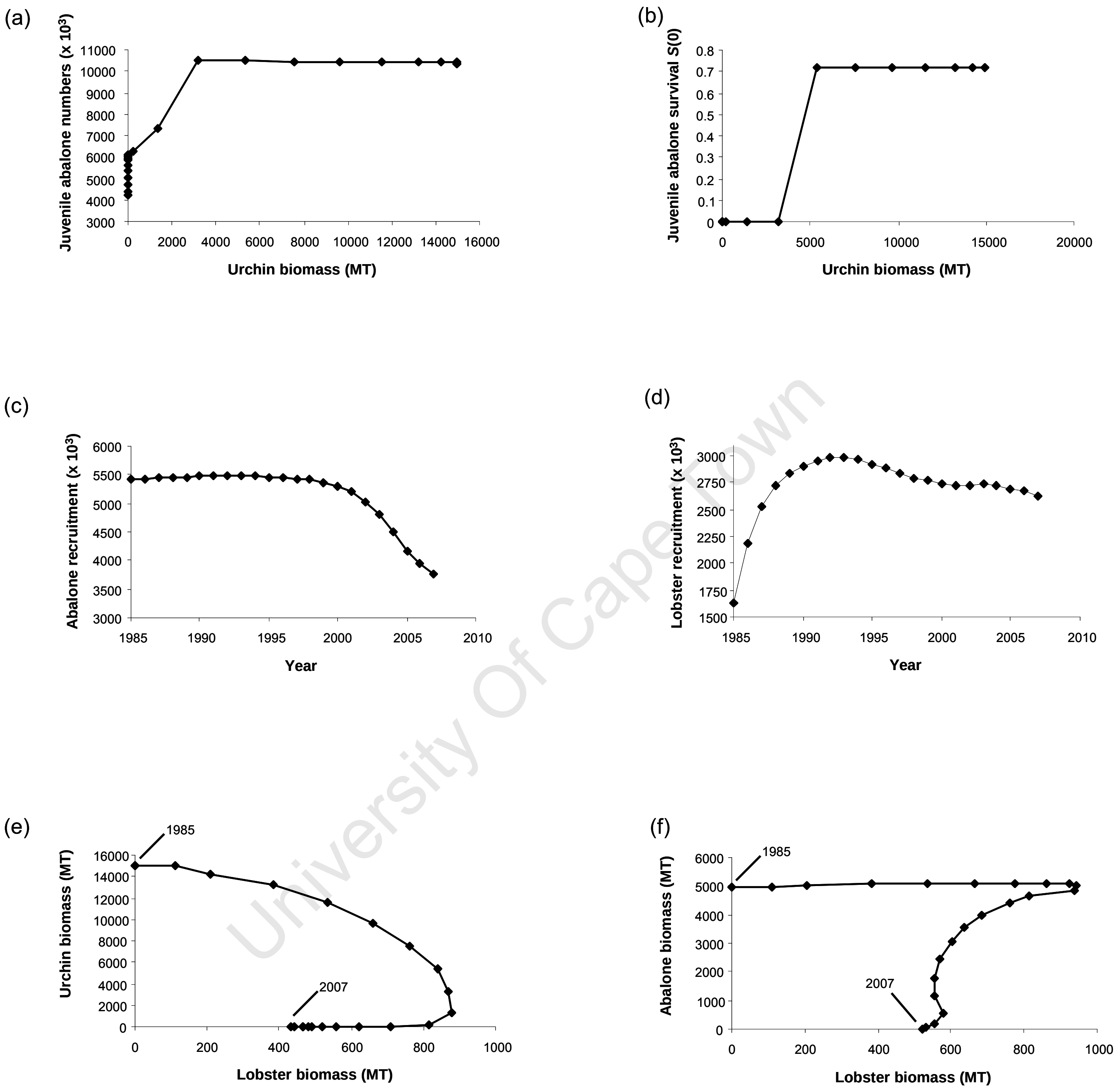


Fig 4.06: Species interactions in Zone D showing (a) juvenile abalone (numbers) and (b) juvenile abalone survival *S*(0) relative to urchin biomass, (c) abalone recruitment (numbers) and (d) lobster recruitment (numbers) over time, (e) urchin biomass and (f) inshore abalone biomass relative to lobster biomass through model time course (1985-2007).

Zone D

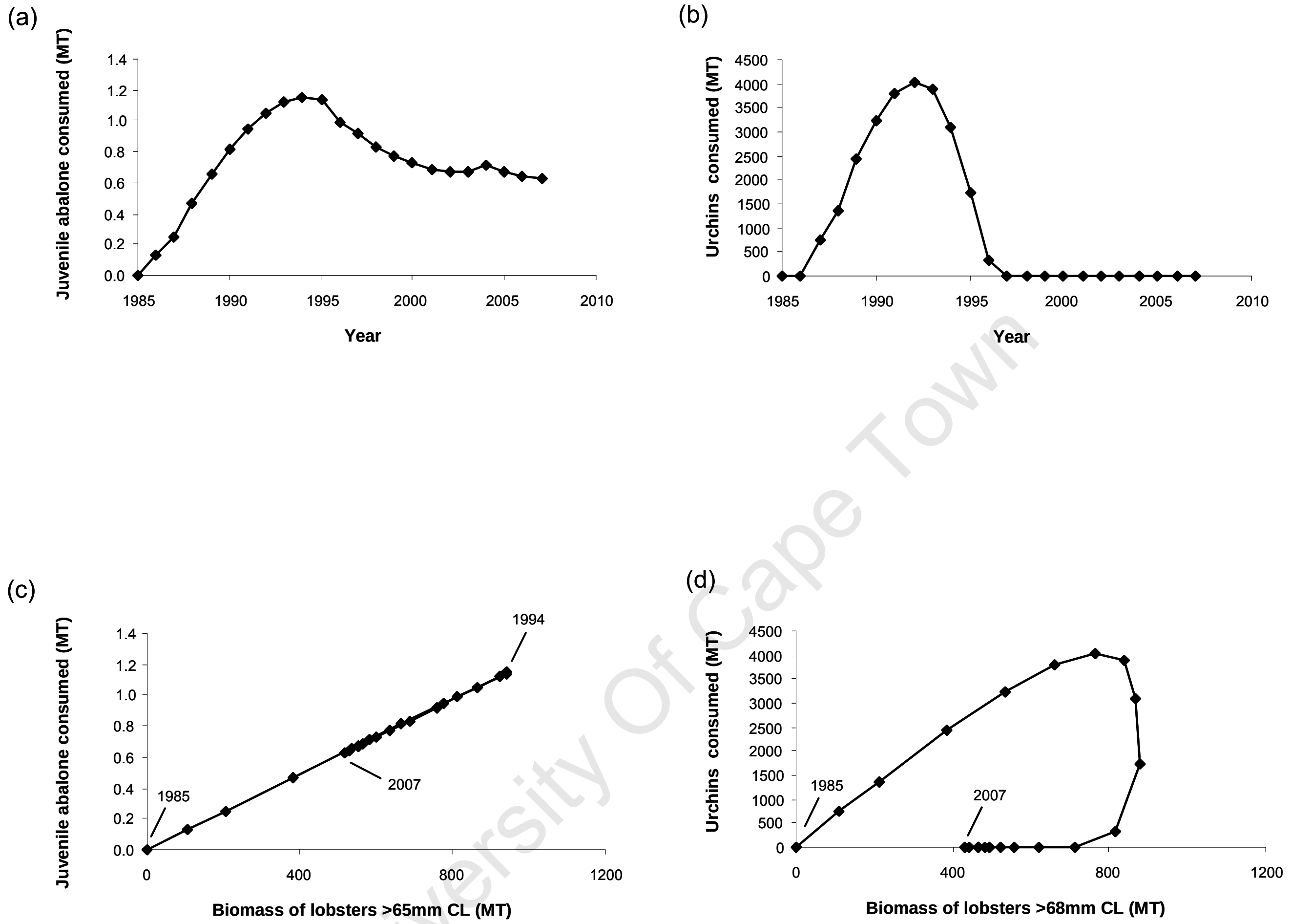
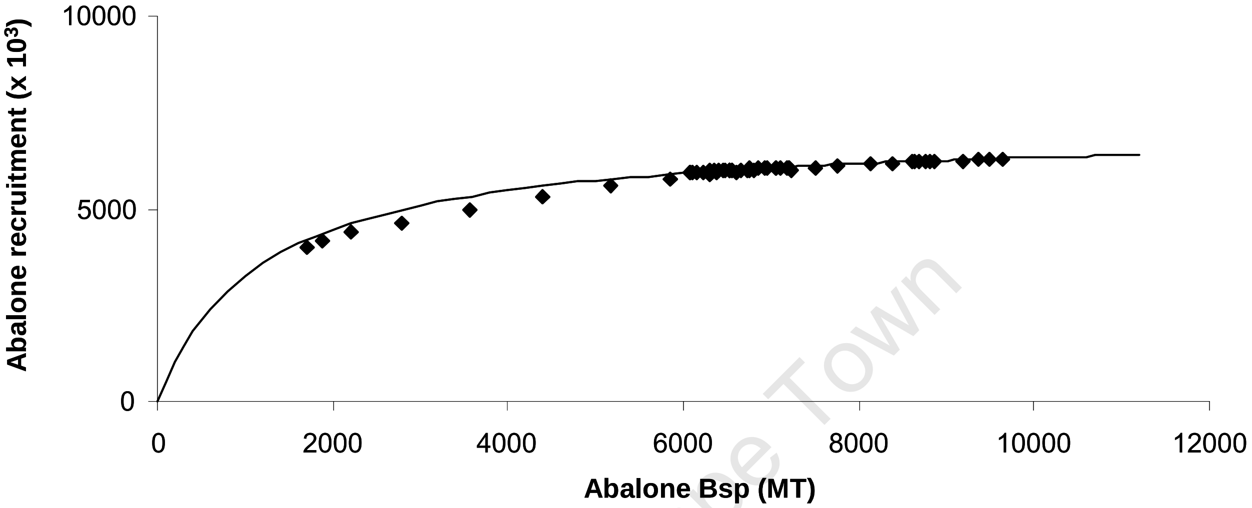


Fig 4.07: Consumption of (a) juvenile abalone and (b) urchins in Zone D over time, (c) juvenile abalone consumed relative to biomass of lobsters larger than 65 mm CL (minimum size to eat abalone) over model time period and (d) urchins consumed relative to biomass of lobsters larger than 68 mm CL (minimum size to eat urchins) over model time period.

(a)



(b)

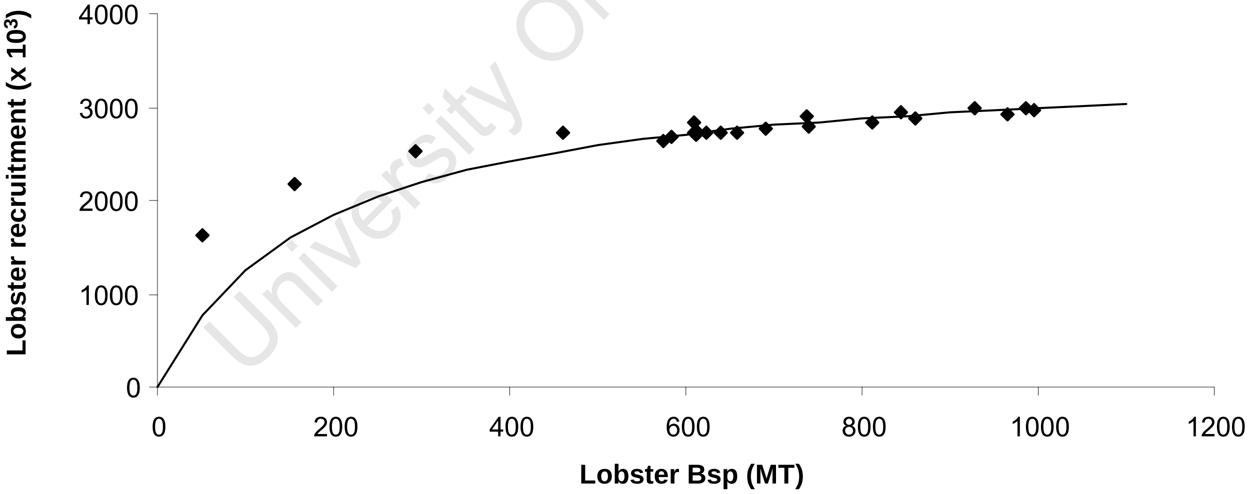


Fig 4.08: Spawner biomass - recruitment curves using a Beverton-Holt relationship, for (a) abalone and (b) rock lobster. Recruitment is in numbers and spawning biomass is in MT.

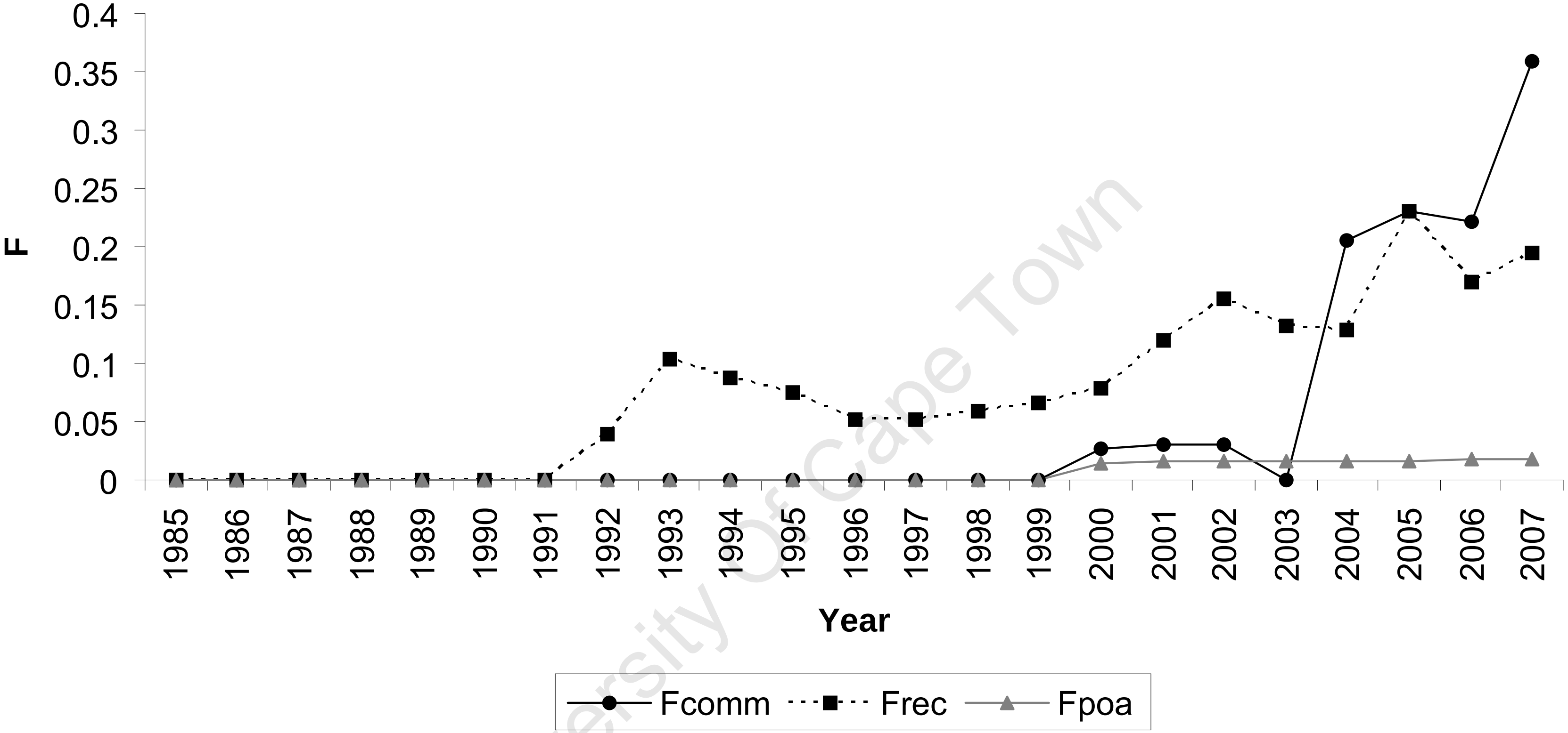


Fig 4.09: Rock-lobster fishing mortality '*F*' (proportion of biomass harvested) shown for the three fishing sectors: the commercial (Fcomm), recreational (Frec) and illegal fishery (Fpoa) in Zone D.

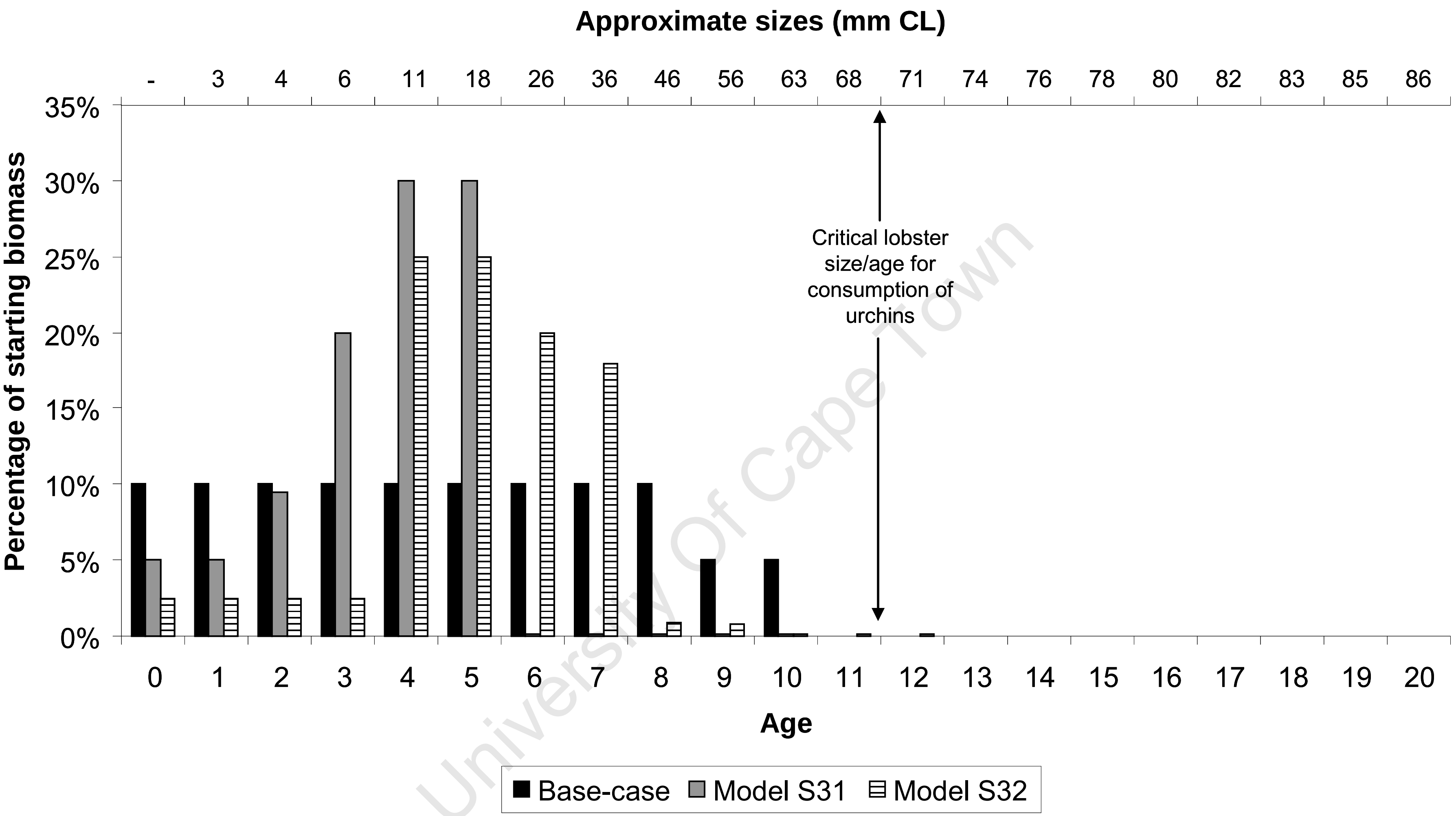


Fig 5.01: The percentage biomass for each age class that contributed to the initial rock-lobster starting biomass that was used in the base-case model starting in 1985, and in the sensitivity analyses. The base-case model used an age-structure that, by 1990, would have mimicked an adult rock-lobster immigration into the EOCH area; Model S31 used an age-structure that would, by 1990, have produced a population that mimicked increased juvenile settlement in the early 1980s and Model S32 used an age-structure that was an intermediate between the base-case and Model S31.

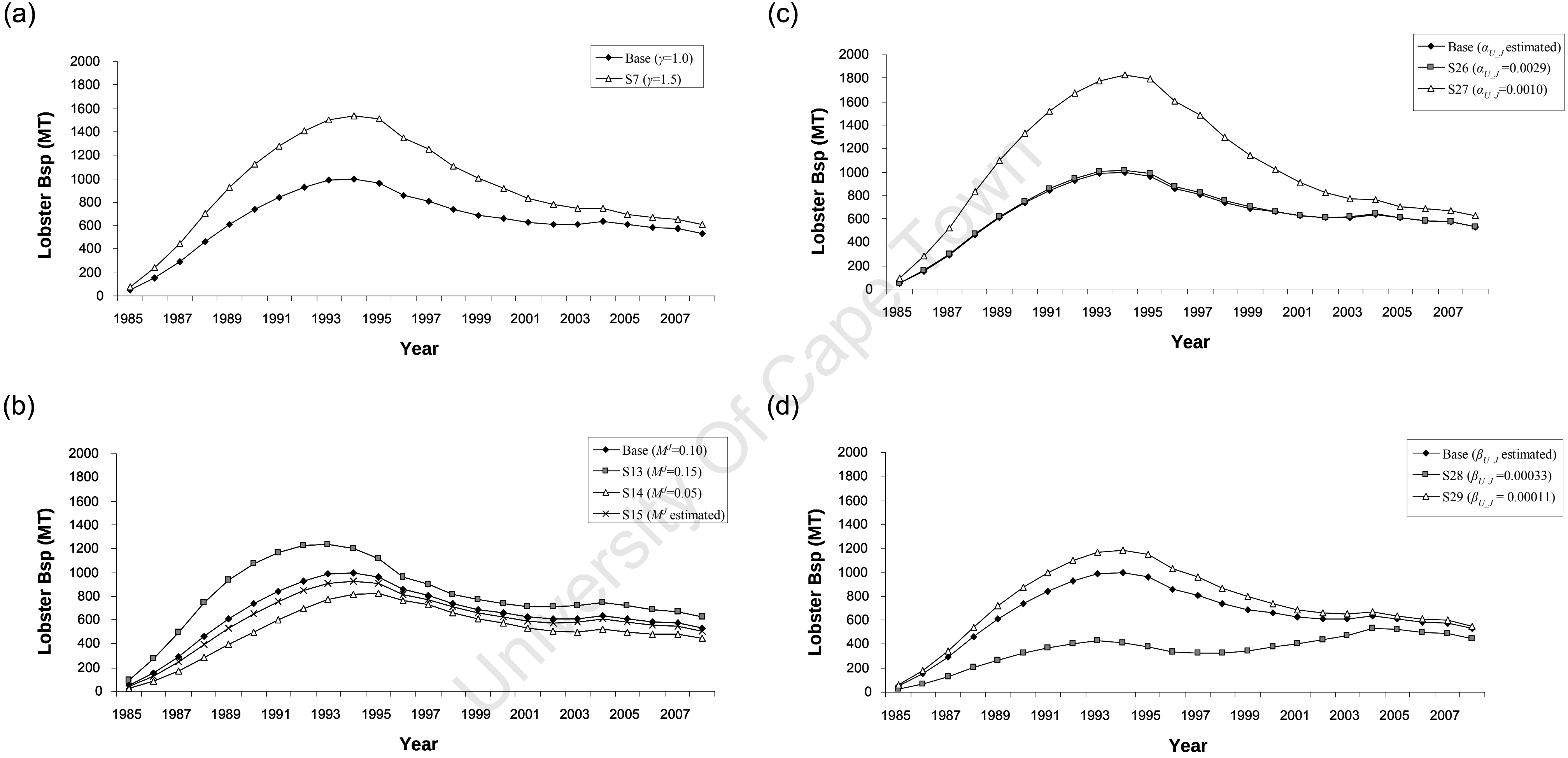


Fig 5.02: Rock-lobster spawning biomass (Bsp) trends resulting from sensitivity analyses on (a) the rock-lobster spawner-recruit parameter γ, (b) the rock-lobster natural mortality parameter M^J, (c) the urchin-lobster parameter α_{U_J} and (d) the urchin-lobster parameter β_{U_J}.

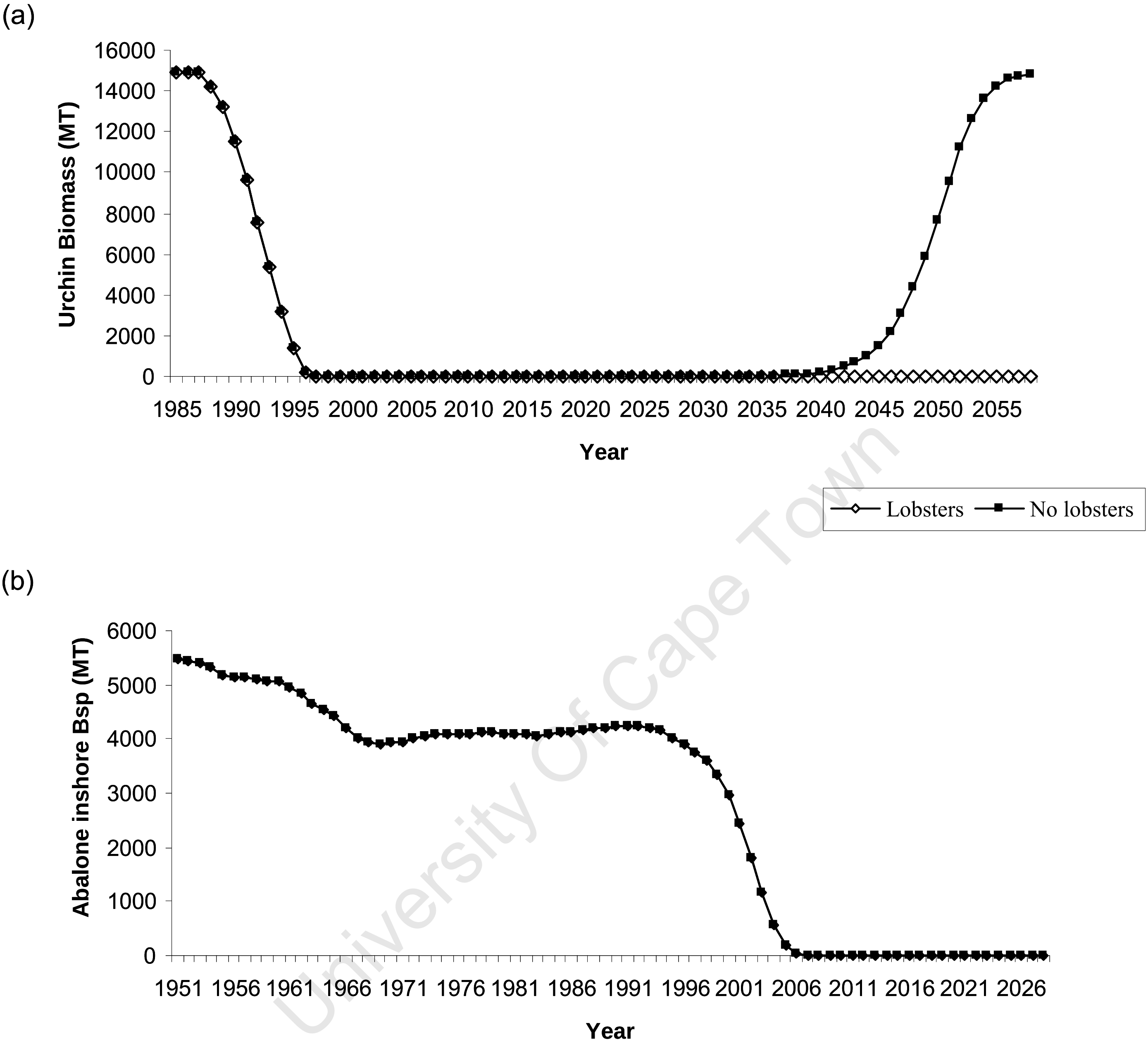


Fig 5.03: Future projections for (a) urchin biomass for the period 1985-2058 and (b) the abalone inshore spawning biomass for the period 1951-2028. 'Lobsters' = the base-case model continued for either 20 or 50 years into the future with no changes to the model i.e. a continuation of lobster predation. 'No lobsters' = the removal of rock lobsters from 2008-2058 i.e. an absence of lobster predation. In (b) the data for both ‘lobsters’ and ‘no lobsters’ track identical paths.

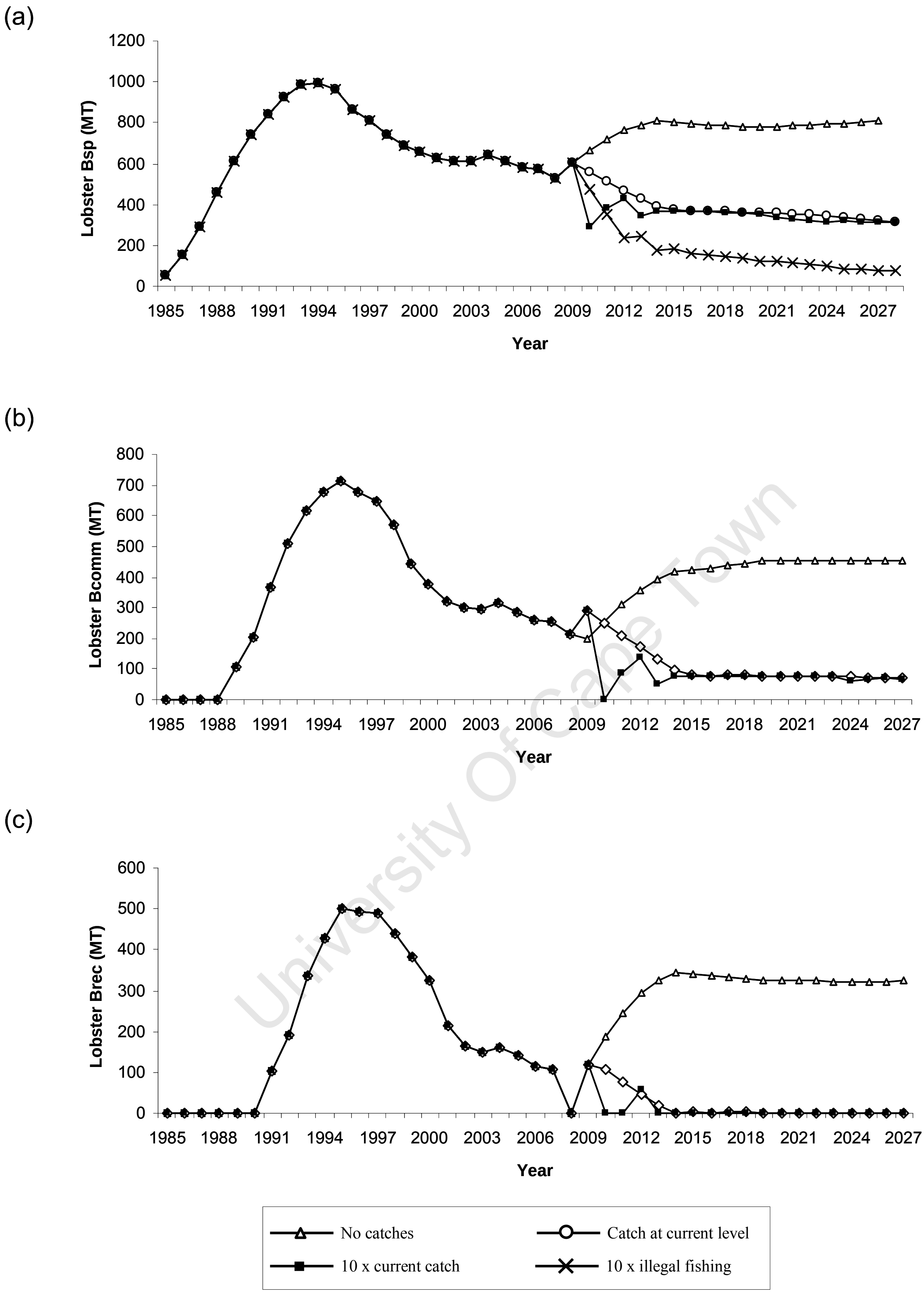


Fig 5.04: Future projections for (a) rock-lobster spawning biomass, (b) rock-lobster available commercial biomass and (c) rock-lobster available recreational biomass, under different rock-lobster catch scenarios employed for the period 2008-2028.

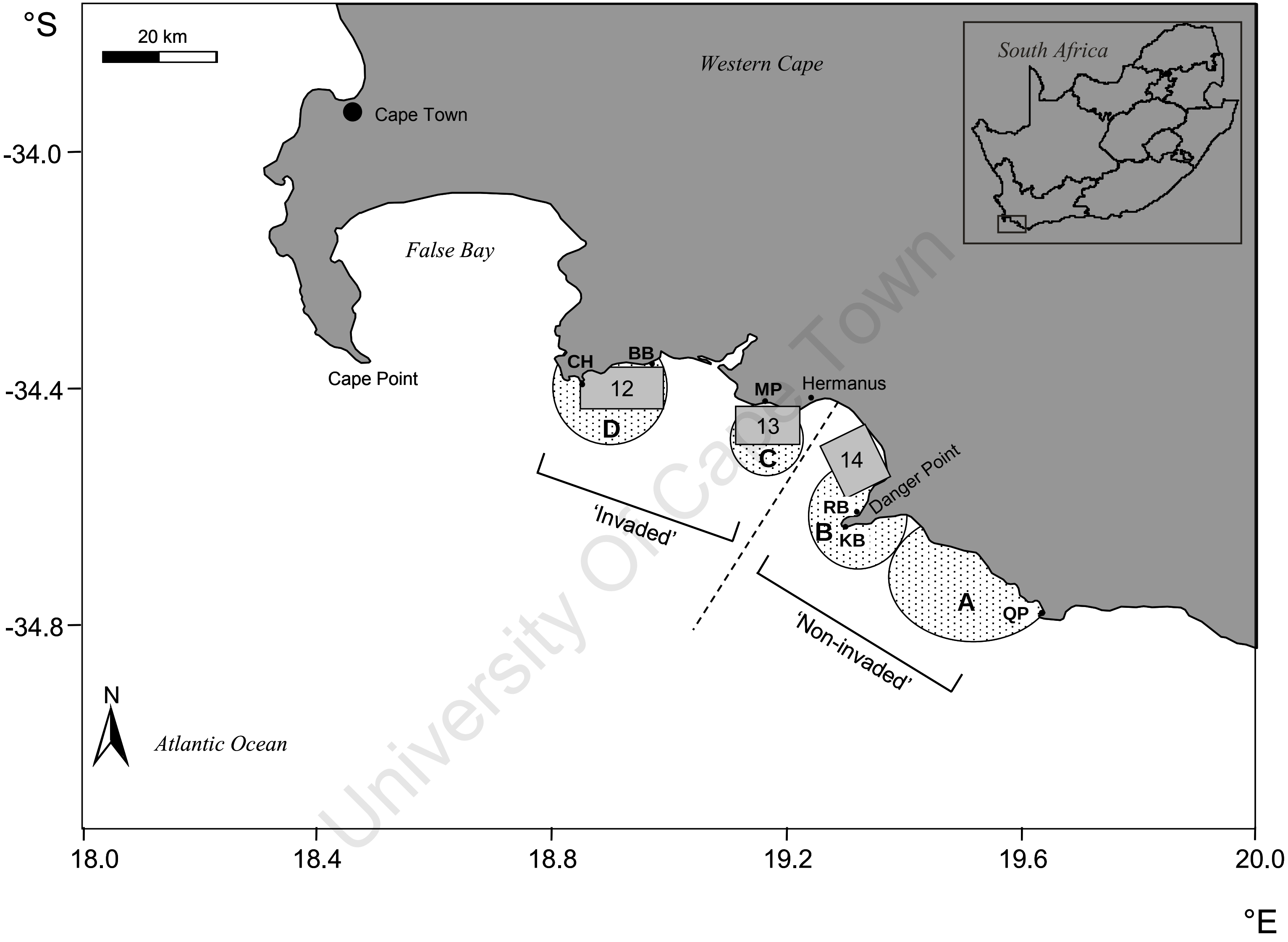


Fig 6.01: Map showing the lobster-invaded and non-invaded regions along south-west coast and associated fishing zones/areas. Zones A-D are the commercial abalone fishing zones and Areas 12-14 are the commercial rock-lobster fishing areas EOCH: Area 12 Kleinmond, Area 13 Hermanus and Area 14 Gansbaai. CH = Cape Hangklip, BB = Betty's Bay, MP = Mudge Point, RB = Romans Bay, KB = Kruismans Bay and QP = Quoin Point.

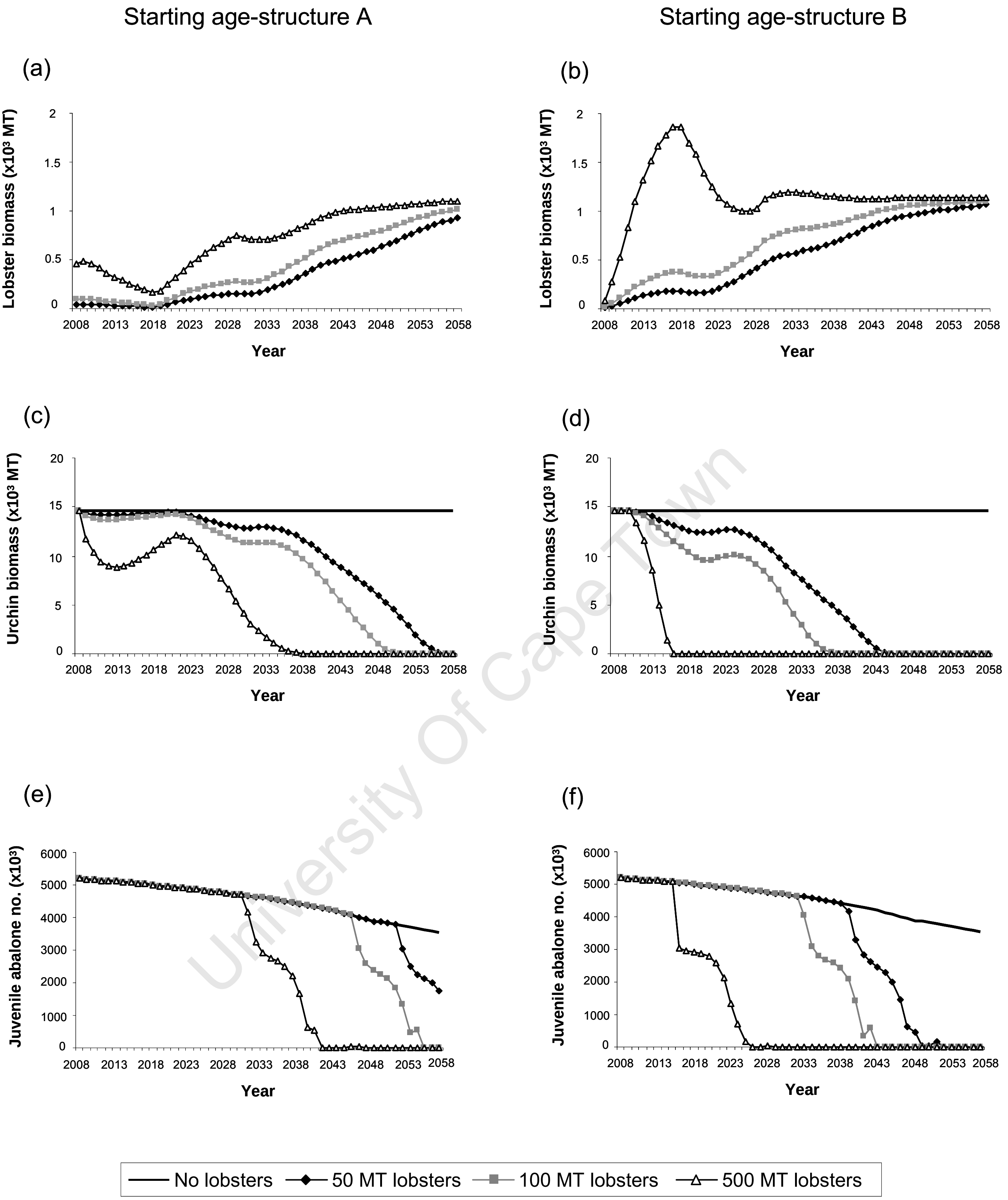


Fig 6.02: Zone B rock-lobster, urchin and juvenile abalone future projections using an initial rock-lobster starting biomass of 0 MT, 50 MT, 100 MT and 500 MT under two different rock-lobster starting age-structures. 50-year future projections are shown for (a,b) rock lobsters (MT) (c,d) urchins (MT) and (e,f) juvenile abalone (numbers).

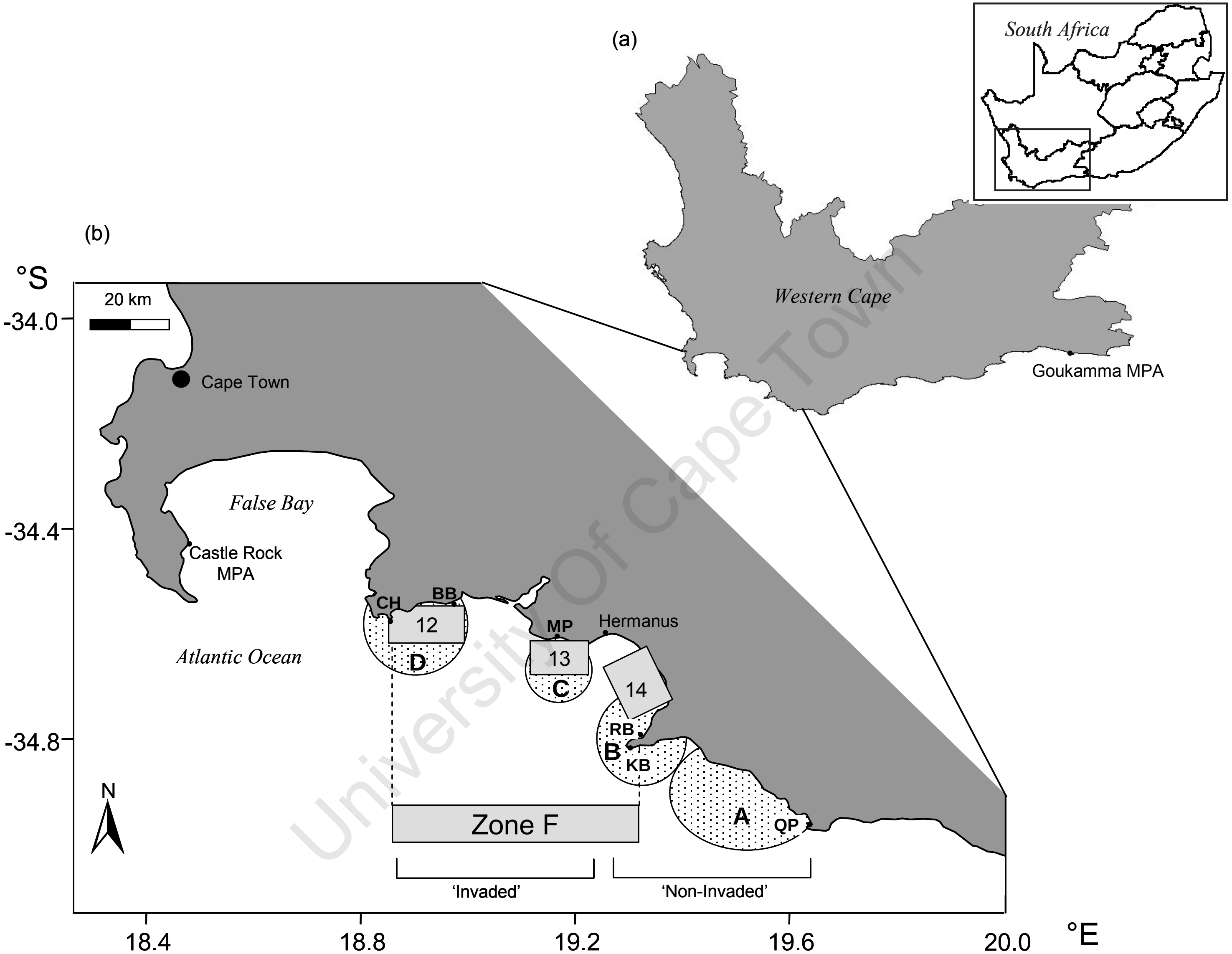


Fig 7.01: Map showing (a) the Western Cape along which (b) the south-west coast and associated fishing zones are situated. Zones A-D are the commercial abalone fishing zones and Zone F is one of the west coast rock lobster fishing zones. Zone F is sub-divided into three areas: Area 12 Kleinmond, Area 13 Hermanus and Area 14 Gansbaai. CH = Cape Hangklip, BB = Betty's Bay, MP = Mudge Point, RB = Romans Bay, KB = Kruismans Bay and QP = Quoin Point.

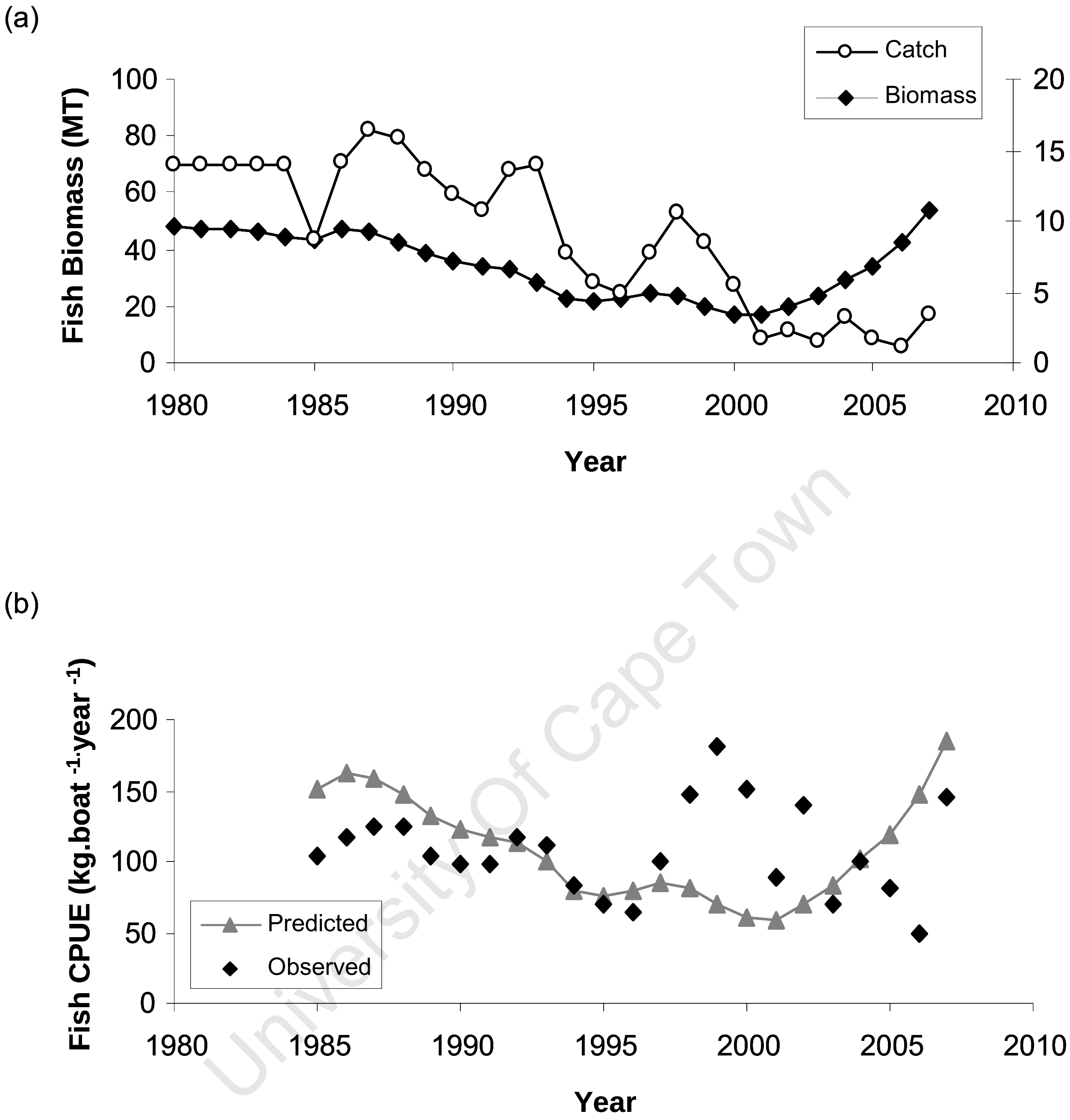


Fig 7.02: (a) Empirical data for commercial fish catches 1980-2007, and fish biomass (MT) predicted by the ‘current fish’ model. (b) observed vs. predicted fish CPUE (kg.boat^{-1}.year^{-1}) for the years 1985-2007.

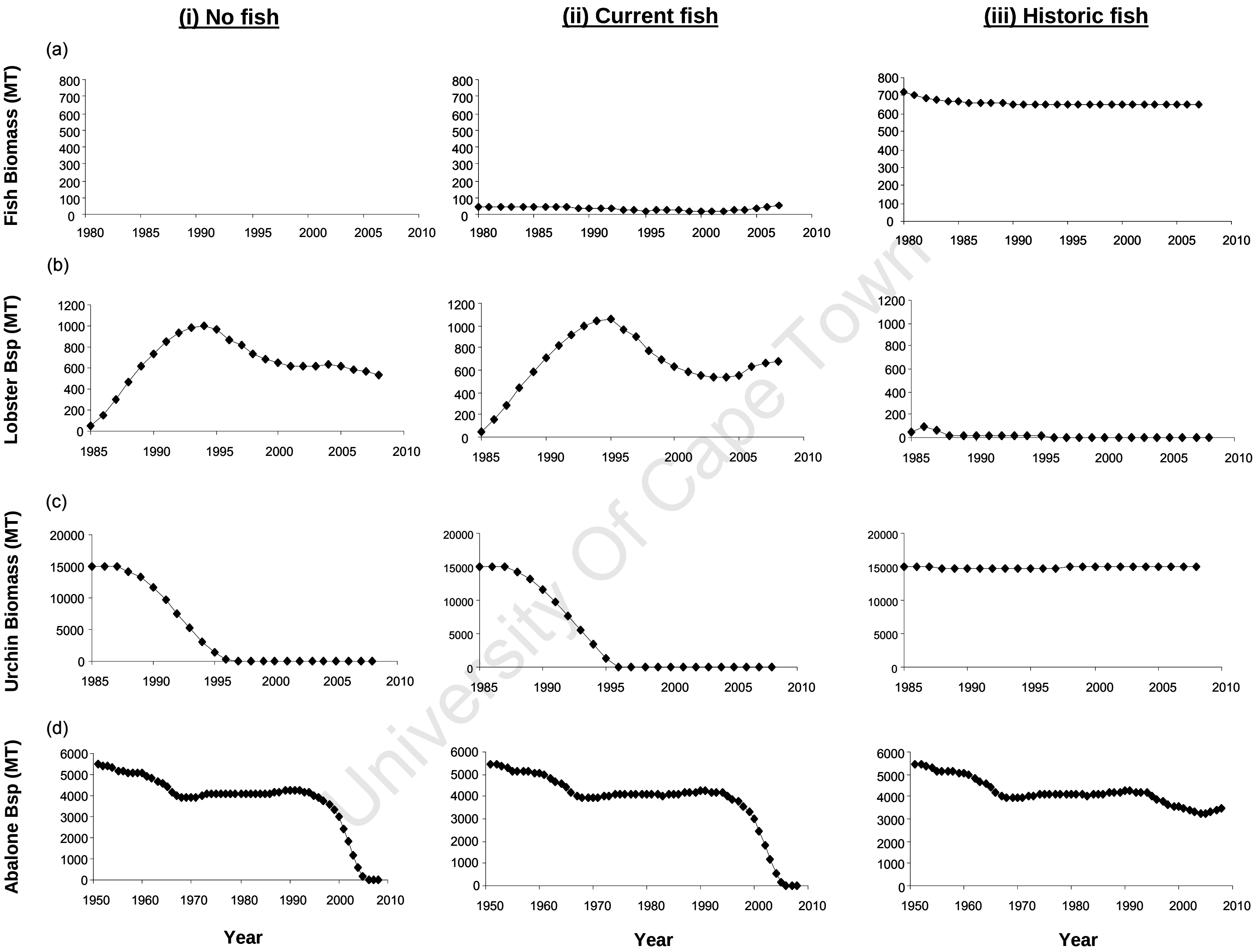


Fig 7.03: Population trajectories for (a) fish biomass, (b) rock-lobster spawning biomass, (c) urchin biomass and (d) abalone inshore spawning biomass using three model scenarios: (i) no fish (i.e. base-case model), (ii) current fish levels (i.e. 1980s-2000s) and (iii) historic fish level (i.e. late-1890s/early-1900s).

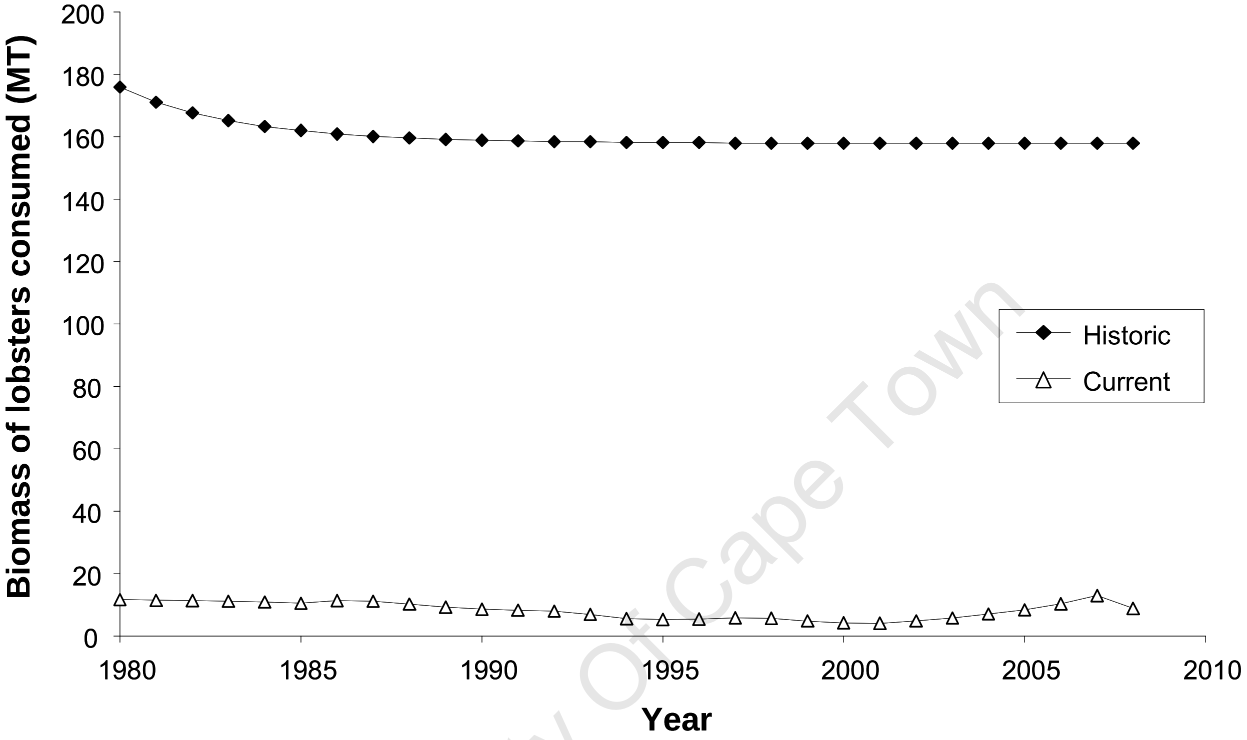


Fig 7.04: The total biomass of lobsters consumed over time at both historic (pristine) and current (overfished) fish biomasses.

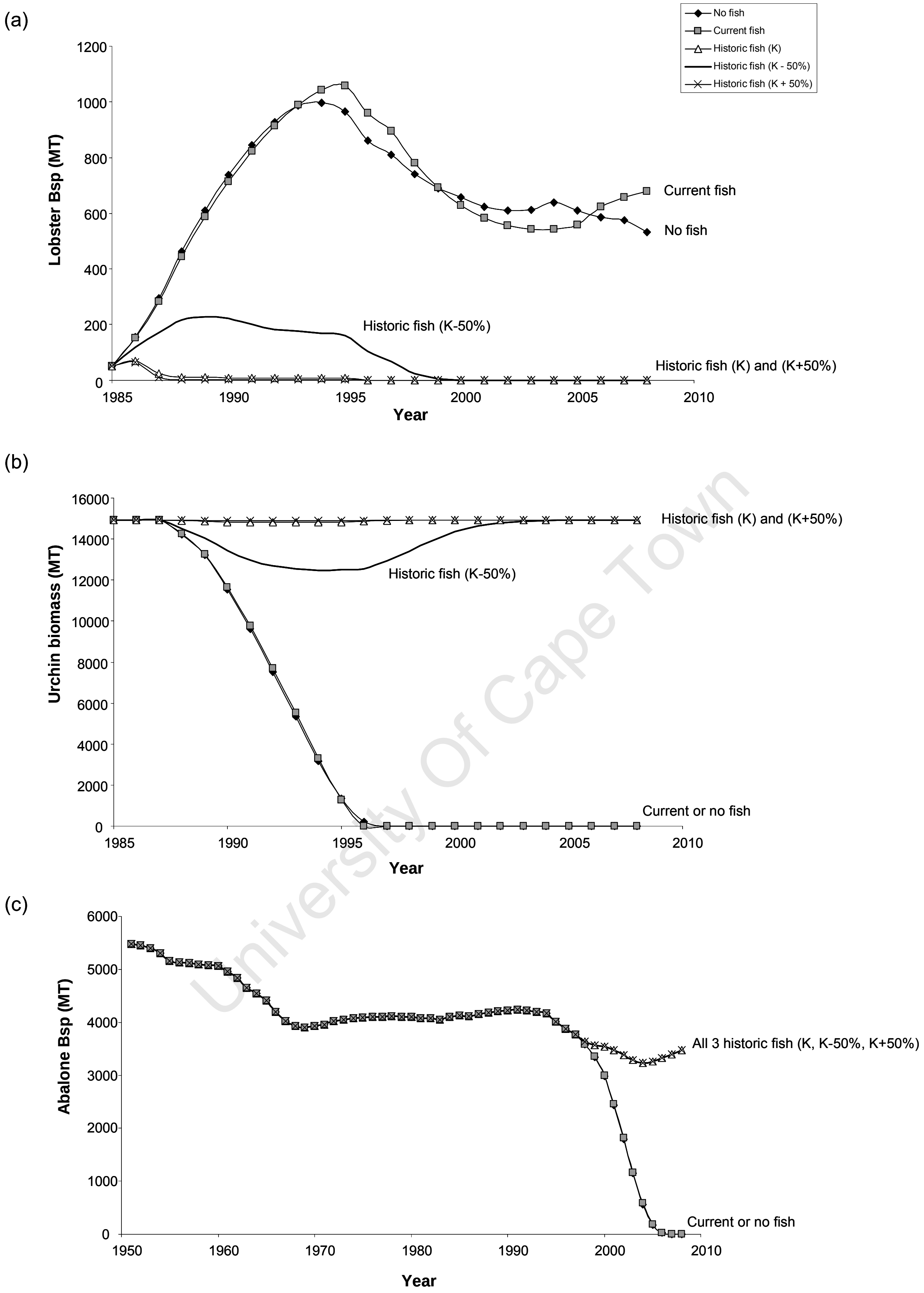


Fig 7.05: Population trajectories for (a) rock-lobster spawning biomass, (b) urchin biomass and (c) abalone inshore spawning biomass using three different starting levels of historic biomass (i.e. carrying capacity K_f), as well as the current fish biomass and no fish.

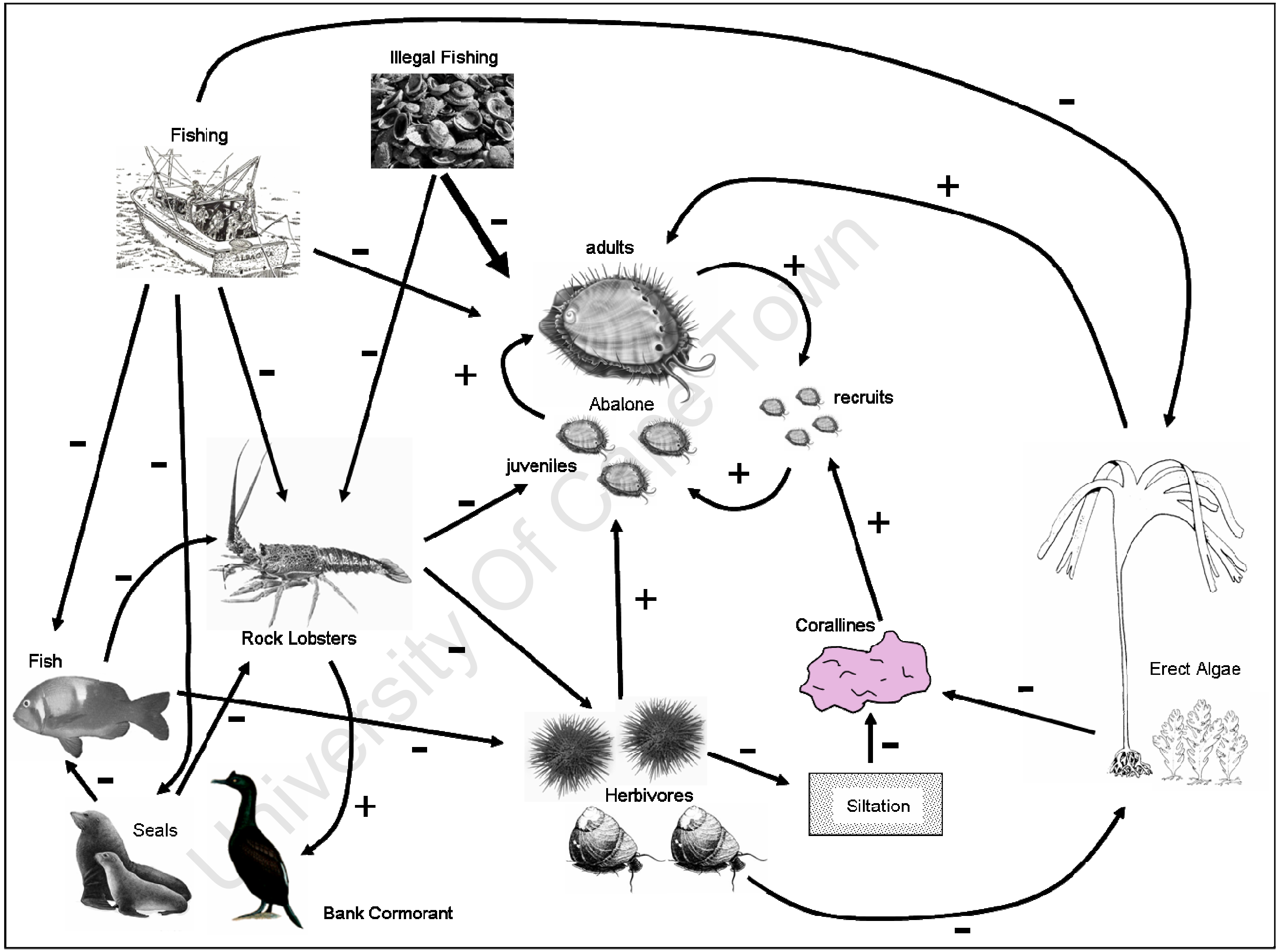


Fig 7.06: An overview of the EOCH ecosystem, indicating interactions that could be added to the multispecies model. Positive and negative associations between top predators (fish, seals, and cormorants), rock lobster, abalone, herbivores, encrusting corallines and erect algae are shown, as well as the harvesting of fish, seals, rock lobsters, abalone and kelp.

Table 2.01: A summary of sources, data and sampling methods used for analyses in this chapter. 'Major species' = *Jasus lalandii*, *Parechinus angulosus*, *Haliotis midae*, *Ecklonia maxima* and *Laminaria pallida*. Spp = species level, FG = functional- or taxonomic-group level, T = transect, Q = quadrats per transect. When sampling methods involved 0.25-m^2 quadrats, kelps were recorded in 1-m^2 quadrats due to their size.

Site	Dates sampled	Source of data	Taxa sampled	Resolution	Sampling methods	Replication	Data units
Betty's Bay	**Pre-invasion** 1978/1979	Field *et al.* (1980a)	All benthic taxa	Spp	1300-m transect, 50-m intervals, 1-m^2 quadrats	T: n = 1 Q: n = 3	kJ.m^{-2}
	Post-invasion 1996/1997	Mayfield (1998)	Rock lobsters, urchins	Spp	26-m transect, 0.25-m^2 quadrats	T: n = 1 Q: n = 45	Density
	1998	MCM unpublished data	Major species & benthic algae	Spp FG	100-m transect, 10-m intervals, 0.25-m^2 quadrats	T: n = 1 Q: n = 10	Density or % cover
	2001	Reaugh (2001)	Major species & other benthos	Spp FG	One Transect, 0.25-m^2 quadrats	T: n = 1 Q: n = 10	Density or % cover
	2005/2006	Present surveys	All benthic taxa	Spp	10-m transects, 0.25-m^2 quadrats	T: n=3 Q: n = 6	g.m^{-2} wet weight
Cape Hangklip	**Pre-invasion** 1988/1989	Jackleman (1996)	Major species, understory algae & other invertebrates	Spp Spp FG	One Transect, 0.25-m^2 quadrats	T: n = 1 Q: n = 10	g.m^{-2} wet weight
	Post-invasion 1996/1997	Mayfield (1998)	Rock lobsters, urchins	Spp	26-m transect, 0.25-m^2 quadrats	T: n = 1 Q: n = 40	Density
	2001	Reaugh (2001)	Major species & other benthos	Spp FG	One Transect, 0.25-m^2 quadrats	T: n = 1 Q: n = 10	Density or % cover
	2005/2006	Present surveys	All benthic taxa	Spp	10-m transects, 0.25-m^2 quadrats	T: n=3 Q: n = 6	g.m^{-2} wet weight

Table 4.01: Minimum/maximum size and age of rock lobsters, abalone and/or urchins used to define selectivities in the model. CL= carapace length, SL= shell length, SW = shell width and TD = test diameter.

Description	**Size**	**Units**	**Age**	**Units**	**Reference for size**	**Reference for age**
Minimum size/age lobsters must reach to eat urchins	69	mm CL	12	Years	Mayfield and Branch (2000)	Johnston and Butterworth (2001)
Minimum size/age lobsters must reach to eat juvenile abalone	65	mm CL	11	Years	Van Zyl *et al.* (2003)	Johnston and Butterworth (2001)
Largest abalone that can be consumed by lobsters	50	mm SL	4	Years	G.M. Branch pers. comm.	Plagányi (2004)
Size of juvenile abalone under urchins	3-35	mm SL	0-2	Years	Day and Branch (2000a,2000b)	Plagányi (2004)
Maximum size of urchin consumed by lobsters	60	mm TD	-	-	Mayfield *et al.* (2001), Mayfield and Branch (2000)	-
Size of urchin able to offer protection to abalone	40	mm TD	-	-	Day and Branch (2000a,2000b)	-
Size of female lobster at 50% maturity	65-70	mm CL	11	Years	Pollock and Beyers (1981); Pollock *et al.* (1982); Beyers and Goosen (1987)	Johnston and Butterworth 2001
Size of male lobster at maturity	60-65	mm CL	10	Years	Heydorn (1969)	Johnston and Butterworth 2001
Minimum size (lobster) taken by commercial fishers	75	mm CL	14	Years	-	Johnston and Butterworth 2001
Minimum size (lobster) taken by recreational fishers	80	mm CL	16	Years	-	Johnston and Butterworth 2001
Minimum size (lobster) taken by illegal fishers	65	mm CL	11	Years	S. Johnston pers. comm.	S. Johnston pers. comm.
Minimum size (lobster) taken by FIMS	55	mm CL	9	Years	MCM unpub. data	MCM unpub. data
Minimum size (lobster) counted on transect	55	mm CL	9	Years	Blamey (2009), unpub. data	Blamey (2009), unpub.data
Minimum size (abalone) taken by commercial fishers	114	mm SW	8	Years	Plagányi (2004)	Plagányi (2004)

Table 4.02: Densities of rock lobster, abalone and urchins used as inputs into the model.

Description	**Density/numbers**	**Units**	**References**
Minimum urchin density required for juvenile abalone to take shelter	5	m²	Mayfield and Branch (2000)
Density of large lobsters required to reduce urchin density to 5/m²	0.08	m²	Mayfield and Branch (2000)
Minimum urchin density required to achieve replenishment of juvenile abalone	30	m²	Mayfield and Branch (2000)
Mean urchin density observed at Danger Point Peninsula (‘Non-invaded’)	30.5	m²	Mayfield and Branch (2000)
Mean urchin density at Romans Bay (‘Non-invaded’)	74.4	m²	Blamey (2009), unpub. data
Density of large lobsters required to eliminate urchins	0.25	m²	Mayfield and Branch (2000)
Average daily consumption of urchins by a lobster of sufficient size	6.11	number.day^{-1}	Mayfield *et al.* (2001)
Mean number of juvenile abalone under an urchin (all urchins)	1	number	Day (1998)

Table 4.03: Starting (1985) age-structure of the rock lobster population.

Age (Year)	Population %
0	10
1	10
2	10
3	10
4	10
5	10
6	10
7	10
8	10
9	5
10	5
11	0
12	0
13	0
14	0
15	0
16	0
17	0
18	0
19	0
20	0

Table 4.04: Parameters used in the rock lobster component of the model.

Rock Lobster Parameters					
Parameter	**Notation**	**Value**	**Units**	**Source**	**Estimated/Fixed**
Natural mortality	M^J	0.105	-	S. Johnston pers. comm.	Fixed
Carrying capacity (spawning biomass)	K_J^{sp}	1511	MT	-	Estimated
Starting lobster biomass	B_{y0}^J	314	MT	-	Estimated
Steepness of stock-recruitment relationship	h	0.7	-	-	Fixed
Spawning biomass-recruitment parameter	γ	1.00	-	-	Fixed
Lobster-abalone interaction parameter 1	α_{Ab_J}	0.007	-	-	Estimated
Lobster-abalone interaction parameter 2	β_{Ab_J}	5.768	-	-	Estimated
Pristine lobster density at Betty's Bay after invasion had taken place	$U_{pristine}$	0.943	number.m^{-2}	Reaugh (2001), unpub. data	Fixed

Table 4.05: Parameters used in the urchin component of the model.

Urchin Parameters

Parameter	**Notation**	**Value**	**Units**	**Source**	**Estimated/Fixed**
Intrinsic growth rate	r_u	0.5	-	-	Fixed
Carrying capacity	K_u	14943.57	MT	calculated based on habitat area and density estimates	Fixed
Initial urchin biomass in 1985	U_{1985}	14943.57	MT	calculated based on habitat area and density estimates	Fixed
Lobster-urchin interaction parameter 1	α_{U_J}	0.0019	-	-	Estimated
Lobster-urchin interaction parameter 2	β_{U_J}	0.0002	-	-	Estimated
Urchin threshold relative to carrying capacity	U_{thresh}	0.3	-	Mayfield and Branch 2000	Fixed
Minimum survival	$S_{\min}$	0.01	-	-	Fixed
Additional variance	σ_{AD}	0.2	-	-	Fixed

Table 4.06: Model settings and variables used for the rock lobster and urchin model components.

Rock Lobster and urchin starting values				
Parameter	**Notation**	**Value**	**Units**	**Source**
Number of seasons	q	4	-	-
Plus group	z	20	years	-
Mean weight-at-age	w_a^J	see Appendix 2 Table A2.03	grams	Johnston and Butterworth (2001)
Pristine lobster density at Betty's Bay	$J_{pristine}$	0.943	number.m^{-2}	Reaugh (2001), unpub. data
Pristine urchin density estimate	$U_{pristine}$	80	urchins	Mayfield and Branch (2000)
Urchins density at Cape Hangklip before invasion	U_{1980}	23	urchins	Field *et al.* (1980a)
Mean weight of an urchin	W_u	28.5	grams	Blamey (2009) unpub. data
Weight penalty	w_{pen}	500	-	-
Delta	δ	0.05	-	-
Area B	$Area^B$	4 276 873	m^2	Plagányi (2004)
Area D	$Area^D$	4 474 754	m^2	Plagányi (2004)
habitat multiplication factor	$hfact$	1.5	-	Plagányi (2004)

Table 4.07: Estimated parameters with 90% confidence intervals.

Parameter description	**Notation**	**Value**	**90% confidence interval**	
Starting lobster biomass (MT)	B_{y0}^{J}	314	0	942
Lobster-abalone interaction parameter 1	α_{Ab_J}	0.0070	0	16.14
Lobster-abalone interaction parameter 2	β_{AB_J}	5.7680	0	19 679
Lobster-urchin interaction parameter 1	α_{U_J}	0.0019	0	0.0063
Lobster-urchin interaction parameter 2	β_{U_J}	0.0002	0.0001	0.0004
Lobster spawning biomass carrying capacity (MT)	K_{J}^{sp}	1510.6	1085.7	1935.5

Table 4.08: Log-likelihood contributions for the multispecies model.

Parameter	**Notation**	**Value**
Likelihoods for:	**Abalone likelihoods Zone B**	
Abalone CPUE	-*ln* L CPUE	-49.9
Abalone FIAS	-*ln* L FIAS	-8.2
Commercial catch-at-age	-*ln* L age CS	-18.2
Recreational catch-at-age	-*ln* L age RS	-7.0
Poaching catch-at-age	-*ln* L age PS	-1.6
FIAS catch-at-age	-*ln* L age FIAS	-8.4
Old survey catch-at-age	-*ln* L age OS onshore	-1.1
Old survey offshore catch-at-age	-*ln* L age OS offshore	-1.4
Industry catch-at-age	-*ln* L age IS	-1.0
Overall likelihood for Zone B	-*ln* L Zone B	-96.9
Likelihoods for:	**Abalone likelihoods Zone D**	
Abalone CPUE	-*ln* L CPUE	-30.9
Abalone FIAS	-*ln* L FIAS	3.6
Commercial catch-at-age	-*ln* L age CS	-10.1
Recreational catch-at-age	-*ln* L age RS	-6.4
Poaching catch-at-age	-*ln* L age PS	0.2
FIAS catch-at-age	-*ln* L age FIAS	-1.4
Old survey catch-at-age	-*ln* L age OS onshore	-1.1
Old survey offshore catch-at-age	-*ln* L age OS offshore	-2.0
Overall likelihood for Zone D	-*ln* L Zone D	-48.1
Likelihoods for:	**Lobster likelihoods**	
Lobster CPUE	-*ln* L CPUE	-9.7
Lobster FIMS	-*ln* L FIMS	-1.9
Overall lobster likelihood	-*ln* L lobster	-12.7
Likelihoods for:	**Juv. abalone and urchin likelihoods**	
Juvenile abalone survey	-*ln* L ab_surv	-1.9
Urchin survey	-*ln* L urch_surv	1.6
	Overall likelihood	
Overall Total Likelihood	***-ln* L Total**	**-156.7**

Table 5.01: Experimental and commercial CPUE (kg/bakkie/day) for the West Coast rock lobster fishery - Area 12 (Zone F).

Year	Commercial CPUE	Fishery
2000	246.00	Experimental
2001	244.00	Experimental
2002	273.00	Experimental
2004	186.47	Commercial
2005	170.58	Commercial
2006	196.64	Commercial
2007	161.28	Commercial
2008	123.87	Commercial

Table 5.02: Six different scenarios under which biomass future projections are made. All rock lobster catches are in MT, + denotes a presence and **–** denotes an absence of rock lobsters.

	Urchin and abalone biomass		Rock lobster biomass			
	Scenario 1 rock lobster predation	**Scenario 2** no rock lobster predation	**Scenario 3** no catch	**Scenario 4** current catch	**Scenario 5** 10 x current catch	**Scenario 6** 10 x illegal catch
Rock lobsters	+	**–**	+	+	+	+
Commercial lobster catch	91	0	0	91	910	0
Recreational lobster catch	20.5	0	0	20.5	205	0
Illegal lobster catch	9	0	9	9	9	90

Table 5.03: Sensitivity results for the model using various values of *h* (steepness of the stock-recruitment curve). *p* is the number of estimated parameters, *-lnL* is the negative log likelihood and AIC is the Akaike Information Criterion goodness of fit test; B_{y0}^{J} is the initial total rock lobster biomass in 1985, α_{Ab_J} is the abalone-lobster interaction parameter 1, β_{Ab_J} is the abalone-lobster interaction parameter 2, α_{U_J} is the urchin-lobster interaction parameter 1, β_{U_J} is the urchin-lobster interaction parameter 2 and K_{J}^{sp} is the spawning biomass-recruitment parameter for lobsters.

Model	**Manipulated parameter**	**No. of parameters**	**Goodness of fit**		**Responses of other parameters**					
	h	*p*	-lnL	AIC	B_{y0}^{J}	α_{Ab_J}	β_{Ab_J}	α_{U_J}	β_{U_J}	K_{J}^{sp}
Base model (*h* = 0.7)	0.70	6	-156.7	-301.4	314.03	0.0070	5.7680	0.0019	0.00022	1510.58
S1 (*h* = 0.55)	0.55	6	-156.6	-301.2	321.75	0.0069	5.7716	0.0019	0.00023	1545.15
S2 (*h* = 0.6)	0.60	6	-156.6	-301.3	319.27	0.0070	5.7685	0.0019	0.00023	1533.58
S3 (*h* = 0.75)	0.75	6	-156.8	-301.5	310.80	0.0071	5.7680	0.0019	0.00023	1499.62
S4 (*h* = 0.8)	0.80	6	-156.8	-301.7	306.552	0.0071	5.7680	0.0020	0.00023	1489.28
S5 (*h* = 0.85)	0.85	6	-156.9	-301.8	300.148	0.0073	5.7680	0.0020	0.00023	1479.70
S6 (*h* estimated)	0.99	7	-157.3	-300.6	196.501	0.0089	5.8369	0.0033	0.00026	1431.06

Table 5.04: Sensitivity results for the model using (S7) a spawner-recruitment parameter (γ) value of 1.5 which would mimic a Ricker spawner-recruit relationship, and (S8) estimating γ. See Table 5.03 for parameter definitions.

Model	Manipulated parameter	No. of parameters	Goodness of fit		Responses of other parameters					
	γ	p	$-lnL$	AIC	B_{y0}^{J}	α_{Ab_J}	β_{Ab_J}	α_{U_J}	β_{U_J}	K_{J}^{sp}
Base model (γ = 1.00)	1.00	6	-156.7	-301.4	314.03	0.0070	5.7680	0.0019	0.00022	1510.58
S7 (γ = 1.50)	1.50	6	-156.9	-301.8	477.50	0.0046	5.8064	0.0012	0.00021	1465.93
S8 (γ estimated)	1.49	7	-156.9	-299.8	477.50	0.0047	5.9676	0.0012	0.00021	1465.93

Table 5.05: Sensitivity results for the model using (S9) a 50% increase in K_J^{sp} (rock lobster spawning carrying capacity) and (S10) a 25% decrease in K_J^{sp}. See Table 5.03 for parameter definitions.

Model	**Manipulated parameter**	**No. of parameters**	**Goodness of fit**		**Responses of other parameters**				
	K_J^{sp}	p	$-lnL$	AIC	B_{y0}^J	α_{Ab_J}	β_{Ab_J}	α_{U_J}	β_{U_J}
Base model ($\ln(K_J^{sp})$ estimated)	1510.6	6	-156.7	-301.4	314.03	0.0070	5.7680	0.0019	0.00022
S9 $\ln(K_J^{sp}) = 7.03$	1132.9	5	-153.9	-297.8	561.37	0.0039	5.7754	0.0010	0.00021
S10 $\ln(K_J^{sp}) = 7.72$	2265.9	5	-156.3	-302.7	124.89	0.0143	5.7669	0.0060	0.00031

Table 5.06: Sensitivity results for the model using (S11) a 50% increase in K_u (urchin carrying capacity) and (S12) a 50% decrease in K_u. See Table 5.03 for parameter definitions.

Model	**Manipulated parameter**	**No. of parameters**	**Goodness of fit**		**Responses of other parameters**					
	K_u	p	$-lnL$	AIC	B_{y0}^{J}	α_{Ab_J}	β_{Ab_J}	α_{U_J}	β_{U_J}	K_J^{sp}
Base model ($\ln(K_u) = 9.61$)	14 943.6	6	-156.7	-301.4	314.03	0.0070	5.7680	0.0019	0.00022	1510.58
S11 ($\ln(K_u) = 10.02$)	22 471.4	6	-156.7	-301.4	314.02	0.0073	5.9650	0.0019	0.00015	1510.59
S12 ($\ln(K_u) = 8.92$)	7 471.8	6	-156.7	-301.4	314.02	0.0086	7.0127	0.0019	0.00046	1510.58

Table 5.07: Sensitivity results for the model using (S13) a 50% increase in M^J (rock lobster natural mortality), (S14) a 50% decrease in M^J and (S15) estimating M^J. See Table 5.03 for parameter definitions.

Model	**Manipulated parameter**	**No. of parameters**	**Goodness of fit**		**Responses of other parameters**					
	M^J	p	$-lnL$	AIC	B^J_{y0}	α_{Ab_J}	β_{Ab_J}	α_{U_J}	β_{U_J}	K^{sp}_J
Base model (M^J = 0.10)	0.100	6	-156.7	-301.4	314.03	0.0070	5.7680	0.0019	0.00022	1510.58
S13 (M^J = 0.15)	0.150	6	-156.4	-300.8	588.64	0.0067	5.8651	0.0019	0.00035	1144.39
S14 (M^J = 0.05)	0.050	6	-156.5	-301.0	165.89	0.0039	6.2009	0.0020	0.00016	3103.94
S15 (M^J estimated)	0.087	7	-156.7	-299.5	260.93	0.0082	5.7872	0.0020	0.00021	1713.05

Table 5.08: Sensitivity results for Model S16 when abalone natural mortality (*M*) is estimated. See Table 5.03 for parameter definitions.

Model	**Manipulated parameter**	**No. of parameters**	**Goodness of fit**		**Responses of other parameters**					
	M	p	$-lnL$	AIC	B_{y0}^{J}	α_{Ab_J}	β_{Ab_J}	α_{U_J}	β_{U_J}	K_{J}^{sp}
Base model (*M* fixed)	0.126	6	-156.7	-301.4	314.03	0.0070	5.7680	0.0019	0.00022	1510.58
S16 (*M* estimated)	0.128	7	-156.8	-299.6	311.76	0.0073	5.7679	0.0019	0.00022	1511.85

Table 5.09: Sensitivity results for the model using different urchin intrinsic growth rates (r_u): (S17) a 50% decrease, (S18) a 50% increase, (S19) a 100% increase, (S20) a 200% increase and (S21) r_u estimated. See Table 5.03 for other parameter definitions.

Model	**Manipulated parameter**	**No. of parameters**	**Goodness of fit**		**Responses of other parameters**					
	r_u	p	$-lnL$	AIC	B^J_{y0}	α_{Ab_J}	β_{Ab_J}	α_{U_J}	β_{U_J}	K^{sp}_J
Base model (r_u = 0.5)	0.5	6	-156.7	-301.4	314.03	0.0070	5.7680	0.0019	0.00022	1510.58
S17 (r_u = 0.25)	0.25	6	-157.0	-301.9	320.33	0.0067	5.8004	0.0016	0.00025	1507.27
S18 (r_u = 0.75)	0.75	6	-156.6	-301.1	307.59	0.0072	5.7680	0.0023	0.00021	1514.28
S19 (r_u = 1.0)	1.00	6	-156.5	-300.9	301.35	0.0074	5.7812	0.0026	0.00020	1518.20
S20 (r_u = 1.5)	1.5	6	-156.3	-300.7	289.89	0.0077	5.7812	0.0034	0.00018	1526.31
S21 (r_u estimated)	0.100	7	-157.1	-300.3	323.80	0.0069	5.8236	0.0014	0.00026	1505.56

Table 5.10a: Sensitivity results for the model when the first abalone-lobster interaction parameter (α_{Ab_J}) was (S22) halved (50% decrease) or (S23) multiplied by 1½ (50% increase). See Table 5.03 for other parameter definitions.

Model	**Manipulated parameter**	**No. of parameters**	**Goodness of fit**		**Responses of other parameters**				
	α_{Ab_J}	*p*	*-lnL*	AIC	B_{y0}^{J}	β_{Ab_J}	α_{U_J}	β_{U_J}	K_{J}^{sp}
Base model (α_{Ab_J} estimated)	0.0070	6	-156.7	-301.4	314.03	5.7680	0.0019	0.00022	1510.58
S22 (α_{Ab_J} * ½)	0.0035	5	-156.7	-303.4	314.03	5.7680	0.0019	0.00023	1510.58
S23 (α_{Ab_J} * 1½)	0.0105	5	-156.7	-303.4	314.03	8.6037	0.0019	0.00023	1510.583

Table 5.10b: Sensitivity results for the model when the second abalone-lobster interaction parameter (β_{Ab_J}) was (S24) halved (50% decrease) or (S25) multiplied by 1½ (50% increase). See Table 5.03 for other parameter definitions.

Model	**Manipulated parameter**	**No. of parameters**	**Goodness of fit**		**Responses of other parameters**				
	β_{Ab_J}	*p*	*-lnL*	AIC	B_{y0}^{J}	α_{Ab_J}	α_{U_J}	β_{U_J}	K_{J}^{sp}
Base model (β_{Ab_J} estimated)	5.7680	6	-156.7	-301.4	314.03	0.0070	0.0019	0.00022	1510.58
S24 (β_{Ab_J} * ½)	2.8840	5	-156.7	-303.4	314.03	0.0035	0.0019	0.00023	1510.58
S25 (β_{Ab_J} * 1½)	8.6520	5	-156.7	-303.4	314.03	0.0070	0.0019	0.00023	1510.58

Table 5.10c: Sensitivity results for the model when the first urchin-lobster interaction parameter (α_{U_J}) was (S26) halved (50% decrease) or (S27) multiplied by 1½ (50% increase). See Table 5.03 for other parameter definitions.

Model	**Manipulated parameter**	**No. of parameters**	**Goodness of fit**		**Responses of other parameters**				
	α_{U_J}	*p*	*-lnL*	AIC	B_{y0}^{J}	α_{Ab_J}	β_{Ab_J}	β_{U_J}	K_{J}^{sp}
Base model (α_{U_J} estimated)	0.0019	6	-156.7	-301.4	314.03	0.0070	5.7680	0.00022	1510.58
S26 (α_{U_J} * ½)	0.0010	5	-156.5	-303.1	565.27	0.0038	5.7809	0.00021	1499.05
S27 (α_{U_J} * 1½)	0.0029	5	-153.9	-297.9	318.59	0.8546	2.6391	0.00046	1507.80

Table 5.10d: Sensitivity results for the model when the second urchin-lobster interaction parameter (β_{U_J}) was (S28) halved (50% decrease) or (S29) multiplied by 1½ (50% increase). See Table 5.03 for other parameter definitions.

Model	**Manipulated parameter**	**No. of parameters**	**Goodness of fit**		**Responses of other parameters**				
	β_{U_J}	*p*	*-lnL*	AIC	B_{y0}^{J}	α_{Ab_J}	β_{Ab_J}	α_{U_J}	K_{J}^{sp}
Base model (β_{U_J} estimated)	0.00022	6	-156.7	-301.4	314.03	0.0070	5.7680	0.0019	1510.58
S28 (β_{U_J} * ½)	0.00011	5	-154.2	-298.3	370.86	0.0047	4.2942	0.0011	1489.55
S29 (β_{U_J} * 1½)	0.00033	5	-156.5	-303.0	137.58	0.0164	6.8573	0.0056	1999.89

Table 5.11: Sensitivity results for the model when CPUE data from the rock lobster commercial fishery for the years 2000-2002 were added. These data were from experimental catches that were made EOCH before the full-scale commercial fishery opened in this area. See Table 5.03 for parameter definitions.

Model	**Parameters**								
	p	$-lnL$	AIC	B_{y0}^{J}	α_{Ab_J}	β_{Ab_J}	α_{U_J}	β_{U_J}	K_{J}^{sp}
Base model	6	-156.7	-301.4	314.03	0.0070	5.7680	0.0019	0.00022	1510.58
S30 (Additional CPUE data)	6	-159.5	-307.0	383.05	0.0057	5.7712	0.0015	0.00022	1425.18

Table 5.12: Results from the sensitivity analyses using different starting age-structures to test hypotheses: (1) A starting age-structure that mimics an adult migration was used in the base-case model, (2) an age-structure that mimics increased larval settlement in the early 1980s was used in Model S31 and (3) an age-structure that is an intermediate of the first two hypotheses was represented by Model S32. See Table 5.03 for parameter definitions.

Model	**Parameters**								
	p	$-lnL$	AIC	B_{y0}^{J}	α_{Ab_J}	β_{Ab_J}	α_{U_J}	β_{U_J}	K_{J}^{sp}
Base model (Adult immigration)	6	-156.7	-301.4	314.03	0.0070	5.7680	0.0019	0.00022	1510.58
S31 (Increased larval settlement)	6	-135.9	-259.8	365.22	0.6676	6.7144	0.0533	0.17677	4817.06
S32 (Intermediate)	6	-154.5	-296.9	232.82	0.0024	0.0084	0.5833	0.22464	1365.56

Table 6.01: Rock lobster and urchin starting values for Zone B.

Parameter	Notation	Value	Units	Source
Maximum observed urchin density at Roman's Bay (Zone B)	U_{roman}	74.4	no. per m^2	Chapter 3
Pristine urchin density estimate	$U_{pristine}$	80	no. per m^2	Mayfield and Branch (2000)
Urchin carrying capacity	K_{uB}	14 267	MT	Calculated
Area B	$Area^B$	4 276 873	m²	Tarr (1993)
Area D	$Area^D$	4 474 754	m²	Tarr (1993)
habitat multiplication factor	$hfact$	1.5	-	Plagányi (2004)
Rock lobster carrying capacity	K^{sp}	2000	MT	Assumed
Rock lobster starting biomass I	$B_I^{J\_B}$	50	MT	-
Rock lobster starting biomass II	$B_{II}^{J\_B}$	100	MT	-
Rock lobster starting biomass III	$B_{III}^{J\_B}$	500	MT	-

Table 7.01: Model settings and variables used in the fish model.

Parameter	**Notation**	**Value**		**Units**	**Source**
		Fished Area	**Historic**		
Fish consumption/biomass ratio	Q/B	4.86	4.86	-	Calculated (Eq 7.3)
Area of Zone D	$Area^D$	4474754	4474754	m^2	Tarr (1993)
Mean density of redfish	$P_{density}$	0.0138[§]	0.1189[†]	number.m^{-2}	[§]Kerwath *et al.* (2008), [†]estimate
Mean weight of redfish	W_P	0.775[*]	1.36[#]	kg	[*]Götz (2005), [#]Gilchrist (1900)
Initial number of redfish	N_{1980}^P	61 931	532 353	numbers	Calculated
Initial starting biomass	P_{1980}	48.00	724.00	MT	Calculated/estimated
Biomass of prey eaten each yr	P_y^{prey}	233.46	3518.64	MT	Calculated
% of fish diet comprising lobsters	ξ	5	5	%	Assumed

Table 7.02: Variables used to calculate the consumption/biomass ratio as described by Palomares and Pauly (1998).

Parameter	Notation	Value	Units	Source
Aspect ratio	A	2.96	-	Fishbase.org
Mean temperature for False Bay	T	16.50	°C	Jury (1991)
Mean temperature for False Bay	T'	3.45	1000/K	Calculated
VBGF asymptotic length	L_∞	512.86	mm	Götz (2005)
Intercept of length-weight relationship	a	0.00002	g	Götz (2005)
Slope of length-weight relationship	b	3.07	$\mathrm{g.mm^{-1}}$	Götz (2005)
VBGF asymptotic weight	W_∞	4175.67	g	Calculated
Herbivore parameter	H	0	-	Palomares and Pauly (1998)
Detritivore parameter	D	0	-	Palomares and Pauly (1998)

Table 7.03: Sensitivity results for the model using intrinsic fish growth rates (r_P) of 0.25 (S1) and 0.35 (S2). K_P is the fish carrying capacity, p is the number of estimated parameters, *-lnL* is the fish negative log likelihood and AIC is the Akaike Information Criterion goodness of fit test.

Model	Parameters				
	r_P	K_P	p	$-\ln L$	AIC
Fish base $r_P = 0.3$	0.3	723.78	1	-7.23	-12.46
S1 $r_P = 0.25$	0.25	70.59	1	8.58	19.16
S2 $r_P = 0.35$	0.35	229.16	1	-6.23	-10.46