Effects of marine reserves on the biology of rocky intertidal limpets along the southeast coast of South Africa

Thesis submitted in fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

of

RHODES UNIVERSITY

By

MOTEBANG DOMINIC VINCENT NAKIN

April 2008

Abstract

Limpets are harvested by people in South Africa, but are selected in terms of species and size. The effects of marine reserves on the biology of commonly exploited (*Helcion concolor* and *Scutellastra longicosta*) and rarely exploited species (*Cellana capensis* and *Scutellastra granularis*) were investigated on the southeast coast of South Africa at two reserve and two non-reserve sites. For each species, a 4-way nested ANOVA was used to test the effects of month, reserve, site (nested within reserve) and area (nested within site and reserve) on population density, size structure and recruitment of these limpets. The data were collected monthly over 20 months.

The overall results indicated a gradient of exploitation among species, *S. longicosta* was the most heavily exploited species and *S. granularis* the least exploited species. However, there was also a gradient of exploitation between reserves and non-reserves. Xhora was the most heavily exploited site while Nqabara was less heavily exploited. Of the two reserve sites, Cwebe had more poachers than Dwesa.

In most analyses, the month x area (reserve (site)) interaction was significant. However, this was largely an artifact due to comparisons of areas in different sites and significant differences between areas within sites occurred in relatively few months.

Densities were greater inside reserves for all species except *C. capensis*. For *S. longicosta* and *H. concolor* this was expected but not for *S. granularis* and the result possibly reflects its opportunistic exploitation in the absence of the preferred species or indirect effects of reserves. Commonly exploited species and the rarely exploited *C. capensis* clearly showed greater mean and maximum sizes in reserves but there were month/site (reserve) interactions. Months with significant differences between reserves and non-reserves in both mean and maximum sizes generally occurred more often for commonly exploited than rarely exploited species, but *C. capensis* showed the strongest reserve effect on maximum size. Interview surveys showed that, although not normally exploited, *C. capensis* is sometimes mistaken for *H. concolor* and this suggests that large individuals are unintentionally harvested outside reserves.

There were no significant reserve effects on recruitment for any species. Although Xhora had the lowest densities and limpet sizes, it showed the highest recruitment especially for *S. longicosta*, suggesting that larvae can be transported far from where they are released and settle in non-reserve sites regardless of adult densities. Reserve as a main factor was not significant for the rarely exploited species, but there was a significant month x reserve interaction, with non-reserves having greater GSI values than reserves in most months.

Growth rates were examined using individual tagging and cohort analysis. The two techniques gave different results, with individual tagging giving higher growth estimates than cohort analysis. Except for the territorial species *S. longicosta*, growth was higher in non-reserves and inversely correlated with population density. Mortality estimates using the Cormack-Jolly-Seber model indicated that the rarely exploited species had significantly greater capture probabilities in reserves while no significant reserve effects were observed for the commonly exploited species. Reserve effects on survival probability were significant only for *S. longicosta*, with reserves being greater than non-reserves and no significant effects for any other species. Enhanced survival in reserves was attributed to the effects of human exploitation**.**

In theory, marine protected areas show increases in densities, sizes and reproductive output of exploited species, but the present results revealed that the efficacy of reserves depends on the status of the species, not only whether it is exploited or non-exploited, but also whether it is territorial.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Acknowledgements

First and foremost, I would like to thank my supervisor Prof. C.D. McQuaid for providing me with the opportunity to further my studies part-time. His endless support, guidance and constructive criticism have made this project possible. The work on modeling owes much to Prof. T. Booth who sacrificed his time in assisting me. I would also like to thank Prof. S. Radloff for advice on statistical analysis.

Many people have shared their ideas with me while at Rhodes University, especially the Coastal Research Group but very particular thanks are due to Francesca Porri, Gerardo Zardi**,** Eliecer Diaz, Jackie Hill and Katy Nicastro. Walter Sisulu University (former University of Transkei) and Rhodes University were invaluable in providing grounds for many of my ideas. I am indebted to my colleagues from WSU in the Department of Biological Sciences. The financial support of WSU and National Research Foundation as well as the logistic support provided by Rhodes University brought this project to term. The Eastern Cape Parks Board is also thanked for providing access to Dwesa and Cwebe Nature Reserves. I thank all those who participated in field sampling, especially, Mzolelwa Nkaitshana ("Mzo") and Siyambusa Sodinga ("Siya").

As always, the enthusiastic and loving support of my wife Mandisa has been the most important factor allowing me to complete this work. My warmest thanks go to all my family and in-laws, especially my father, Monaheng and mother, the late Nontsikelelo "Mantsane" for their invaluable contributions, constant support and encouragement

throughout my study time. May God bless you! Ntsane ("Pat-Pat") your contributions and support to our father is acknowledged. Tsólo ("T.O."), Mookameli ("Mrey") and Buhle ("Buhleza"), I thank you for looking after my two sons, Molemo ("Lemo") and Thabang ("T-bos") during the time when I have been away from home. I also want to thank all other people who contributed in various ways either mentally, spiritually, physically and socially.

I won't forget the kindness of Mr Dez Weeks and Ms Elizabeth Cloete who solved my dispersed accommodation needs during my stay in Grahamstown!

CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

Anthropogenically driven climate change, coupled with rapidly expanding coastal human populations has the potential to intensify both direct and indirect effects of exploitation of natural populations and increases the probability of important synergisms between climatic variability and fishing (Harley *et al.* 2006). The effects of climate change and fishing depend partly on the characteristics of the exploited species, including their resistance to various forms of disturbance (e.g. thermal extremes, storm-induced disturbance and human collection) and their resilience, or ability to recover following a disturbance (Harley & Rogers-Bennett 2004).

Due to the ongoing direct depletion of the world's marine resources as well as the indirect effects of harvesting, no-take marine reserves are being promoted as an ecosystem-level management tool (Pillans *et al*. 2005). No-take marine reserves prohibit extractive activities such as harvesting, offering a way to conserve marine biodiversity whilst at the same time sustaining fisheries (Roberts & Hawkins 1999; Halpern 2003; Lubchenco *et al*. 2003). They may restore fish stocks, particularly spawning stocks, within their boundaries and act as sources of larvae that could eventually settle outside of the reserve (Rakitin & Kramer 1996). Thus, marine reserves provide an additional fisheries management tool that has the potential to reverse dramatically the detrimental effects of fishing (Dugan & Davis 1993**;** Roberts & Hawkins 1999). There is much evidence suggesting that establishing well-designed and managed marine reserves can result in rapid increases in the size and abundance of once exploited-species (Halpern 2003; Gell & Roberts 2003; Lubchenco *et al*. 2003). Branch and Odendaal (2003) reported 57 areas that receive some protection in South Africa. Of the whole coastline, about 4.7% was reported to be fully protected and about 10% receives substantial protection (Attwood *et al.* 1997). The efficacy of these reserves was found to vary, depending largely on the degree of management. Reserves are known to offer an opportunity to carry out a valid comparison between protected and unprotected areas where resources are continuously removed (Walters & Holling 1990). Thus, studies involving monitoring of marine reserves are an important tool for identifying the general impacts of exploitation and assessing the "health" condition of the coast. Therefore, monitoring of exploited sites associated with marine reserves also provides valuable information on long-term trends in the coastal environment, including those related to global warming and introduced species (Dye 1998; Edgar *et al.* 2004).

Fishing pressure on rocky shores is high in most parts of the world, with important consequences for intertidal communities (Thompson *et al*. 2002). Populations of intertidal and shallow-water grazers are highly vulnerable to over-exploitation because their habitat is both restricted and accessible. The impacts of shellfish exploitation have led to decreased biomass, decreased species richness and shifts in community composition worldwide (Littler & Murray 1975; Durán & Castilla 1989; Lasiak 1998). There is also evidence that fishing reduces the abundance and size of the most reproductively valuable members of a population (Chapman & Kramer 1999; Edgar & Barrett 1999; Johnson *et al*. 1999; McClanahan *et al*. 1999; Williamson *et al*. 2004). Previously, declines in rocky intertidal biodiversity have largely been ascribed to chronic, persistent disturbances including sewage discharge and industrial effluents (Littler &

Murray 1975). However, more episodic disturbances can result from visitor foot traffic (Keough & Quinn 1998). Climate change can enhance species' vulnerability to overexploitation, just as exploitation can make species particularly vulnerable to change in climate. The combined influence of exploitation and adverse environmental change tends to reduce and fragment exploited populations, making them more vulnerable to Allee effects (Harley & Rogers-Bennett 2004). Fishing pressure may therefore reduce population sizes to the point where additional stresses from rare environmental catastrophes (e.g. extreme high temperature, winter storms) place populations at risk of local extinction (Gascoigne & Lipcius 2004).

Limpets dominate certain zones of rocky shores worldwide and play a major role not only in the structuring of intertidal communities through their grazing activities, but also by providing secondary habitats for other invertebrates that settle either on top of, or beneath their shells (Branch 1981, 1985; Hawkins & Hartnoll 1983; Pal & Hodgson 2004). By providing habitats for other species, limpets contribute to overall diversity of the shore. In addition, they are heavily exploited at a subsistence level and used as food and bait by people in several parts of the world (Hockey & Bosman 1986; Ortega 1987; Keough *et al*. 1993; Pombo & Escofet 1996; Murray *et al*. 1999; Kido & Murray 2003; Roy *et al*. 2003). Other authors have found that the removal of larger grazing gastropods facilitates the growth of algae (Underwood 1980; Hockey & Bosman 1986; Dye 1993, 1995; Johnson *et al*. 1997; Jenkins & Hartnoll 2001; Coleman *et al*. 2004; Davies *et a*l. 2007), which leads to further changes within the rocky shore community (Underwood &

Jernakoff 1984; Coleman 2002; Forster *et al*. 2003; Jenkins *et al*. 2005; Coleman *et al*. 2006b).

The exploitation of limpets can have secondary effects on other species that interact with grazers, including their predators, competitors, food plants and parasites. For instance, Hockey (1987) reported that human exploitation of limpets may have contributed to the extinction of the Canarian black oystercatcher *Haematopus meadewaldoi*. Due to their specialized methods of prey capture, adult oystercatchers feed their chicks for prolonged periods and are particularly vulnerable to the effects of food shortage during this time. Depletion of their prey, coupled with disturbance, may have made it impossible for adult birds to glean sufficient food to meet both their own needs and those of their chicks. Parasites are an additional group of organisms that may be adversely affected by exploitation of limpets (Mouritsen & Poulin 2005).

Patterns of shellfish exploitation vary from place to place and from time to time (Bosman *et al*. 1988; Durán & Castilla 1989; Van Herwerden *et al*. 1989; Underwood & Chapman 1996). Some geographic patterns of distribution and abundance of molluscs are general, with little variation at small scales (Forster *et al.* 2003), while other patterns are specific to particular places or times (Forster *et al*. 2003; Morrisey *et al.* 1992; Underwood & Chapman 1998). Understanding these patterns of variation in distribution and abundance and how they change in time and space is important to understanding the ecology of the organism or assemblage being studied (Underwood 2000).

Shellfish gatherers have exploited the marine resources of the South African coastline for at least the past 100 000 years (Thackery 1988). The intensity and the distribution of such activities have, however, varied markedly through time. The Transkei coast is subject to intense subsistence exploitation due to high population density and poverty. Thus, local people rely on shellfish for protein (Bigalke 1973; Hockey & Bosman 1986; Bosman *et al.* 1988; Lasiak 1991a). This coast is also utilized to a lesser extent by recreational and commercial fishers (Hockey *et al.* 1988; Fielding *et al.* 1994; Lasiak 1997). Shellfish-gatherers are highly selective in terms of size, selecting bigger animals and species, preferring mussels and various species of limpets (Bigalke 1973; Siegfried *et al.* 1985; Hockey & Bosman 1986; Lasiak & Dye 1989; Lasiak 1991a; 1992). Humans collect intertidal species mainly for use as food or fishing bait or for their shells (Pombo & Escofet 1996; Lasiak 1997), or for recreational activities. People also collect intertidal organisms for home aquariums (Griffiths & Branch 1997), and other purposes such as the exploratory manipulation of rocks and specimens (Addessi 1994).

The spatial pattern of subsistence exploitation in South Africa has changed considerably over time in response to demographic changes in human populations. In addition, modern techniques, such as underwater breathing apparatus, which allows more efficient collecting of subtidal organisms, has expanded the range of species that can easily be gathered. The advent of the coastal tourism industry, and the practices of commercial operators (Fielding *et al.* 1994; Siegfried *et al.* 1994; Griffiths & Branch 1997), are also important, as are the effects of anthropogenic disturbance including indirect effects, such as sewage and industrial effluent (Littler & Murray 1975; Liu & Morton 1998), and more direct effects, such as harvesting and development (Durán & Castilla 1989; Underwood & Kennelly 1990; Povey & Keough 1991; Kingsford *et al.* 1991). However, the exploitation on the Transkei coast is almost entirely for food. Studies along the Transkei coast on the southeast coast of South Africa (Fig. 1.1) suggest that the selective removal of patellid limpets results in a marked increase in macroalgal cover, and that this in turn, reduces the availability of primary space for other species (Lasiak & White 1993; Dye 1995).

In South Africa, the exploitation of intertidal organisms is currently controlled by regulations promulgated under the Marine Living Resource Act of 1998. The objective of these regulations is to ensure the maintenance of viable populations of species subject to exploitation. These regulations are supposedly based on best available information. The fact that shellfish-gathering practices along the Transkei coast take place in a way that is unconstrained by any firmly enforced conservation legislation is a matter of great concern to marine ecologists. Siegfried *et al.* (1985) have demonstrated over-exploitation of some shellfish stocks while Hockey & Bosman (1986) and Lasiak & Field (1995) noted that over-exploitation has led to modifications in intertidal community structure and functioning. Another issue of concern is that, although there are strong biogeographic effects along coast (Emanuel *et al.* 1992) and marked regional differences in community structure (Van Erkom Schurink & Griffiths 1990; Lasiak 1997; McQuaid & Payne 1998), similar control measures are applied all around the coast. The problem is further complicated as there are also marked differences in recruitment rates around the South African coast (Harris *et al.* 1998).

Human impacts on marine systems are increasing, both directly through fishing and indirectly through anthropogenic warming. The effects of either climate change or fishing alone are sufficient to alter dramatically marine populations and ecosystems and may drive abundant species to extinction (Roberts & Hawkins 1999; Dulvy *et al.* 2003). Harley & Rogers-Bennett (2004) suggest that future management strategies must shift their emphasis from correlative data to a more mechanistic understanding of the effects of environmental variability and its interactions with fishing. Conservation of exploited marine populations requires knowledge of interannual variation in the characteristics of and relationships between the spawning stock and recruitment, which determine population resilience and persistence (Lipcius & Stockhausen 2002).

Climate change and fishing are both likely to have major effects on the distribution and abundance of marine species. As rates of climate change and exploitation accelerate, additive and synergistic interactions between them are becoming increasingly important to the dynamics of marine ecosystems and the sustainability of marine fisheries (Harley & Rogers-Bennett 2004). The management and conservation of any resource requires information on standing stocks and the direct impact of population exploitation (Foster & Hodgson 2000). Effective management requires a detailed understanding of ecological impacts resulting from anthropogenic disturbances as well as a detailed knowledge of the system itself. The structure of intertidal assemblages results from many interacting processes, including predation and competition (Dayton 1971; Fairweather & Underwood 1991), settlement and/or recruitment (Broitman *et al*. 2005) and disturbances (Chapman & Underwood 1998). Understanding the structure and dynamics of these assemblages is, however, not possible without knowledge of the ecology of the component species (Dayton 1971). A minimum viable population (MVP) density may be necessary for reproduction and sustained recruitment to maintain the population in the long term (Siegfried *et al.* 1994). Part of the difficulty of predicting the effects of human exploitation on grazers is that each species has particular characteristics that influence its vulnerability to exploitation.

Despite the intensity of human exploitation, few researchers have quantitatively estimated the magnitude or the relative importance of the effects of human exploitation or compared them with naturally occurring processes (Keough & Quinn 1993; Pombo & Escofet 1996; Lasiak 1997; Lindberg *et al.* 1998; Murray *et al.* 1999; Kido & Murray 2003). Thus, the primary objectives of the present study were to investigate the effects of marine reserves on the population density, size structure, recruitment, growth rates, mortality rates and reproductive output of four species of patellid limpets on the southeast coast of South Africa. These were: *Helcion concolor, Scutellastra longicosta* and *Cellana capensis* and *Scutellastra granularis*. Owing to the fact that different limpets have different life-history characteristics which influence their vulnerability to exploitation, each limpet was investigated separately (Branch 1974a; Lasiak 1991b; Branch & Odendaal 2003). Creese & Ballantine (1983) have pointed out that for effective evaluation of rocky intertidal communities, it is useful to have an understanding of the life history characteristics and population dynamics of the component species. These characteristics can vary spatially and temporally so that comparisons at different shores through time allow a greater understanding of the demography of species and variability among populations (Dunmore & Schiel 2003). Information from such studies could lead to more effective management and to regulations based on defensible scientific information (Griffiths & Branch 1997).

The South African coast supports a very wide diversity of limpets. However, some species occur throughout the area, while others are limited to particular biogeographic regions, e.g. the cool temperate west coast, the warm temperate south or the subtropical east coast (Emanuel *et al*. 1992). In most cases where a species extends around the entire coast-line, individuals from the west coast are markedly larger than those from the warmer coasts (Branch 1974b; Ridgway *et al*. 1998). Some patellid limpets on South African shores are highly specialized and feed on a single species of algae, and several have specialized relationship in which they territorially guard particular species of algae in "gardens" (Branch 1971). Most limpets are slow-moving, browsing animals that feed on algae, lichens and diatoms. They are predominantly intertidal or infratidal, and are zoned fairly rigidly both vertically and geographically. Thus overlap between habitats of the different species is relatively restricted. Some species occupy fixed positions on the shore. The individuals become so established in one position that they form well defined scars on the substratum. From these, they undertake feeding excursions, subsequently returning to their own particular "home scar" (Branch 1971). According to Branch (1975b), limpets have evolved two basic mechanisms to reduce intraspecific competition. Firstly, they may migrate progressively away from the site of settlement, or secondly, they may remain in a fixed zone and develop behavioural patterns to reduce competition.

Thus South African limpets can be grouped either as migratory species or non-migratory species. Migratory species (e.g. the study species *S. granularis*, *H. concolor,* and *C. capensis*) are all generalized grazers, feeding on any available food (Branch 1971, 1975a). Conversely, non-migratory species (e.g. *S. longicosta*) all occupy relatively fixed zones in the low intertidal and undergo no vertical migration from the site of settlement. Most adults are known to have a fixed scar, and defend the territory around this scar, reacting aggressively to others of the same species (Branch 1974a). Homing and scars are used for different functions such as territorial maintenance and reduction of predation. For example, a large proportion of *S. longicosta* juveniles are found on the shells of *Oxystele sinensis*, a winkle that shows strong avoidance reactions to the predatory starfish *Marthasterias glacialis* and thus the limpets may also benefit from these escapes (Branch 1974b). Home scars are also important in the prevention of desiccation.

1.2 STUDY SITES AND SPECIES

The Transkei coast is located on the southeast coast of South Africa (Figs. 1.1 & 1.2) near the junction of two marine biogeographic provinces, the warm temperate south coast and the subtropical east coast (Kilburn & Rippey 1982; Emanuel *et al*. 1992). Sampling was conducted at four study sites, between the Nqabara and Xhora rivers on the Transkei coast of South Africa (Fig. 1.1). This stretch of coast is approximately 40 km long, and the sites were approximately 5-10 km apart. Two sites (Dwesa and Cwebe) are marine nature reserves, separated by the Mbashe River and have recently been combined as one reserve called the Dwesa-Cwebe Nature Reserve. These reserves will be regarded as separate throughout the present study. Adjacent to Dwesa and Cwebe were two non-reserve sites, Nqabara and Xhora. The non-reserve sites were chosen on the basis of proximity to reserve sites (no more than 10 km north or south of the reserves), habitat similarities and hydrodynamic conditions such as flow rates and wave exposure. Within each of the four sites, two areas (~ 100 m apart) were established.

The shores in the southern region of Transkei are a mixture of dolerite, mudstone or shale platforms, those in the central region are sandstone while those in northern region are formed of quartzitic sandstone (Hockey *et al*. 1988). The rocky shore at Nqabara (the south most site) is in the form of gently-sloping, slightly stepped mudstone platforms with occasional shale and dolerite intrusions while Dwesa is very gently sloping and mainly shale. The rocky shores at Cwebe and Xhora are formed mainly of sandstone platforms, with Xhora being more gently-sloping with fewer gulleys than Cwebe. Various studies have documented the underlying geological substrata (Hockey *et al*. 1988), and standing stocks of exploited intertidal invertebrates (Fielding *et al*. 1994) and intensity of exploitation (Lasiak 1997) in this region.

All study areas were selected subjectively to have similar aspect and shore topography, but standardization of study sites on the basis of rock type was not feasible owing to the heterogenous nature of the underlying geological substrata along the Transkei coast (Hockey *et al*. 1988). Clarke and Green (1988) suggested a need to control potential confounding physical and biotic variables within set limits when sites are selected.

Originally, four species were selected that were believed to comprise two exploited and two unexploited species. However, later interview survey results revealed that the unexploited species were occasionally taken either by mistake or in the absence of the preferred species. Therefore, the term “rarely exploited species” has been used instead of “unexploited species” throughout the thesis.

Scutellastra granularis

S. granularis is the most widespread of the study species, with regard to both vertical and geographic distribution. It occurs around the entire South African coast, from Rocky Point in Namibia to Umpangazi near the Mozambique border (Penrith & Kensley 1970) (Fig. 1.2), and can reach a maximum size of 60 mm (Branch *et al.* 2002). It occurs intertidally and is distributed from the infratidal fringe to the upper balanoid zone. Small individuals are restricted to the lower shore, indicating settlement, or survival, of larvae in this region. Size increases higher on the shore, to a maximum in the balanoid zone, suggesting upward migration as the limpets age.

Scutellastra longicosta

This is characteristically a ‘warm water’ species which is recorded from Isipingo on the east coast to Saldanha Bay on the west coast (Branch 1974a). It occurs in the lower balanoid zone, below the main concentration of *Cymbula oculus* and can reach a maximum size of 70 mm (Branch *et al.* 2002). This species changes its habitat at different stages of its life (Branch 1974a). For instance, during the first year, animals occur on other shells (particularly *Oxystele sinensis* and other *S. longicosta*) and feed on the encrusting red algae *Ralfsia*, growing there. In the second year, they move on to rock and feed on the encrusting coralline algae *Lithothamnion* until they establish a *Ralfsia* garden (or occupy an empty scar). Gardens vary in size according to the size of the limpet, but most are about 150 cm^2 in area (Branch 1974b). These transitions in habitat and food are known to reduce competition between age groups.

Cellana capensis and ***Helcion concolor***

These two species occur between Port Alfred on the southeast coast of South Africa and Kenya (Fig. 1.2) and can reach a maximum size of 50 mm (Branch *et al.* 2002). In the intertidal area, these two species broadly overlap in distribution, zonation and food, but differences exist in their microhabitats, *C. capensis* prefers dry rocks and avoids sand-covered rocks, while *H. concolor* predominates in damp areas, often where sand scours or forms a film over the rocks (Branch 1976).

1.3 RANKING OF SITES AND SPECIES IN TERMS OF EXPLOITATION

To determine whether shellfish collections were random or species-specific, 4 interview surveys were carried out at each non-reserve site (i.e. 2 in each of two months at each site) during four spring low tides in September and December 2005, when exploitation pressure is especially heavy during the holiday season (Lasiak 1997). The questionnaires (Appendix A.1) focused mainly on short questions about limpet species identification and their order of preference. These questions were asked confidentially of each individual interviewed and their responses were recorded. A total of 191 and 114 respondents were interviewed at Xhora and Nqabara, respectively. A Chi-square test (X^2) was used to examine whether shellfish collectors showed random or species-specific collection patterns.

The X^2 test showed significant ($p < 0.05$) results, indicating that the shellfish collectors have clear species preferences. The ranking of the species was the same at each site (Table 1.1), *S. longicosta* was the most favoured species, while *S. granularis* was the least exploited species.

A t-test was used to determine whether the mean numbers of shellfish collectors were different between Xhora and Nqabara. The t-test indicated significant ($p < 0.05$) results, suggesting that the number of shellfish collectors between the two non-reserve sites were different. Exploitation pressure is greatest on *S. longicosta* at Xhora and least on *S. granularis* at Nqabara. Therefore, interviews indicated that a gradient in exploitation exists among sites and among species. Xhora had more shellfish collectors than Nqabara (Table 1.1). Similarly, Lasiak (1997) estimated that the number of shellfish collectors ranged between 16-28 per km of shore in the central region (closer to Xhora) and 1-6 per km of shore in the southern region (closer to Nqabara).

While the reserves are theoretically “no take” zones, it was recognized that some poaching does occur. Information on the number of poachers at these sites (Table 1.2) was obtained from the nature reserves’ office records. The data were patchy and counts were not always contemporary at the two sites, but these represent the best information available. Only data that were comparable between the two reserves were considered, spanning the period from January 2003 to May 2007. Although the total number of poachers was greater at Cwebe (141) than at Dwesa (137), a t-test on mean number per month revealed the results to be non-significant ($p > 0.05$).

1.4 OUTLINE OF THE THESIS

This thesis consists of eight chapters.

Chapter 1 provides a general introduction – exploring patterns of exploitation and species life-history characteristics and defining the study sites and species.

Chapter 2 estimates population densities and compares commonly exploited and rarely exploited species in reserve and non-reserve sites.

Chapter 3 examines the population structures of the study species – mean and mean maximum sizes and size frequency distributions.

Chapter 4 compares recruitment of commonly exploited and rarely exploited species in reserve and non-reserve sites.

Chapter 5 investigates the growth rates of commonly exploited and rarely exploited species at the four study sites, using individual tagging and cohort analysis. This allowed the comparison of age and growth rates between reserves and non-reserves.

Chapter 6 deals with their reproductive biology – gonado-somatic index (GSI), sex ratios and size at sexual maturity.

Chapter 7 investigates the mortality rates of commonly exploited and rarely exploited species at the four study sites from tagged individuals using the Cormack-Jolly-Seber model.

Chapter 8 concludes the thesis with a general discussion.

Table 1.1: Results from a four days survey to determine species preferences for consumption at the two non-reserve sites, Xhora and Nqabara.

	Xhora (n = 191) $X^2 = 208.85$, df = 3 , $p < 0.0001$	**Nqabara** (n = 114) $X^2 = 113.39$, df = 3 , $p < 0.0001$
Species	Mean rank	Mean rank
S. longicosta	1.20	1.33
H. concolor	2.04	1.64
C. capensis	2.52	2.20
S. granularis	3.98	3.97

Table 1.2: Data on the number of poachers collecting shellfish at each of the reserve sites, Dwesa and Cwebe.

<table>
<tr><th colspan="5">Dwesa</th></tr>
<tr><th>Year</th><th>Month</th><th>No. of months</th><th>Total no. of people</th><th>Mean no. of people per month</th></tr>
<tr><td>2002</td><td>Jan-Dec</td><td>12</td><td>20</td><td>1.67</td></tr>
<tr><td>2003</td><td>Jan-Oct</td><td>10</td><td>28</td><td>2.8</td></tr>
<tr><td>2004</td><td>Jul-Dec</td><td>6</td><td>39</td><td>6.5</td></tr>
<tr><td>2005</td><td>Feb-Dec</td><td>11</td><td>50</td><td>4.5</td></tr>
<tr><th colspan="5">Cwebe</th></tr>
<tr><th>Year</th><th>Month</th><th>No. of months</th><th>Total no. of people</th><th>Mean no. of people per month</th></tr>
<tr><td>2002</td><td>Nov</td><td>1</td><td>3</td><td>3</td></tr>
<tr><td>2003</td><td>Jan-Nov</td><td>11</td><td>92</td><td>8.3</td></tr>
<tr><td>2004</td><td>Jan-Dec</td><td>12</td><td>27</td><td>2.25</td></tr>
<tr><td>2005</td><td>Jul- Nov</td><td>5</td><td>19</td><td>3.8</td></tr>
</table>

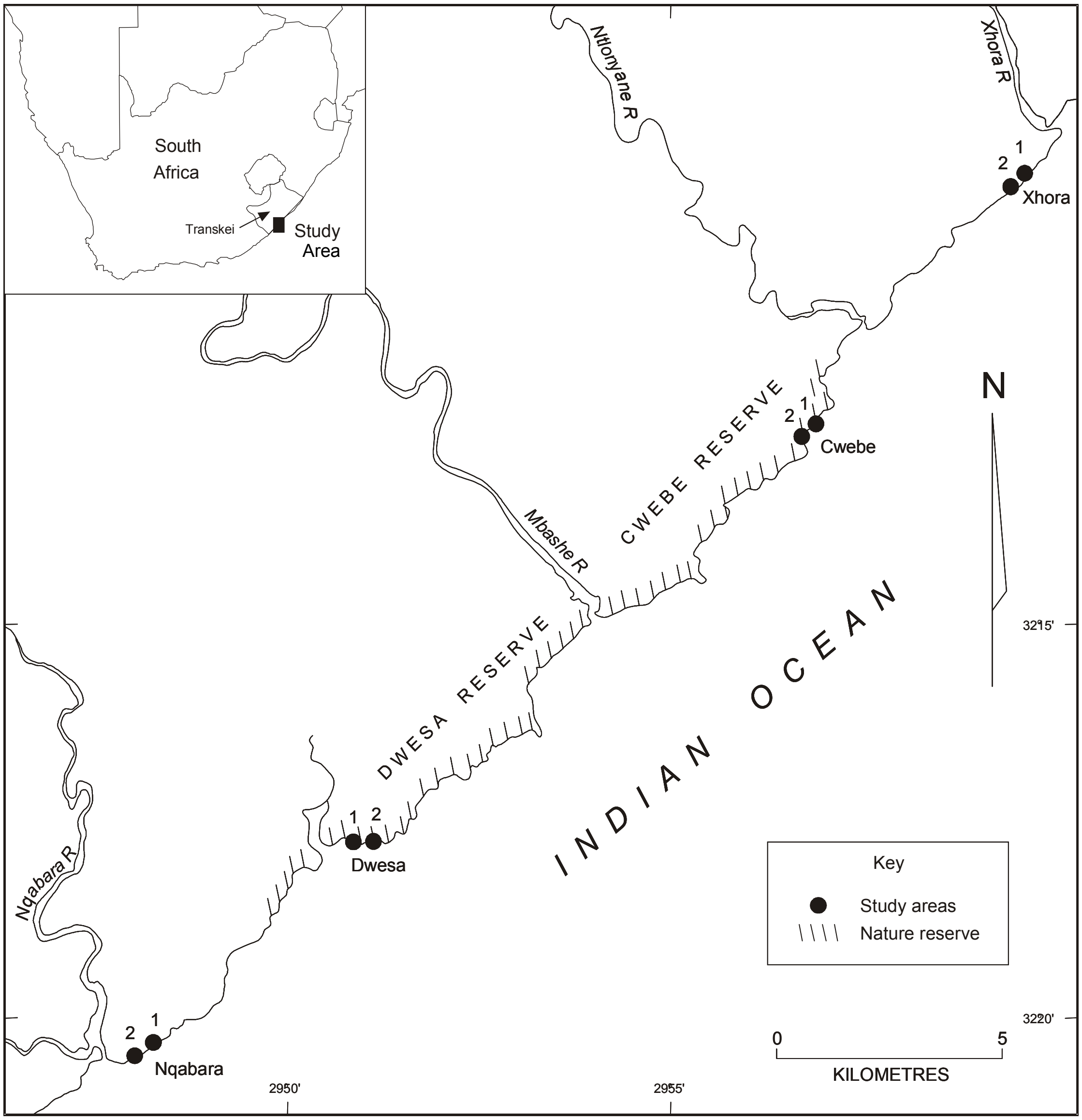


Fig. 1.1: Map showing the location of the four study sites on the Transkei coast of South Africa. Numerals 1 and 2 attached to study sites mean areas.

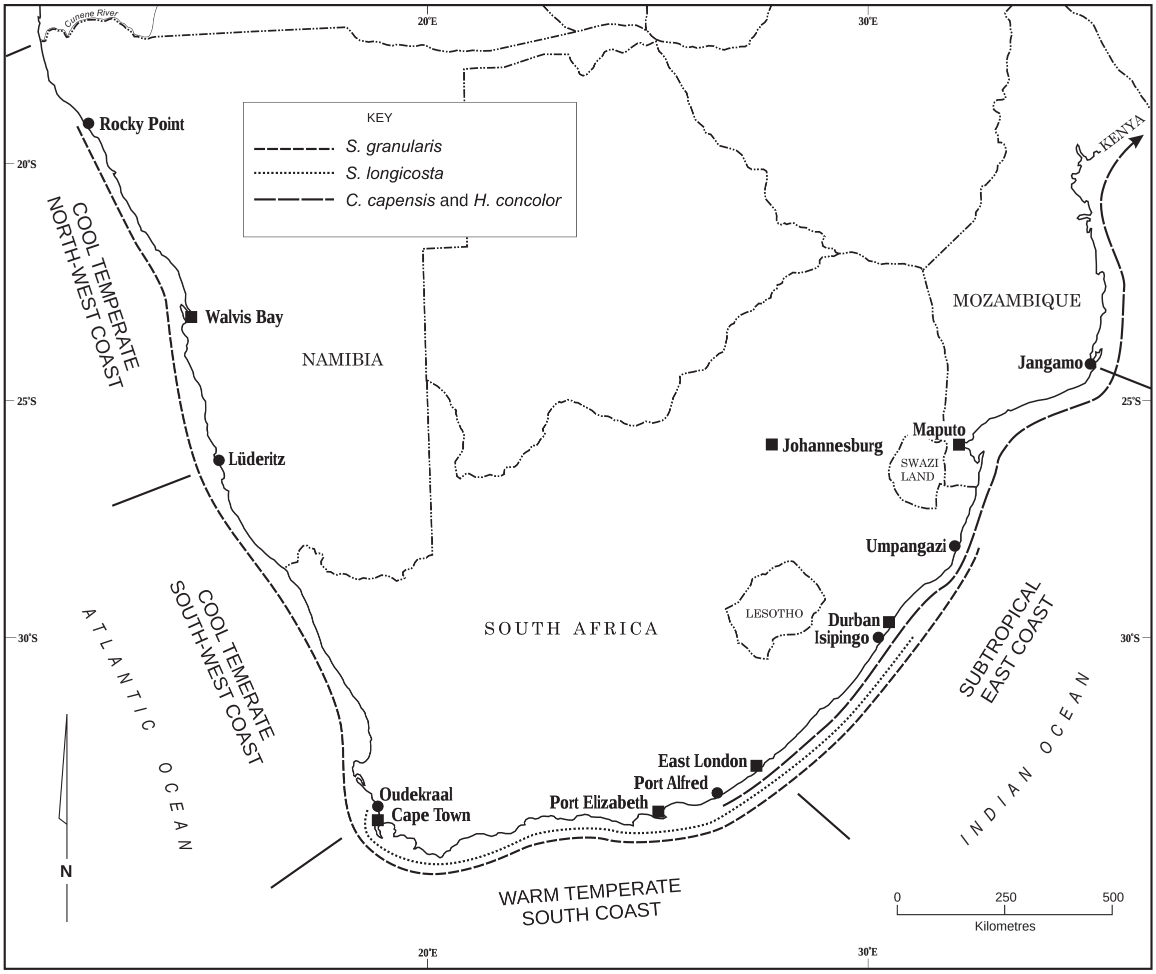


Fig. 1.2: Map showing the distribution of the four limpet species and biogeographic provinces on the South African coast. ------ = *Scutellastra granularis*, ········· = *S. longicosta*, and — — — = *Cellana capensis* and *Helcion concolor*.

CHAPTER 2

POPULATION DENSITIES

2.1 INTRODUCTION

There is much evidence to show that shellfish populations throughout the world have been exploited by humans at a subsistence level for thousands of years (e.g. Branch 1975a; Moreno *et al.* 1984; Thackery 1988; Keough *et al.* 1993). Often such research was prompted by recent pronounced declines in stocks (Bustamante & Castilla 1987; Griffiths & Branch 1997; Lasiak 1997, 1998). The reasons for these declines were found to have come about as a result of, among other factors, rapid increases in human population growth along the coast, the replacement of subsistence by commercial exploitation and technological advances in methods of collection, processing, storage and transportation (Eekhout *et al.* 1992; Griffiths & Branch 1997). As a result the effects of human exploitation relative to natural processes in determining populations of harvested marine invertebrates are an issue of substantial interest in contemporary ecology and conservation biology (Pombo & Escofet 1996). Researchers have long been concerned with the processes that limit and regulate the size of natural populations, with the aim of determining why some species are rare and others common (Breen 1972; Underwood & Chapman 2000; Kurihara 2002; Lasiak 2006). Tanner (1997) categorised the processes influencing population size based on whether they limit the population size (density independent factors) or regulate the population size (density-dependent factors).

Most studies of population regulation in benthic marine ecosystems tend to emphasize intra- and inter-specific competition (Lewis & Bowman 1975; Lasiak 1993, Gray & Hodgson 1997; Keough *et al.* 1997; Edgar & Barrett 1999; Boaventura *et al.* 2003; Dunmore & Schiel 2003; Steffani & Branch 2003b), while the factors that limit populations include natural predators (Marsh 1987; Bosman *et al.* 1989, Lindberg *et al.* 1998; Coleman *et al.* 1999), pollution (Tablado *et al.* 1994; Liu & Morton 1998), wave action (Denny *et al.* 1985; McQuaid & Lindsay 2000), and naturally occurring physical disturbances (Cadeë 1999).

The increased concern over depletion of exploited shellfish species in South Africa centres on illegal commercialisation in case of abalone (Griffiths & Branch 1997). Over-collecting by subsistence shellfish gatherers can cause reductions in population density and the impact of such activities on target populations has been well documented for the Transkei region of South Africa (Branch 1975a; Siegfried *et al.* 1985; Hockey & Bosman 1986; Lasiak & Dye 1989; Lasiak 1991a & b, 1992, 1993; Dye *et al.* 1994; Lasiak 1997) and elsewhere (Moreno *et al.* 1984; Keough *et al.* 1993; Addessi 1994; Pombo & Escofet 1996; Griffiths & Branch 1997; Lindberg *et al.* 1998; Murray *et al*. 1999; Kido & Murray 2003; Roy *et al.* 2003). By reducing species densities, human exploitation can decrease the reproductive output of intertidal invertebrate populations especially for species that show an increase in individual fecundity with body size (Branch 1974a, 1975b; Creese 1980; Levitan 1991; Tegner *et al.* 1996). However, this will only influence density if the population is relatively closed (Caley *et al*. 1996) or if recruitment intensity correlates with adult density (McQuaid *et al.* 2000).

The effects of humans as predators have generally been examined by contrasting intertidal populations and communities between areas that are open or closed to human access (Keough *et al.* 1993). The most popular procedure for determining population regulation is to examine long-term series of estimates of population size (Tanner 1997). On the Transkei coast, the existing information that compares exploited and unexploited sites has focussed largely on the effects of subsistence exploitation on balanoid zone community structure (Hockey & Bosman 1986), overall community structure (Lasiak 1993), structure of infratidal assemblages (Lasiak & Field 1995) and the structure of macrofaunal assemblages (Lasiak 1998). Despite the intensity of human exploitation, few researchers have quantitatively estimated the magnitude or relative importance of the effects of humans, or compared them to natural processes (Keough *et al.* 1993). Other researchers have proposed a need to address the population dynamics of limpet species (Lasiak & Dye 1989), as such information is thin in Transkei.

The main objective of this study was to test the hypothesis that exposure to exploitation outside reserves leads to a decrease in mean density of commonly exploited species. In order to test this hypothesis, the variability in densities inside and outside reserves was compared. This was complemented by the concomitant hypothesis that density of rarely-exploited species will not show an effect of reserves. The null hypothesis is that the mean density of both commonly exploited and rarely exploited species is the same inside and outside reserves. In order to test these hypotheses, population densities of two commonly exploited limpets that occur outside reserves, *Scutellastra longicosta*, *Helcion concolor*, and of two rarely exploited limpets *S. granularis* and *Cellana capensis* were investigated. Species were classified as commonly exploited and rarely exploited on the basis of interviews conducted with shellfish collectors at each of the two non-reserve sites examined (Chapter 1, Table 1.1).

2.2 MATERIALS AND METHODS

Sampling was conducted at approximately monthly intervals, between November 2002 and June 2004 (a period of 20 months), during spring low tides. On each occasion, 20 quadrats (50 x 50 cm^2) were haphazardly thrown within the zone of occurrence of each species in each area of each site (Chapter 1, Fig. 1.1). The densities of limpet populations were estimated by counting the numbers of individuals found within each quadrat. The data obtained were then used to estimate the mean density of each limpet species for each month, allowing comparisons of mean densities among sites. All data were converted to density per square metre for the analysis.

2.2.1 Statistical analysis

The effects of marine reserves on limpet densities were analysed separately for each species, using a four-factor nested analysis of variance (ANOVA) to test the effects of month, reserve, site (nested in reserve) and area (nested in reserve and site). The factors month, site and area were treated as random while reserve was treated as fixed. Multiple comparison tests (Tukey HSD tests) were subsequently run on significant results ($p < 0.05$) from ANOVA tests. Prior to the use of ANOVA, the data were tested for normality and homogeneity of variances using Kolmogorov-Smirnov and Cochran’s tests (Zar 1996; Underwood 1997), respectively. No transformation was necessary.

2.3 RESULTS

Reserve as the main factor had no significant effect for any species. Except for *Cellana capensis*, month was always significant, indicating variations in mean density among months. The month/site (reserve) interaction was significant for all species, indicating temporal variation on scales of 10 km. Except for *Helcion concolor*, the month/area (reserve (site)) interaction was significant, indicating temporal variation on scales of 100 m within sites. Thus the lowest level effect was generally the month/area (reserve (site)) interaction.

In many cases these interactions occurred because there were a few months in which the areas within a site differed, while in most months this was not the case. In fact of the 160 possible cases of areas differing within a site (20 months x 4 species x 4 sites), there was a total of only 4 cases where these differences were significant. In addition, the month/area (reserve (site)) interaction often arose because of meaningless comparisons. For example, area 1 at Dwesa versus area 2 at Xhora. These interactions tended to mask the effects of reserve. Consequently, I have described the significant effects, and have included reserve effects even if they were not statistically significant.

2.3.1 Commonly exploited species

Helcion concolor

There was a significant effect of site and of the month/site (reserve) interaction, while all other effects were not significant (Table 2.1).

Month x Reserve

Population density was moderately stable with a suggestion of repeated recruitment events in January 2003, June 2003, September 2003 and April 2004 and a gradual overall decline between these events (Fig. 2.1.1). Reserves showed considerable variation for the first 11 months and a general decline for the last 9 months. After September 2003, post-hoc tests showed no obvious patterns among months. Non-reserves generally had lower and more stable densities, with only slight variability throughout the sampling period. Densities in reserves were generally greater than in non-reserves (Fig. 2.1.2). The lowest mean densities in reserves and non-reserves were 4.42 ± 0.34 and 4.06 ± 0.67 per m^2 (June 2004 and May 2003, respectively), while the highest mean densities were 8.36 ± 0.67 and 6.33 ± 0.64 per m^2 (September 2003 and October 2003, respectively).

Month x Site (Reserve)

The overall mean densities of *H. concolor* (Fig. 2.1.3) were, in descending order, Cwebe (6.29 ± 0.17) > Nqabara (6.05 ± 0.16) > Dwesa (5.52 ± 0.14) > Xhora (4.27 ± 0.12). However, there was a month/site (reserve) interaction.

The mean density of *H. concolor* was fairly stable throughout the sampling period and differed among months only in detail. Post-hoc tests revealed 7 out of 20 months with significant differences among (see Fig. 2.1.4). In 2 months (Mar and Apr 2003) this was because Xhora had especially low densities, while for 3 months it was because Cwebe had especially high densities.

Scutellastra longicosta

Four-way nested ANOVA showed significant effect of month, site (reserve) and area (reserve (site)), including the interactions of month/site (reserve) and month/area (reserve (site)) (Table 2.2).

Month x Reserve

The mean density of *S. longicosta* was highly variable throughout the sampling period with a general decrease from March to June 2003 and then an overall increase (Fig. 2.2.1). High variability occured in both reserves and non-reserves, which showed very similar trends that differed only in detail. Mean densities of reserves were always greater than non-reserves (Fig. 2.2.2).

The lowest mean densities in reserves and non-reserves were 5.90 ± 0.34 and 3.68 ± 0.40 per m^2 (July 2003 and June 2003, respectively), while the highest mean densities were 10.76 ± 0.59 and 7.48 ± 0.81 per m^2 (May 2004 and March 2003, respectively).

Month x Site (Reserve)

The overall mean density of *S. longicosta* (Fig. 2.2.3) was, in decreasing order, Dwesa (8.17 ± 0.17) > Cwebe (8.14 ± 0.17) > Nqabara (7.51 ± 0.18) > Xhora (3.87 ± 0.14). However, there was a month/site (reserve) interaction.

The population mean density of *S. longicosta* generally showed slight variations in the early months of sampling and subsequently became constant until the end of sampling. Tukey HSD tests on the month/site (reserve) effect of mean density of *S. longicosta* showed 17 months out of 20 with significant differences (see asterisks in Fig. 2.2.4). This was due to the fact that Xhora had the lowest mean densities in all months where there were significant differences among sites.

Month x Area (Reserve (Site))

Post-hoc tests on the interaction of month and area (reserve (site)) effect revealed a significant difference only in April 2003 between the two areas at Nqabara (Fig. 2.2.5).

2.3.2 Rarely exploited species

Cellana capensis

There were significant effects of month, site and area but also significant effects were the interactions of month/site (reserve) and month/area (reserve (site)) (Table 2.3).

Month x Reserve

The mean density of *C. capensis* was relatively stable for the first 9 months of the sampling period (until July 2003) and this was followed by a clear long-term, progressive increase over the remaining 11 months (Fig. 2.3.1). This broad trend was true for both reserves and non-reserves and the patterns differed only in detail (Fig. 2.3.2).

Densities were generally greater in reserves than in non-reserves (Fig 2.3.2). There were also 5 months when mean densities of reserves and non-reserves were almost identical (February, May, September, October 2003, and June 2004). The lowest mean densities in reserves and non-reserves were 12.5 ± 0.84 and 8.35 ± 0.61 per m^2 (May and June 2003, respectively), while the highest mean densities were 23.24 ± 1.03 and 23.34 ± 0.88 per m^2 (January 2004 and June 2004, respectively). Thus, the differences between reserves and non-reserves was generally strongest in the early part of the sampling period, when populations were relatively stable and densities in reserves were often greater than in non-reserves. The differences diminished during the period of population increase (after July 2003). During this period, densities were frequently identical (September, October, June 2004), or very similar (December, January, April, May 2004).

Month x Site (Reserve)

The overall mean density of *C. capensis* (Fig. 2.3.3) among sites in descending order was, Cwebe (18.89 ± 0.36) > Xhora (16.07 ± 0.34) > Nqabara (15.32 ± 0.31) > Dwesa (14.95 ± 0.29). However, there was a month/site (reserve) interaction.

The mean density of *C. capensis* revealed a variable but similar pattern among sites throughout the sampling period. Post-hoc tests on the month/site (reserve) effect on mean density of *C. capensis* indicated 9 months with significant differences (see asterisks in Fig. 2.3.4). In all months where the effect was significant, sites could be clearly ranked by density. However, while the two reserve sites ranked highest in the earlier months (Mar, Apr, Jun '03), and Cwebe often had the highest density, there was no clear ranking of reserve versus non-reserve sites during the later months.

Month x Area (Reserve (Site))

Tukey HSD tests on the effect of month/area interaction on the mean density of *C. capensis* showed a significant difference between areas within a site on only 1 occasion at Dwesa, in March 2003 (Fig. 2.3.6).

Scutellastra granularis

Four-way nested ANOVA tests revealed significant effects of month and site including the interactions of month/site (reserve) and month/area (reserve (site)) (Table 2.4).

Month x Reserve

The mean density of *S. granularis* was remarkibly stable for the first 9 months of the sampling period. This was followed by a clear long-term, progressive increase over the remaining 11 months from August 2003 onwards (Fig. 2.4.1). This trend was true for both reserves and non-reserves and the patterns differed only in detail (Fig. 2.4.2). In particular, the increase after July was stronger for reserves.

In 17 months, densities in reserves were greater than in non-reserves while densities of non-reserves were marginally greater than in reserves for 2 months (Fig. 2.4.2).

The lowest mean densities in reserves and non-reserves were 10.76 ± 0.65 and 9.80 ± 0.56 per m^2 (July 2003 and November 2002, respectively), while the highest mean densities were 27.84 ± 1.25 and 25.48 ± 1.29 per m^2 (February 2004 and April 2004, respectively).

Month x Site (Reserve)

The overall mean density of *S. granularis* (Fig. 2.4.3) was in decreasing order, Cwebe (19.50 ± 0.41) > Dwesa (17.84 ± 0.35) > Nqabara (16.76 ± 0.34) > Xhora (14.60 ± 0.29). However, there was a month/site (reserve) interaction.

Tukey HSD tests on the month/site (reserve) effect on mean density of *S. granularis* showed 9 months with significant differences between sites (see asterisks in Fig. 2.4.4). Ranking of sites differed among months with no clear consistent pattern.

Month x Area (Reserve (Site)

Post-hoc tests on the month/area (reserve (site)) effect on mean density of *S. granularis* indicated only 2 months with significant differences between areas in the same site (Fig. 2.4.5). This was observed at the reserve site, Cwebe in November 2003 and in May 2004 at both non-reserve sites, Nqabara and Xhora.

2.4 DISCUSSION

The present study showed marked differences among sites and through time for all species. Reserve as a main factor had no significant effect for any species. Most differences in mean densities were at the level of site, not area. Differences between areas within sites for three species, *Cellana capensis*, *Scutellastra granularis* and *S. longicosta*, provide evidence of occasional variation in density at small (100 m) scales. However, such small-scale differences were rare. Post-hoc tests showed that they occurred on only 4 out of 160 possible occasions, indicating generally very high consistency in densities between areas within each site. Commonly exploited species showed clear consistency in ranking of sites among months, with reserves having greater limpet densities than non-reserves in more months than the reverse. In contrast, rarely exploited species showed no consistency in differences among sites.

The lack of consistency in mean densities among sites for rarely exoloited species may be due to species preference by harvesters. For example, Lasiak (1993) reported that *C. capensis* is not subject to intense exploitation but rather to opportunistic exploitation which occurs in the absence of preferred species such as mussels. This is also supported by the results from interviews (Chapter 1, Table 1.1), which showed a similar ranking of species by order of preference at non-reserve sites. Previous studies on the Transkei coast (Hockey & Bosman 1986; Lasiak 1991a, 1993) found no reduction in the density of *C. capensis* at exploited sites. These authors attributed this to the fact that this species may not have been subjected to such intense exploitation as some of the other organisms taken.

The lack of reserve effects may possibly have been due to masking by significant month/area effects, although these were based largely on meaningless comparisons of areas between sites and different months. Neverthless, the significant month/site interactions showed that commonly exploited species had greater mean densities in reserves than in non-reserves in most months, while there was no clear pattern for rarely exploited species. The possible reason for this may be that this species may be subject to opportunistic exploitation in the absence of preferred species or to variation in density resulting from interactions with other species so that the reserve effect for *S. granularis* is a secondary one. Interactions between limpets and barnacles often occur and may have both negative and positive effects on limpet survival. Since barnacles are able to retain moisture at low tide, and provide shade from sunlight and shelter from wave action, they can increase the survival of limpets (Branch 1975b; Lewis & Bowman 1975; Choat 1977). This may be true for *S. granularis*, which is mostly found where barnacles dominate. Some researchers noted that such associations provide protection against dislodgement (Dayton 1971; Monteiro *et al*. 2002; Dunmore & Schiel 2003). Moreno *et al*. (1984) noted that the exclusion of harvesters from marine reserve results in an increase in the abundance of limpets (*Fissurella* spp.), coupled with a dramatic decline in the abundance of the mid-intertidal macroalgae, *Iridaea boryana*. In contrast, the presence of barnacles can be detrimental to the survival of some species of limpets, as barnacles can dominate the substratum (Branch 1976), and hence reduce the area on which adult limpets can graze effectively (Lewis & Bowman 1975; Branch 1976). Moreover, interactions between limpets and algae can reflect variation in the presence and abundance of limpets from year to year at the same site (Johnson *et al*. 1997). For example, limpets may be “swamped” by intense algal recruitment. There is also the likelihood that *S. granularis* interacts positively with barnacles as there are more barnacles at reserve than non-reserve sites (*pers. obs*.), where *S. granularis* also showed higher mean density.

Variations in densities in both reserves and non-reserves over time, from month to month and from year to year, reflect periods of recruitment, mortality and predation (Underwood & Chapman 2000; Moore *et al.* 2007). Density is known to vary with time and space as a result of changes in both local conditions and more general fluctuations in annual recruitment (Lewis & Bowman 1975; Kurihara 2002) and climate indices (Thompson *et al*. 2002; Herbert *et al.* 2007). Steffani and Branch (2003b) noted that the intensity of competition among mussels varies both temporarily and spatially as a function of wave exposure. Underwood and Chapman (1996) noted that different ecological processes influence the densities of intertidal organisms on rocky shores at different spatial scales. In most intertidal species that disperse via a planktonic larval stage and have restricted adult mobility, differences in recruitment and mortality may lead to differences in abundances from one site to another, at scales of kilometres (Noda 2004). More recent studies on mussels show variation in settlement and recruitment at much smaller scales (Lawrie & McQuaid 2001; Erlandsson & McQuaid 2004).

The intensity of competition is likely to be greater in reserves than non-reserves due to the relatively high mean densities. Many studies have shown that inter- and intra- specific competition may lead to a reduction in species densities (Creese & Underwood 1982;

Underwood 1984; Ortega 1985; Lasiak & White 1993). Among limpets, the intensity of competition has been found to vary on a temporal and spatial basis according to the availability of microalgal film and to the densities and mixtures of grazing species (Fletcher 1984a; Lasiak & White 1993; Jenkins & Hartnoll 2001; Thompson *et al*. 2002). Branch (1975b) pointed out that individuals of closely related species usually have a great overlap in the resources they require and can therefore compete if they coexist. Furthermore, intraspecific competition is likely to be more intense than interspecific competition, as individuals of the same species have very similar requirements (Branch 1976; Creese & Underwood 1982).

Although there were month/site (reserve) interaction, in 3 out of the 4 species examined, Cwebe generally had the highest densities while Xhora had the lowest densities. Nqabara had the second lowest mean densities for 3 of the 4 species and Dwesa was highly variable in this respect. The density of *S. longicosta* was lowest at Xhora in 17 out of 20 months and this can be attributed to human exploitation pressure as this is a highly preferred species (Chapter 1, Table 1.1). Exploitation gradients exist among sites on the Transkei coast (Lasiak 1997), with more exploitation pressure occurring in central than southern sites. Although Xhora is in the southern region, it is closer to the central region than its counterpart non-reserve site, Nqabara, which shows a higher mean density of *S. longicosta*. Lasiak (1997) estimated that the number of shellfish collectors ranged from 1-6 per km of shore in the southern region and 16-28 per km of shore in the central region. Similarly, data from interview surveys on limpet preferences (Chapter 1, Table 1.1) showed that more shellfish collectors were observed at Xhora than at Nqabara while

Xhora had the lowest mean density for all limpet species except C. *capensis*. It has been shown that even if animals are not actively collected and removed by visitors, trampling and turning of boulders exposes animals to potential predators, or may crush and dislodge molluscs and other organisms, thus resulting in a decrease of intertidal populations (Povey & Keough 1991; Pombo & Escofet 1996; Lasiak 1997).

Temporal differences in densities of the limpet species among sites can also be attributed partly to the influence of dispersal processes on recruitment patterns, (Lewis & Bowman 1975). Chapman (1994a) reported similar significant variation in densities of *Nodilittorina* among sites. The differences in densities were found to be strongly correlated to the distribution of particular microhabitats, especially cracks, crevices and pits within the rock surfaces (Chapman 1994a). Lewis and Bowman (1975) reported that changes in the abundance of species along the coast may be due to the presence of unsuitable substrata or salinity, decreased habitat area or larval wastage due to the effects of offshore currents. Another potential factor that can influence the mean density of these species is predation. Predation of limpets has been shown to be important in maintaining bare rock in small-scale patches (Berlow & Navarrete 1997). However, relative to other parts of the world, predation is generally less important in South African intertidal shores (Branch & Steffani 2004).

The observed month/area effect on the mean densities of *S. longicosta*, *C. capensis* and *S. granularis,* indicates a temporal variation of these species on these small (100 m) scales. Snails are known to move over relatively short distances, and respond to small-scale features of their habitat (Chapman 1994a). They can also aggregate in response to cues from the habitat and each other (Chapman & Underwood 1996). As a result, differences in density among areas may potentially result in quite different responses and patterns of variance. Within a single shore, mobile animals can show considerable small-scale (< 10 m) variability in abundance, which is primarily determined by behavioural responses to the habitat (Underwood 1976; Underwood & Chapman 1989; Olabarria & Chapman 2001; Coleman 2002; Pfister & Peacor 2003).

Analysis of spatial patterns in four intertidal snails at scales of 10 to 100 m and between shores separated by approximately 20-30 km showed large-scale spatial patterns that were reported to be caused by differences in recruitment and /or mortality (Underwood & Chapman 1996). Similar variation in densities at scales of 100 m was found in *Littorina unifasciata* (Chapman 1994b). These differences appeared to be caused by larval behaviour, reflected by variation in recruitment or by mortality after recruitment. Variations at these scales were not very strong possibly due to the fact that limpets are much less mobile than *Littorina* species. Moreover, much of the observed variability could be accounted for by variability among replicate quadrats, probably reflecting behavioural processes (Chapman 1994b). Differences in densities within sites at scales of 100 m are probably due to differences in recruitment among patches within sites, although variations due to mortality may be possible (Dayton 1971; Underwood *et al.* 1983; Fairweather & Underwood 1991; Menge *et al.* 1994).

Harvesting of limpets results in reduction of limpet populations, and this can enhance barnacle densities (Dye 1993, 1995) and lead to the proliferation of algae (Davies *et al.* 2007). Subsistence harvesting can lead to an increase in the proportion of inedible species and a decrease in species diversity (Hockey & Bosman 1986; Lasiak & Field 1995; Lasiak 1998). Branch and Odendaal (2003) reported that, without the existence of protected areas along the heavily harvested Transkei coast, it would have been impossible to quantify the magnitude of the effects of harvesting. The observed differences in densities among sites, suggest variation in recruitment/mortality that may be determined by processes that vary within a site, causing patchiness in densities (Underwood & Chapman 1996). It is also noted from this study that significant differences in the mean density of these limpets exist not only between non-reserves but also between reserve sites. In reserves, this may be attributable to poaching by shellfish collectors. This kind of activity can therefore, cause a significant negative impact on the density of protected intertidal species and other marine organisms.

In conclusion, the intention was to test the effects of reserves versus non-reserves on harvested versus non-harvested species. Theoretically, these categories of sites and species are clear cut. In reality, non-reserve sites are exploited to different degrees and there is evidence of poaching within reserves. Commonly exploited species can be ranked by preference and rarely exploited species are sometimes taken by mistake or in the absence of preferred species. Consequently, we have not categories, but continua of sites and species on a gradient of degree of exploitation. Despite this, the categorical approach taken using ANOVA produced easily interpretable results.

There were generally marked differences among months in the mean density of all species with different temporal patterns for each species. Density was generally lowest in winter but species differed in the timing of major recruitment events. Temporal patterns were generally very similar between reserves and non-reserves, implying that the same external factors, such as weather or recruitment events, have an over-riding influence on density. The number of months when densities were higher in reserves was greater for commonly exploited species than for rarely exploited species. These limpet species showed different patterns of variation that may be associated with different patterns of recruitment. For instance, *C. capensis* and *S. granularis* showed a similar long trend of increasing densities with time, which may indicate protracted recruitment. *S. longicosta* revealed a parallel pattern, indicating that the effect of exploitation was not as strong as the effect of natural mortality (i.e. no indication that population decline in non-reserves was faster than in reserves).

In reserves, *Helcion concolor* showed more pronounced fluctuation in mean densities in reserves than in non-reserves, decreasing through time. *H. concolor* was the only species to show no significant month effect. There was a lack of reserve effects in all the species. However, there were strong, significant month/site (reserve) effects in all the species, with mean densities in reserves generally being greater than in non-reserves for the commonly exploited species. The possible lack of a reserve effect may either be due to masking by the month/area interaction or because exploitation of even preferred limpets was not very strong in some months. Fluctuations in mean densities were further complicated by the fact that this study revealed that Nqabara is moderately exploited, relative to Xhora, which is heavily exploited and their combined mean densities made it more difficult to see the effect of reserve than if they were considered separately. Moreover, exploitation gradients exist among limpet species (i.e. they show different levels of exploitation). Lastly, the interaction between month and site (reserve) has implications for tests of the effect of surveys of sites, as the results may differ among months.

Table 2.1: Results of 4-way ANOVA based on mean density estimates of *H. concolor*. * denotes a significant effect at p < 0.05, ** = < 0.001 and *** = < 0.0001.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	802.36	19	42.23	1.512	0.189
Reserve	248.84	1	248.84	0.611	0.521
Site (Reserve)	843.49	2	421.74	9.333	< 0.05*
Area (Reserve (Site))	59.11	4	14.78	1.267	0.291
Month x Reserve	530.75	19	27.93	0.664	0.829
Month x Site (Reserve)	1599.08	38	42.08	3.607	< 0.0001***
Month x Area (Reserve (Site))	886.75	76	11.67	1.235	0.084
Error	28716.57	3040	9.45		

Table 2.2: Results of 4-way ANOVA based on mean density estimates of *S. longicosta*. * denotes a significant effect at p < 0.05, ** = < 0.001 and *** = < 0.0001.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	71.55	19	3.77	3.764	< 0.001**
Reserve	141.23	1	141.23	1.963	0.300
Site (Reserve)	146.39	2	73.20	0.885	< 0.05*
Area (Reserve (Site))	20.75	4	5.19	7.261	< 0.0001***
Month x Reserve	19.01	19	1.00	0.444	0.969
Month x Site (Reserve)	85.58	38	2.25	3.153	< 0.0001***
Month x Area (Reserve (Site))	54.28	76	0.71	1.686	< 0.001**
Error	1287.55	3040	0.42		

Table 2.3: Results of 4-way ANOVA based on mean density estimates of *C. capensis*. * denotes a significant effect at p < 0.05, ** = < 0.001 and *** = < 0.0001.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	472.77	19	24.88	11.169	< 0.0001***
Reserve	14.12	1	14.12	0.489	0.563
Site (Reserve)	60.60	2	30.30	4.50	< 0.05*
Area (Reserve (Site))	17.52	4	4.38	3.347	< 0.05*
Month x Reserve	42.33	19	2.23	0.608	0.876
Month x Site (Reserve)	139.14	38	3.66	2.798	< 0.0001***
Month x Area (Reserve (Site))	99.45	76	1.31	1.872	< 0.001**
Error	2125.24	3040	0.70		

Table 2.4: Results of 4-way ANOVA based on mean density estimates of *S. granularis*. * denotes a significant effect at p < 0.05, ** = < 0.001 and *** = < 0.0001.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	48683.3	19	2562.3	19.603	< 0.0001***
Reserve	4047.8	1	4047.8	5.539	0.182
Site (Reserve)	1672.1	2	836.1	4.654	< 0.05*
Area (Reserve (Site))	121.3	4	30.3	0.349	0.843
Month x Reserve	2483.4	19	130.7	0.554	0.915
Month x Site (Reserve)	8967.8	38	236.1	2.722	< 0.0001***
Month x Area (Reserve (Site))	6588.4	76	86.7	2.344	< 0.0001***
Error	112455.0	3040	37.0		

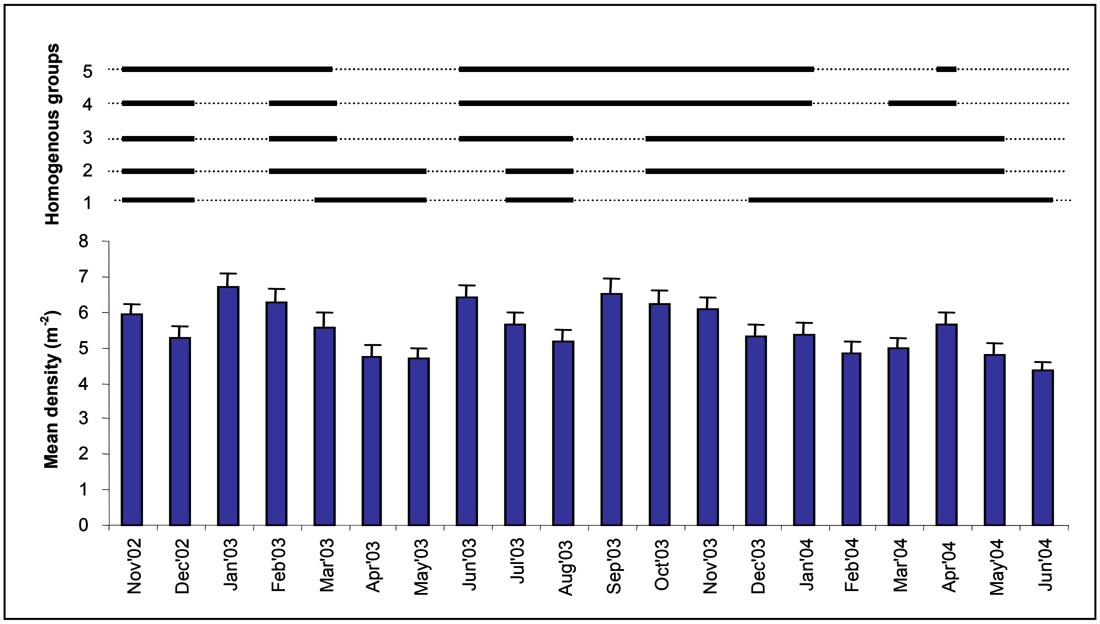


Fig. 2.1.1: Overall mean density (+SE) of *H. concolor* at all sites over time Solid lines above the bar columns connect months that were not significantly ($p > 0.05$) different from each other (Tukey HSD test).

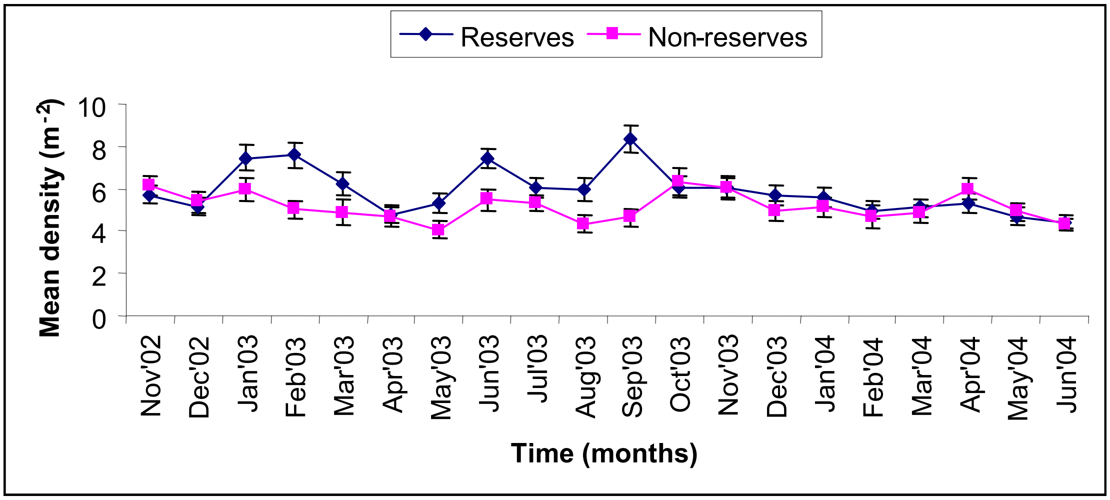


Fig. 2.1.2: Mean density (±SE) of *H. concolor* in reserves and non-reserve sites through sampling period. * = significant difference between reserves and non-reserves in this month.

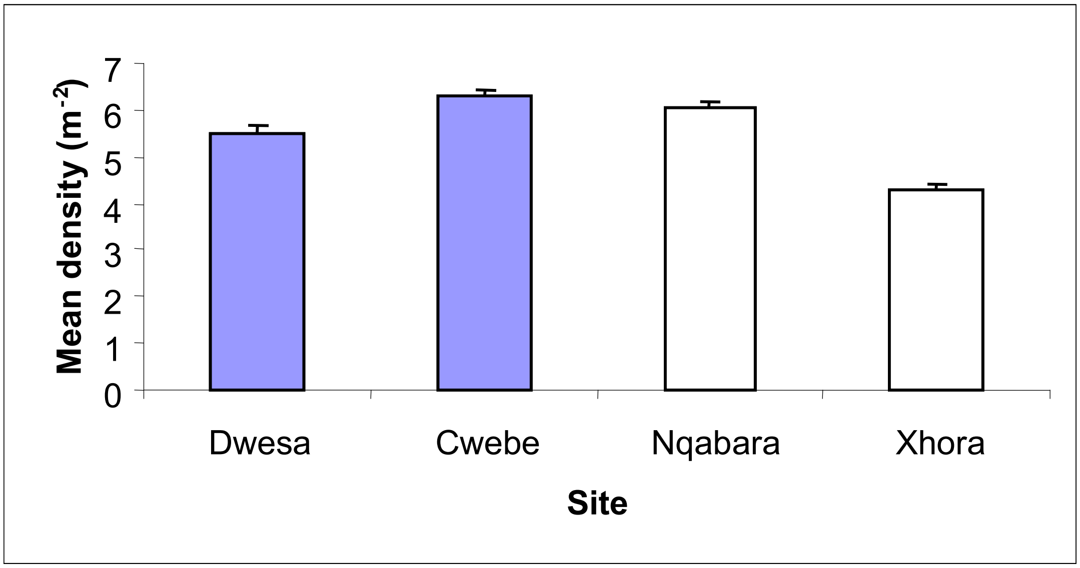


Fig. 2.1.3: Mean density (+SE) of *H. concolor* at each of the four study sites. Dwesa and Cwebe are reserves while Nqabara and Xhora are non-reserves.

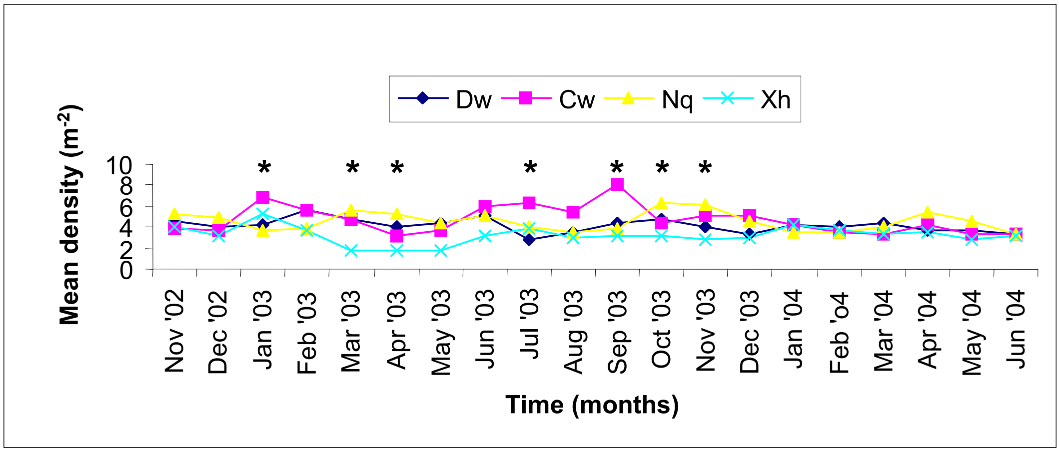


Fig. 2.1.4: Monthly mean density (Standard errors (SE) were omitted for clarity) of *H. concolor* at each of the four study sites. * = significant difference ($p < 0.05$). Post-hoc test results: Jan'03 C>X>D>N; Mar'03 N>C=D>X; Apr, Oct'03 N>D>C>X; Jul '03 C>N>X>D; Sep'03 C>D>N>X; Nov'03 N>C>D>X.

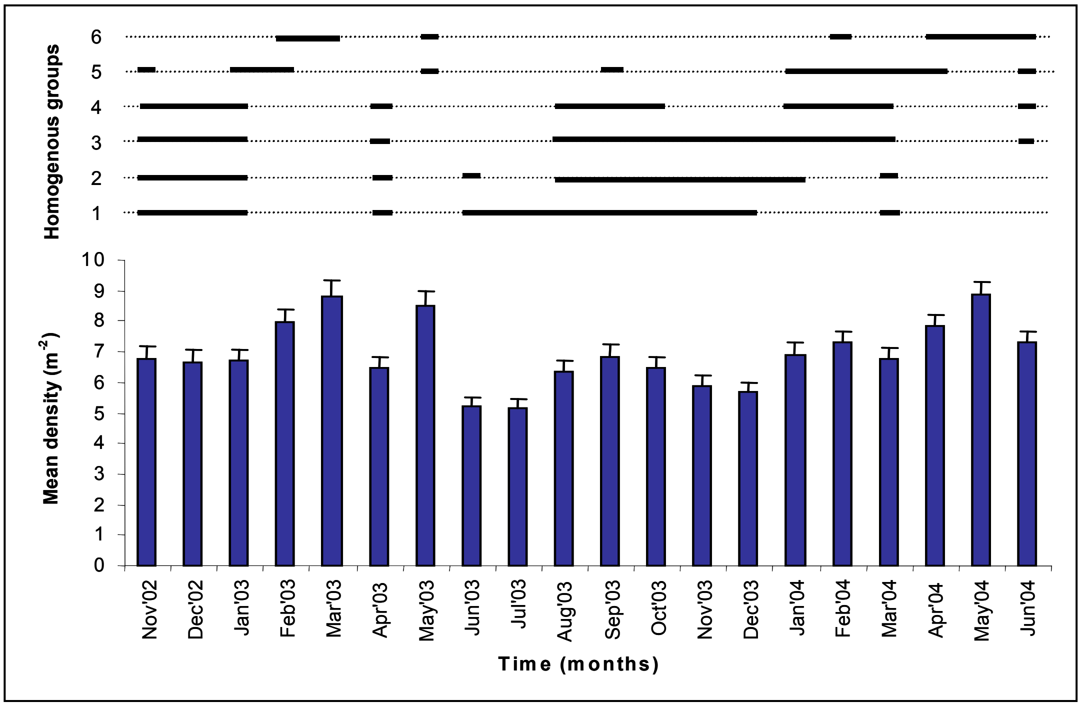


Fig. 2.2.1: Overall mean density (+SE) of *S. longicosta* at all sites over time. Solid lines above the bar columns connect months that were not significantly ($p < 0.05$) different from each other (Tukey HSD test).

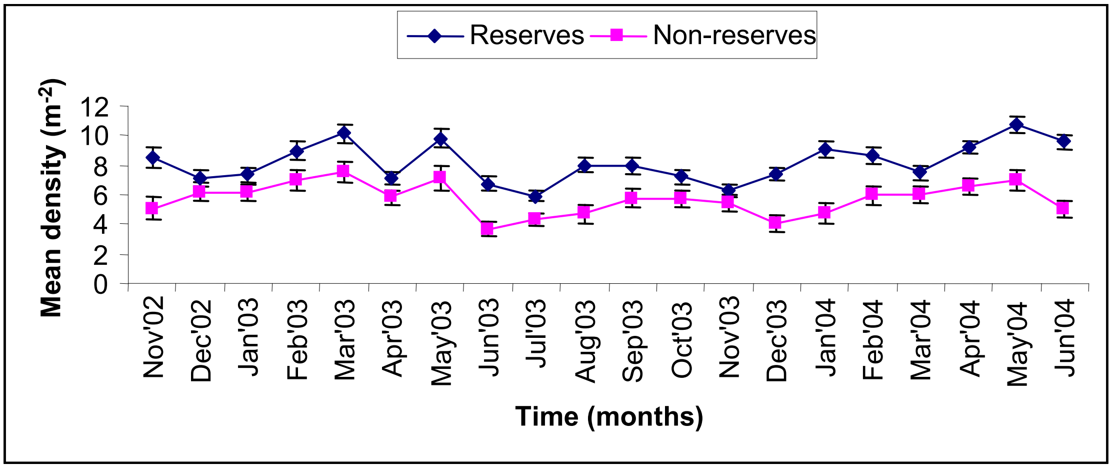


Fig. 2.2.2: Mean density (±SE) of *S. longicosta* in reserves and non-reserve sites through sampling period.

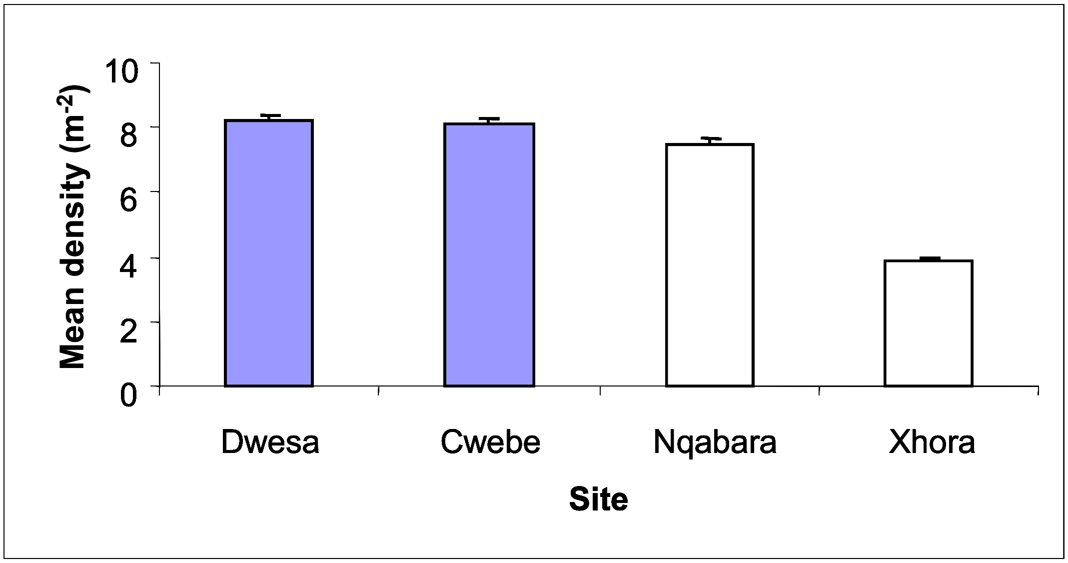


Fig. 2.2.3: Mean density (+SE) of *S. longicosta* at each of the four study sites. Dwesa and Cwebe are reserves while Nqabara and Xhora are non-reserves.

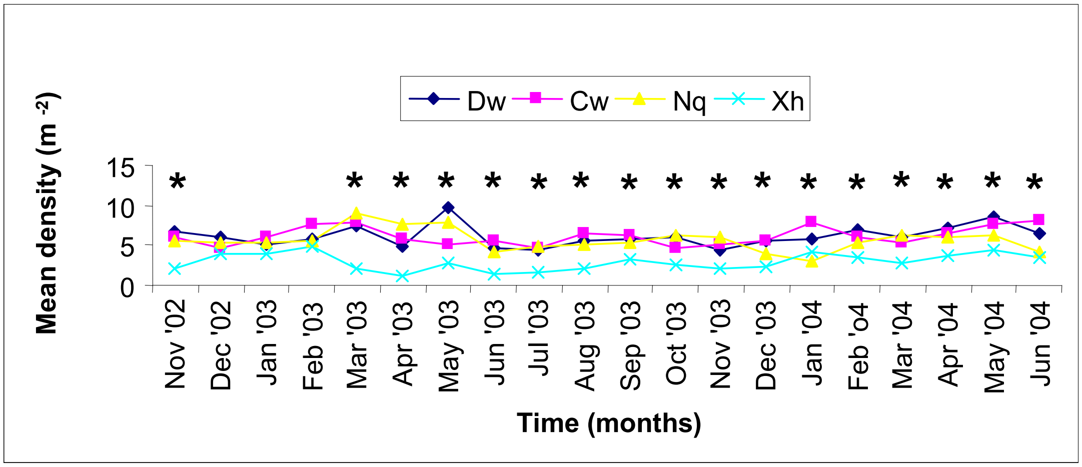


Fig. 2.2.4: Monthly mean density (Standard errors (SE) were omitted for clarity) of *S. longicosta* at each of the four study sites. * = significant difference ($p < 0.05$). Post-hoc test results: Nov'02, Feb'03, Apr'03, May'03, May'04 D>C>N>X; Mar'03, Apr'03, Nov'03 N>C>D>X; Jun'03, Aug'03, Sep'03, Jan'04, Jun'04 C>D>N>X; Jul'03 C>N=D>X; Oct'03 & Mar'04 D=N>C>X; Dec'03 C=D>N>X; Jan'04 C>D>X>N.

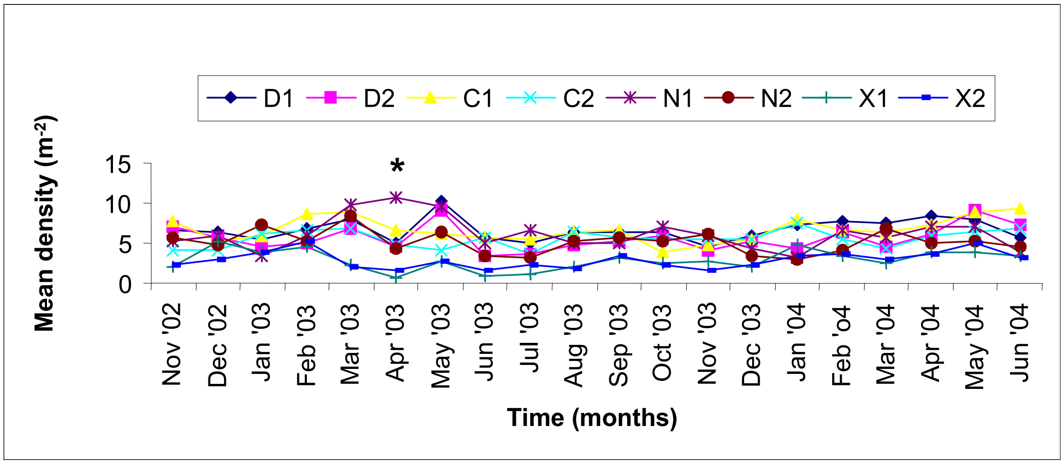


Fig. 2.2.5: Monthly mean density (Standard errors (SE) were omitted for clarity) of *S. longicosta* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Apr'03 N1>N2.

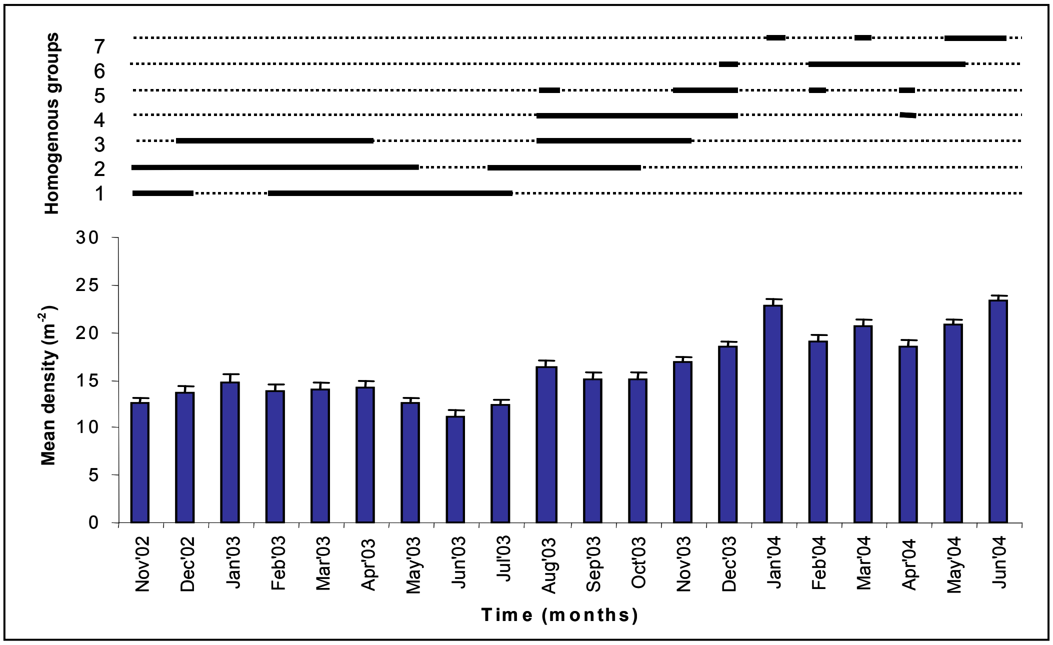


Fig. 2.3.1: Overall mean density (+SE) of *C. capensis* at all sites over time. Solid lines above the bar columns connect months that were not significantly ($p < 0.05$) different from each other (Tukey HSD test).

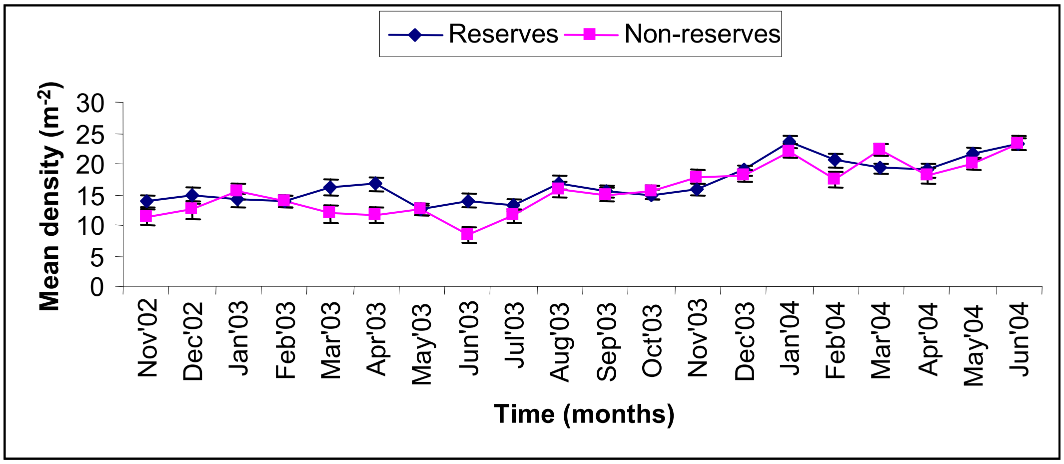


Fig. 2.3.2: Mean density (±SE) of *C. capensis* in reserves and non-reserve sites through sampling period.

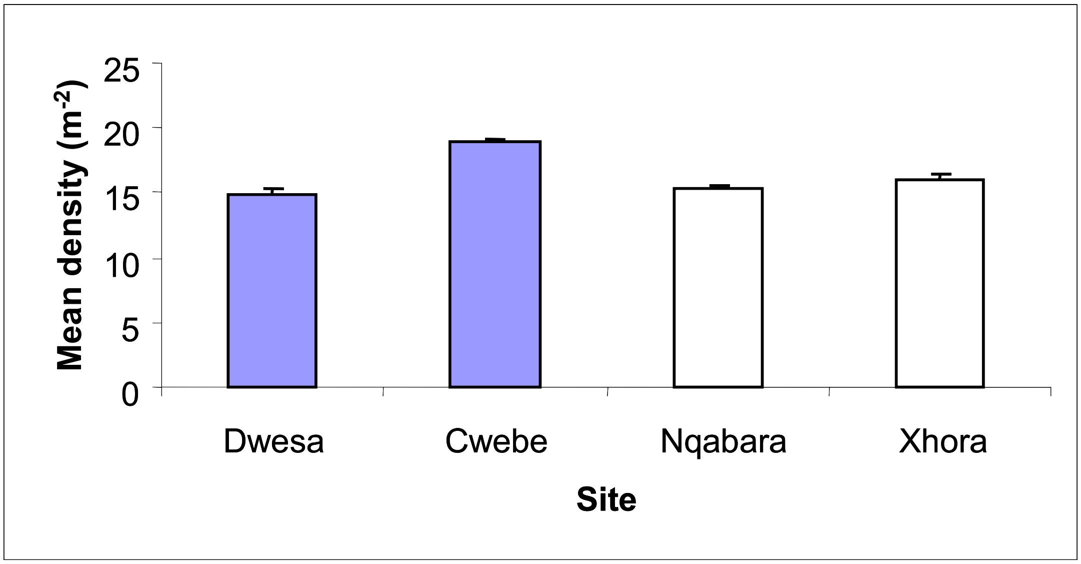


Fig. 2.3.3: Mean density (+SE) of *C. capensis* at each of the four study sites. Dwesa and Cwebe are reserves while Nqabara and Xhora are non-reserves.

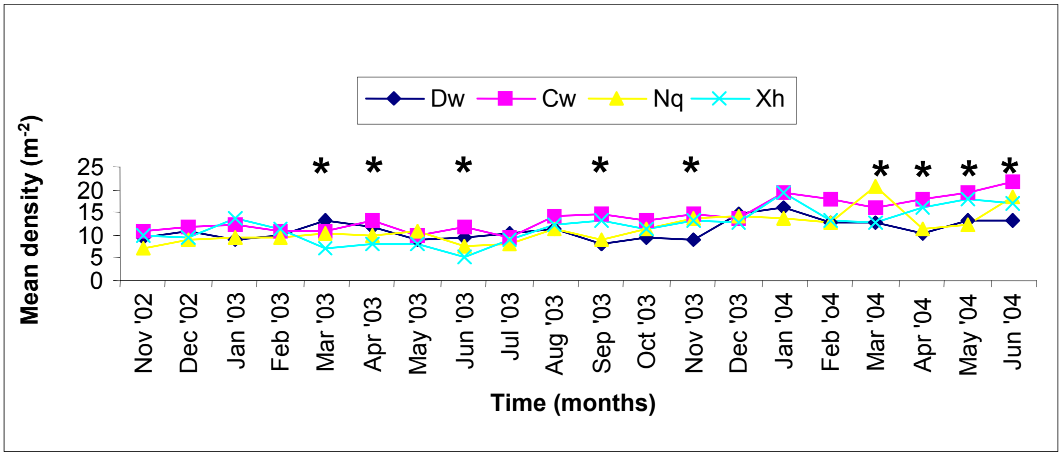


Fig. 2.3.4: Monthly mean density (Standard errors (SE) were omitted for clarity) of *C. capensis* at each of the four study sites. * = significant difference ($p < 0.05$). Post-hoc test results: Mar '03 D>C>N>X; Apr'03, Jun'03 C>D>N>X; Sep'03 & Apr'04 C>X>N>D; Nov'03 & Jun'04 C>N>X>D; Mar'04 N>C>D=X; May'04 C>X>D>N.

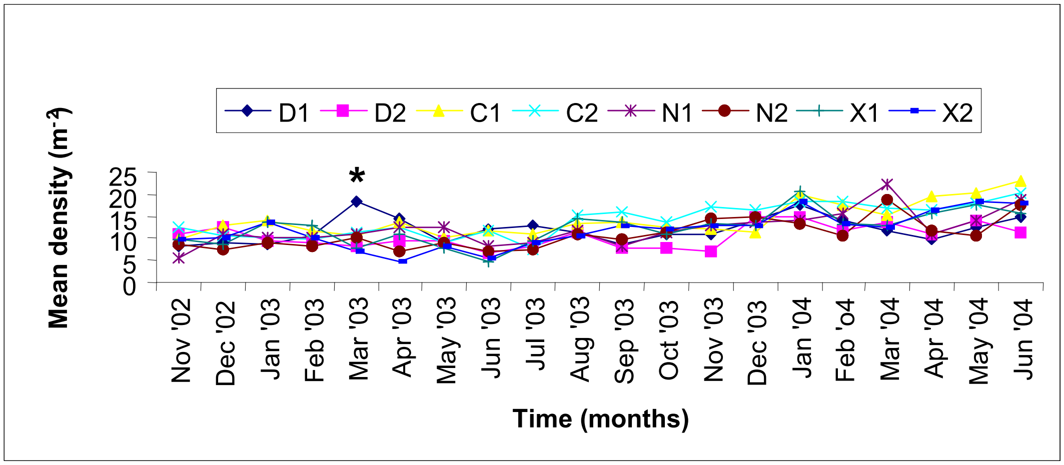


Fig. 2.3.5: Monthly mean density (Standard errors (SE) were omitted for clarity) of *C. capensis* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Mar'03 D1>D2.

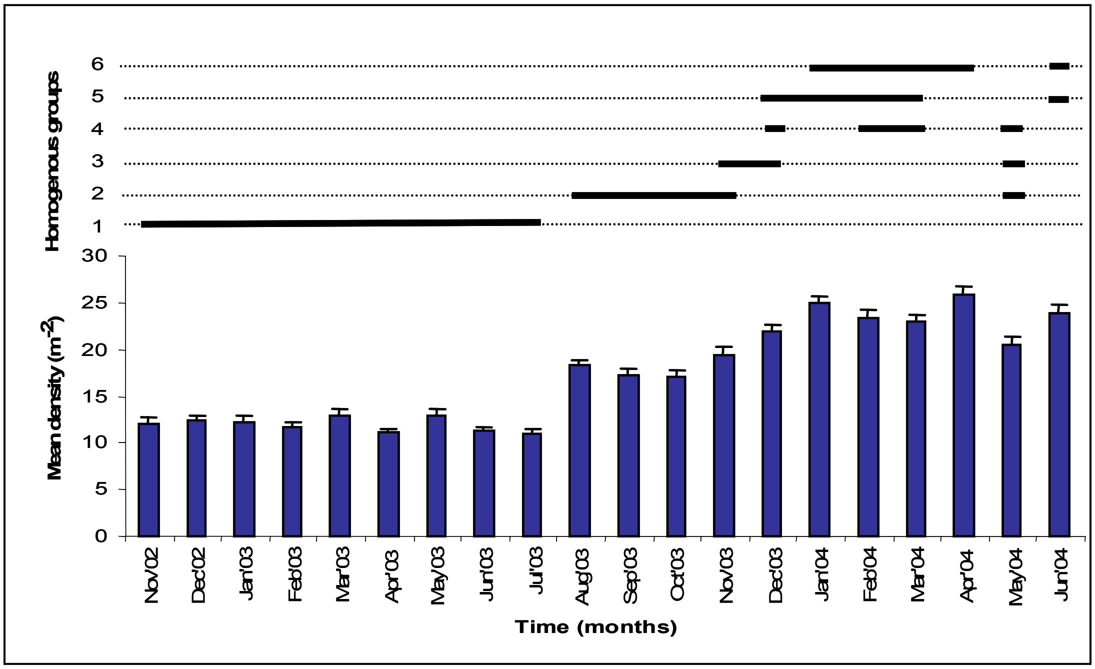


Fig. 2.4.1: Overall mean density (+SE) of *S. granularis* at all sites over time. Solid lines above the bar columns connect months that were not significantly ($p < 0.05$) different from each other (Tukey HSD test).

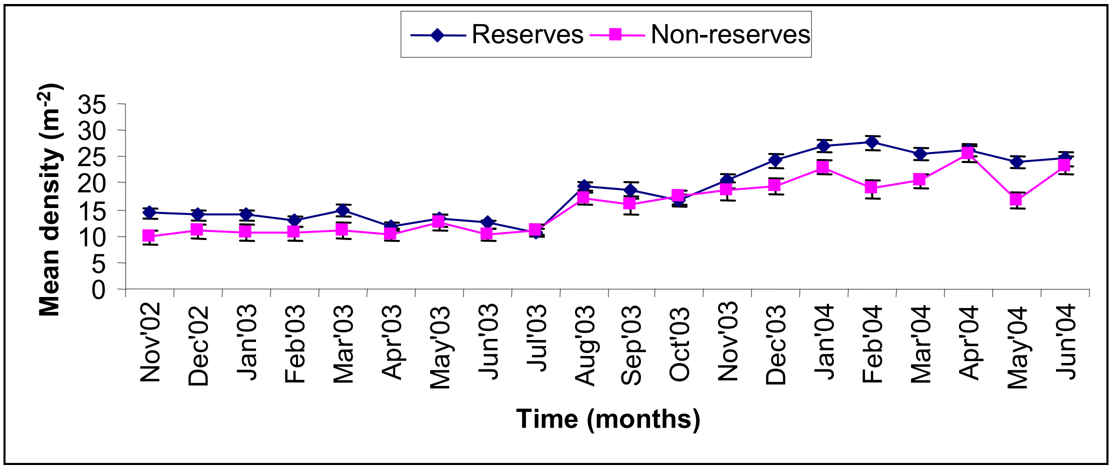


Fig. 2.4.2: Mean density (±) of *S. granularis* in reserves and non-reserve sites through sampling period.

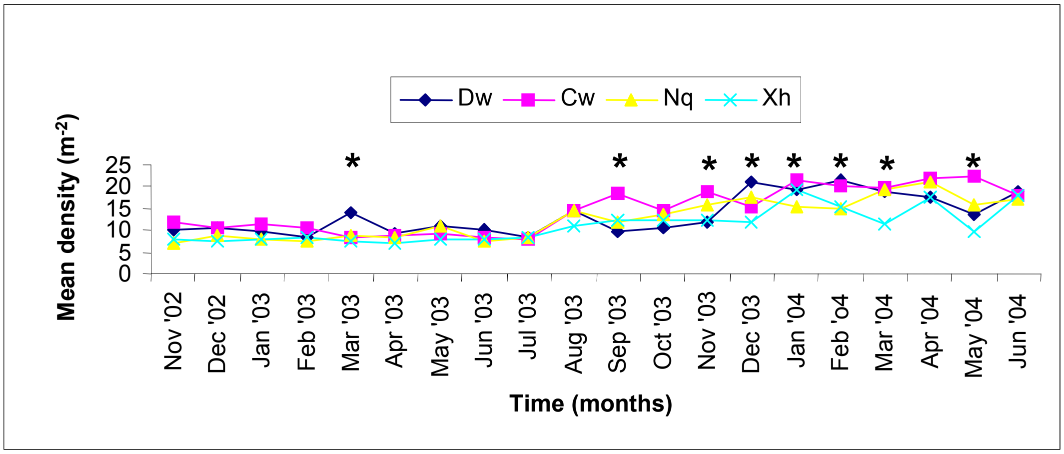


Fig. 2.4.3: Monthly mean density (Standard errors (SE) were omitted for clarity) of *S. granularis* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Mar'03 D>C=N=X; Sep'03 C>X=N>D; Nov'03 C>N>D=X; Dec'03 D>N>C>X; Jan'04 C>D=X>N; Feb'03 D=C>X=N; Mar'04 C=D=N>X; May'04 C>N>D>X.

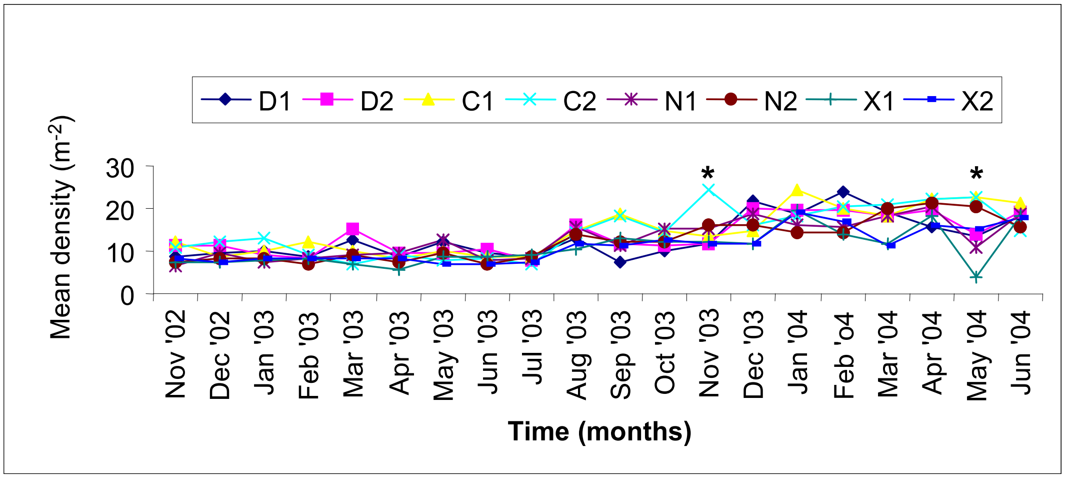


Fig. 2.4.4: Monthly mean density (Standard errors (SE) were omitted for clarity) of *S. granularis* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Nov'03 C1>C2; May'04 N2>N1, X2>X1.

CHAPTER 3

POPULATION SIZE STRUCTURE

3.1 INTRODUCTION

The size of a limpet is of crucial importance in determining its food requirements, ability to access food and the outcome of interference interactions (Marshall & Keough 1994). Within the intertidal area, variations in both the physical and biological environment often lead to distinct intraspecific zonation in the distribution and abundance of marine organisms (Alfaro & Carpenter 1999). The upper boundaries of upper intertidal species have been explained by physical factors such as temperature and desiccation stress, wave action and crevice availability, rock surface slope and topography, surface complexity and microhabitats refuges, and recruitment site (Raffaelli & Hughes 1978; Chapman 1994b) while biological factors such as predation and competition are thought to influence lower distribution limits. In this context, Vermeij (1972) proposed that there are two general patterns exhibited by rocky intertidal gastropods. For species inhabiting the upper intertidal, shell size tends to increase in an upshore direction, while for species inhabiting the lower intertidal, shell size tends to decrease with increasing tidal height.

Patterns of vertical zonation among rock intertidal organisms have been extensively documented (Dayton 1971; Vermeij 1972; Branch 1981; Martins *et al*. 2007). The factors causing size-specific gradients in molluscs are many and varied (McQuaid 1981; McCormock 1982). Factors that affect the population structure of limpet species include associations with other species (Johnson *et al.* 1997), discharge of sewage effluent (Hindell & Quinn 2000), limpet density (Boaventura *et al*. 2002b), predation in terms of age structure (Lewis & Bowman 1975; Frank 1982), size (Bosman *et al*. 1989) and species composition (Wootton 1992).

Sedentary and sessile invertebrates like mussels can form complex beds that provide interstices that offer refuge from birds, and limpets often occur at high densities within these interstices (Ruiz Sebastian *et al*. 2002). Small size is advantageous for finding shelter among and within empty barnacle shells on exposed rocky shores (Raffaelli & Hughes 1978). Many limpets exhibit "homing" behaviour and the role of a home scar as a defence against predators has been well documented (Branch 1981; Garrity & Levings 1983; Iwasaki 1993, 1995; Lindberg 2007). The home scar is important for defence in 'low shore' species. Homing to a fixed scar not only reduces predation but also desiccation (Branch 1981) and individuals change their home scars over periods of months or even years (Little 1989).

As humans constantly and selectively collect limpets from some rocky shores, it can be expected that human exclusion will modify the density and population structure of these limpets (Oliva & Castilla 1986). Over-collection of larger animals by humans has been found to result in a shift in the size structure of exploited populations towards domination by smaller limpets (Branch 1975a; Pambo & Escofet 1996; Griffiths & Branch 1997; Lindberg *et al.* 1998; Roy *et al.* 2003; Kido & Murray 2003). Some authors have noted that the degree of exploitation by humans is related to declines in size structure and densities of targeted populations of limpets (Moreno *et al*. 1984; Hockey & Bosman 1986; Oliva & Castilla 1986; Ortega 1987; Kyle *et al.* 1997; Lindberg *et al.* 1998; Roy *et al*. 2003), other gastropods (McLachlan & Lombard 1981; Castilla & Durán 1985; Moreno *et al.* 1986; Durán & Castilla 1989; Foster & Hodgson 2000), mussels (Hockey & Bosman 1986; Lasiak & Dye 1989) and even algae (Jenkins & Hartnoll 2001).

Through reductions in density and shifts toward smaller individuals, human exploitation can also decrease the reproductive output of intertidal invertebrate populations in which there is an increase in individual fecundity with body size (Branch 1974a; 1975b; Levitan 1991; Tegner *et al*. 1996). In many areas where grazing by limpets is reduced, there is rapid colonization by foliose macroalgae (Underwood 1980; Dye 1993; Davies *et al*. 2007). Despite the existence of regulations in South Africa (Marine Living Resources Act of 1998) that limit the number and minimum sizes of animals that may be collected, many researchers have noted that it has become increasingly difficult to find large limpets intertidally, except in marine reserves (McLachlan & Lombard 1981; Hockey & Bosman 1986; Lasiak & Dye 1989; Griffiths & Branch 1997; Foster & Hodgson 2000).

The main objective of this chapter was to test the null hypothesis that there is no limpet size difference between resereves and non-reserves for both commonly and rarely exploited species. The two hypotheses tested were:

1) that the mean and mean maximum sizes of commonly exploited species will be smaller in non-resereve than in resereves.

2) that the mean and mean maximum sizes of rarely exploited species will not differ between reserves and non-reserves.

3.2 MATERIALS AND METHODS

Monthly sampling to determine the size-frequency distribution of target species was conducted at the same sites as in the previous chapter. Quadrats of 0.5 x 0.5 m were thrown haphazardly and repeatedly in each zone of each species occurrence until about 200 limpets had been measured. A fixed minimum number of individuals was used instead of a fixed number of plots to enable a comparison of size structure among areas and over time with a similar sample size (Silva *et al.* 2003). However, adverse weather conditions limited this to species in some months. Within each quadrat, all individuals were measured *in situ* for total shell length (greatest distance of the anterior and posterior axis) using a ruler and a pair of dividers to obtain size frequency distributions. On each occasion, thorough searches were made during sampling to include smaller, identifiable limpets of each species, including those residing on the shells of older limpets (e.g. *Scutellastra longicosta*). All measurements were taken without removing the individuals from the substratum. The data were then plotted as histograms to indicate the size structure of each limpet population over time and to identify the recruits (Dunmore & Schiel 2003). Size frequency distributions were developed for each population after placing measured limpets into 2.5 mm size classes. In order to reduce the confounding effects of sampling in different habitats, animals found in rock pools were excluded. Mean maximum size was derived from the lengths of the 10 largest individuals for each species each month.

3.2.1 Statistical analysis

The effects of marine reserves on limpet mean and maximum size were analysed separately for each species, using a four-factor nested analysis of variance (ANOVA) to test the effects of month, reserve, site (nested in reserve) and area (nested in reserve and site). The factors month, site and area were treated as random while reserve was treated as fixed. Multiple comparison tests (Tukey HSD tests) were subsequently run on significant results ($p < 0.05$) from ANOVA tests. Prior to the use of ANOVA, the data were tested for normality and homogeneity of variances using Kolmogorov-Smirnov and Cochran's tests (Zar 1996; Underwood 1997), respectively. No transformation was necessary.

3.3 RESULTS

The ANOVA results revealed no significant effects of reserve for any species. The mean and mean maximum size generally showed a similar pattern in time in all species. Except for mean maximum sizes of *Cellana capensis*, the month/site (reserve) interaction was always significant, indicating that temporal variations were different among sites separated on scales of 10 km. The month/area (reserve (site)) interaction was also significant for each species, indicating spatio-temporal variation on scales of 100 m within sites. As the effect of reserve was masked by meaningless comparisons between areas within sites, the month/reserve interaction will be discussed even though they were not statistically significant.

3.3.1 Mean and mean maximum sizes

3.3.1.1 Commonly exploited species

Helcion concolor

There were significant effects of month and area but also were the interactions of month/site (reserve) and month/area (reserve (site)) (Tables 3.1 & 3.2).

Month x Reserve

The mean and mean maximum sizes of *H. concolor* were markedly stable throughout the sampling period (Fig. 3.1.1). Although there were no significant month/reserve interactions, patterns of both parameters between reserves and non-reserves were similar and differed only in detail. The mean sizes in reserves were greater than in non-reserves for 19 months but were significantly different in only 8 months. Mean sizes in non-reserves were greater than in reserves in only 1 month (March 2003) and this difference was not significant (Fig. 3.1.2).

The mean maximum sizes in reserves were greater than in non-reserves for 10 months (Fig. 3.1.3). In 2 months (August and November 2003), mean maximum sizes in non-reserves were greater than in reserves. Mean maximum size was almost identical in reserves and non-reserves for 8 months (March, June, July, October and December 2003, February, April and May 2004). The lowest mean sizes for *H. concolor* in reserves and non-reserves were 15.61 ± 0.35 and 13.91 ± 0.37 mm, attained in March 2003 and November 2002, respectively, while the highest mean sizes were 23.30 ± 0.29 and 21.93 ± 0.31 mm, respectively, both attained in February 2004. The lowest mean maximum sizes for *H. concolor* in reserves and non-reserves were 26.73 ± 0.67 and 23.01 ± 0.67

mm, in March 2003 and November 2002, respectively, while the highest mean maximum sizes were 34.18 ± 0.67 and 31.99 ± 0.67 mm, in November 2002 and February 2004, respectively.

Month x Site (Reserve)

Post-hoc tests on the interaction of month/site (reserve) on the mean sizes of *H. concolor* revealed significant differences in the months showed by asterisks with biggest and smallest mean sizes obtained at Dwesa and Xhora, respectively (Fig. 3.1.4(a)). In contrast, post-hoc tests on the mean maximum sizes showed no clear pattern for the biggest sizes but for the smallest sizes which occurred at Xhora ((Fig. 3.1.4(b)).

Month x Area (Reserve (Site))

In both analyses, there was a significant ($p < 0.05$) area effect which was nested within site and reserve (Fig. 3.1.5(a) & (b)). The area effects on both parameters occurred mostly at Dwesa and Nqabara (Table 3.3).

Scutellastra longicosta

Four-way ANOVA revealed significant ($p < 0.05$) effects of month, site and area including the interactions of month/site (reserve) and month/area (reserve (site)) (Tables 3.4 & 3.5).

Month x Reserve

The sizes of *S. longicosta* were generally constant, with a slight progressive increase in mean and mean maximum sizes over the sampling period (Fig 3.2.1). Although there was no significant month/reserve interaction, the mean sizes in reserves were greater than in non-reserves for all 20 months (Fig. 3.2.2) while the mean maximum sizes, were greater for reserves than non-reserves in 19 months (Fig. 3.2.3). Mean maximum size was greater in non-reserves than in reserves in only one month (July 2003) (Fig. 3.2.3).

The lowest mean sizes of *S. longicosta* in reserves and non-reserves were 21.59 ± 0.37 and 18.93 ± 0.41 mm, in May and February 2003, respectively, while the highest mean sizes were 29.19 ± 0.38 and 24.60 ± 0.37 mm, in July 2003 and December 2002, respectively. The lowest mean maximum size of *S. longicosta* in reserves and non-reserves were 35.21 ± 0.72 and 31.07 ± 0.84 mm, in July 2003 and December 2002, respectively, while the highest mean maximum sizes were 47.78 ± 0.72 and 39.73 ± 0.72 mm, in February 2004 and November 2003, respectively.

<u>Month x Site (Reserve)</u>

Tukey HSD tests on the mean and mean maximum size of *S. longicosta* indicated significant ($p < 0.05$) differences among sites, with lowest mean and maximum sizes always at Xhora (see asterisks in Figs. 3.2.4(a) & (b)). Although there was a month/site (reserve) interaction, so that the order occasionally changed, the general pattern for mean sizes of *S. longicosta* was, in decreasing order Nqabara (26.87 ± 0.12) > Dwesa (26.09 ± 0.13) > Cwebe (24.96 ± 0.13) > Xhora (16.60 ± 0.15) while the overall decreasing order of mean maximum sizes were, Nqabara (45.53 ± 0.23) > Dwesa (44.40 ± 0.22) > Cwebe (39.76 ± 0.22) > Xhora (26.51 ±0.23).

<u>Month x Area (Reserve (Site))</u>

Poat-hoc tests on the interaction of month and area (reserve (site)) effect revealed significant differences in months showed by asterisks (Figs. 3.2.5(a) & (b)). The area effect occurred mostly at Dwesa and Cwebe for both mean and mean maximum sizes (Table 3.6).

3.3.1.2 Rarely exploited species

Cellana capensis

Four-way ANOVA tests on the mean sizes of *C. capensis* revealed significant ($p < 0.05$) effects of month, site (reserve) area (reserve (site)) including the interactions between month/site (reserve) and between month/area reserve (site)) (Tables 3.7). Except for month and month/site interaction, the same significant effects on mean sizes were also significant for the mean maximum sizes (Table 3.8).

Month x Reserve

The mean sizes of *C. capensis* generally showed a stable pattern with little variation throughout the sampling period (Fig. 3.3.1). Although there were no significant month/reserve interactions, the mean and mean maximum sizes were greater in reserves than non-reserves for all 20 months (Figs. 3.3.2 & 3.3.3).

The lowest mean size of *C. capensis* in reserves and non-reserves were 15.73 ± 0.16 and 13.62 ± 0.15 mm, in May 2004 and October 2003, respectively, while the highest and lowest mean size of *C. capensis* were 19.78 ± 0.20 and 16.86 ± 0.22 mm, in January 2003 and June 2003, respectively. The lowest mean maximum sizes of *C. capensis* in reserves and non-reserves were 24.85 ± 0.58 and 21.03 ± 0.67 mm, in May 2004 and October 2003, respectively, while the highest mean maximum sizes were 34.01 ± 0.57 and 24.96 ± 0.58 mm, in December 2002 and June 2003, respectively.

Month x Site (Reserve)

Post-hoc tests on the month/site (reserve) interaction for mean sizes of *C. capensis* revealed significant differences in months indicated by asterisks with highest and lowest mean sizes at Dwesa and Xhora, respectively (Fig. 3.3.4(a)).

Site (nested in reserve) had a significant effect on the mean maximum size of *C. capensis* (Tables 3.5 & 3.6). Tukey HSD tests indicated that the the mean maximum sizes of *C. capensis* at Dwesa were significantly ($p < 0.05$) higher than at Nqabara and Cwebe, which were higher than at Xhora. This reflected that the highest and lowest mean maximum size of 32.69 ± 0.18 and 20.04 ± 0.19 mm, were found at Dwesa and Xhora, respectively (Fig. 3.3.4(b)).

The overall mean size of *C. capensis* was, in decreasing order, Dwesa (20.32 ± 0.06) > Nqabara (17.13 ± 0.06) > Cwebe (14.29 ± 0.06) > Xhora (12.90 ± 0.05) while for mean maximum sizes was, Dwesa (32.69 ± 0.18) > Nqabara (26.50 ± 0.18) ≥ Cwebe (25.95 ± 0.18) > Xhora (20.04 ± 0.19).

Month x Area (Reserve (Site))

Tukey HSD tests on the interaction of month and area (reserve (site)) showed significant differences in months indicated by asterisks (Figs. 3.3.5 (a) & (b)). Most area effects for both parameters were found at Dwesa and Cwebe (Table 3.9).

Scutellastra granularis

There were significant ($p < 0.05$) effects of site (reserve) and area (reserve (site) including the month/site (reserve) and month/area (reserve (site) interactions (Tables 3.10 & 3.11).

Month x Reserve

There were no significant month or month/reserve effects, and the mean and maximum size of *S. granularis* generally exhibited a markedly stable pattern throughout the sampling period (Fig. 3.4.1). Although there was a sharp increase in both mean and mean maximum sizes of *S. granularis* in the last month (June'04), this seems likely to be an artifact (Fig. 3.4.1).

In all months except June 2004, the mean sizes of *S. granularis* in reserves were almost identical to those in non-reserves (Fig. 3.4.2). For mean maximum sizes of *S. granularis*, reserves were greater than non-reserves for 7 months. There were 3 months (July, December 2003 and June 2004) when mean maximum sizes of *S. granularis* in non-reserves were greater than in reserves (Fig. 3.4.3).

The lowest mean sizes of *S. granularis* in reserves and non-reserves were 12.49 ± 0.11 and 12.83 ± 0.12 mm attained in December 2003, respectively, while the highest mean size structure were 15.36 ± 0.17 and 18.69 ± 0.15 mm, respectively both in November 2002 and June 2004. The lowest mean maximum size of *S. granularis* in reserves and non-reserves were 21.0 ± 0.51 and 20.47 ± 0.53 mm, in January 2004 and March 2004, respectively, while the highest mean maximum sizes were 26.22 ± 0.51 and 43.82 ± 0.74 mm, in November 2002 and June 2004, respectively.

Month x Site (Reserve)

Post-hoc tests on the effect of month/site interaction showed significant differences in months indicated by asterisks with almost similar pattern (Figs. 3.4.4(a) & (b)).

The overall mean size of *S. granularis* was, in decreasing order, Nqabara (15.37 ± 0.05) > Dwesa (14.42 ± 0.05) > Cwebe (12.83 ± 0.04) = Xhora (12.56 ± 0.05). For mean maximum size, these were Nqabara (25.54 ± 0.16) > Dwesa (24.62 ± 0.17) > Cwebe (22.11 ± 0.16) > Xhora (21.28 ± 0.21), although there was a month/site (reserve) interaction.

<u>Month x Area (Reserve (Site))</u>

Tukey HSD tests of the month/area interaction in the mean and maximum sizes of *S. granularis* revealed significant differences in months, shown by asterisks, with almost the same pattern for the two parameters (Figs. 3.4.5(a) & (b)). For mean sizes, most area effects occurred at Dwesa and Nqabara, though a few occurred at Xhora and Cwebe, while for the mean maximum sizes they occurred mostly at Dwesa and a occurred equally at Nqabara and Xhora (Table 3.12).

3.3.2 Size frequency distribution

<u>3.3.2.1 Commonly exploited species</u>

Helcion concolor

Generally, areas within sites showed similar unimodal patterns of size distribution except in months when there were bimodal patterns. These months varied with site, there were 9 for Dwesa (Fig. 3.5.1a), 5 for Cwebe (Fig. 3.5.2b), 9 for Nqabara (Fig. 3.5.3c) and 8 for Xhora (Fig. 3.5.4d). Except for Dwesa, with a modal size class of 25-30 mm, all the other sites had a dominant modal size class of 20-25 mm.

Scutellastra longicosta

Size distribution of *S. longicosta* varied from unimodal to bimodal in different months at each site. Size distribution was bimodal in 15 months at Dwesa, 8 months at Cwebe, 11 at Nqabara, and 3 at Xhora.

The modal size class ranged from 30-35 mm for Dwesa (Fig. 3.6.1(a)), 25-30 mm for Cwebe (Fig. 3.6.2(b)) and Nqabara (Fig. 3.6.3(c)), and from 15 to 20 mm for Xhora (Fig. 3.6.4(d). Xhora showed a very clear marked unimodal pattern of distribution which lacked large animals (i.e. skewed to the left) (Fig. 3.6.4(d)).

3.3.2.2 Rarely exploited species

Cellana capensis

A clear unimodal distribution pattern with a modal size range of 20 to 25 mm was evident at Dwesa in most months except April 2004, (Fig. 3.7.1(a)). Except for November 2003 and March 2004, Cwebe generally showed a unimodal pattern, skewed to the left in all months, with a modal size range of 15 to 20 mm (Fig. 3.7.2(b)). For Nqabara (Fig. 3.7.3(c)) and Xhora (Fig. 3.7.4(d)) all months had a normal distribution pattern with a modal size of 20-25 and 15-20 mm, respectively.

Scutellastra granularis

With the exception of June 2004 for Nqabara (modal size of 25 and 40 mm) (Fig. 3.8.3c), all months had an almost unimodal distribution pattern (Figs. 3.8.1a, 3.8.2b, 3.8.3c and 3.8.4d). The modal sizes were 20 mm for Dwesa, 15–20 mm for Cwebe and Nqabara, and 15 mm for Xhora.

3.4 DISCUSSION

This study revealed no significant reserve effects on mean and mean maximum sizes of either the commonly exploited (*Helcion concolor* and *Scutellastra longicosta*) or the rarely exploited (*Cellana capensis* and *Scutellastra granularis*) species. The lack of a reserve effect may be due to masking by meaningless comparisons of areas within sites. This is shown by clear, marked differences in mean and maximum sizes revealed in the month/reserve interactions, with generally greater limpet sizes in reserves than non-reserves even though the overall effect was not significant.

There were significant month/site (reserve) interactions for all four species for mean size and for 3 out of 4 species for the mean maximum sizes. Except for *C. capensis,* the month/site interaction had a significant effect for all species in mean maximum sizes, providing evidence for high spatio-temporal variability at 10 km scales. Although the patterns for mean and mean maximum sizes were similar, there were more months with significant differences in commonly exploited species than in rarely exploited species. The mean and mean maximum sizes were especially low at Xhora for all the species and generally highest at Dwesa.

The month/area (reserve (site)) interaction on mean and maximum sizes was significant for all species, indicating spatial variation on small (100 m) scales. There were two striking points: 1) for each species and both parameters, this area effect was stronger in reserves than in non-reserves. In addition, this bias towards more frequent area effects in reserve sites was stronger for commonly exploited species in the case of mean maximum size and very much stronger for rarely exploited species in the case of mean size. There is no obvious explanation for this.

2) Of the 4 sites, Dwesa revealed very strong area effects across all the species with Dwesa 1 being greater than Dwesa 2. This may be attributed to the effects of habitat or of natural predation. Cwebe had the fewest number of months with significant area effects.

The observed non-significant effects of the month/site interaction for *C. capensis* on mean maximum size rather than mean size implies that large individuals are often taken. In chapter 1, interviews on limpet preferences among harvesters showed that *C. capensis* may be partially exploited because some harvesters cannot distinguish between this species and *H. concolor*. This agrees with Lasiak's (1992) report that *C. capensis* is taken opportunistically rather than being a target species.

Variations in mean and maximum sizes over time may be attributed to mortality. Dunmore and Schiel (2003) reported that once limpets reach larger sizes, they undergo abrupt mortality. Another agent of mortality (aside from predation) that might favour larger body sizes in 'high shore' snails is desiccation (Rochette *et al*. 2003). Other factors that may account for differences in mean and maximum sizes include low recruitment that may reduce intraspecific competition, and increased growth rates due to a higher availability of food supply or less intraspecific interaction and wave exposure (Silva *et al.* 2003).

Interestingly, despite the fact that *S. longicosta* is commonly exploited, the mean and mean maximum sizes at Nqabara, which is a non-reserve site, were significantly greater than in reserve sites. This may possibly reflect the effects of reduced intraspecific competition. Decreased density at Nqabara (Chapter 2) is associated with better performance in size, growth, weight and gonad development of both large and small limpets, and to a reduction in mortality (Boaventura *et al*. 2003). Furthermore, the removal of larger grazing gastropods facilitates the growth of algae (Hockey & Bosman 1986; Dye 1993; Davies *et al*. 2007), and shells of this species were seen covered with algae, which may act as a camouflage from shellfish harvesters. Most limpets are found on the open rock surface and are easy to locate. Similarly, Lasiak (1993) noted smaller specimens of *Haliotis spadicea* and *Scutellastra longicosta* at Dwesa than at Nqabara and this was attributed to the presence of a gulley that prevented shellfish harvesters from reaching the study site except on good spring tides.

It was also noticeable that the mean and mean maximum sizes of *C. capensis* were lower at Cwebe and Xhora despite its greater mean density at these sites (Chapter 2). This may be due to the presence of more barnacles in these sites (*pers. obs*.) as barnacles inhibit the foraging activity of limpets. Underwood *et al*. (1983) showed that *Cellana tramoserica* migrate away from areas with large densities of barnacles and when forced to stay in such areas, they lose weight and eventually die of starvation. Then the trade-off for limpets however may be reduced growth as evidenced by the growth study (Chapter 5). Similarly, Ruiz Sebastian *et al*. (2002) found that the limpet *Scutellastra argenvillei* moved larger distances and homed less within the matrix of the introduced mussel, *Mytilus galloprovincialis*, than on natural or experimental patches of bare rock. They correlated this to the difficulty in forming home-scars and the inaccessibility of food within mussel beds.

The existence of significant month/area (reserve (site)) interaction suggests spatio-temporal variation on small scales within sites. This effect may also imply differences in the distribution of microhabitats (Chapman 1994b**)**. On rocky shores, snails avoid dislodgment by avoiding smooth rock and seeking out refuges from high water flows (Boulding *et al*. 1993). During spring low tide, *C. capensis* and *S. granularis* were often observed in crevices, between barnacles, inside dead barnacles and deep in beds of algae, while *H. concolor* was seen partially buried by sand (*pers. obs.*). In a similar situation, Raffaelli & Hughes (1978) noted the advantage of small size for finding shelter among and within empty barnacle shells on exposed rocky shores. Denny *et al.* (1985) reported that algal holdfasts and barnacles that protrude up from the substratum may decrease flow velocity. The low mean and maximum sizes of *S. granularis* observed at Cwebe may be due to the effects of barnacles on this species. For example, Dunmore & Schiel (2003) noted that when barnacles were experimentally removed, limpets were larger than in barnacle–covered treatments. In addition, barnacles can provide a refuge for small limpets from competition with larger individuals (Creese 1982), which may be unable to forage effectively in areas of dense barnacle cover (Choat 1977; Ridgway *et a*l. 1998). Hobday (1995) noted that more wave splash in exposed areas, results in less desiccation risk and appeared to promote the survival of small limpets (*Lottia digitalis*) at all tidal heights. Moreover, the owl limpet in Northern California (*Lottia gigantean*) has been shown to control the assemblage of intertidal algae and other smaller limpets in its territory through continuous grazing. Its absence was found to lead to an increase in smaller limpet species which, in turn, limited intertidal algae more severely (Denny & Blanchette 2000).

Except for *H. concolor* and *S. granularis*, there were marked differences among months in the mean and maximum sizes of all species with different temporal patterns for each species. The observed effects of temporal variation in mean and maximum sizes in all species may be related to climatic conditions. For instance, during winter, severe storms occur often and adult limpets have a low probability of surviving the winter. In addition, during severe storms, extreme flows may cause algae to bend over further than during more moderate flows. Although this hypothesis was not tested, the decrease in the height of the algal bed above the substratum may decrease the size of the refuge, making it suitable only for small-sized limpets (Boulding *et al*. 1993). Thus the size of the available refuges is believed to be the reason for the predominance of small snails on rocky shores where the average crevice size is small and wave action heavy. Increasing the size of holes in the rock has been shown to increase the mean adult size of snail populations (Raffaelli 1978) and crevices, cracks or boulder refuges enable large tropical gastropods to survive a typhoon (Kohn 1980).

The rarely exploited species showed bimodal distribution patterns more often than commonly exploited species, which may reflect not only different recruitment existing in those species but exploitation effects. The fact that reserve effects were significant in one commonly exploited (*S. longicosta*) and one rarely exploited (*C. capensis*), suggests a lack of consistency and may imply that each species responds differently to the natural processes, irrespective of exploitation. The fact that large individuals of all four species (even the rarely exploited ones) were relatively rare at Xhora may imply that they are exploited in the absence of the preferred ones. There is evidence that the effects of human exploitation on intertidal organisms result in reduced mean densities (Oliva & Castilla 1986; Keough *et al.* 1993; Pombo & Escofet 1996; Branch & Odendaal 2003; Kido & Murray 2003, Chapter 2). In addition, when size-selective exploitation is high, it may cause selection of heritable traits such as mean size (Marshall & Keough 1994; Lipcius & Stockhausen 2002; Fenberg & Roy 2008).

In summary, mean and mean maximum sizes generally showed very similar patterns in time. Months with significant effects of the month/site interaction for both parameters, generally occurred more often for commonly exploited species than for rarely exploited species. However, interestingly, *C. capensis* showed the strongest area effects on maximum size, indicating that large animals are often taken. This accords with the results from interview surveys, which indicated that this species is partially exploited because some harvesters cannot distinguish it from *H. concolor*. *S. granularis* and *S. longicosta* revealed expected reserve effects on the mean and maximum sizes. Although Xhora and Cwebe showed higher mean densities of *C. capensis* than Dwesa and Xhora (Chapter 2), they had the lowest mean and maximum sizes, suggesting possible intraspecific competition.

Table 3.1: Results of 4-way ANOVA based on mean size estimates of *H. concolor*. * denotes a significant effect at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	35998	19	1895	3.398	< 0.05*
Reserve	25918	1	25918	1.379	0.599
Site (Reserve)	37844	2	18922	3.252	0.133
Area (Reserve (Site))	22058	4	5515	17.206	< 0.001**
Month x Reserve	10594	19	558	0.821	0.670
Month x Site (Reserve)	26048	38	685	2.062	< 0.001**
Month x Area (Reserve (Site))	25961	76	342	9.037	< 0.0001***
Error	621916	16454	38		

Table 3.2: Results of 4-way ANOVA based on mean maximum size estimates of *H. concolor*. * denotes a significant effect at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	4497	19	237	1.249	0.316
Reserve	1577	1	1577	0.386	0.597
Site (Reserve)	8149	2	4075	2.746	0.164
Area (Reserve (Site))	5518	4	1380	18.216	< 0.0001***
Month x Reserve	3599	19	189	1.052	0.432
Month x Site (Reserve)	6843	38	180	2.378	< 0.001**
Month x Area (Reserve (Site))	5756	76	76	7.029	< 0.0001***
Error	15516	1440	11		

Table: 3.3: Month x Area (Reserve (Site)) interaction: Summary of Tukey HDS results on the total number of months with significant differences between areas within sites in mean and mean maximum size of *H. concolor*.

Site		**Mean size**	**Mean maximum size**
Reserve	Dwesa	11	10
	Cwebe	0	0
Non-reserve	Nqabara	6	7
	Xhora	1	1

Table 3.4: Results of 4-way ANOVA based on mean size estimates of *S. longicosta*. * denotes a significant effect at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	59577	19	3136	6.280	< 0.05*
Reserve	59183	1	59183	0.568	0.530
Site (Reserve)	210227	2	105113	21.233	< 0.001**
Area (Reserve (Site))	18018	4	4504	19.901	< 0.0001***
Month x Reserve	9486	19	499	0.617	0.869
Month x Site (Reserve)	31081	38	818	3.549	< 0.0001***
Month x Area (Reserve (Site))	17942	76	236	3.136	< 0.0001***
Error	1445930	19208	75		

Table 3.5: Results of 4-way ANOVA based on mean maximum size estimates of *S. longicosta*. * denotes a significant effect at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	8297	19	437	2.693	< 0.05*
Reserve	14553	1	14553	0.384	0.599
Site (Reserve)	75931	2	37965	81.277	< 0.0001***
Area (Reserve (Site))	1289	4	322	3.659	< 0.05*
Month x Reserve	3081	19	162	0.696	0.799
Month x Site (Reserve)	8853	38	233	2.646	< 0.001**
Month x Area (Reserve (Site))	6690	76	88	7.470	< 0.0001***
Error	16969	1440	12		

Table: 3.6: Month x Area (Reserve (Site)) interaction: Summary of Tukey HDS results on the total number of months with significant differences between areas within sites in mean and mean maximum size of *S. longicosta*.

Site		**Mean size**	**Mean maximum size**
Reserve	Dwesa	6	4
	Cwebe	2	4
Non-reserve	Nqabara	0	0
	Xhora	0	1

Table 3.7: Results of 4-way ANOVA based on mean size estimates of *C. capensis*. * denotes a significant effect at p < 0.05, ** = p < 0.001 and *** = p < 0.0001.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	19229	19	1012	3.245	< 0.05*
Reserve	39321	1	39321	0.474	0.563
Site (Reserve)	166724	2	83362	44.453	< 0.001**
Area (Reserve (Site))	5962	4	1491	7.509	< 0.0001***
Month x Reserve	5926	19	312	0.493	0.949
Month x Site (Reserve)	24277	38	639	3.013	< 0.0001***
Month x Area (Reserve (Site))	16447	76	216	10.195	< 0.0001***
Error	662374	31205	21		

Table 3.8: Results of 4-way ANOVA based on mean maximum size estimates of *C. capensis*. * denotes a significant effect at p < 0.05, ** = p < 0.001 and *** = p < 0.0001.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	3000	19	158	0.988	0.509
Reserve	14469	1	14469	1.665	0.325
Site (Reserve)	17268	2	160	18.973	< 0.05*
Area (Reserve (Site))	1734	4	434	5.336	< 0.001**
Month x Reserve	3035	19	160	1.555	0.121
Month x Site (Reserve)	3904	38	103	1.264	0.191
Month x Area (Reserve (Site))	6175	76	81	10.868	< 0.0001***
Error	10766	1440	7		

Table: 3.9: Month x Area (Reserve (Site)) interaction: Summary of Tukey HDS results on the total number of months with significant differences between areas within sites in mean and mean maximum size of *C. capensis*.

Site		**Mean size**	**Mean maximum size**
Reserve	Dwesa	9	6
	Cwebe	8	7
Non-reserve	Nqabara	0	1
	Xhora	1	0

Table 3.10: Results of 4-way ANOVA based on mean size estimates of *S. granularis*. * denotes a significant effect at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	26183	19	1378	1.625	0.149
Reserve	974	1	974	0.060	0.829
Site (Reserve)	33105	2	16553	12.324	< 0.001**
Area (Reserve (Site))	2328	4	582	4.819	< 0.001**
Month x Reserve	16112	19	848	0.828	0.663
Month x Site (Reserve)	40229	38	1059	7.501	< 0.0001***
Month x Area (Reserve (Site))	11087	76	146	9.746	< 0.0001***
Error	487426	32564	15		

Table 3.11: Results of 4-way ANOVA based on mean maximum size estimates of *S. granularis*. * denotes a significant effect at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	2527.7	19	133.0	0.713	0.766
Reserve	22.9	1	22.9	0.007	0.938
Site (Reserve)	6045.3	2	3022.7	8.012	< 0.05*
Area (Reserve (Site))	1035.5	4	258.9	5.176	< 0.001**
Month x Reserve	3543.1	19	186.5	1.107	0.382
Month x Site (Reserve)	6399.1	38	168.4	3.367	< 0.0001***
Month x Area (Reserve (Site))	3800.9	76	50.0	6.511	< 0.0001***
Error	11060.3	1440	7.7		

Table: 3.12: Month x Area (Reserve (Site)) interaction: Summary of Tukey HDS results on the total number of months with significant differences between areas within sites in mean and mean maximum size of *S. granularis*.

Site		**Mean size**	**Mean maximum size**
Reserve	Dwesa	9	6
	Cwebe	1	0
Non-reserve	Nqabara	4	2
	Xhora	2	2

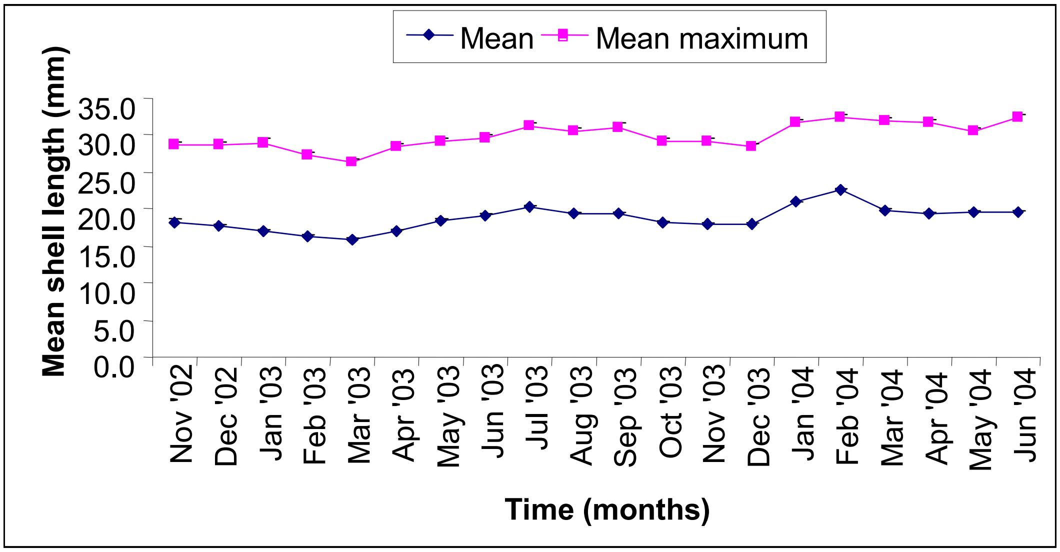


Fig. 3.1.1: Mean and mean maximum (±SE) shell length of *H. concolor* averaged over all sites.

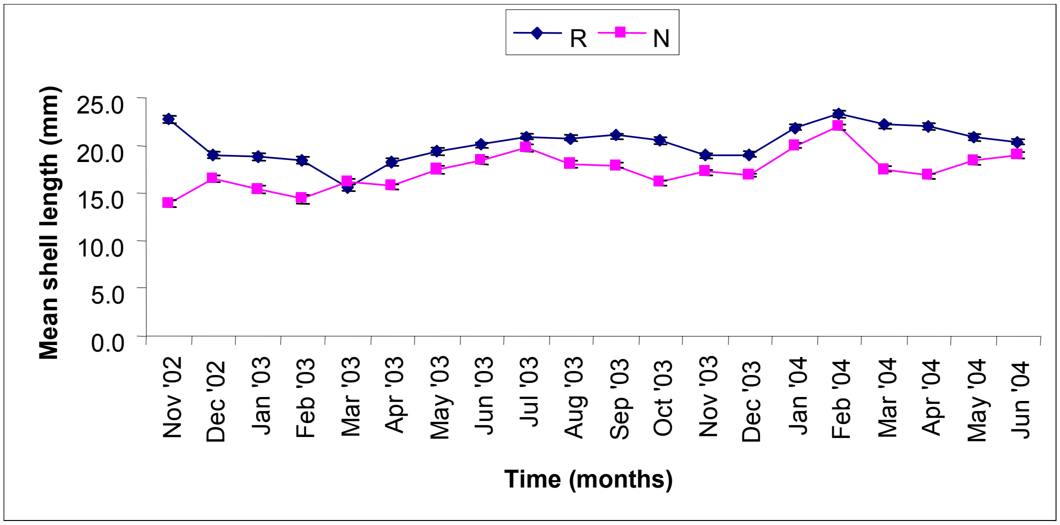


Fig. 3.1.2: Mean (±SE) shell length of *H. concolor* in reserves (R) and non-reserve (N) sites.

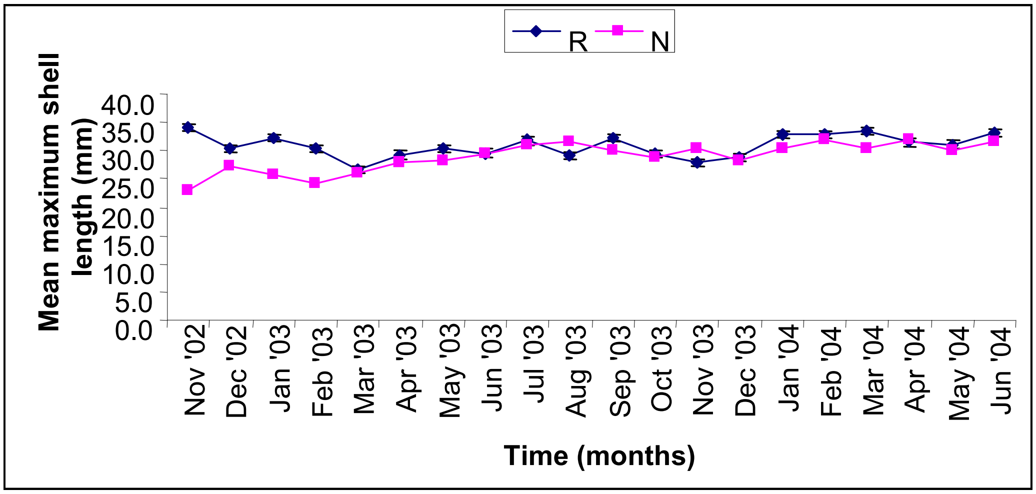


Fig. 3.1.3: Mean maximum (±SE) shell length of *H. concolor* in reserves (R) and non-reserves (N) sites.

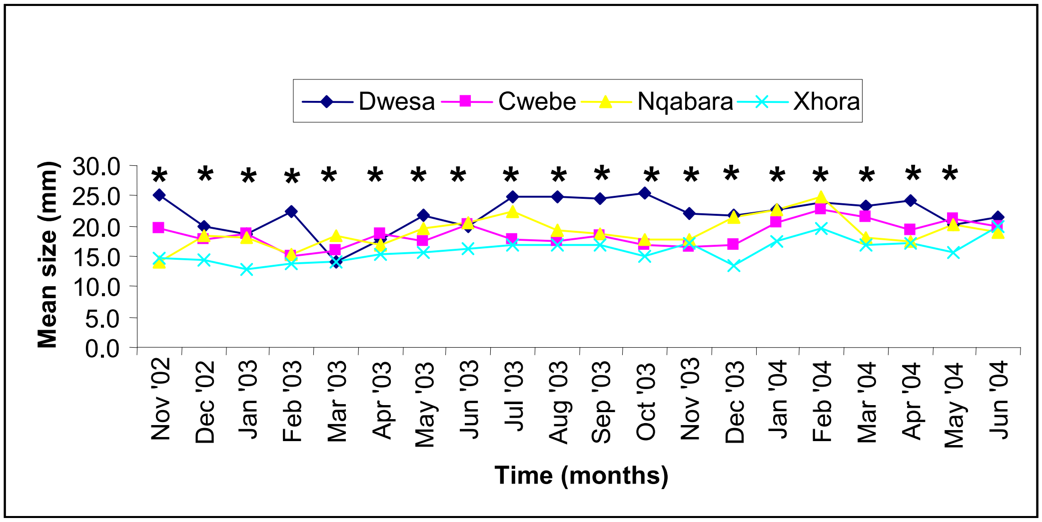


Fig. 3.1.4(a): Monthly mean sizes (Standard errors (SE) were omitted for clarity) of *H. concolor* at each of the four study sites. * = significant difference ($p < 0.05$). D = Dwesa, C = Cwebe, N = Nqabara and X = Xhora. Post-hoc test results: Nov ’02 D>C>X>N; Dec ’02, Feb ’03, Sep ’03, Oct ’03 D>C=N>X; Jan ’03, Jun ’03, May ’04 C=D=N>X; Mar ’03 N>C>D=X; Apr ’03 C=D>N>X; May ’03, Jul ’03 D>N>C>X; Aug ’03 D>N>C=X; Nov ’03 D>N=X>C; Dec ’03, Jan ’04, Feb ’04, Mar ’04 D=N>C>X; Apr ’04 D>C>N=X.

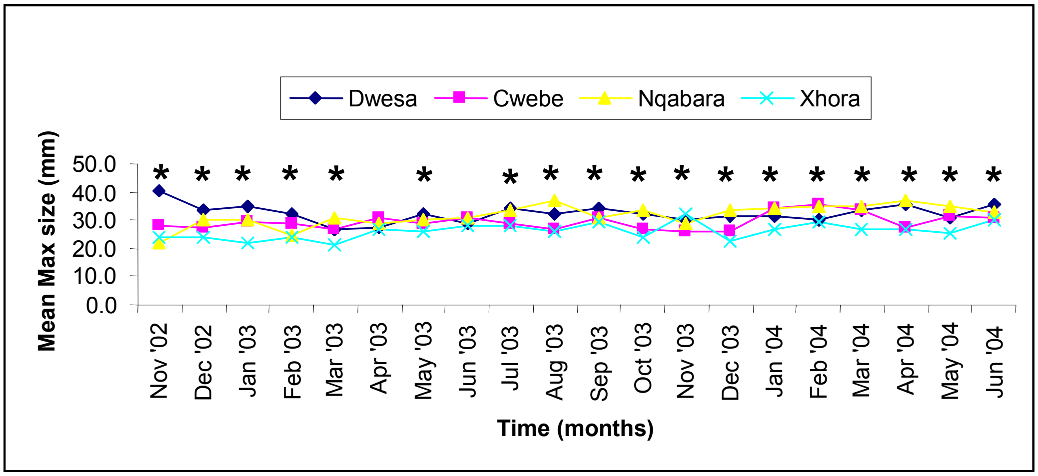


Fig. 3.1.4(b): Monthly mean maximum (Max) sizes (Standard errors (SE) were omitted for clarity) of *H. concolor* at each of the four study sites. * = significant difference ($p < 0.05$). D = Dwesa, C = Cwebe, N = Nqabara and X = Xhora. Post-hoc test results: Nov '02 D>C>X>N; Dec '02, Feb '03 D>N>C>X; Jan '03, May '03, Sep '03 D>C=N>X; Mar '03, May '04 N>C=D>X; Jul '03, Jun '04 D>N>C=X; Aug '03, Apr '04 N>D>C=X; Oct '03, Dec '03 N=D>C>X; Nov '03 X>D>N>X; Jan '04 C>N>D>X; Feb '04 C>N>D=X; Mar '04 C=D=N>X.

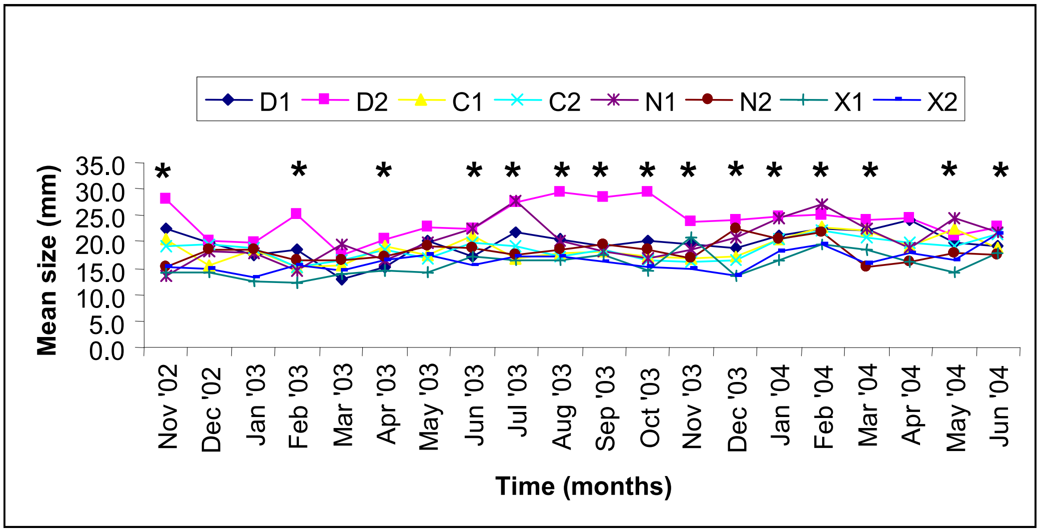


Fig. 3.1.5(a): Monthly mean sizes (Standard errors (SE) were omitted for clarity) of *H. concolor* at each of the areas within sites. * = significant difference ($p < 0.05$). D1 = Dwesa 1, D2 = Dwesa 2, C1 = Cwebe 1, C2 = Cwebe 2, N1 = Nqabara 1, N2 = Nqabara 2, X1 = Xhora 1 and X2 = Xhora 2. Post-hoc test results: Nov ’02, Feb ’03, Apr ’03, Jun’03, Jul ’03, Aug ’03, Sep’03, Oct ’03, Nov ’03, Dec ’03, Jan ‘04 D2>D1; Jul ’03 N1>N2; Nov ’03 X1>X2; Jan ’04, Feb ’04, Mar ’04, May ’04, Jun ‘04 N1>N2.

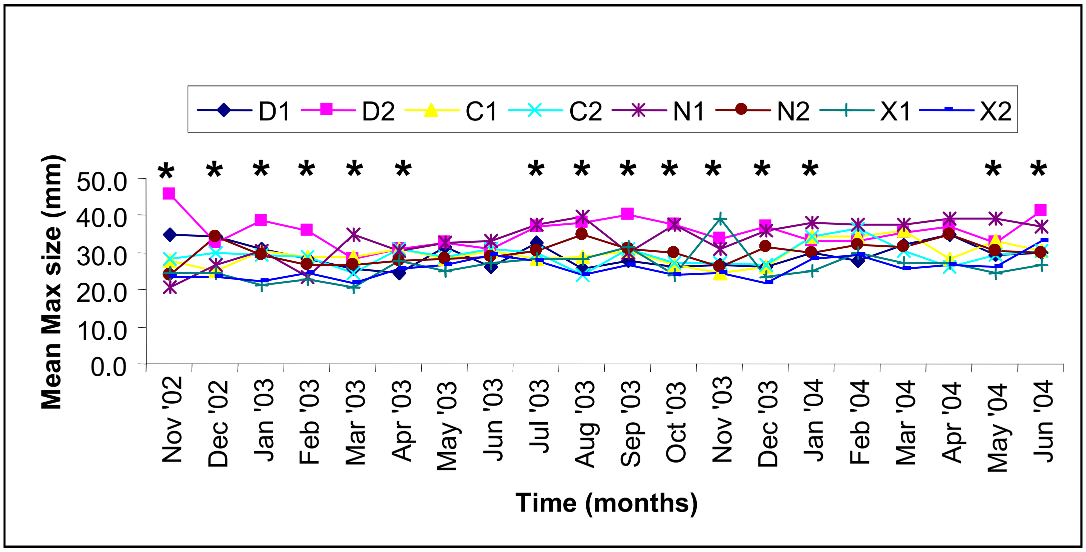


Fig. 3.1.5(b): Monthly mean maximum sizes (Standard errors (SE) were omitted for clarity) of *H. concolor* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Nov ’02, Jan ’03, Feb ’03, Apr ’03, Aug ’03, Sep ’03, Oct ’03, Nov ’03, Dec ’03, Jun ’04 D2>D1; Dec ’02 N2>N1; Mar ’03, Jul ’03, Oct ’03, Jan ’04, May ’04, Jun ’04 N1>N2; Nov ’03 X1>X2.

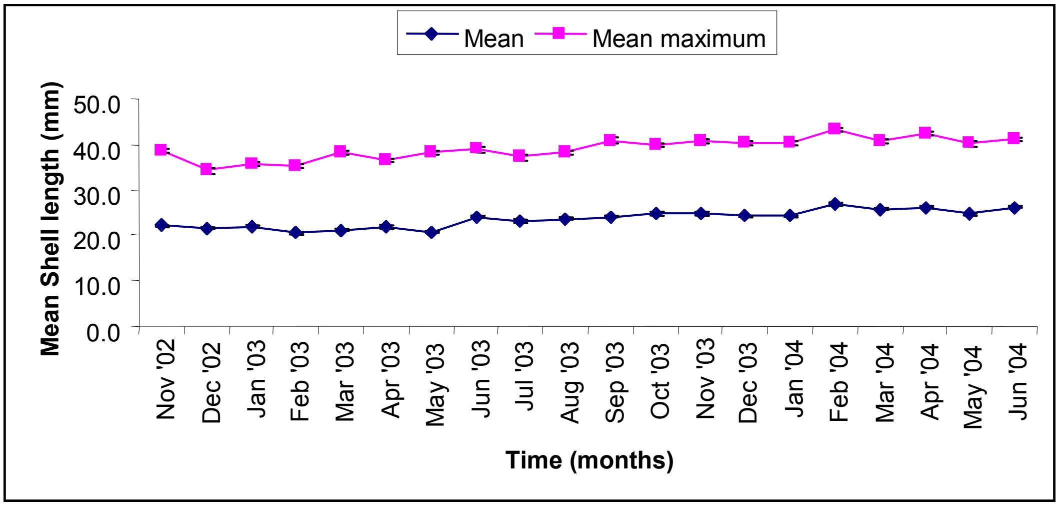


Fig. 3.2.1: Mean and mean maximum (±SE) shell length of *S. longicosta* averaged over all sites.

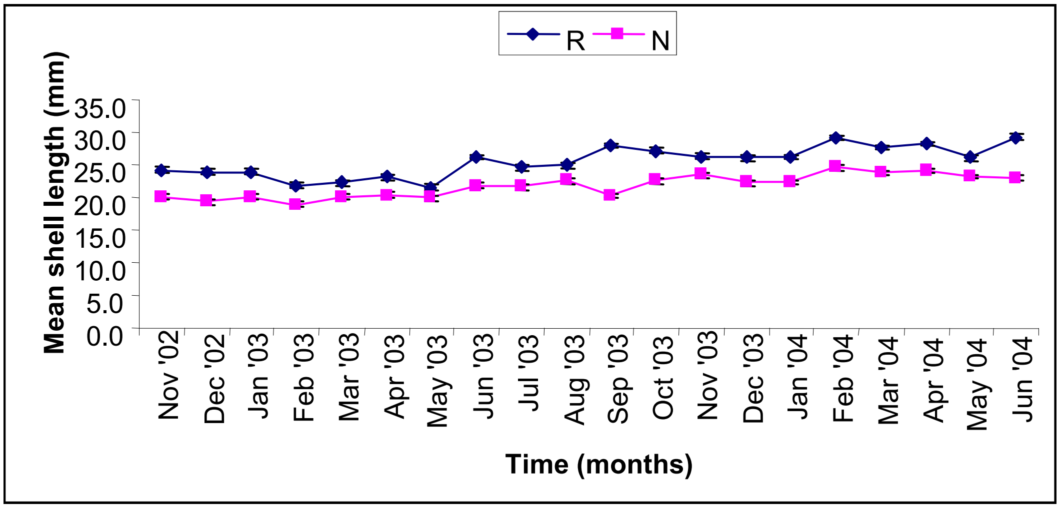


Fig. 3.2.2: Mean (±SE) shell length of *S. longicosta* in reserve (R) and non-reserve (N) sites.

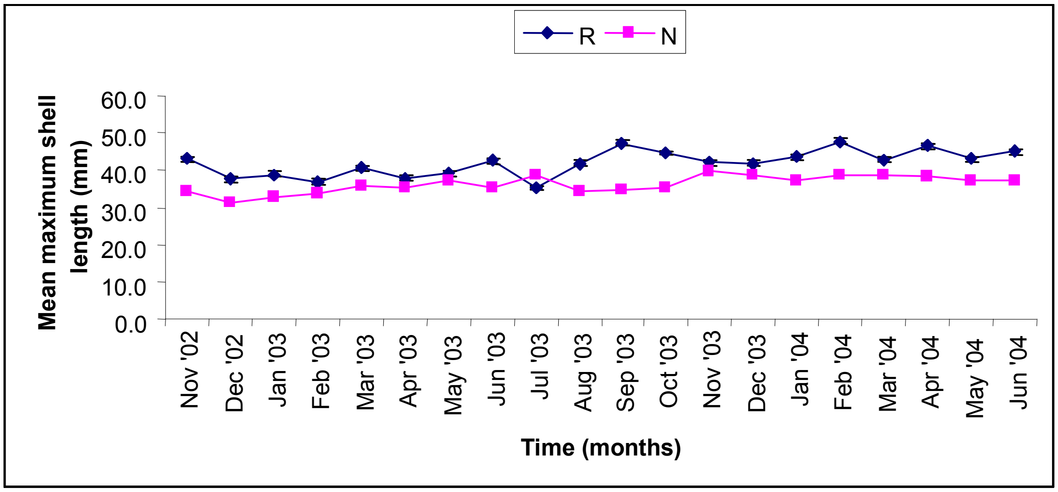


Fig. 3.2.3: Mean maximum (±SE) shell length of *S. longicosta* in reserve (R) and non-reserve (N) sites.

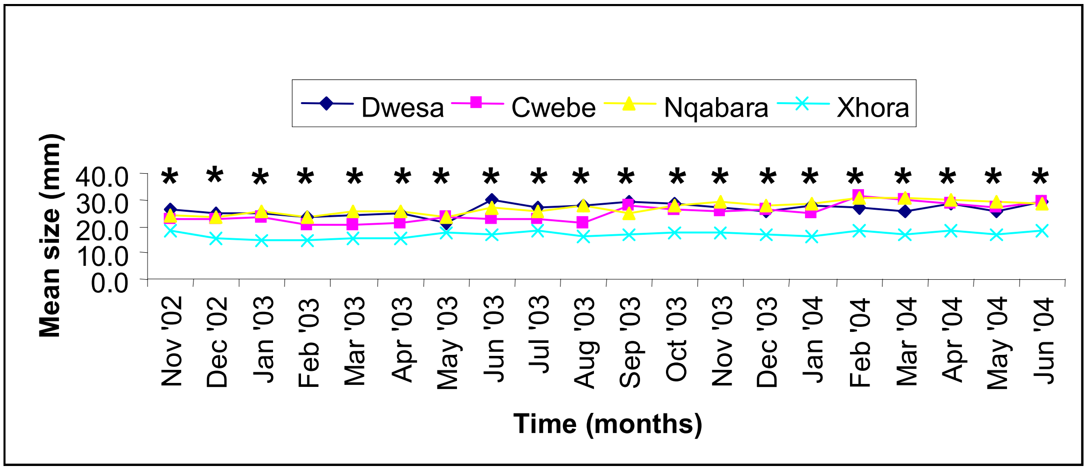


Fig. 3.2.4(a): Monthly mean sizes (Standard errors (SE) were omitted for clarity) of *S. longicosta* at each of the four study sites. * = significant difference ($p < 0.05$). Post-hoc test results: Nov '02, Dec '02, Jan '03, Feb '03, May '03, Oct '03, Nov '03, Dec '03, Apr '04, May '04 D=C=N>X; Mar '03, Apr '03, Jul '03, Aug '03, Jan '04 D=N>C>X; Jun '03 D>N>C>X; Sep '03, Jun '04 D=C>N>X; Feb '04 C>N>D>X; Mar '04 C=N>D>X.

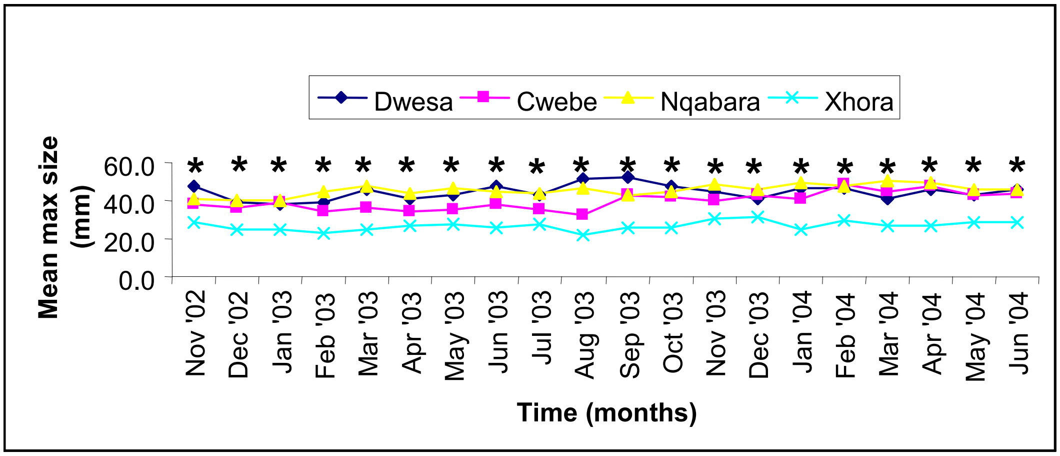


Fig. 3.2.4(b): Monthly mean maximum sizes (Standard errors (SE) were omitted for clarity) of *S. longicosta* at each of the four study sites. * = significant difference ($p < 0.05$). D = Dwesa, C = Cwebe, N = Nqabara and X = Xhora. Post-hoc test results: Nov '02, Sep '03, Oct '03 D>N=C>X; Dec '02, Mar '03, Apr '03, May '03 Jul '03, Jan '04, Feb '04 D=N>C>X; Jan '03, Dec '03, Apr '04, May '04, Jun '04 C=N=D>X; Feb '03, Nov '03, Mar '04 N>D>C>X; Jun '03, Aug '03 D>N>C>X.

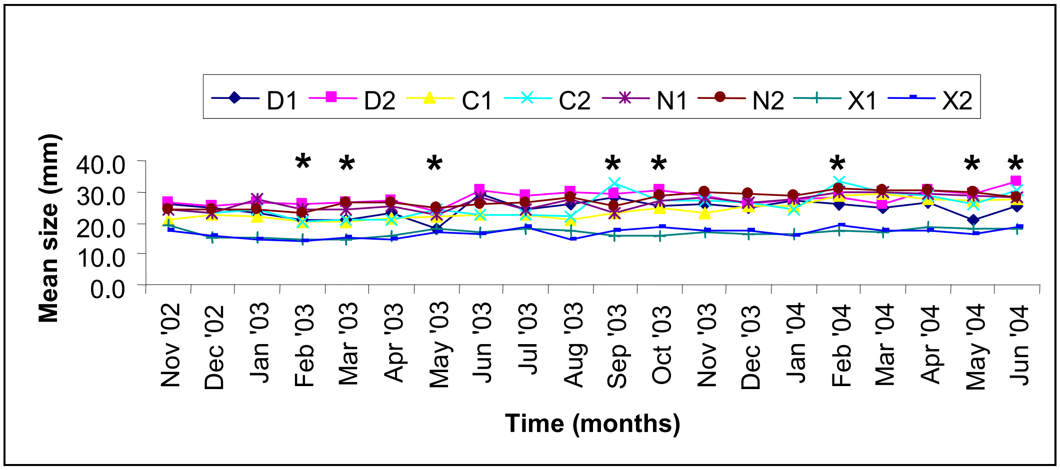


Fig. 3.2.5(a): Monthly mean sizes (Standard errors (SE) were omitted for clarity) of *S. longicosta* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Feb'03, Mar '03, May '03, Oct '03, May '04, Jun '04 D2>D1; Sep '03, Feb '04 C2>C1.

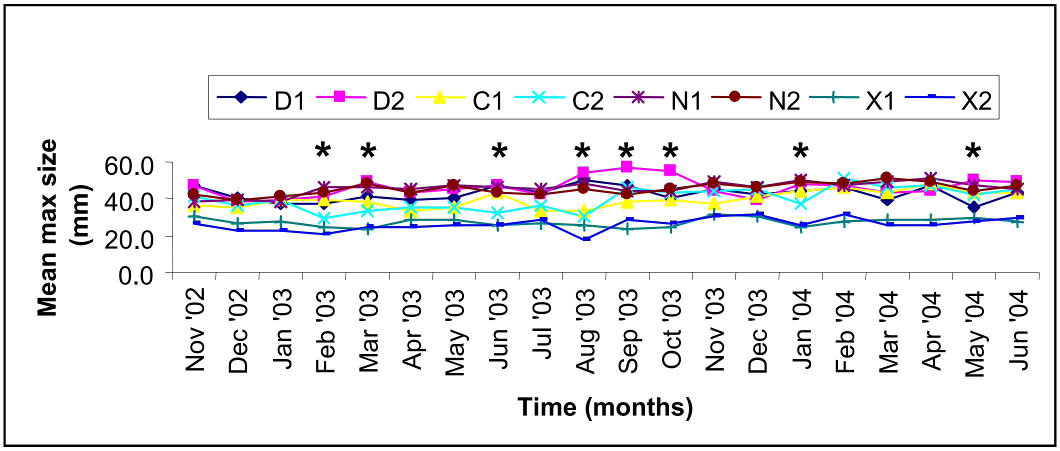


Fig. 3.2.5(b): Monthly mean maximum sizes (Standard errors (SE) were omitted for clarity) of *S. longicosta* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Feb'03, Jun '03, Jan '04 C1>C2; Mar '03, Sep '03, Oct '03, May '04 D2>D1; Aug '03 X1>X2; Sep '03 C2>C1.

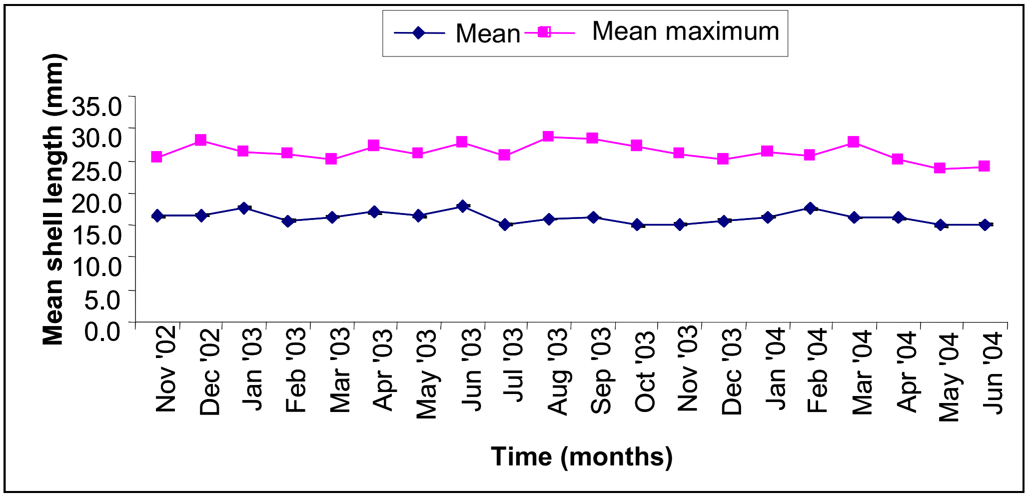


Fig. 3.3.1: Mean and mean maximum (±SE) shell length of *C. capensis* averaged over all sites.

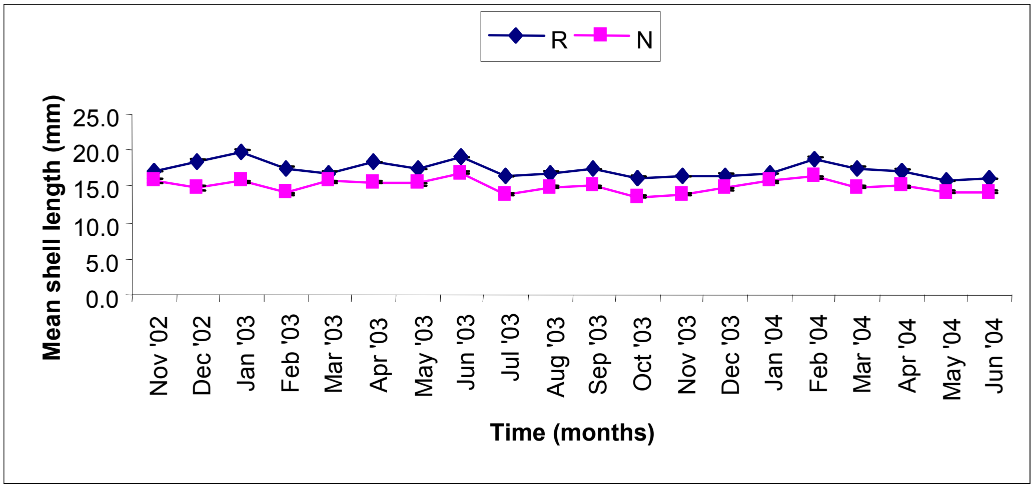


Fig. 3.3.2: Mean (±SE) shell length of *C. capensis* in reserve (R) and non-reserve (N) sites.

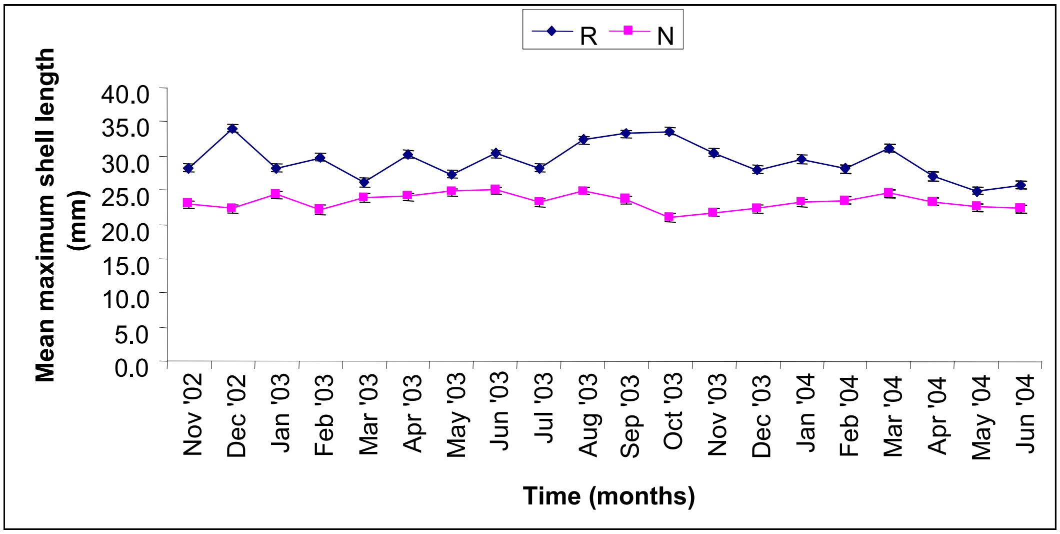


Fig. 3.3.3: Mean maximum (±SE) shell length of *C. capensis* in reserve (R) and non-reserve (N) sites.

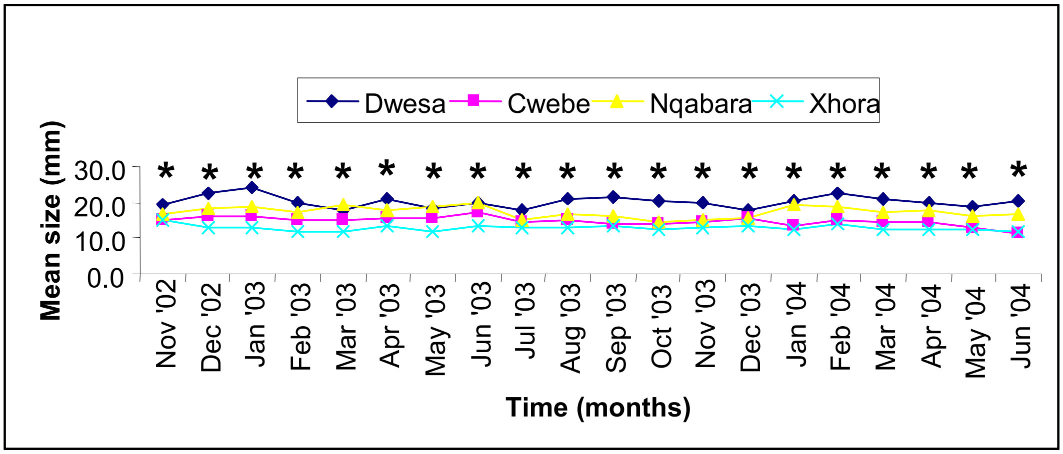


Fig. 3.3.4(a): Monthly mean sizes (Standard errors (SE) were omitted for clarity) of *C. capensis* at each of the four study sites. * = significant difference ($p < 0.05$). Post-hoc test results: Nov '02, Dec '02, Jan '03, Feb '03, Apr '03, Sep '03 Jan '04, Feb '04, Mar '04, Apr '04 May '04, Jun '04 D>N>X=C; Mar '03, May '03, Jun '03 N=D>C>X; Jul '03, Aug '03, Oct '03, Nov '03, Dec '03 D>C=N>X.

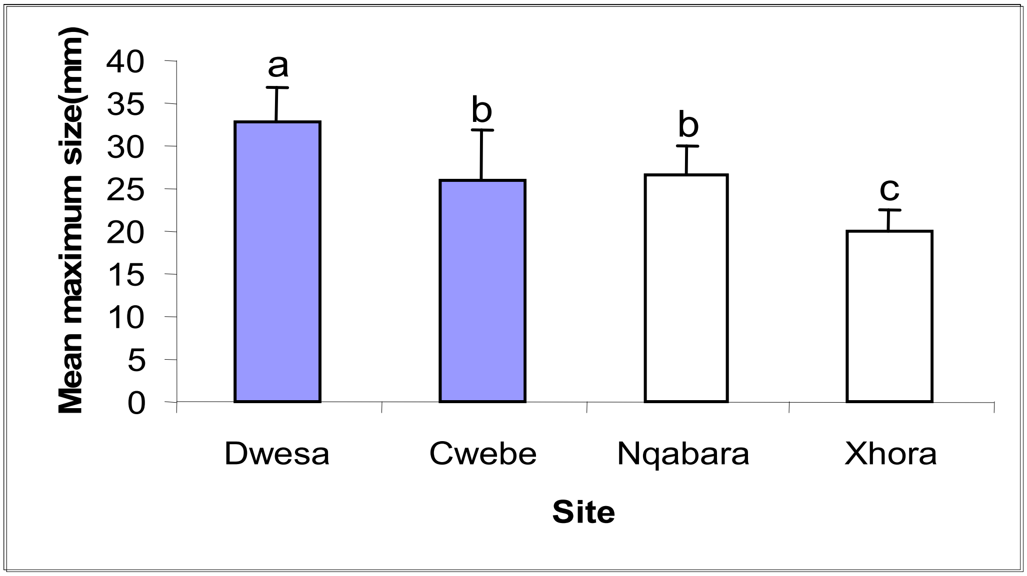


Fig. 3.3.4(b): Mean maximum (+SE) size of *C. capensis* at each of the four the study sites. Letters above the bar columns represent homogenous groups.

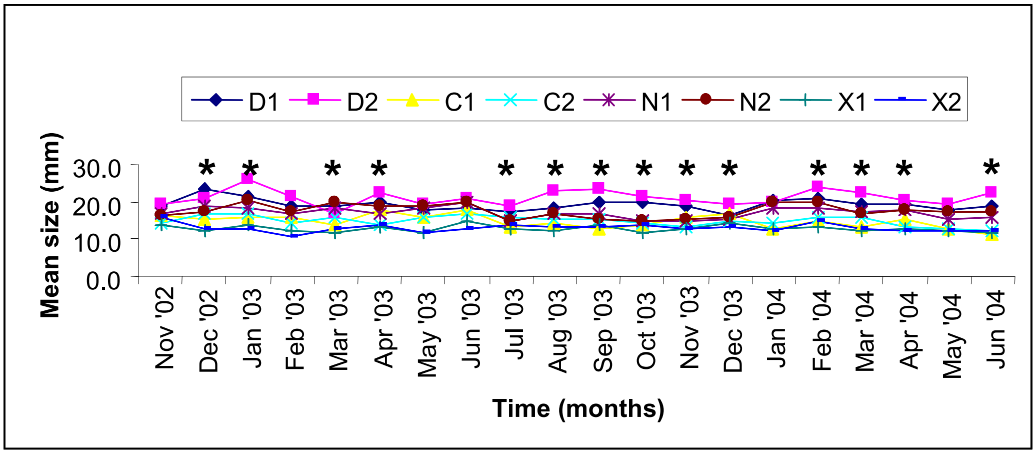


Fig. 3.3.5(a): Monthly mean sizes (Standard errors (SE) were omitted for clarity) of *C. capensis* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Dec '02 D1>D2; Jan '03, Apr '03, Aug '03, Sep '03, Dec '03, Feb '04, Mar '04, Jun '04 D2>D1; Mar '03, Jul '03, Sep '03, Mar '04 C2>C1; Apr '03, Nov '03, Dec '03, Apr '04 C1>C2; Oct '03 X2>X1.

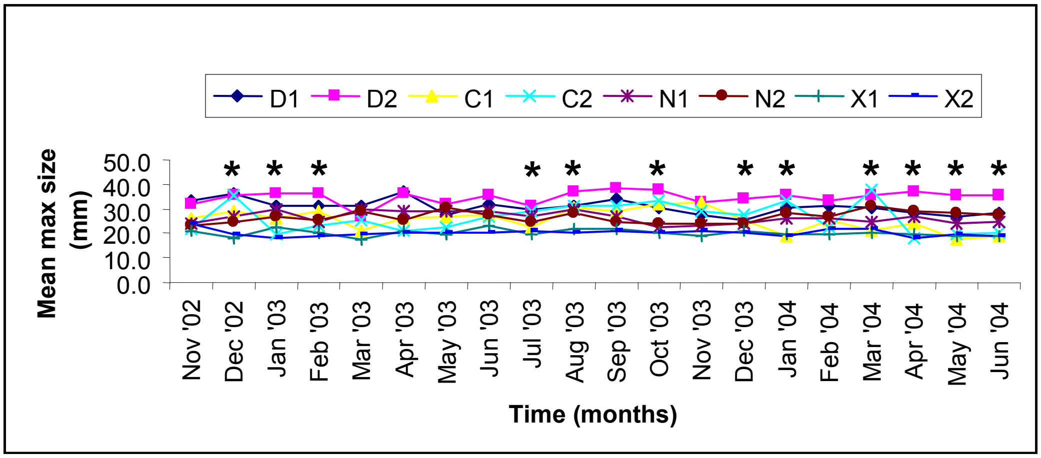


Fig. 3.3.5(b): Monthly mean maximum sizes (Standard errors (SE) were omitted for clarity) of *C. capensis* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Dec '02, Jul '03, Jan '04, Mar '04 C2>C1; Jan '03, Feb '03, Apr '04 C1>C2; Aug '03, Oct '03, Dec '03, May '04, Apr '04, Jun '04 D2>D1; N2>N1.

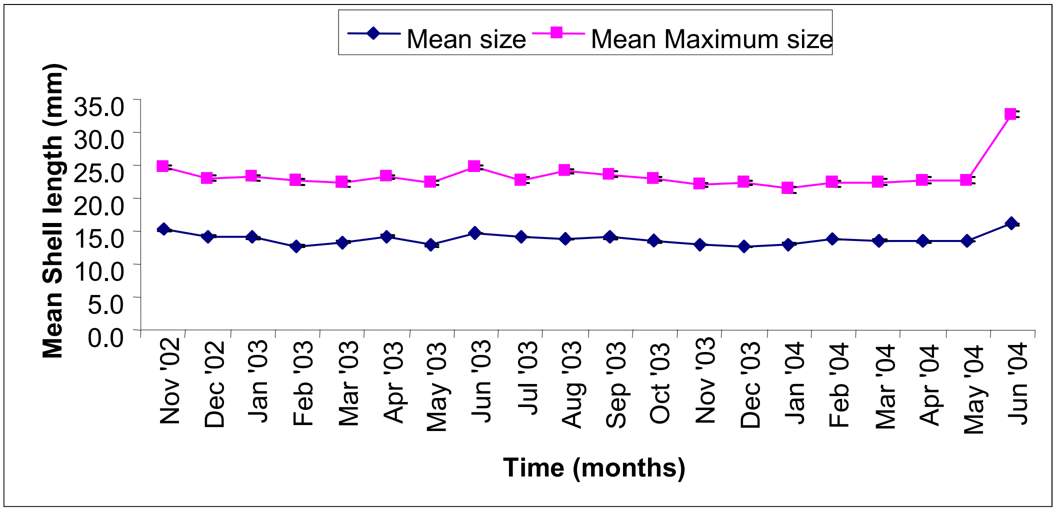


Fig. 3.4.1: Mean and mean maximum (±SE) shell length of *S. granularis* averaged over all sites.

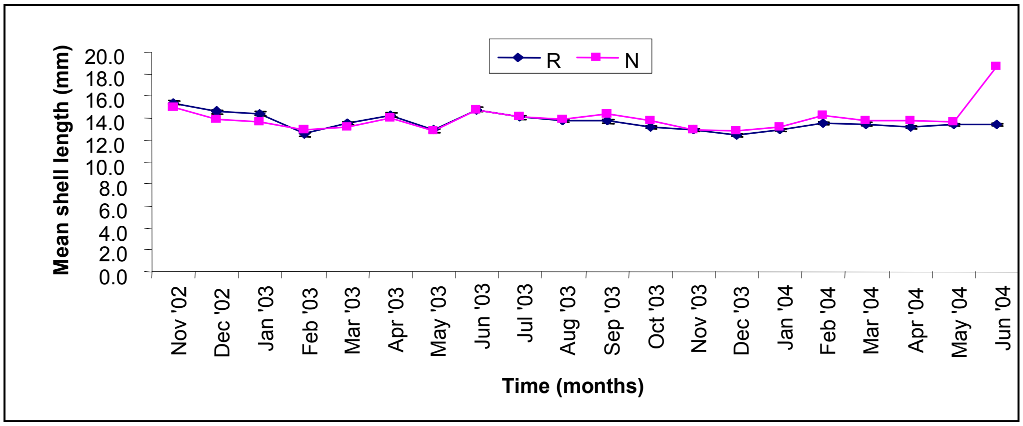


Fig. 3.4.2: Mean (±SE) shell length of *S. granularis* in reserve (R) and non-reserve (N) sites.

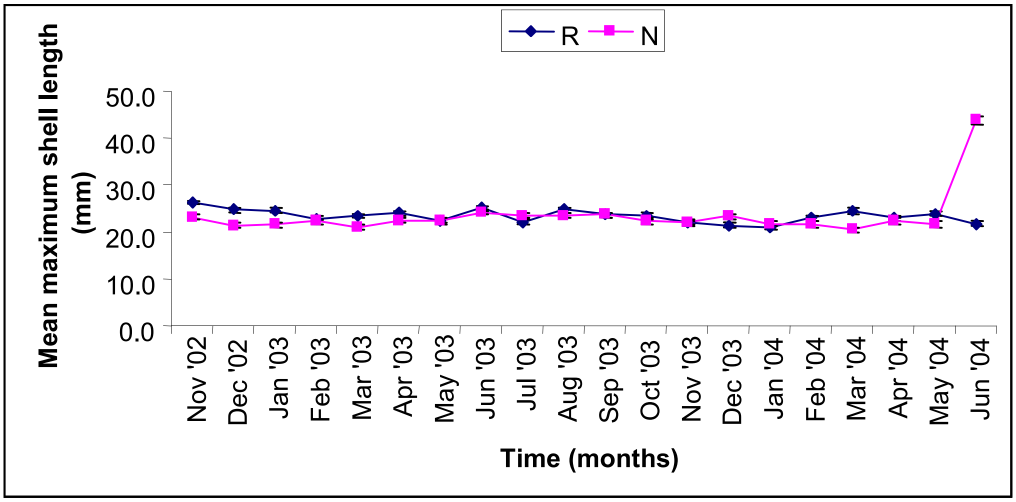


Fig. 3.4.3: Mean maximum (±SE) shell length of *S. granularis* in reserve (R) and non-reserve (N) sites.

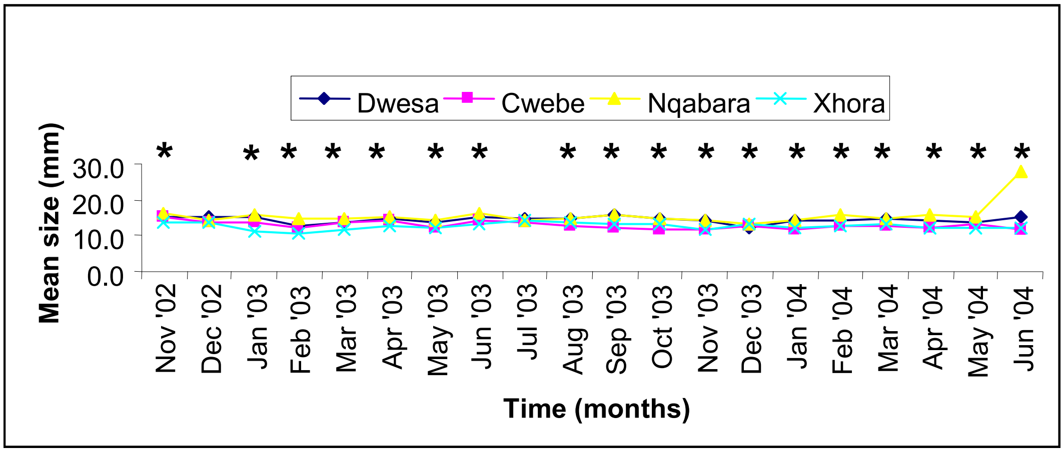


Fig. 3.4.4(a): Monthly mean sizes (Standard errors (SE) were omitted for clarity) of *S. granularis* at each of the four study sites. * = significant difference ($p < 0.05$). Post-hoc test results: Nov '02, Mar '03, Apr '03 C=D=N>X; Jan '03 D>N>C>X; Feb '03 N>D=C>X; May '03, Jun '03, Nov '03, Jan '04, Feb '04, Apr '04, Mar '04, May '04 D=N>X=C; Aug '03, Sep '03 D=N=X>C; Oct '03 D=N>X>C; Dec '03 C=N=X>D; Jun '04 N>D>C=X.

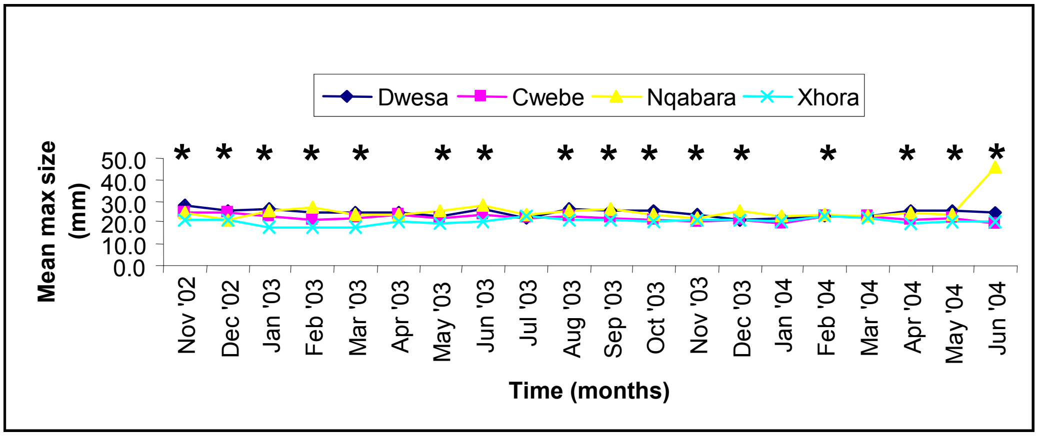


Fig. 3.4.4(b): Monthly mean maximum sizes (Standard errors (SE) were omitted for clarity) of *S. granularis* at each of the four study sites. * = significant difference ($p < 0.05$). Post-hoc test results: Nov ’02, Mar ’03, May ’04 D>C=N>X; Dec ’02, Jan ’03, May ’03 D=C=N>X; Feb ’03, Jun ’03 N=D>C>X; Aug ’03, Oct ’03, Apr ’04 D>N>C>X; Sep ’03 D=N>C=X; Nov ’03 D>N=C=X; Dec ’03 N>D=C=X; Feb’04 C>N=D=X; Jun ’04 N>D>C=X.

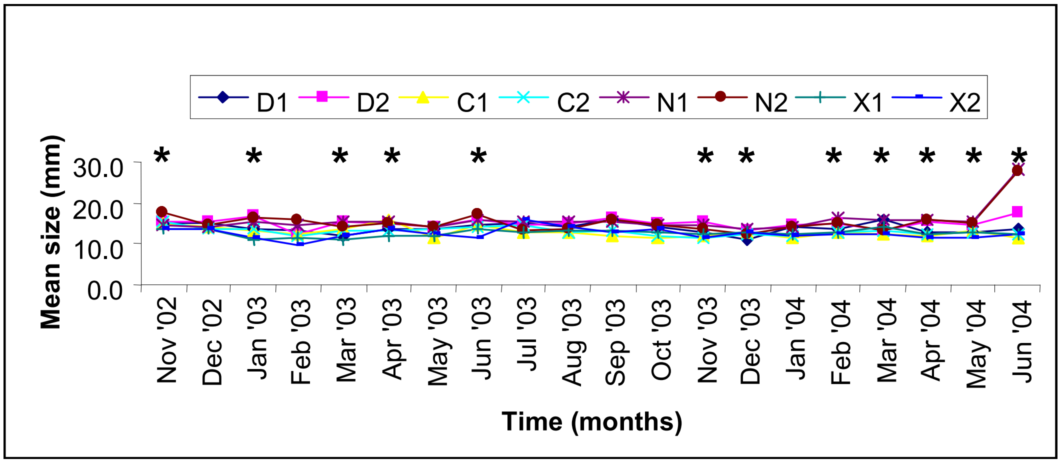


Fig. 3.4.5(a): Monthly mean sizes (Standard errors (SE) were omitted for clarity) of *S. granularis* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Nov '02 N2>N1; Jan '03, Mar '03, Nov '03, Dec '03, Feb '04, Apr '04, May '04, Jun '04 D2>D1; Apr '03 C1>C2; Jul '03, Feb '04, Mar '04 N1>N2, Mar '04 X2>X1; Mar '04 D1>D2.

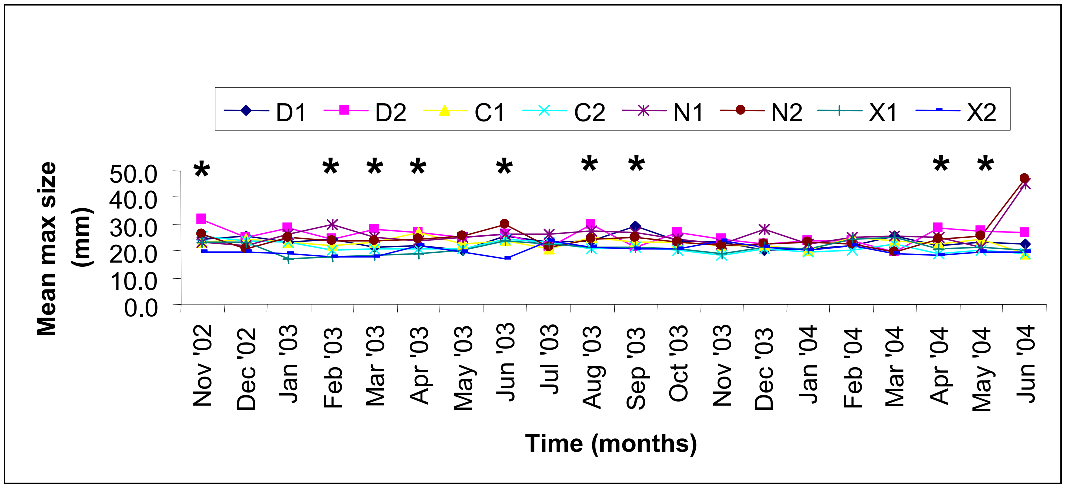


Fig. 3.4.5(b): Monthly mean maximum sizes (Standard errors (SE) were omitted for clarity) of *S. granularis* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Nov ’02, Sep ’03 D1>D2; Feb ’03, Mar ’04 N1>N2; Mar ’03, Aug ’03, Mar ’04, ; Apr ’04 D2>D1; Apr ’03 C1>C2; Jun ’03, Mar ’04 X1>X2.

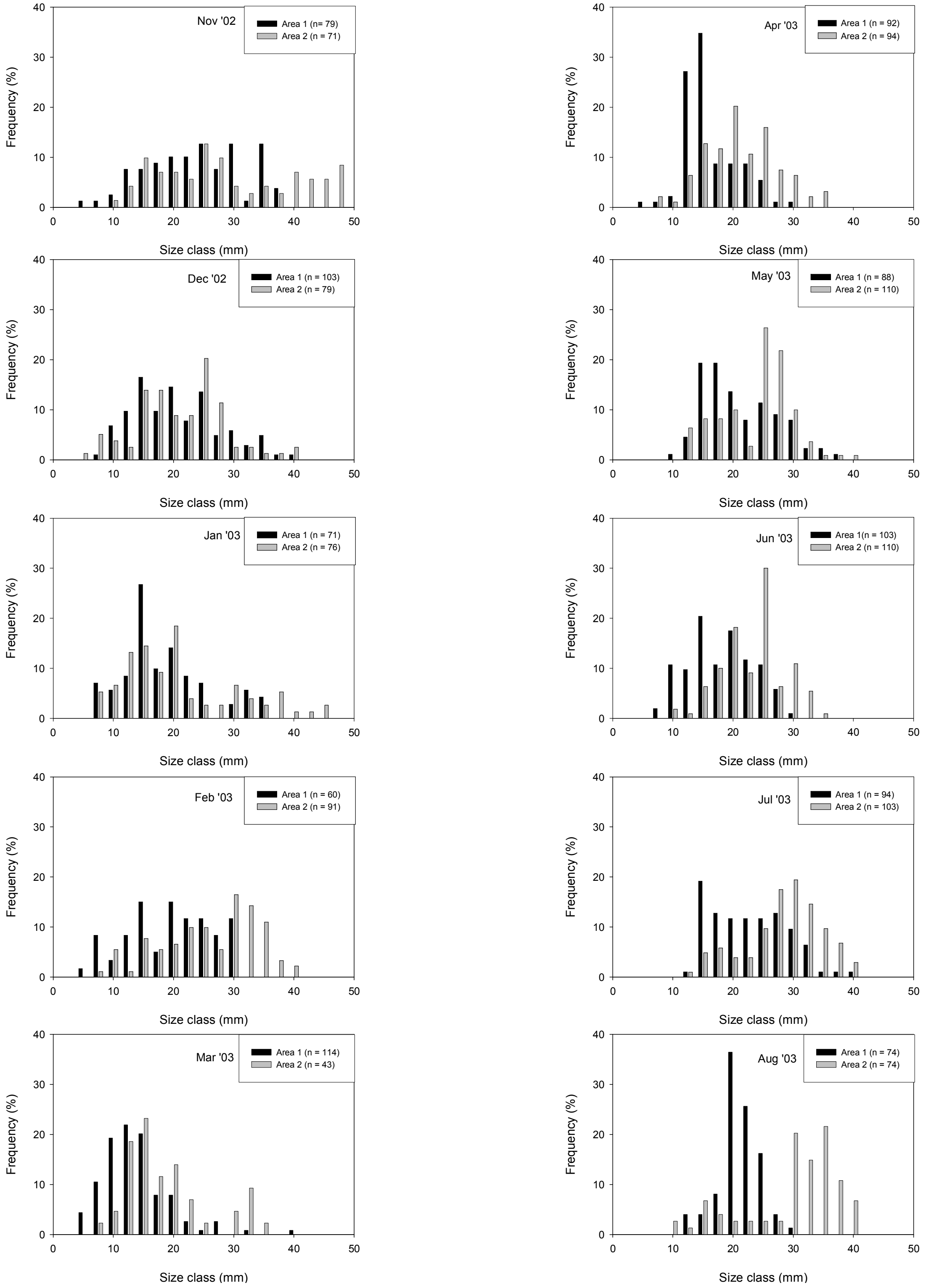


Fig. 3.5.1(a): Size-frequency distribution of *H. concolor* through sampling period at Dwesa.

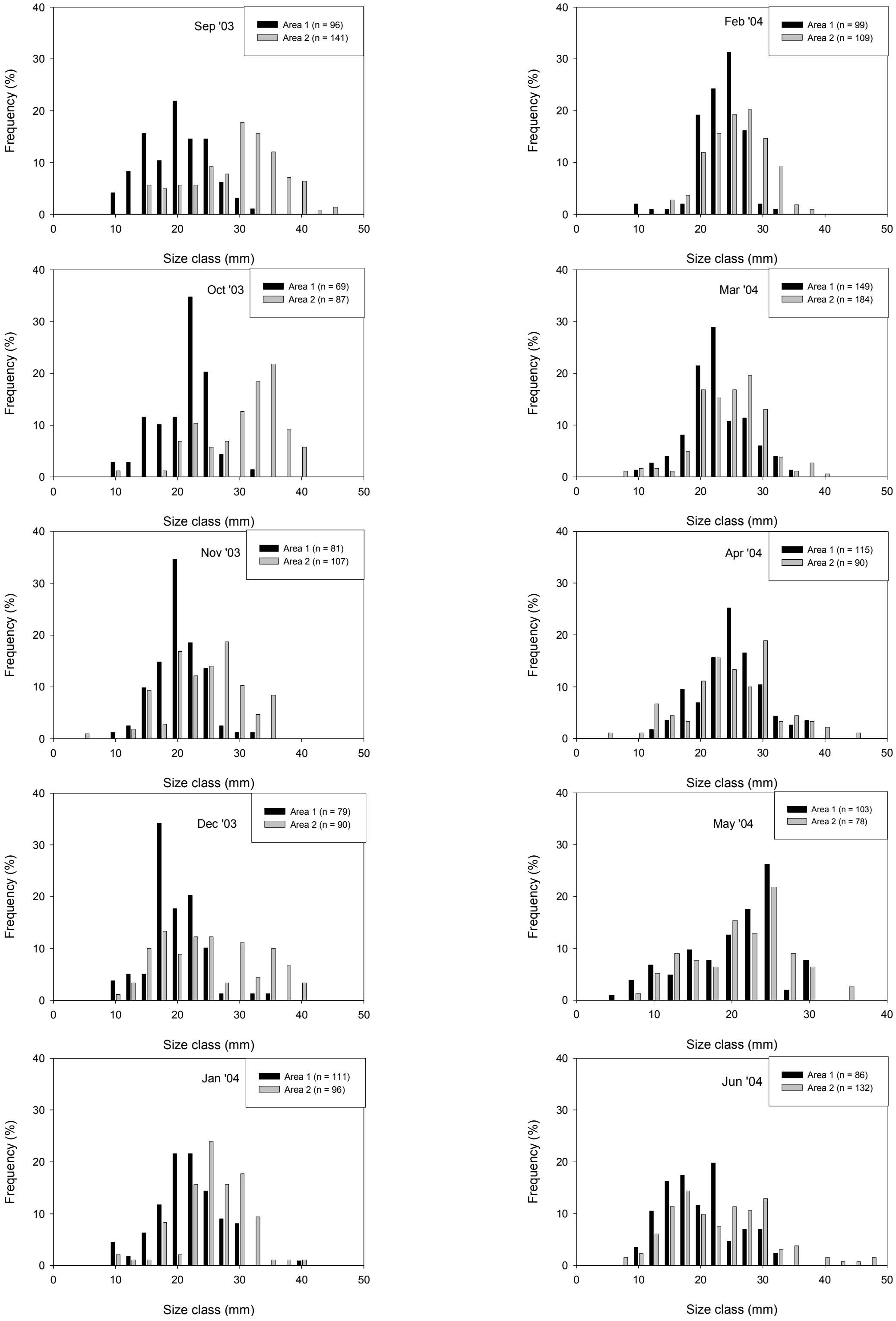


Fig. 3.5.1(a) (Continued): Size-frequency distribution of *H. concolor* through sampling period at Dwesa.

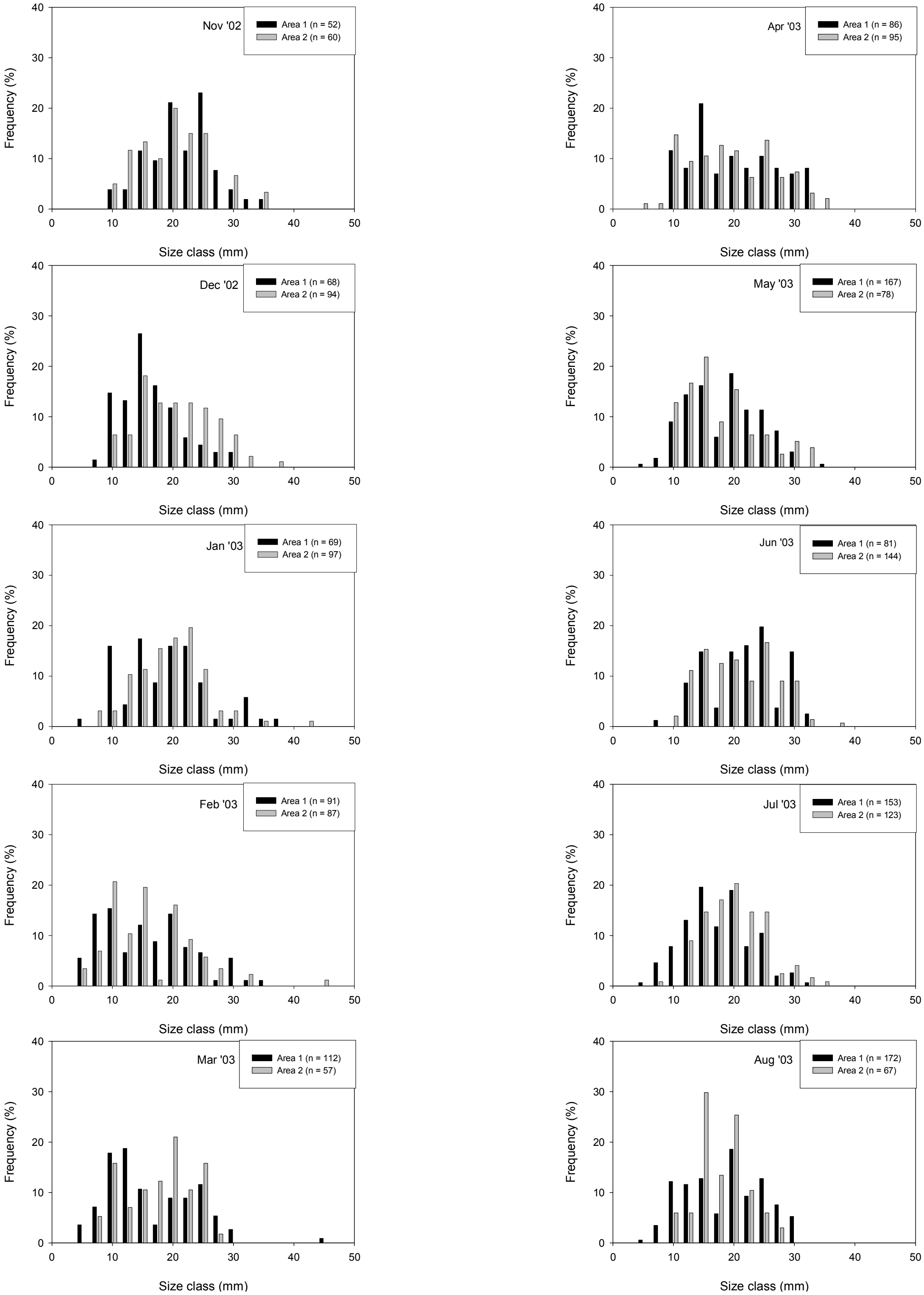


Fig. 3.5.2(b): Size-frequency distribution of *H. concolor* through sampling period at Cwebe.

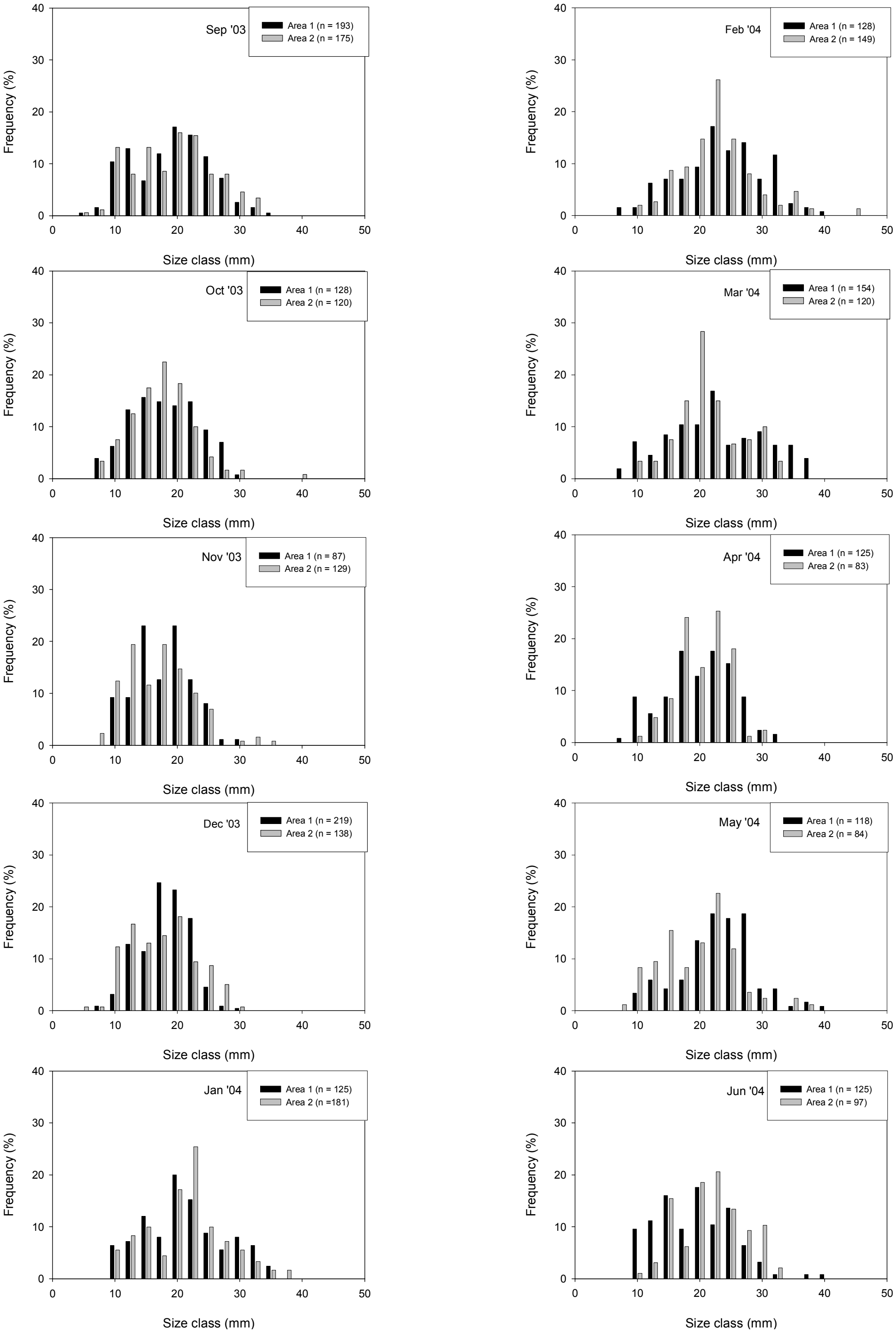


Fig. 3.5.2(b) (Continued): Size-frequency distribution of *H. concolor* through sampling period at Cwebe.

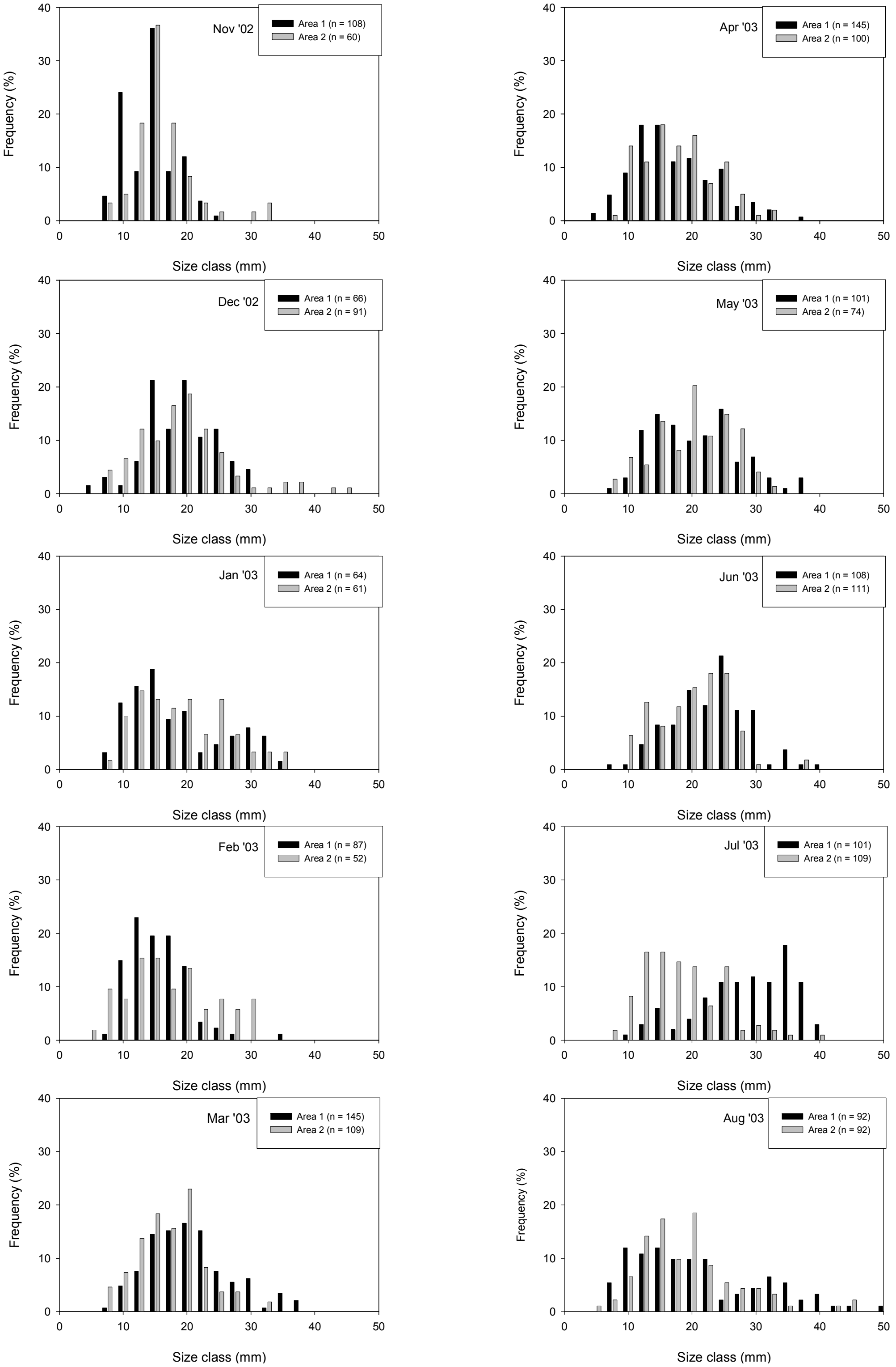


Fig. 3.5.3(c): Size-frequency distribution of *H. concolor* through sampling period at Nqabara.

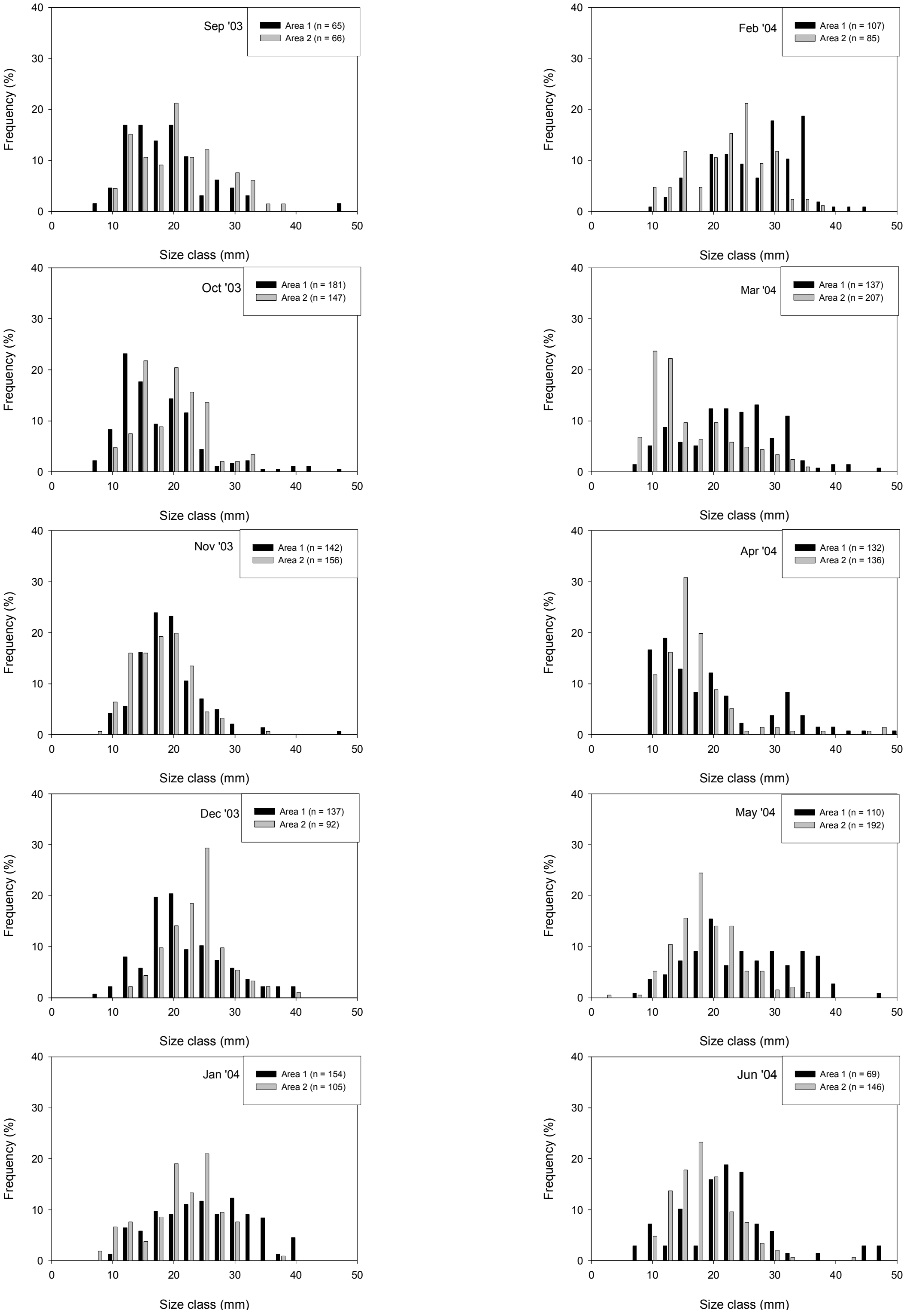


Fig. 3.5.3(c) (Continued): Size-frequency distribution of *H. concolor* through sampling period at Nqabara.

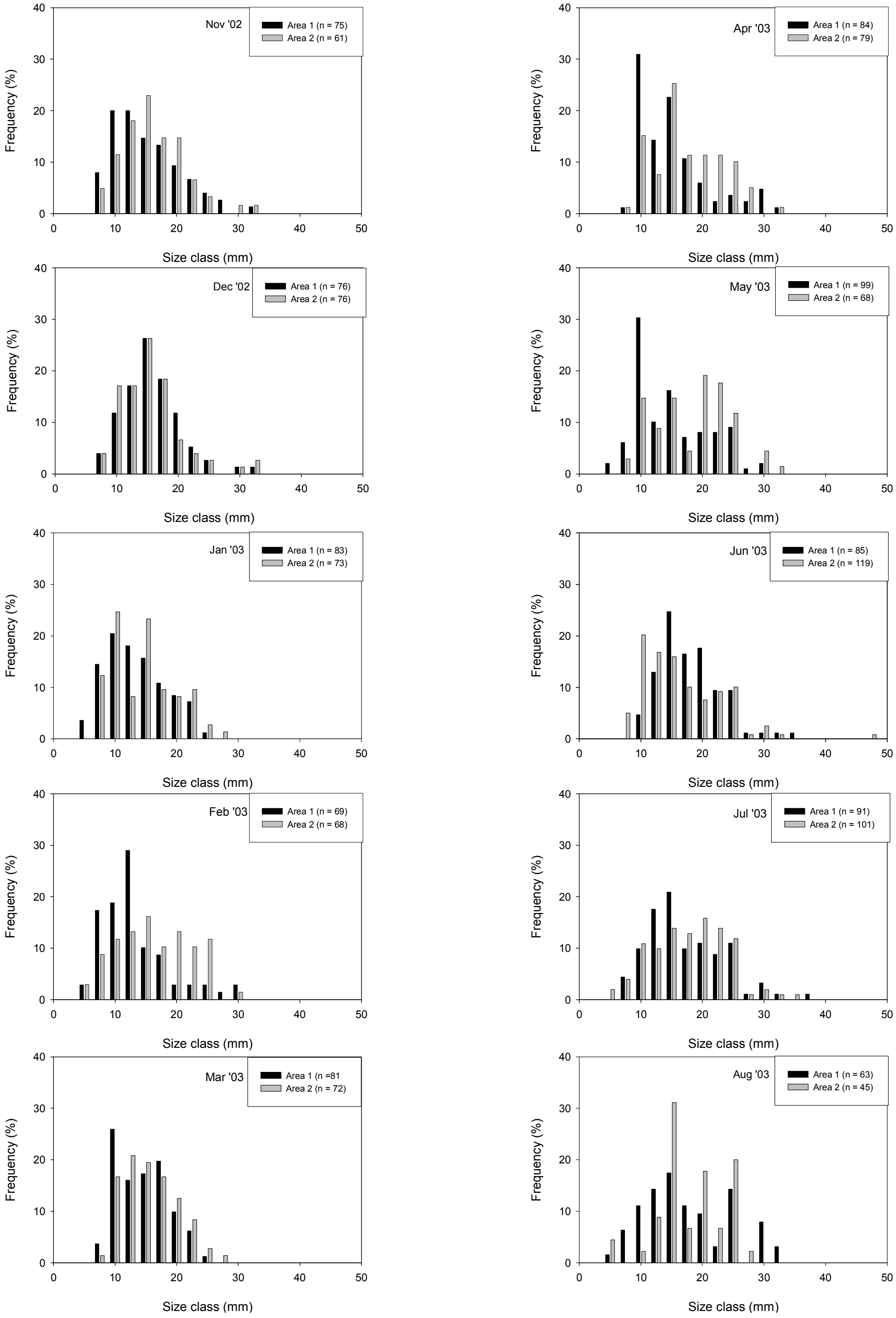


Fig. 3.5.4(d): Size-frequency distribution of *H. concolor* through sampling period at Xhora.

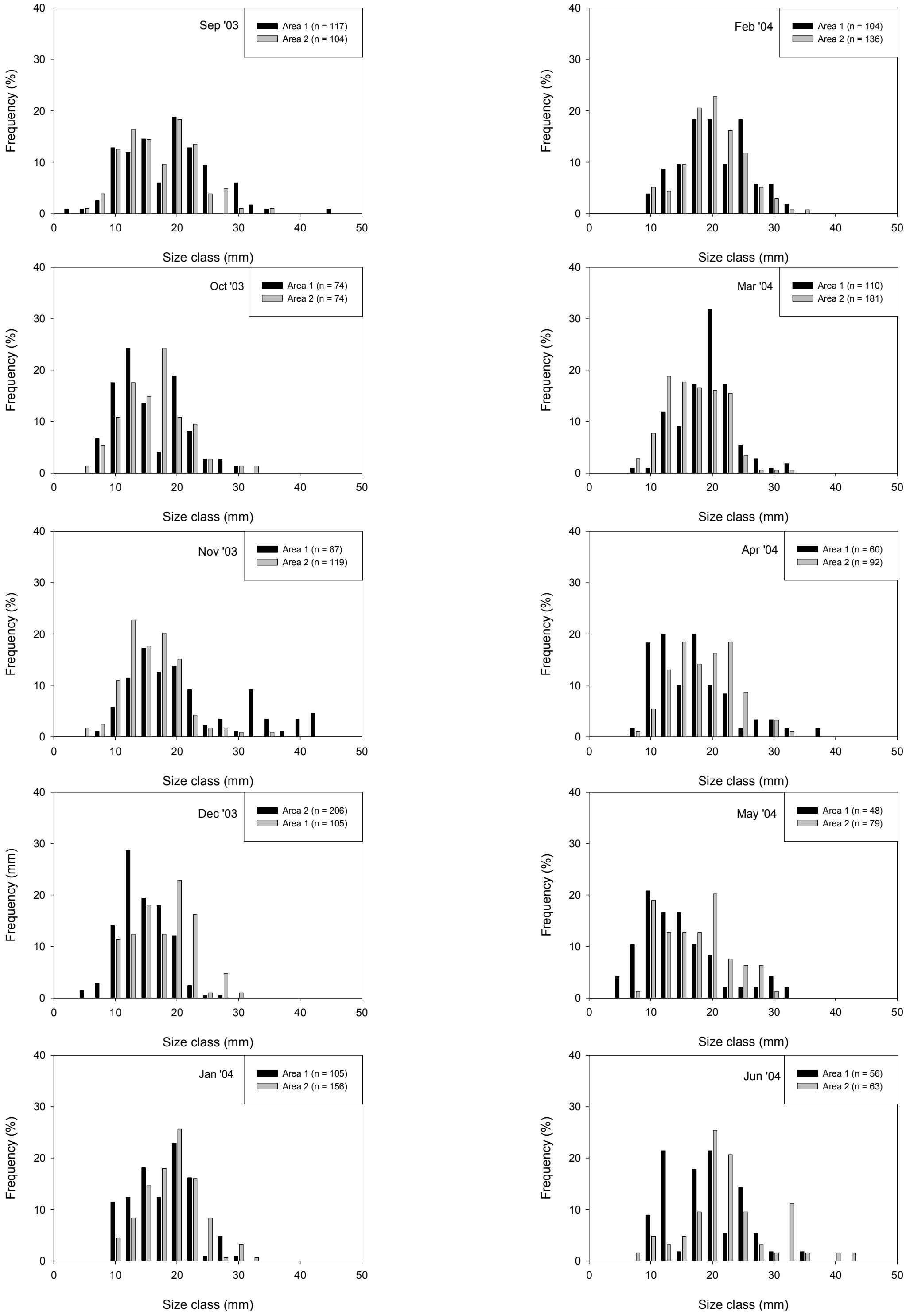


Fig. 3.5.4(d) (Continued): Size-frequency distribution of *H. concolor* through sampling period at Xhora.

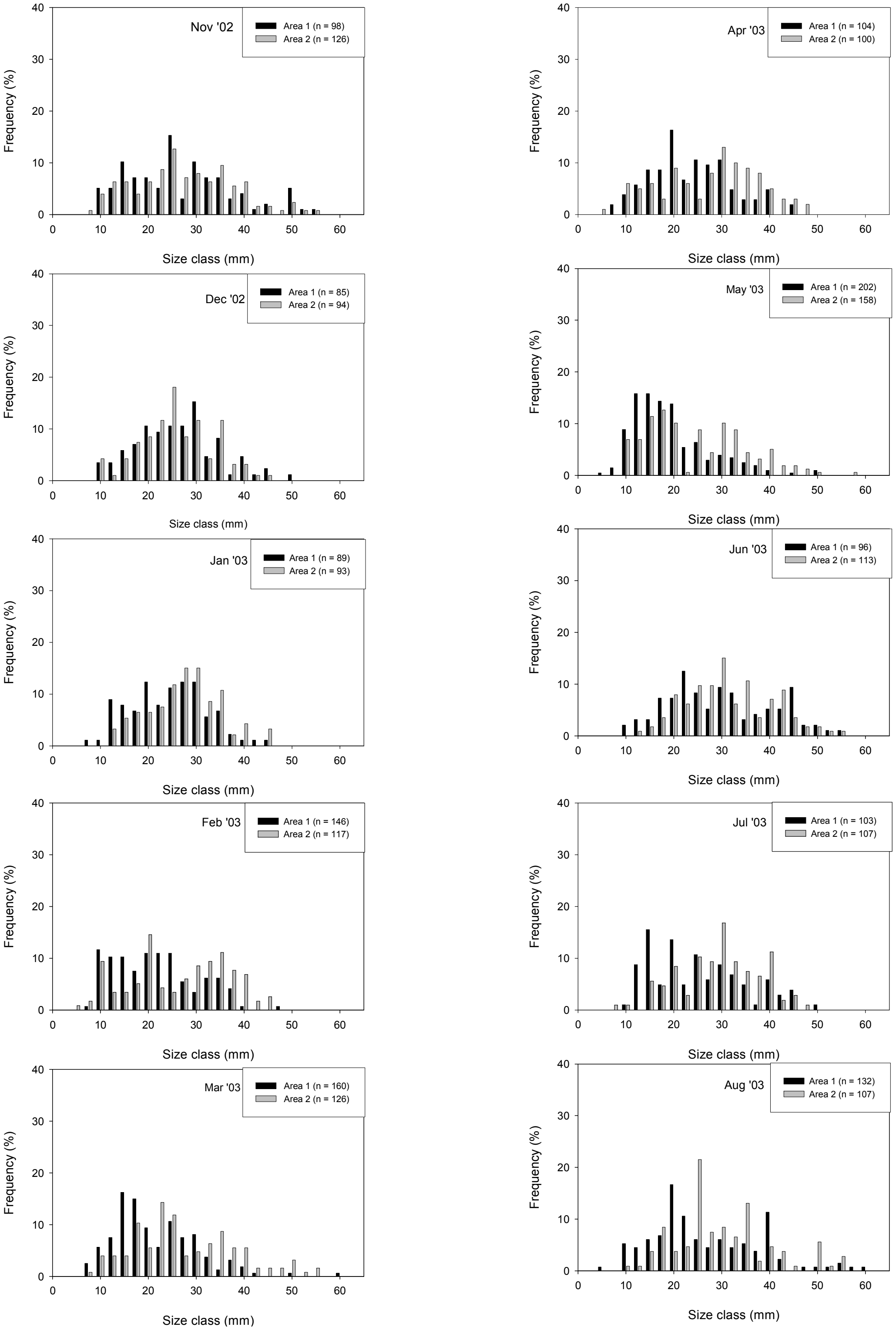


Fig. 3.6.1(a): Size-frequency distribution of *S. longicosta* through sampling period at Dwesa.

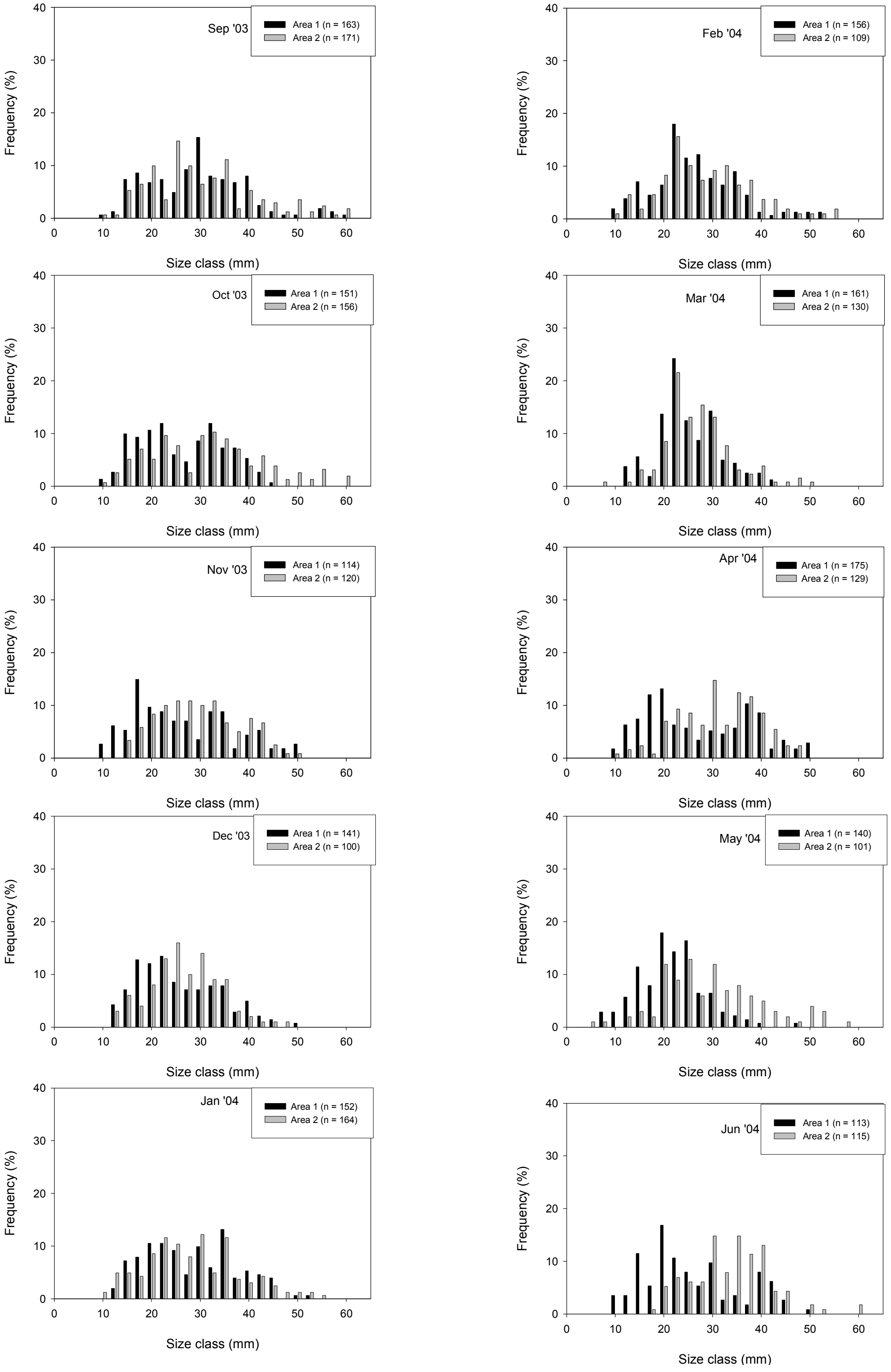


Fig. 3.6.1(a) (Continued): Size-frequency distribution of *S. longicosta* through sampling period at Dwesa.

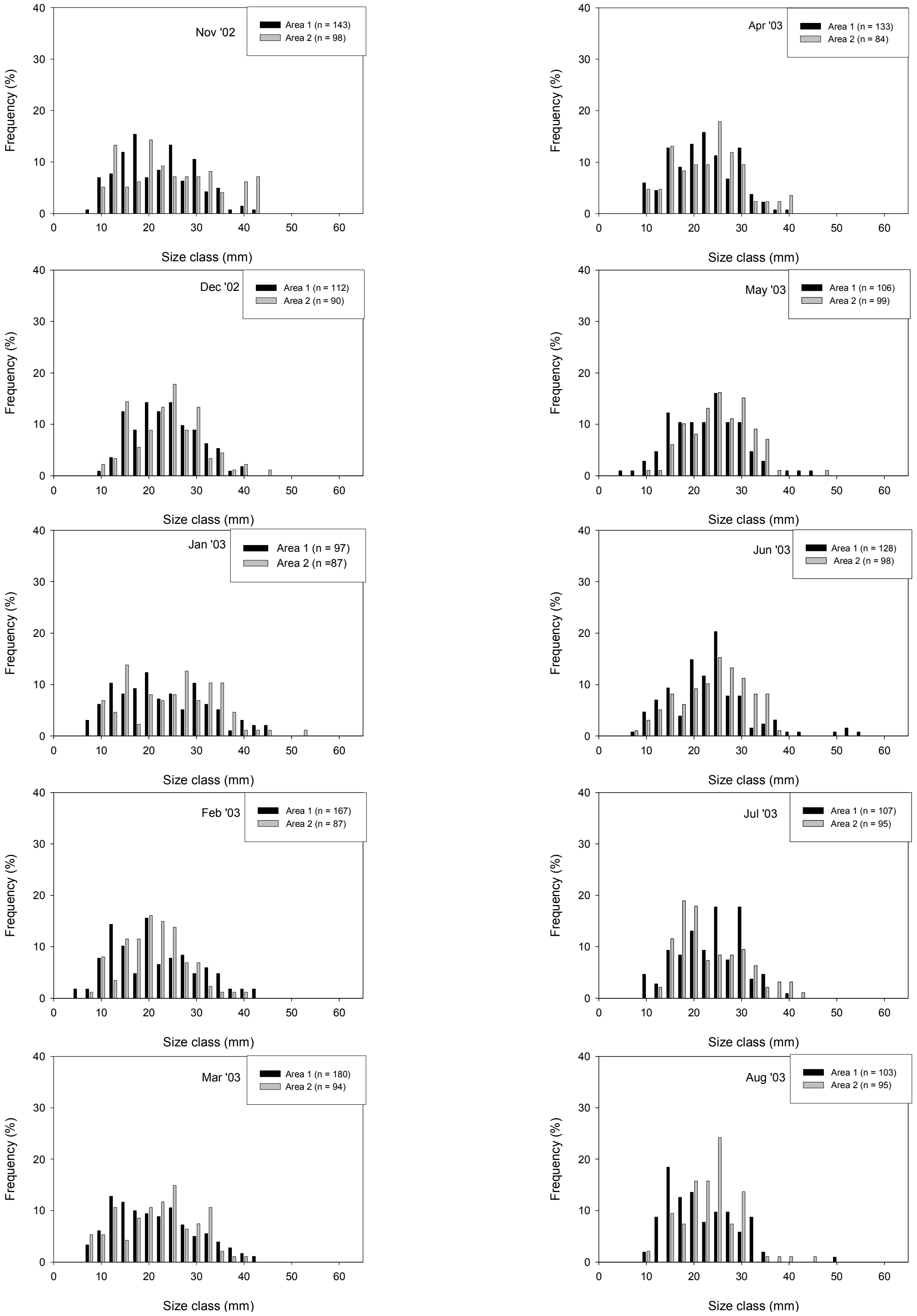


Fig. 3.6.2(b): Size-frequency distribution of *S. longicosta* through sampling period at Cwebe.

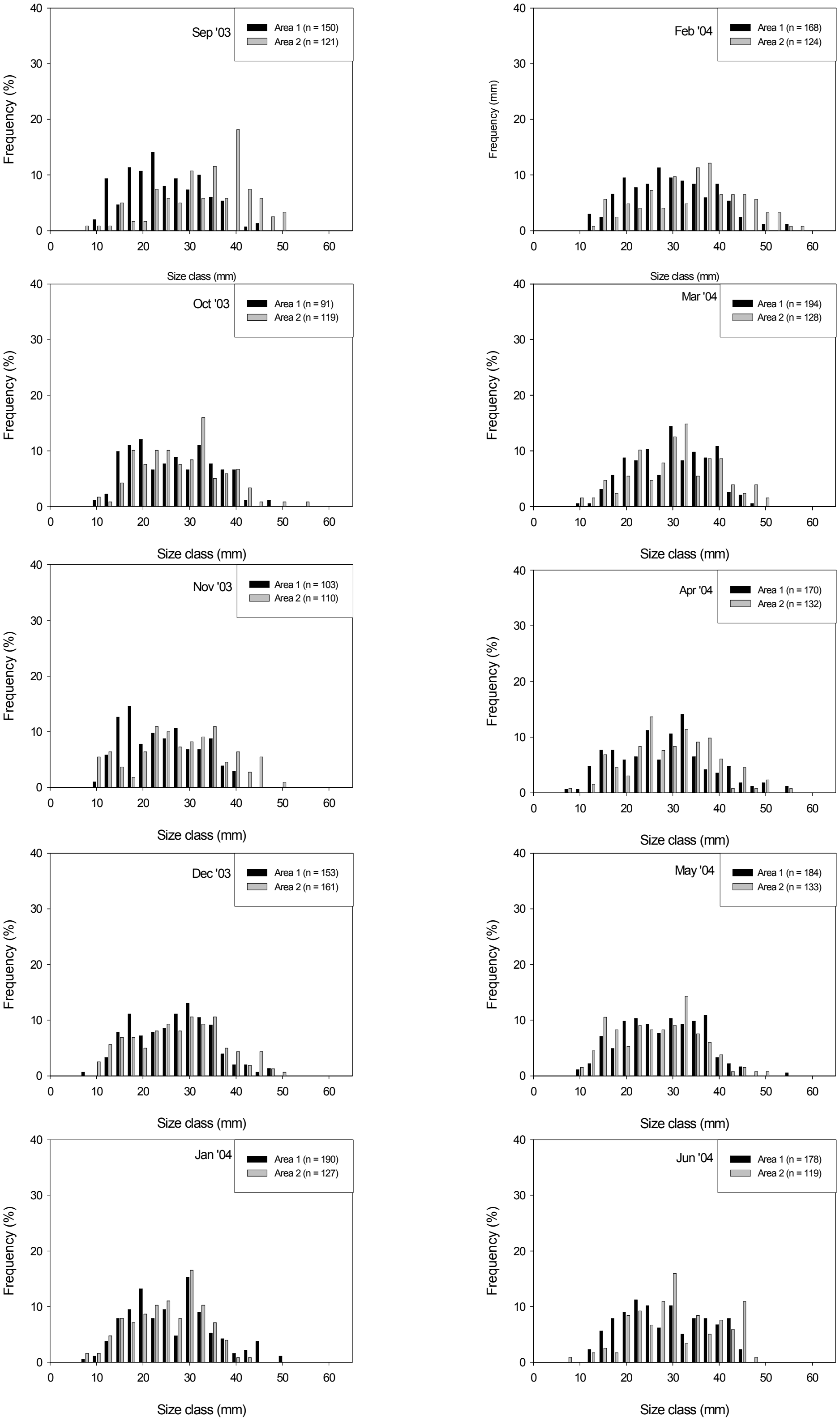


Fig. 3.6.2(b) (Continued): Size-frequency distribution of *S. longicosta* through sampling period at Cwebe.

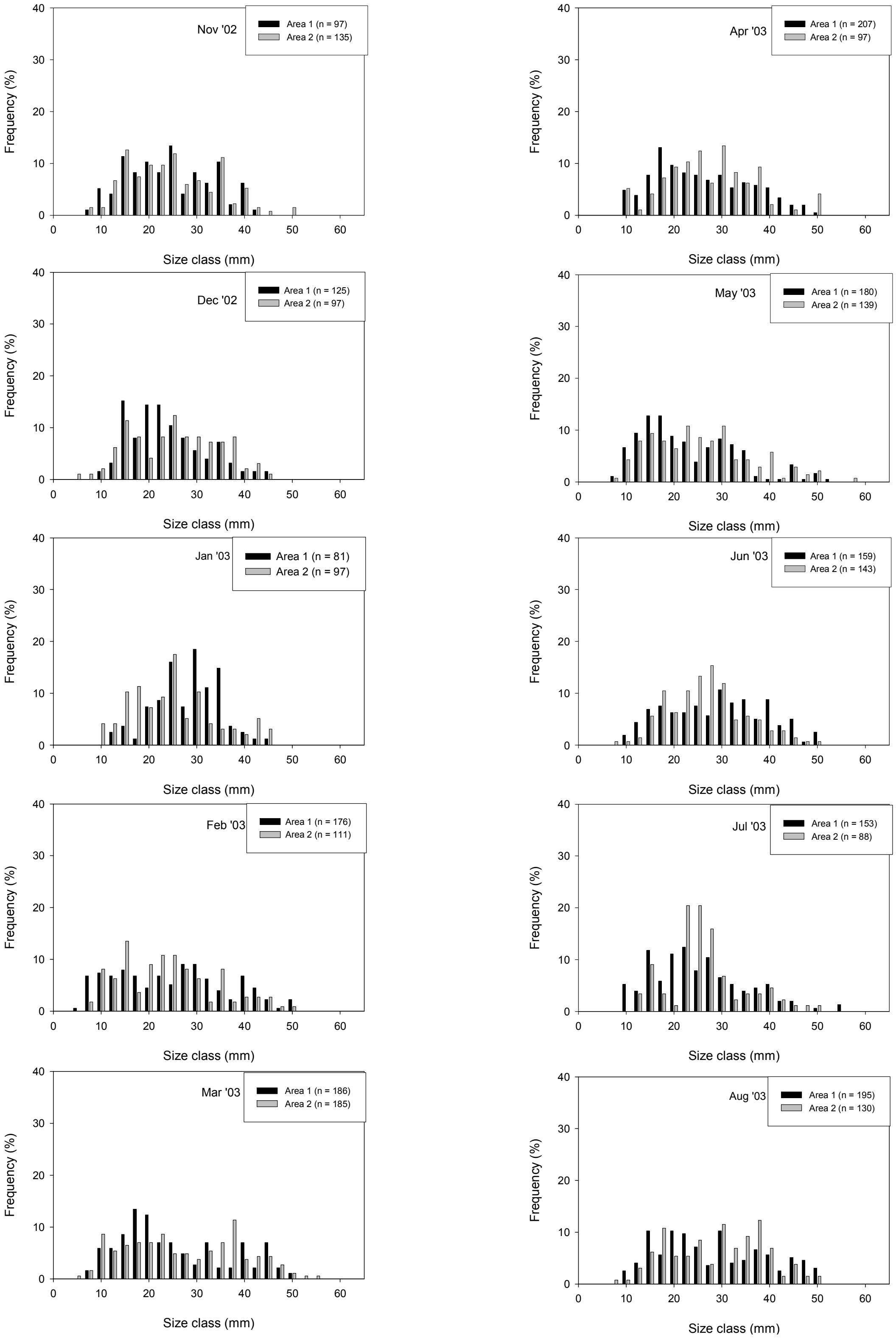


Fig. 3.6.3(c): Size-frequency distribution of *S. longicosta* through sampling period at Nqabara.

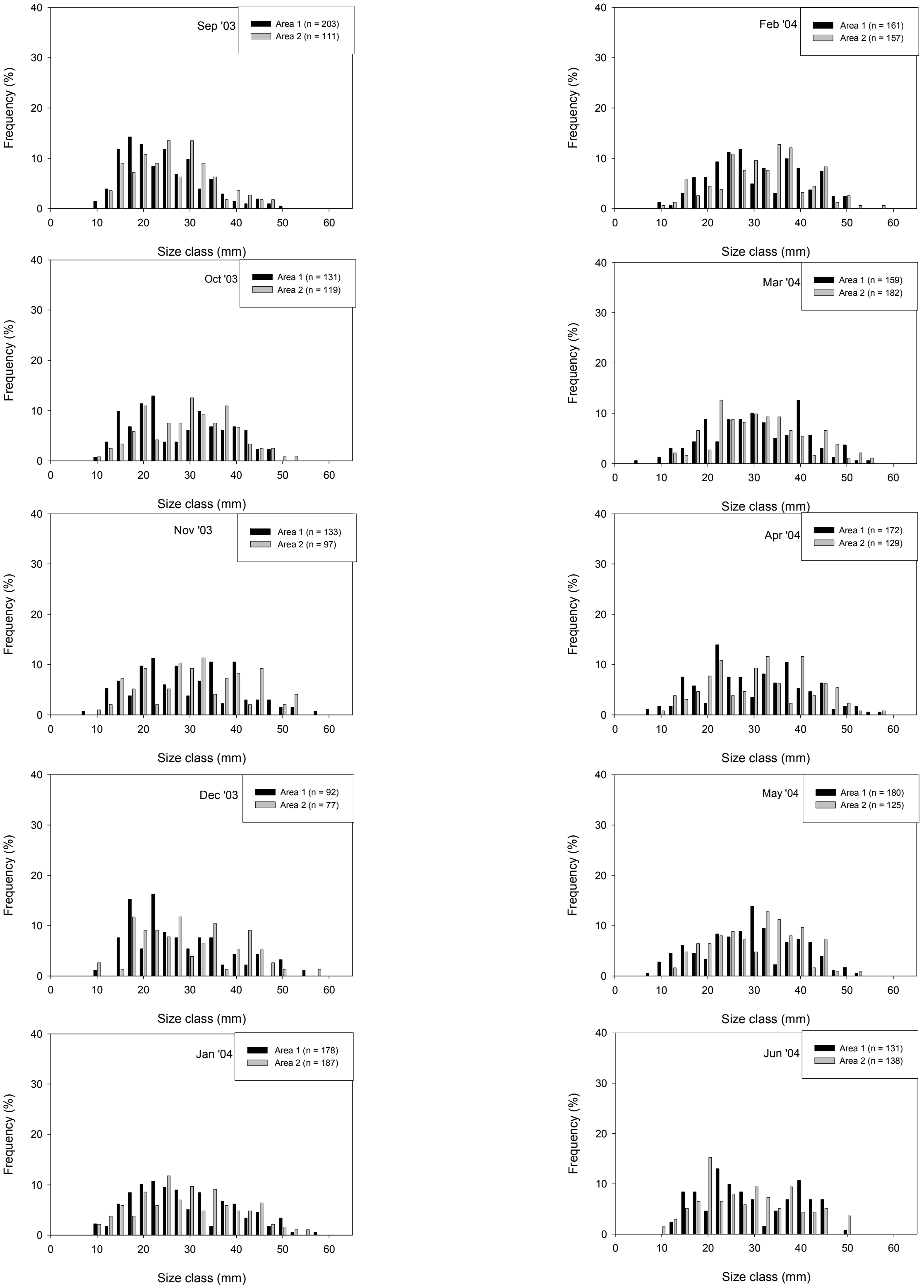


Fig. 3.6.3(c) (Continued): Size-frequency distribution of *S. longicosta* through sampling period at Nqabara.

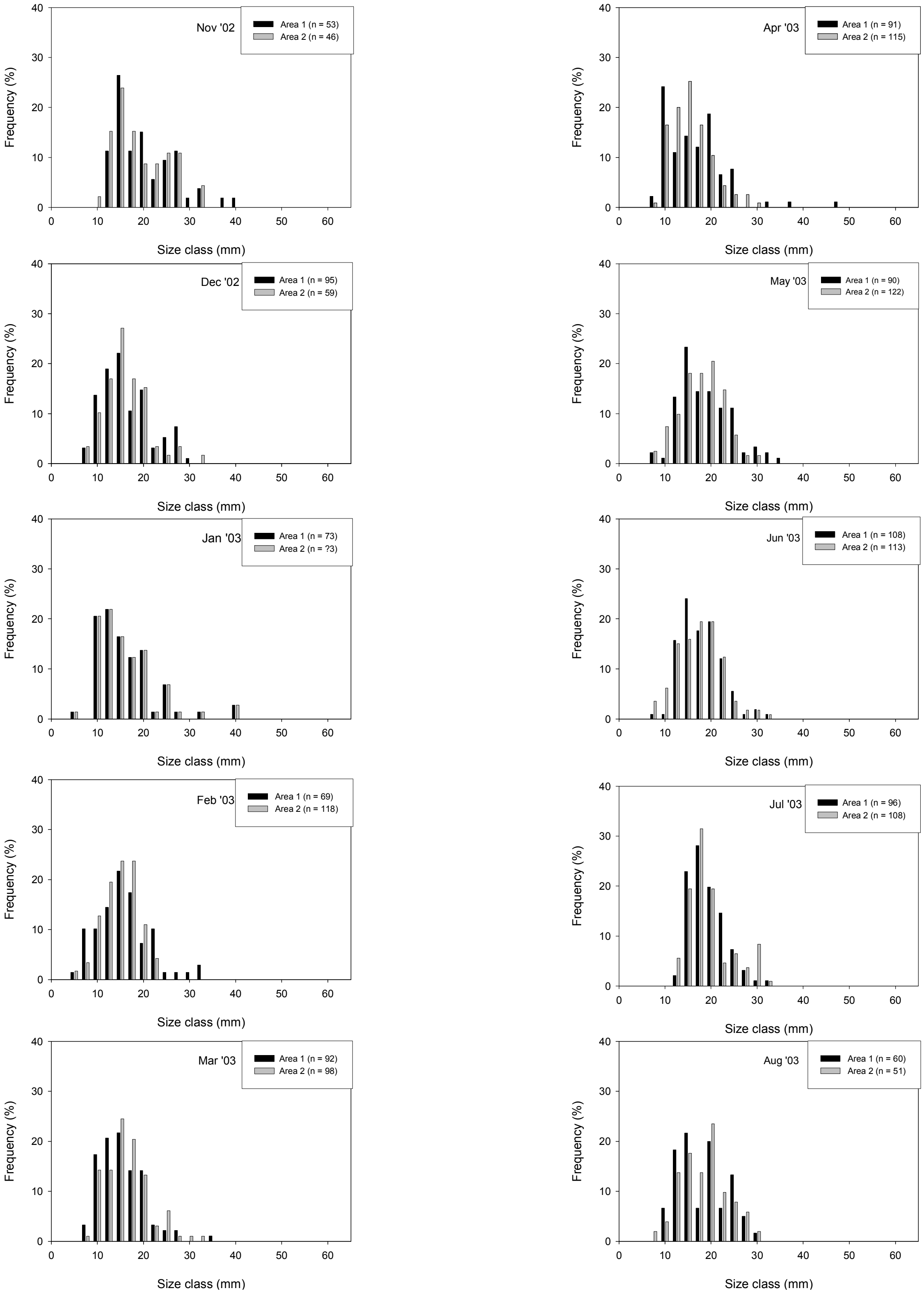


Fig. 3.6.4(d): Size-frequency distribution of *S. longicosta* through sampling period at Xhora.

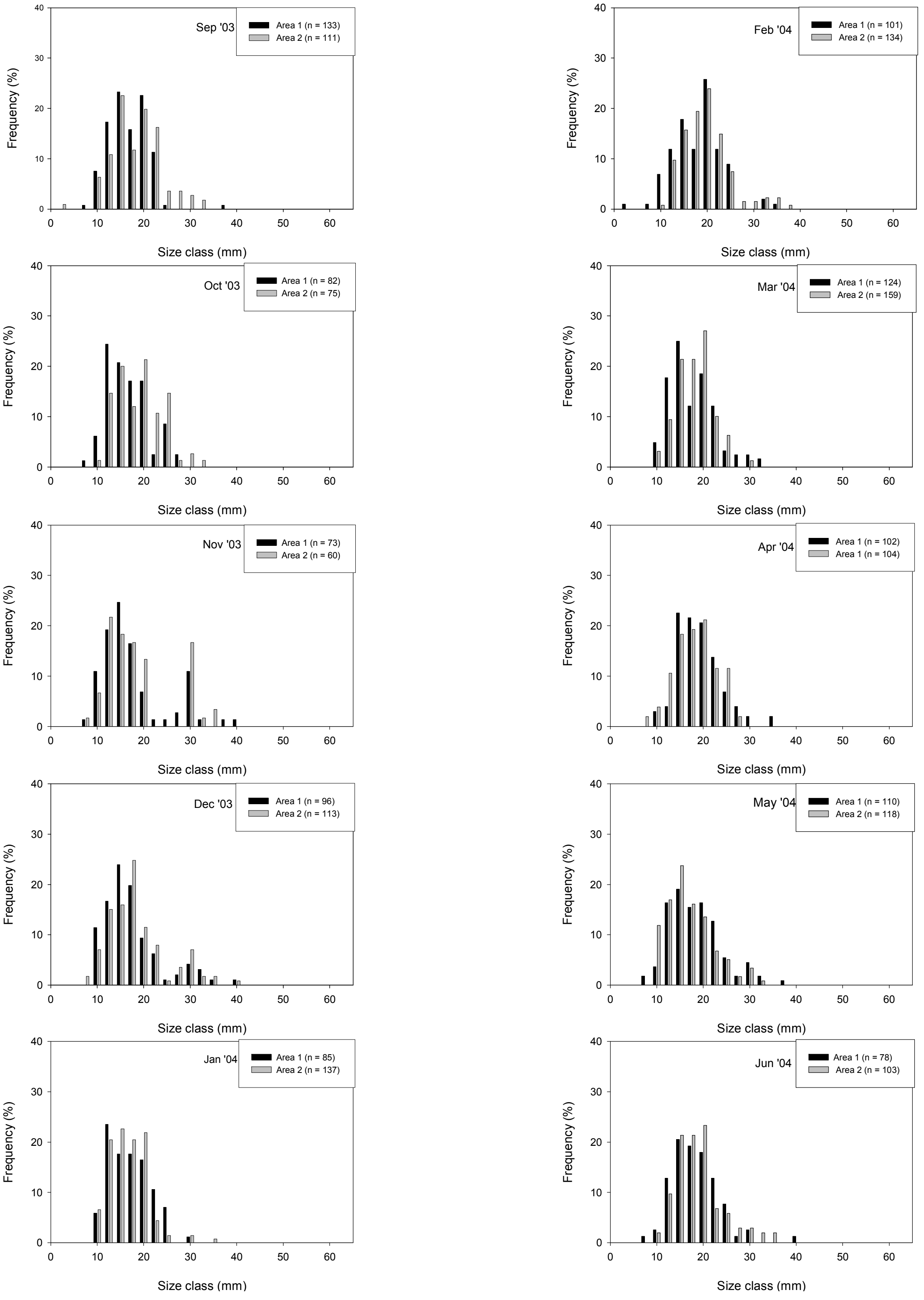


Fig. 3.6.4(d) (Continued): Size-frequency distribution of *S. longicosta* through sampling period at Xhora.

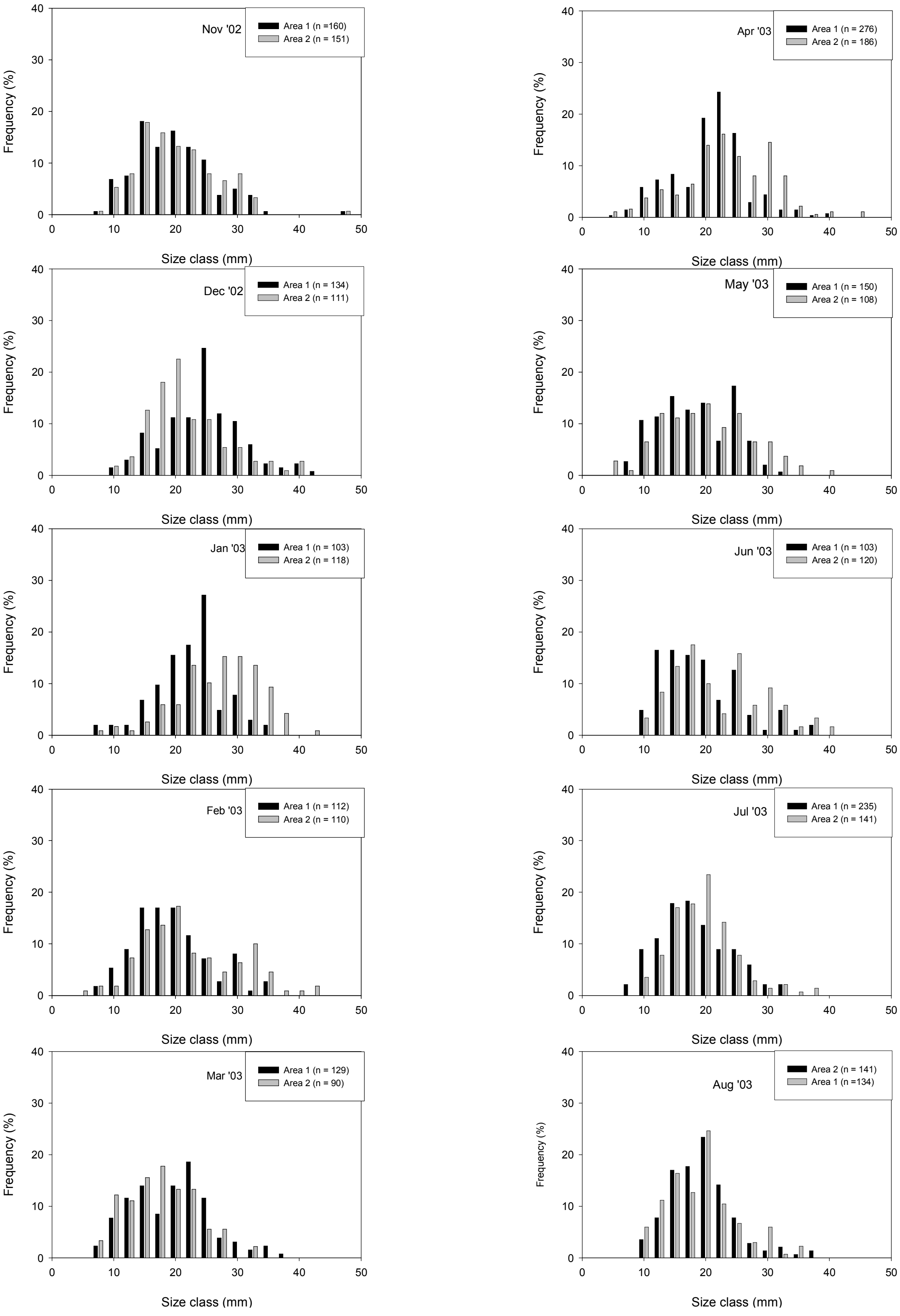


Fig. 3.7.1(a): Size-frequency distribution of *C. capensis* through sampling period at Dwesa.

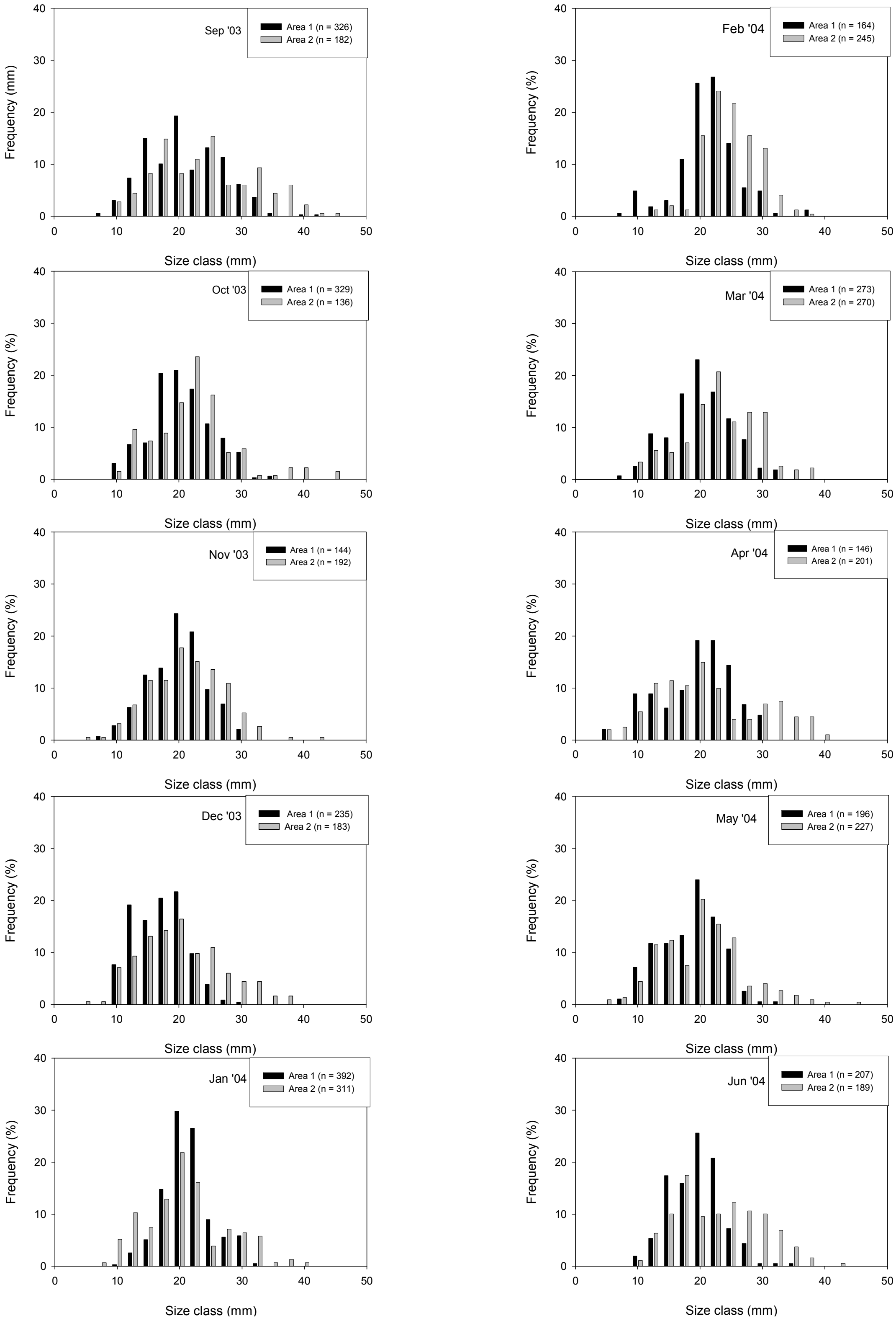


Fig. 3.7.1(a) (Continued): Size-frequency distribution of *C. capensis* through sampling period at Dwesa.

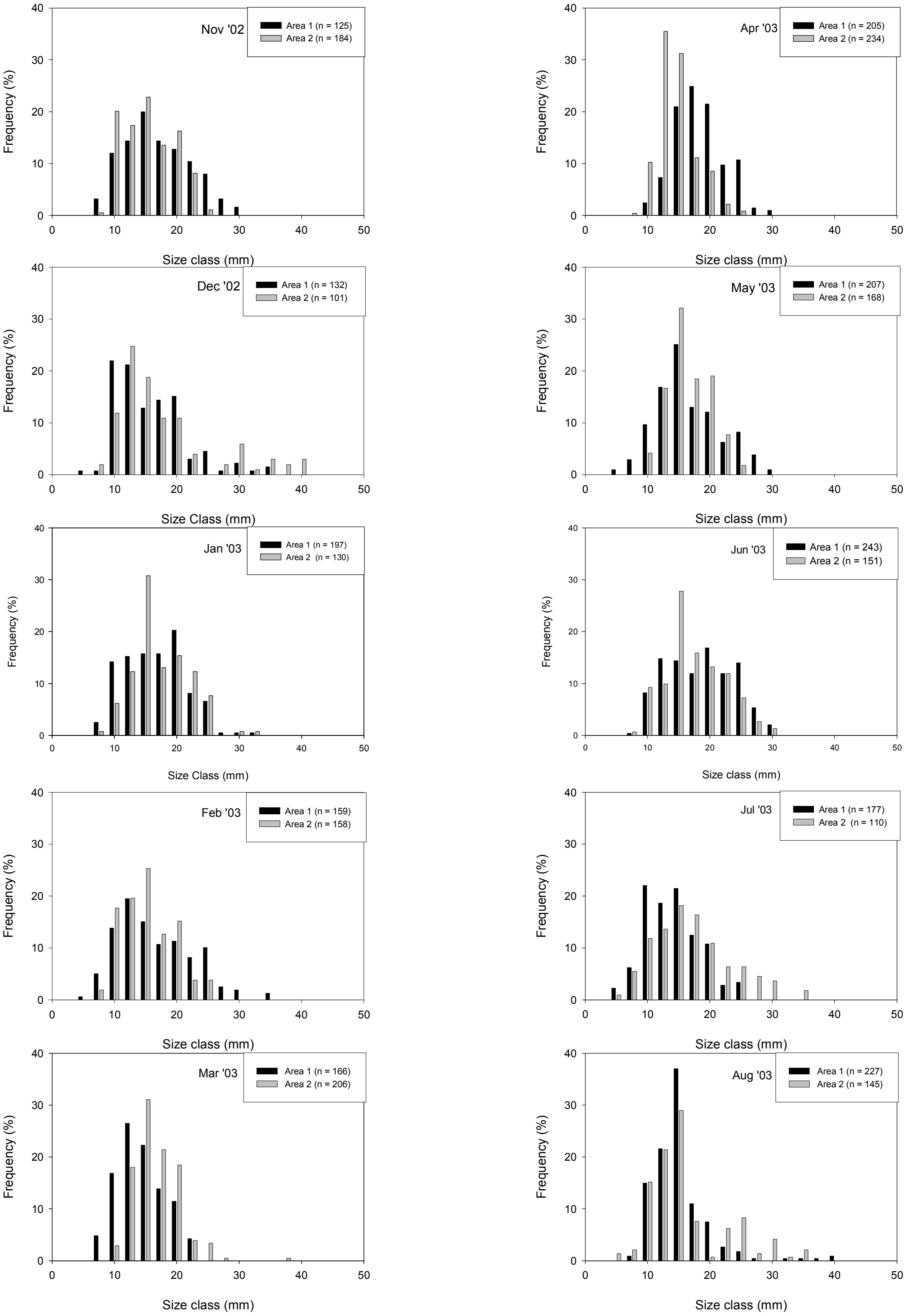


Fig. 3.7.2(b): Size-frequency distribution of *C. capensis* through sampling period at Cwebe.

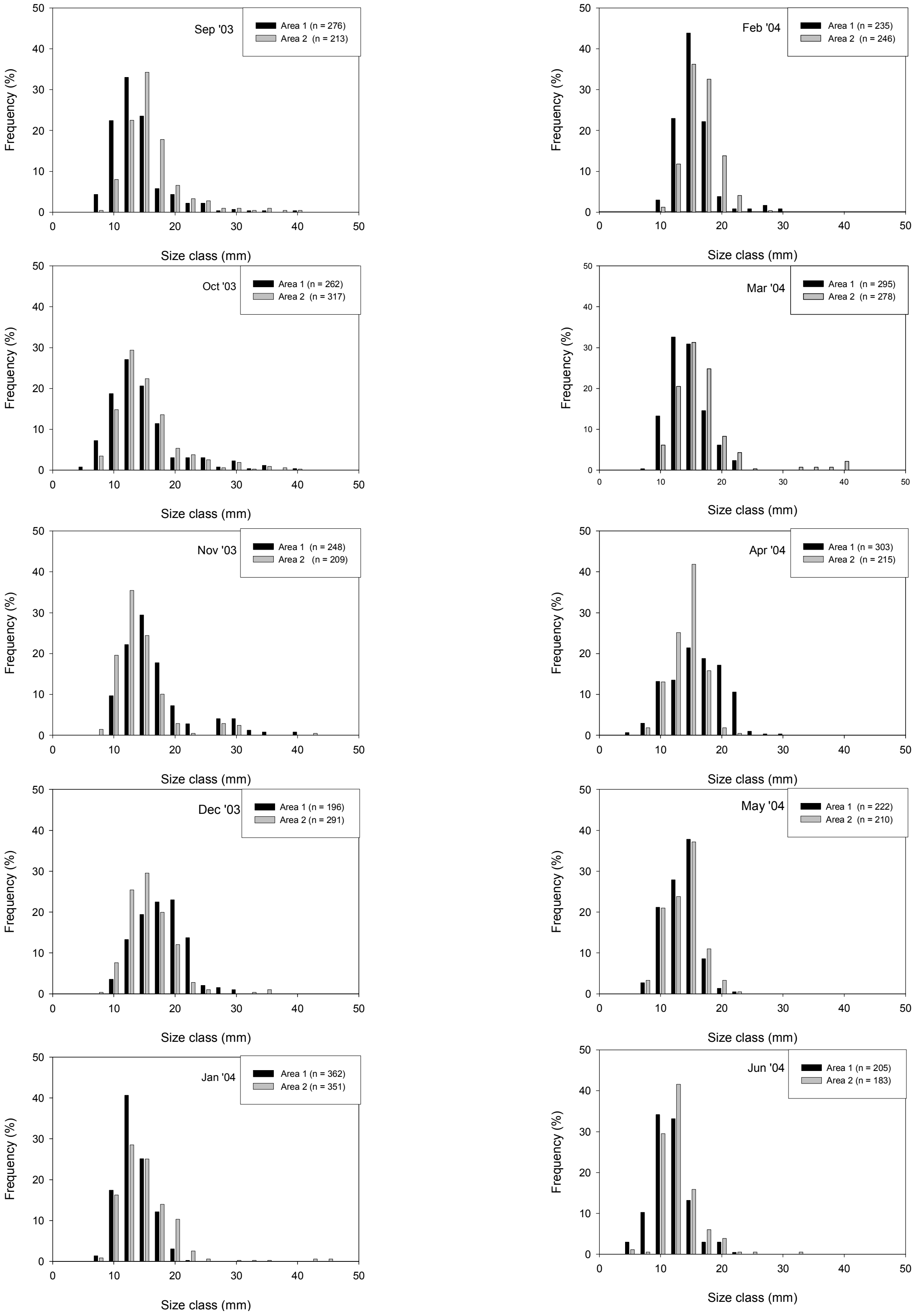


Fig. 3.7.2(b) (Continued): Size-frequency distribution of *C. capensis* through sampling period at Cwebe.

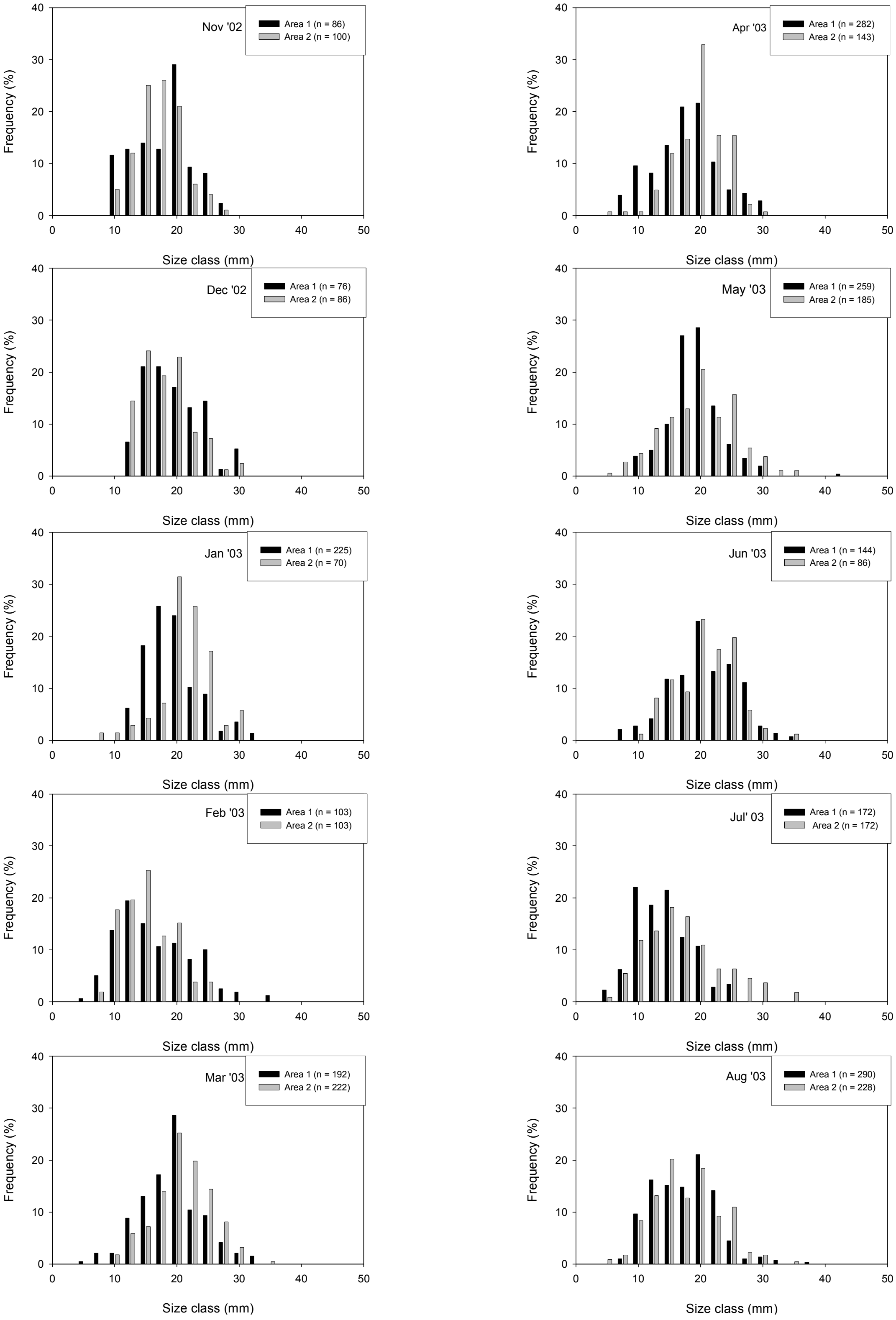


Fig. 3.7.3(c): Size-frequency distribution of *C. capensis* through sampling period at Nqabara.

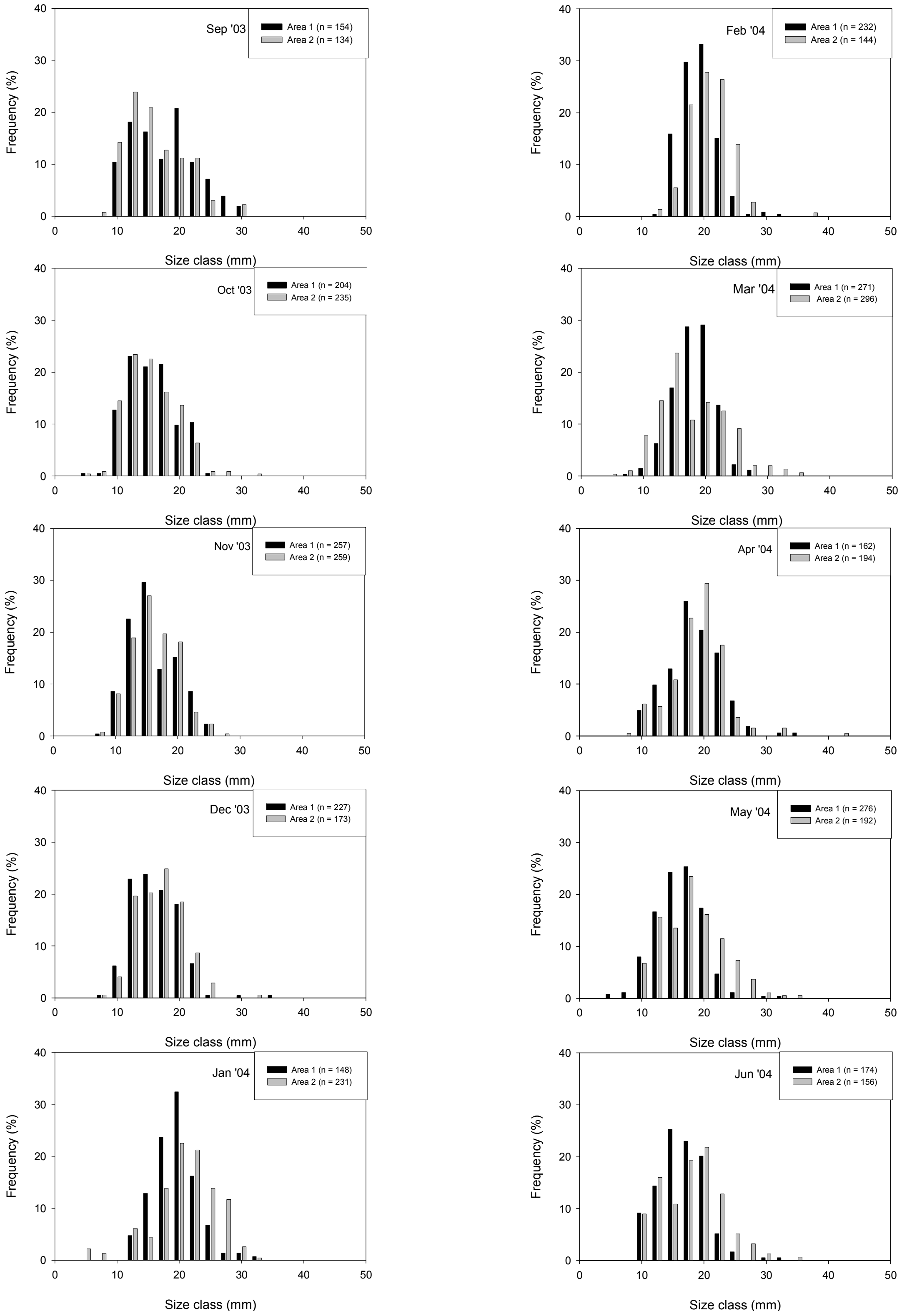


Fig. 3.7.3(c) (Continued): Size-frequency distribution of *C. capensis* through sampling period at Nqabara.

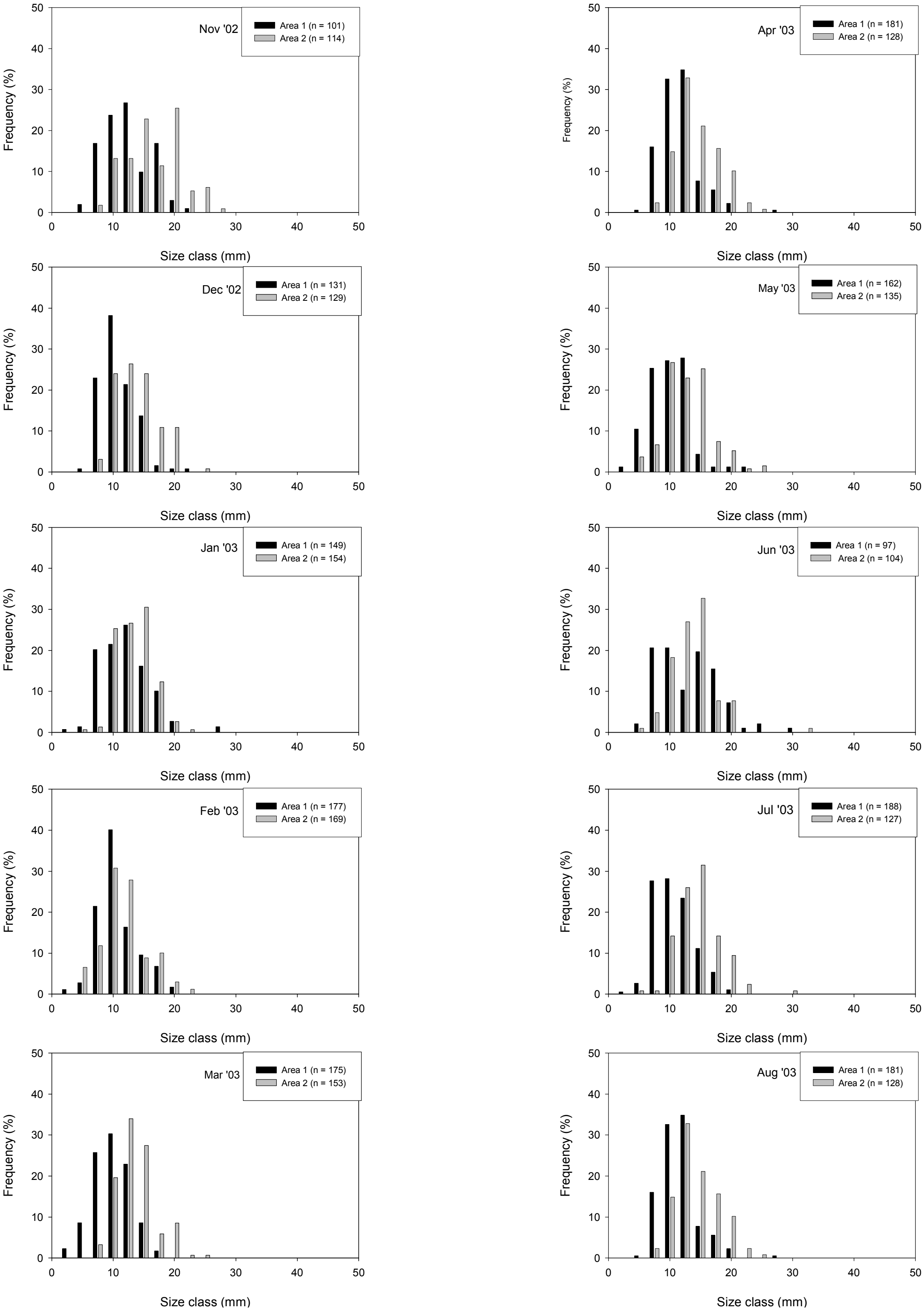


Fig. 3.7.4(d): Size-frequency distribution of *C. capensis* through sampling period at Xhora.

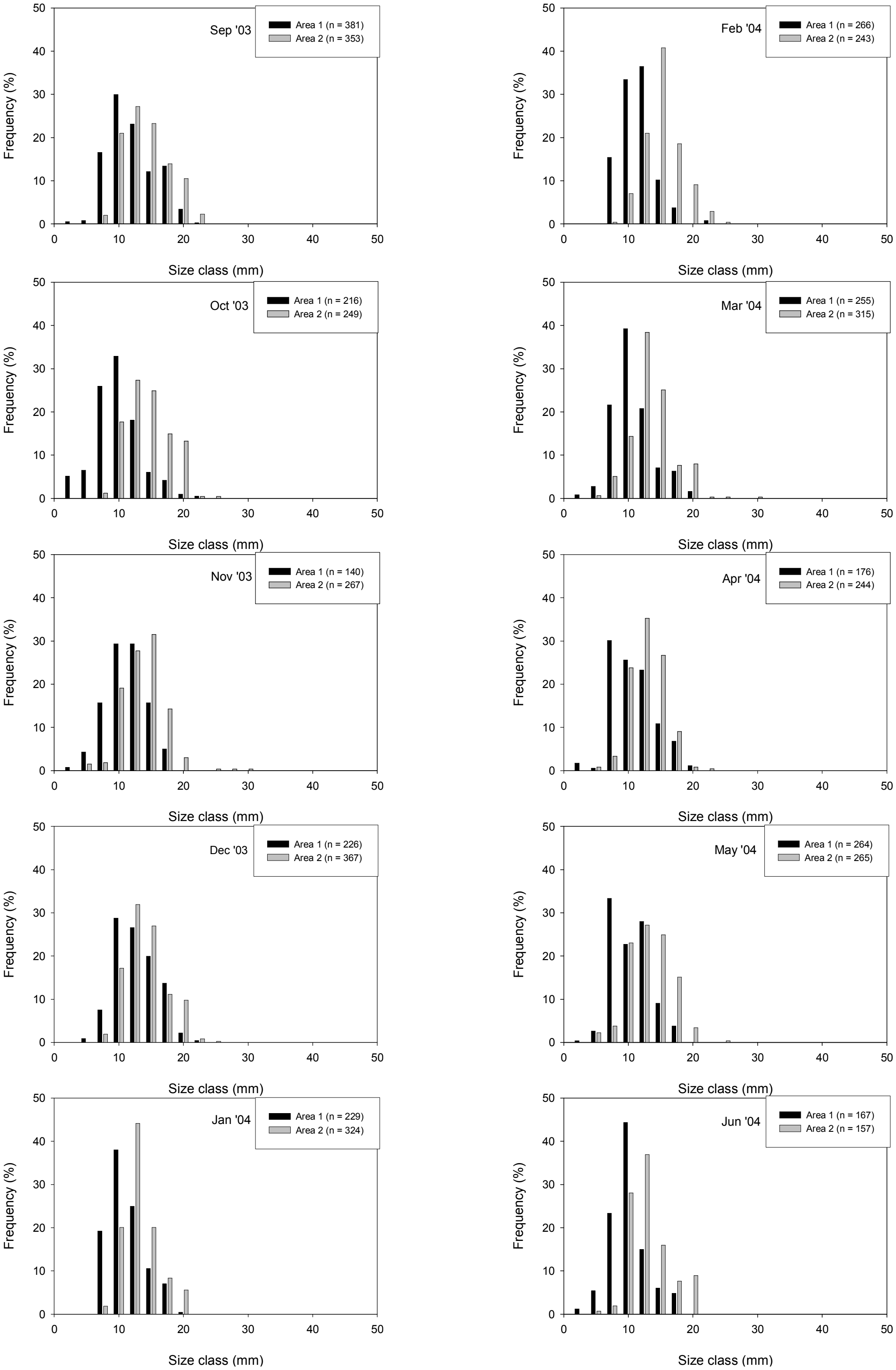


Fig. 3.7.4(d) (Continued): Size-frequency distribution of *C. capensis* through sampling period at Xhora.

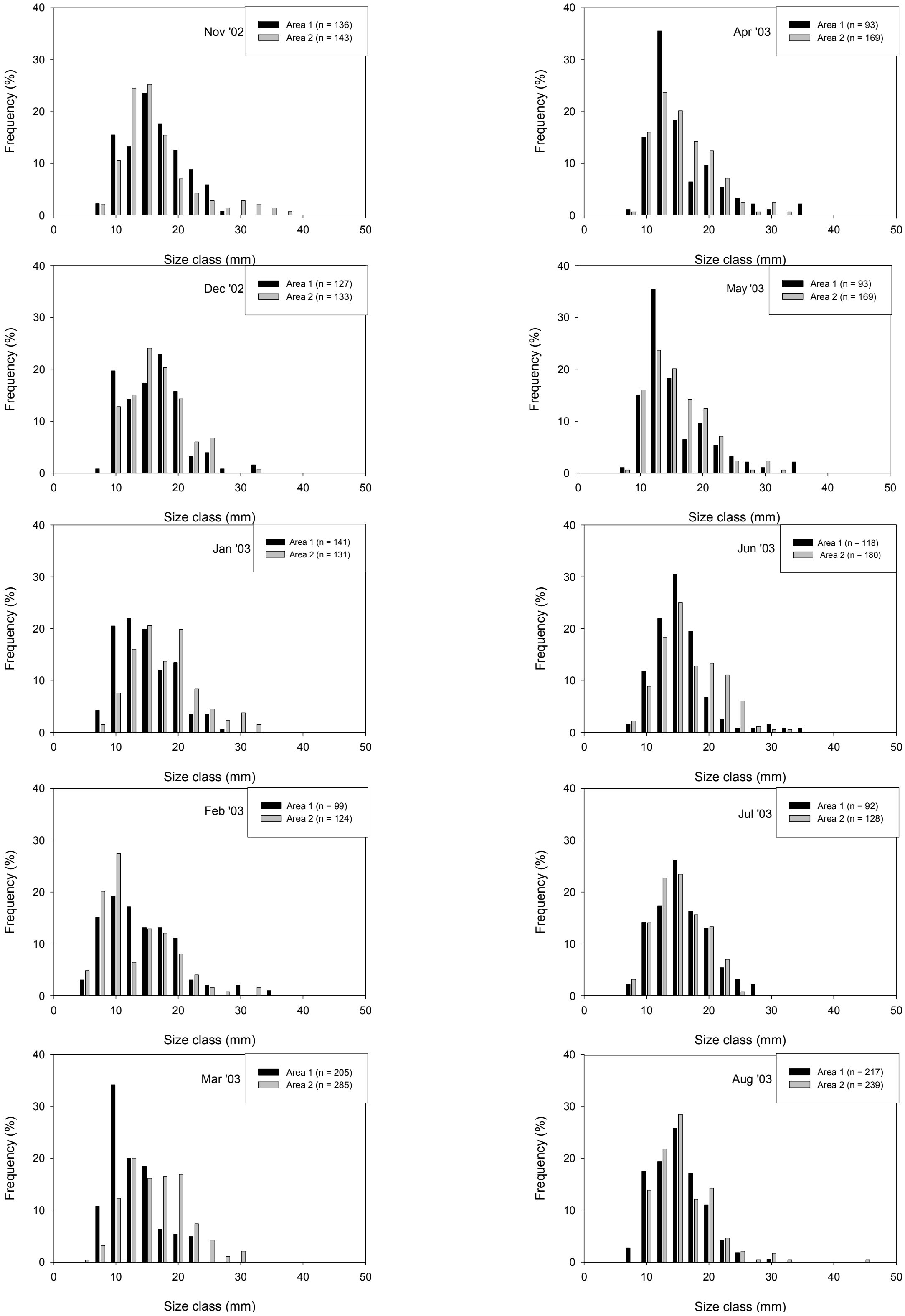


Fig. 3.8.1(a): Size-frequency distribution of *S. granularis* through sampling period at Dwesa.

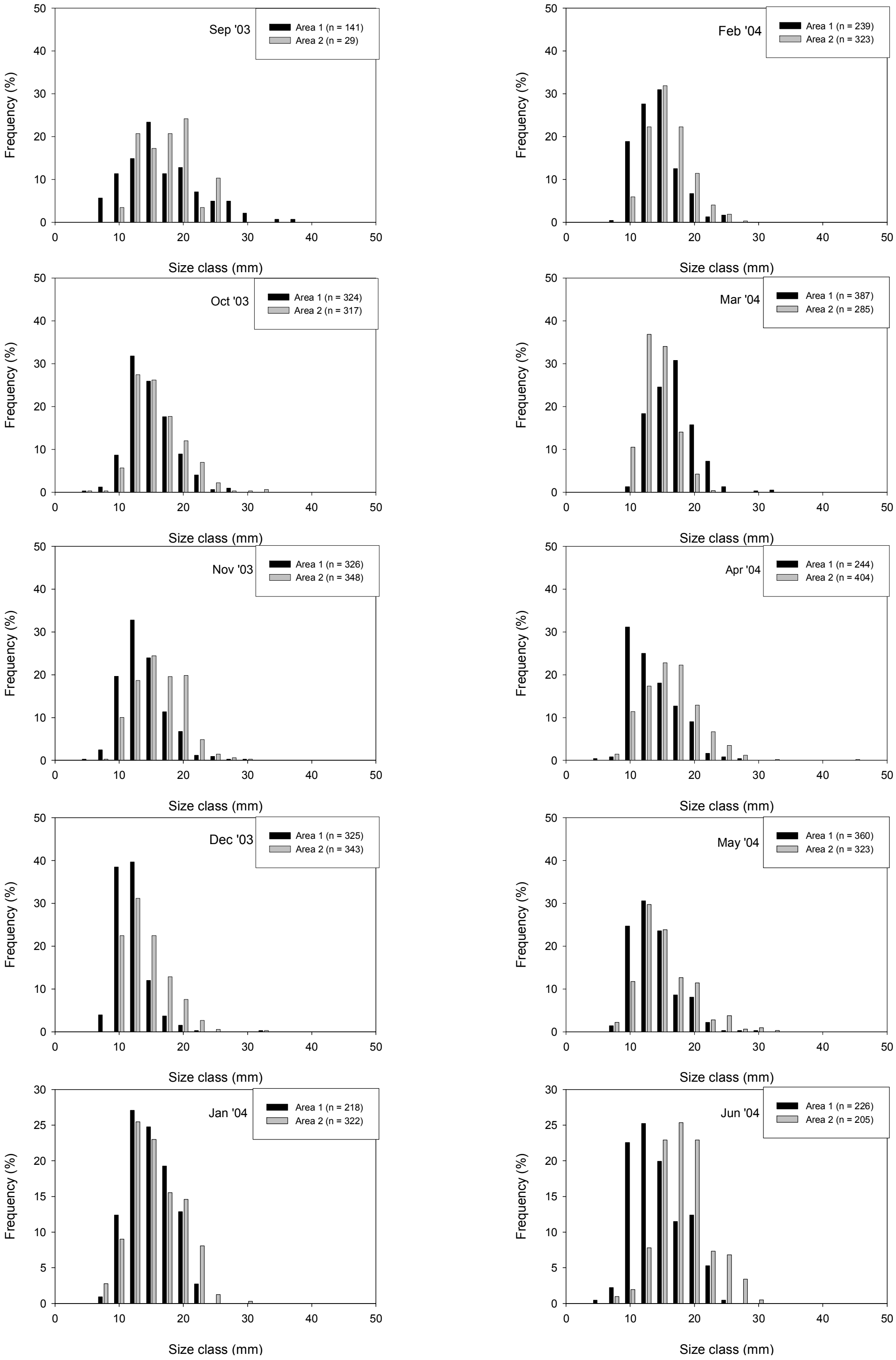


Fig. 3.8.1(a) (Continued): Size-frequency distribution of *S. granularis* through sampling period at Dwesa.

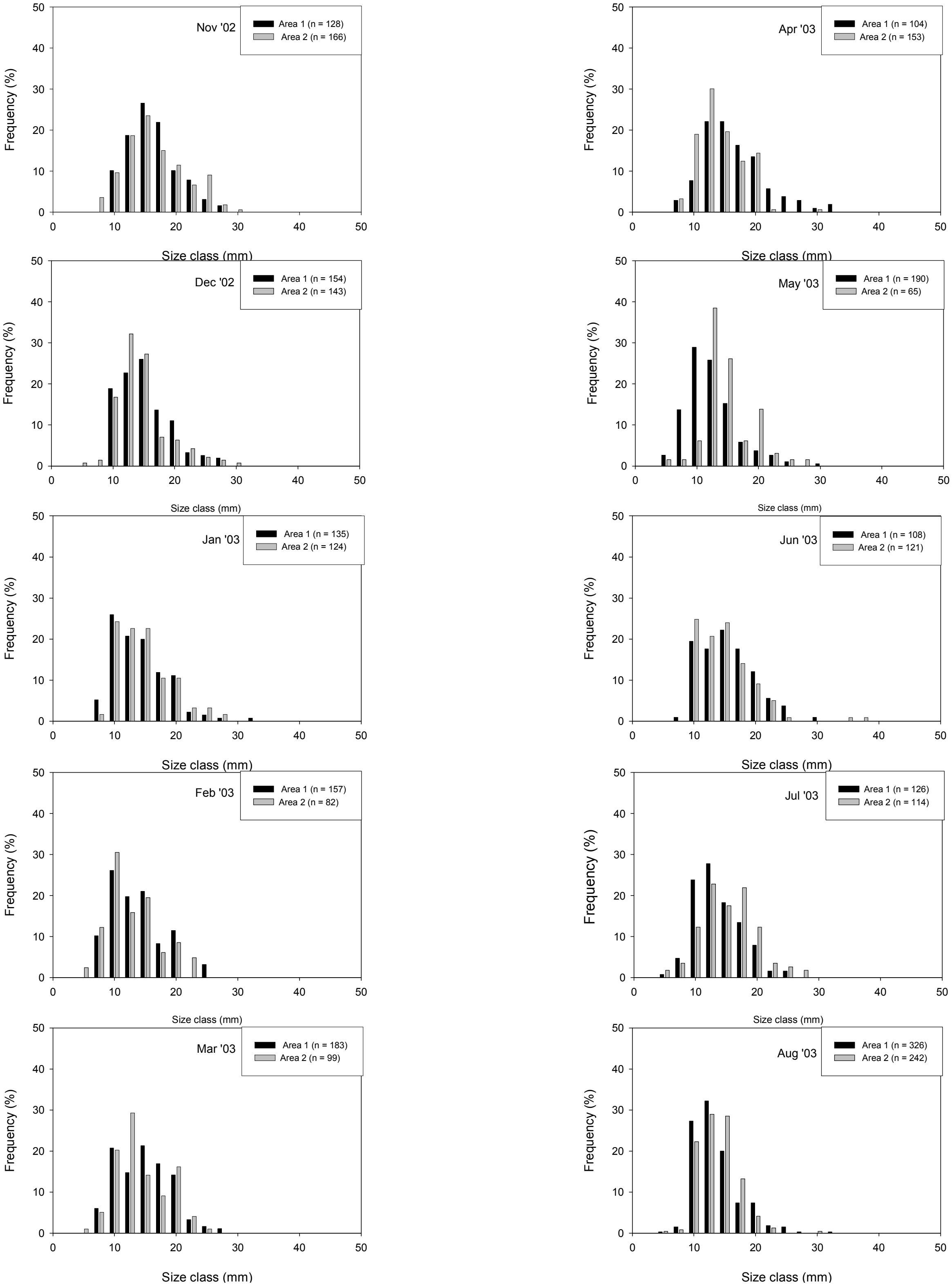


Fig. 3.8.2(b): Size-frequency distribution of *S. granularis* through sampling period at Cwebe.

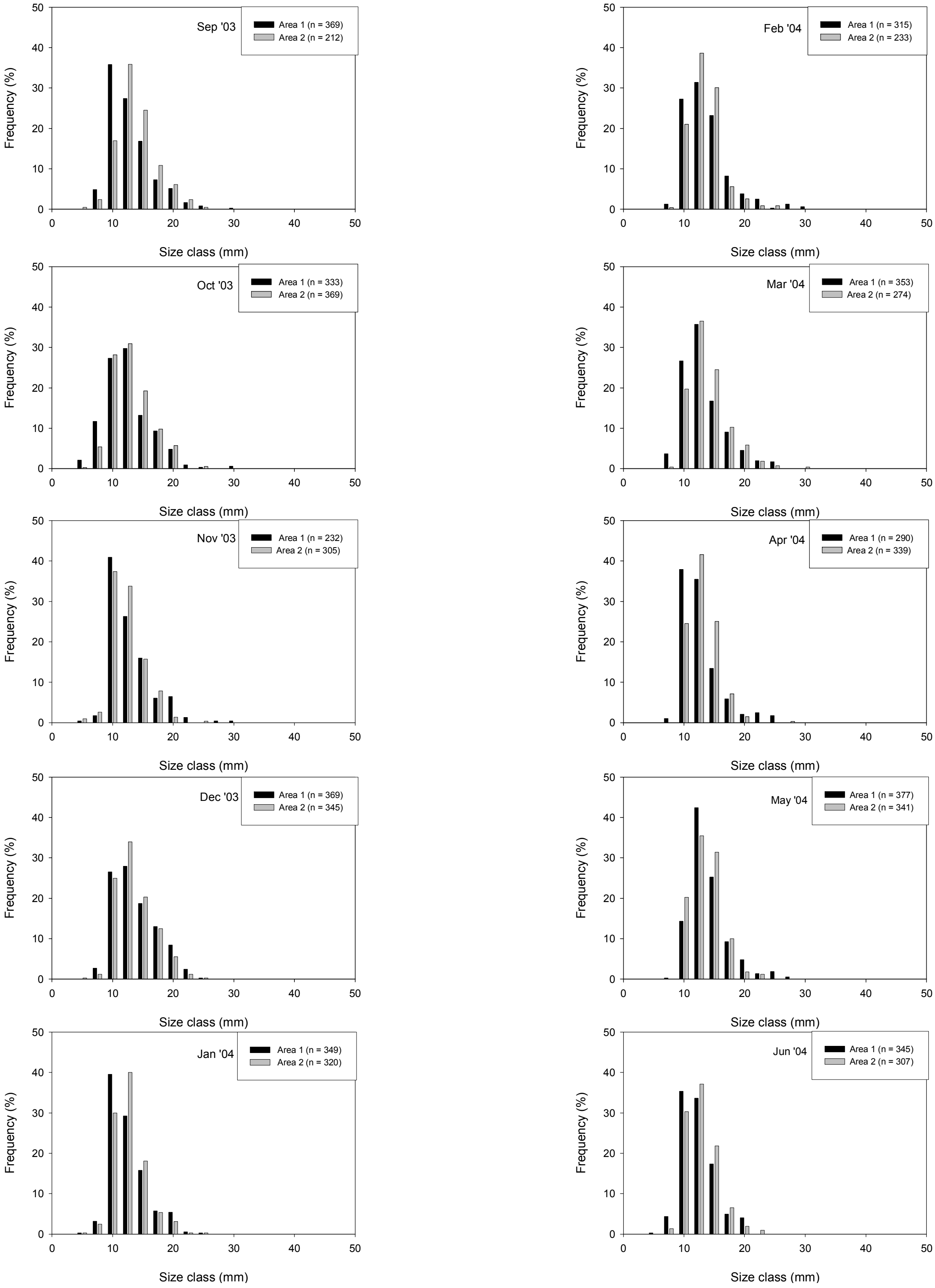


Fig. 3.8.2(b)(Continued): Size-frequency distribution of *S. granularis* through sampling period at Cwebe.

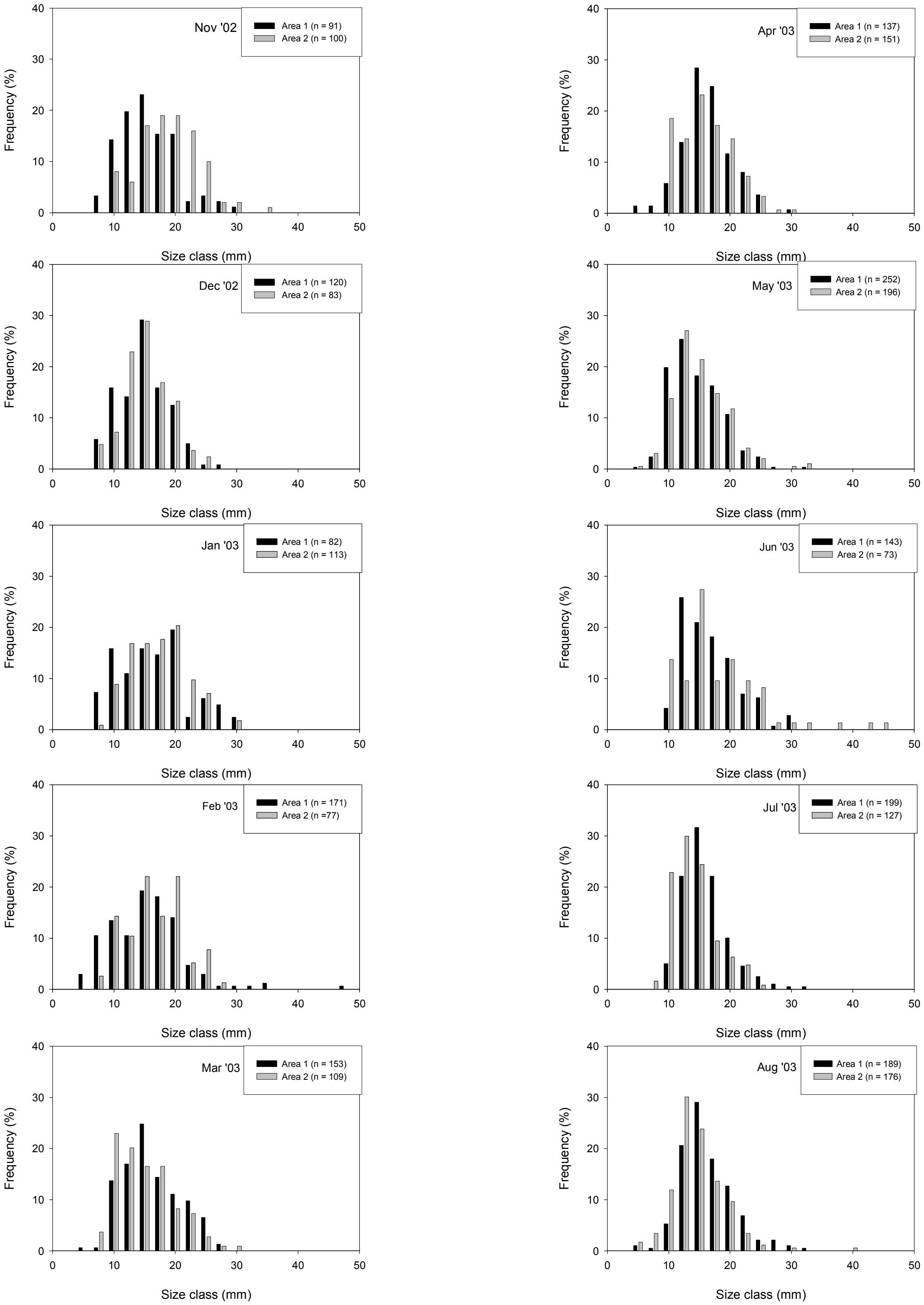


Fig. 3.8.3(c): Size-frequency distribution of *S. granularis* through sampling period at Nqabara.

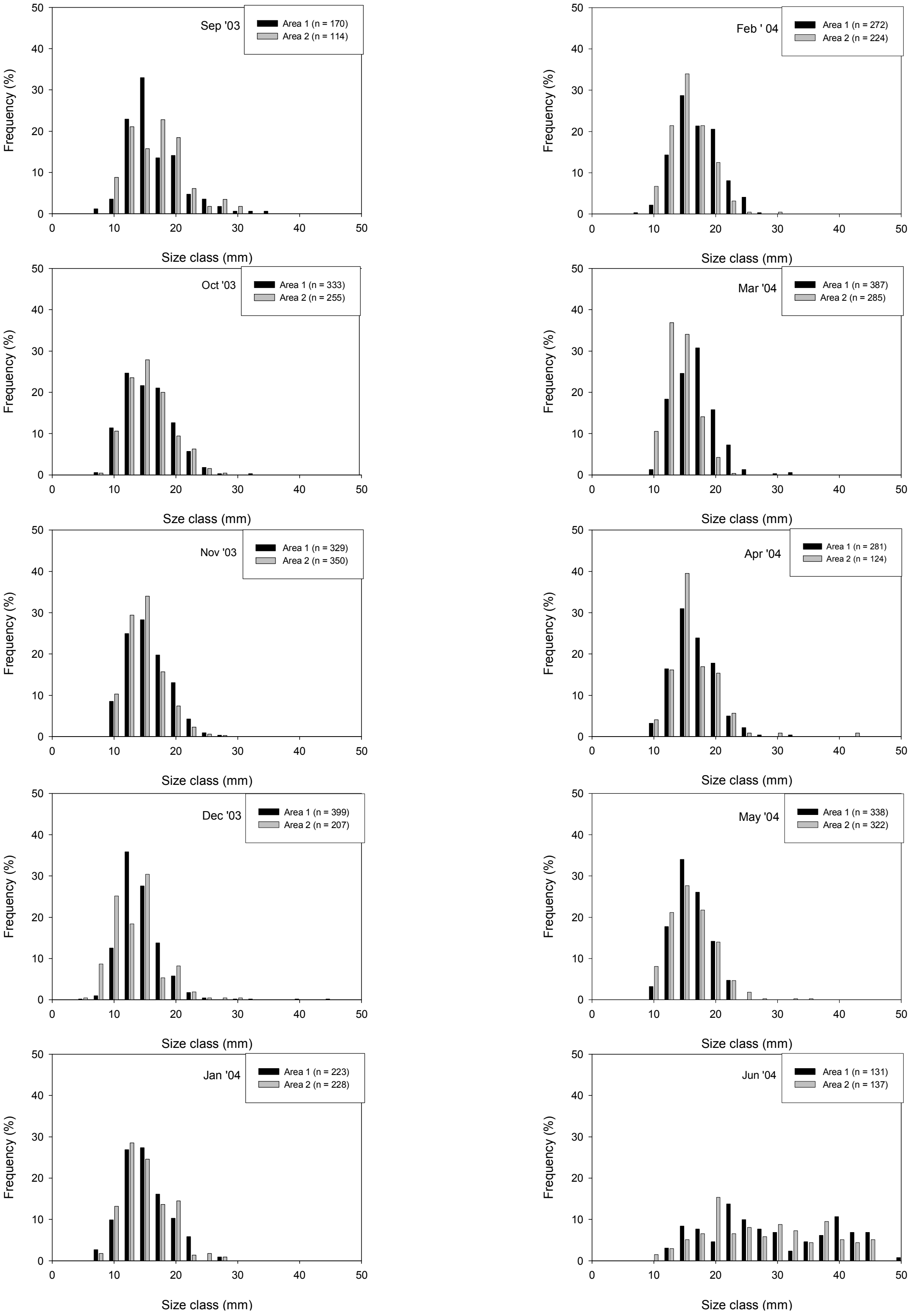


Fig. 3.8.3(c) (Continued): Size-frequency distribution of *S. granularis* through sampling period at Nqabara.

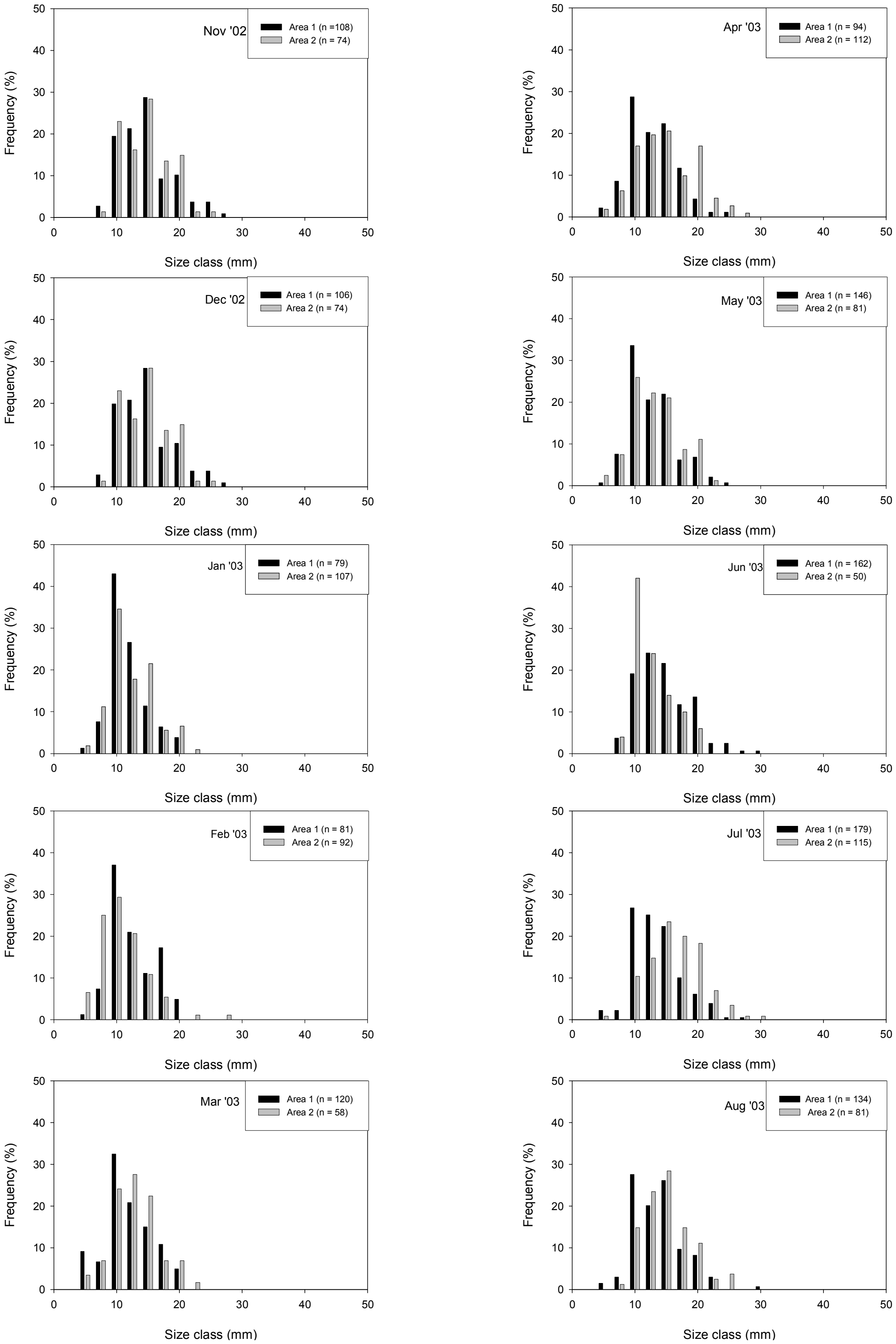


Fig. 3.8.4(d): Size-frequency distribution of *S. granularis* through sampling period at Xhora.

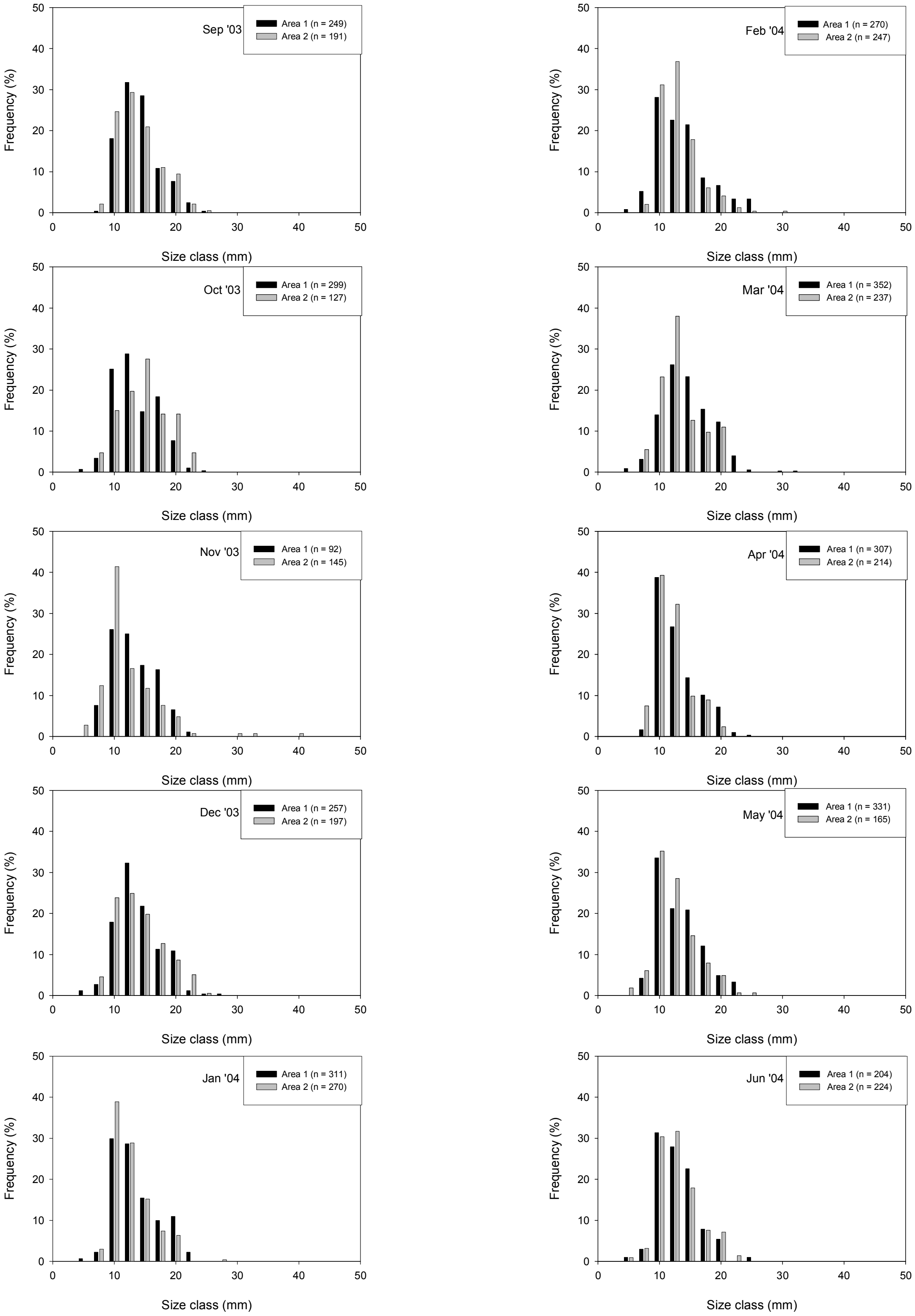


Fig. 3.8.4(d) (Continued): Size-frequency distribution of *S. granularis* through sampling period at Xhora.

CHAPTER 4

RECRUITMENT

4.1 INTRODUCTION

One of the processes that shape community structure in most habitats is the arrival and subsequent survival of new individuals (Connell 1985; Roughgarden *et al.* 1988; Menge 2000; Hutching & Williams 2001; O'Riordan *et al*. 2004). This initial process is responsible for the supply of individuals to existing assemblages, as well as the re-colonization of denuded areas or newly created space (Lubchenco & Menge 1978; Sousa 1984; Zabin & Altieri 2007). The recruitment of marine benthic invertebrates involves both the settlement and metamorphosis of planktonic larvae and the post-settlement survival of these individuals to recognizable recruits (Osman & Whitlatch 1996). Larval supply and subsequent settlement can be difficult to measure due to problems of defining the number of larvae capable of settling at a particular place and time, and of counting small and/or cryptic individuals (Calley *et al*. 1996). Some ecologists have adopted the standard operational definition of recruitment as the number of individuals that have settled and survived between census intervals (Keough & Downes 1982). Settling larvae can vary greatly in their quality and potential for survival and growth (Marshall & Keough 2004). There are a number of sources of variation in larval quality. For example, extension of the larval period negatively affects post-metamorphic survival and growth in a number of marine environments (Ng & Keough 2003).

All patellogastropod limpet species release gametes that ultimately develop into planktonic veliger larvae (Kay 2002). After a brief pelagic life stage, these larvae settle onto appropriate surfaces where they metamorphose and commit to a benthic existence. Two general patterns emerge in studies of limpet recruitment: firstly, some limpet species settle directly into the adult habitat (Breen 1972; Scheibling *et al.* 1990) and secondly, other species recruit indirectly by settling outside and then migrating into the adult habitat (McGrath 1992; Delany *et al.* 1998). A possible third pattern is that settlement is equal in adjacent habitats, but the habitats impose differential post-larval mortality and thereby determine juvenile/adult distributions (Menge 2000; Marshall & Keough 2003a).

For many benthic marine invertebrates with planktonic larvae, settlement tends to be a non-random process that is triggered by environmental cues (Burke 1983; Butman 1987; Rodriguez *et al*. 1993). Environmental cues are typically associated with juvenile or adult habitats, and are assumed to assist in successful recruitment. Larvae of some high-intertidal limpet species settle at a low tidal level or in small pools, where the habitat is distinctly different from that of the adults, and subsequently migrate to join their conspecifics (Corpuz 1981; Delany *et al*. 1998). This indirect recruitment pattern might safeguard young individuals from the physical stresses of the adult habitat (e.g. temperature and desiccation) at a life stage when limpets are most susceptible due to their small size (Wolcott 1973**;** Chow 1975). It also reduces intraspecific competition between age classes. In the present study only rock substrata were sampled, to avoid the confounding effects of different habitats. Therefore, this chapter will focus on recruits, meaning the smallest size class of individuals that are found in the adult habitat.

The intensity of recruitment in marine organisms can vary from time to time and over many spatial scales (Caffey 1985; Raimondi 1990; Noda & Nakao 1996; Connolly *et al*. 2001; Broitman *et al*. 2005). Such spatial variability is likely to be a consequence of numerous processes that act at different spatial scales (Pineda 1994). The occurrence of a planktonic larval stage in many marine organisms introduces the potential for considerable spatial and temporal variation in recruitment to the benthic adult population (Forde & Raimondi 2004). Such variation is a result of abiotic (waves, currents, tides and wind) and biotic (behaviour, predation) factors, which are known to vary markedly in space and time (Gaines & Roughgarden 1985; Menge *et al*. 1994). Understanding variability in recruitment may be useful in determining patterns in assemblage structure of benthic intertidal animals (Gaines & Bertness 1992), especially those with planktonic dispersive larval stages (Denny & Shibata 1989; Marshall & Keough 2003b).

Many physical and biological factors play important roles in the arrival and subsequent survival of recruits in intertidal assemblages. These include processes that act at a limited local scale, such as the impact of benthic grazers and predators (Hawkins & Hartnoll 1983; Caley 1993), substratum type and complexity (Raimondi 1988), and the availability of free-space (Roughgarden *et al.* 1985; Jenkins *et al.* 2007), as well as non-local processes including oceanic currents (Roughgarden *et al.* 1988), changes in climatic conditions (Thieltges *et al.* 2004; Herbert *et al.* 2007) and environmental (physical and chemical) stimuli (Zhao & Qian 2002).

More recently, researchers have begun to investigate the effects of recruitment intensity in pairwise interactions (Minchinton & Scheibling 1993; Robles 1997; Robles & Desharnais 2002). Populations of grazing gastropods are known to fluctuate in density from place to place and from time to time in relation to variability in recruitment and mortality (Branch 1981; Caffey 1985; Caley 1993; Broitman *et al*. 2005). The degree to which adult density affects recruitment density is influenced not only by the attraction of recruits to conspecifics, but also by how demographically open or closed a population is.

The main aim of the present study was to test the hypothesis that if recruits are attracted to adults (or survive better where there are more adults), then commonly exploited species should show higher recruitment inside reserves, with no reserve effect for rarely exploited species.

4.2 MATERIALS AND METHODS

Limpets in each population were classified as either adults, which were sexually mature, or recruits, which were limpets with gonads that could not be classified as males or females, because they were neuter or had not yet developed gender-specific reproductive structures (Branch & Odendaal 2003; Rochette *et al*. 2003). The specific size used to separate recruits from adults in each population was selected based on the typical size at which limpets begin to mature in each species (Etter 1996). The cut-off size for recruits varied among species and was derived from reproduction data (Chapter 6). They were for: *Cellana capensis* (≤ 8 mm), *Helcion concolor* (≤ 9 mm), *Scutellastra granularis* (≤ 7 mm) and *Scutellastra longicosta* (≤ 13 mm). Monthly samples were collected to estimate the mean recruit density for each limpet population. In each of 20 randomly thrown quadrats (0.5 x 0.5 m), all adults and recruits were counted and measured *in situ*, using a pair of dividers and a ruler.

4.2.1 Statistical analysis

The effects of marine reserves on limpet recruit density were analysed separately for each species, using a four-factor nested analysis of variance (ANOVA) to test the effects of month, reserve, site (nested in reserve) and area (nested in reserve and site). The factors month, site and area were treated as random while reserve was treated as fixed. Multiple comparison tests (Tukey HSD tests) were subsequently run on significant results ($p < 0.05$) from ANOVA tests. Prior to use of ANOVA, the data were tested for normality and homogeneity of variances using Kolmogorov-Smirnov and Cochran's tests (Zar 1996; Underwood 1997), respectively. No transformation was necessary.

4.3 RESULTS

Reserve as the main factor had no significant effect in any species. Month was significant for 3 out of the four species, indicating variations in recruitment among months. The interaction between month and reserve was not significant for any species. There were strong month/site interactions for all four species, indicating variation in recruitment on scales of 10 km among sites. The area/month interaction was significant in three of the four species, indicating variation in recruitment on scales of 100 m, within sites. However, there were relatively few months with significant differences between areas. Although the effect of reserve was not significant as it was masked by meaningless comparisons of areas within sites, I will discuss them even though not statistically significant.

4.3.1 Commonly exploited species

Helcion concolor

There were significant ($p < 0.05$) effects of month, area (reserve (site)) and the month/site (reserve) interaction while no other factor was significant (Table 4.1).

Month x Reserve

H. concolor showed 2 major periods of recruitment, between January and March 2003 and between August and December 2003 (Fig. 4.1.1). Although the month/reserve interaction was not significant, non-reserves were markably greater than reserves. There were 14 months when non-reserves were greater than reserves and 2 months when reserves were greater than non-reserves (Fig. 4.1.2).

Month x Site (Reserve)

Tukey HSD tests on the month/site (reserve) effect on mean recruit density of *H. concolor* showed 3 months with significant differences among sites but with no obvious pattern (see asterisks in Fig. 4.1.3).

Area (Reserve (Site))

There was a significant ($p < 0.05$) area effect which was nested within site and reserve (Table 4.1). Mean recruit densities of *H. concolor* differed significantly between areas within all sites, indicating high variability of this species on scales of 100 m within sites (Fig. 4.1.4).

Scutellastra longicosta

Four-way nested ANOVA showed significant ($p < 0.05$) effects of month and area (reserve (site)), including the interaction between month/site (reserve) and between month/area (reserve (site). Other factors were not significant (Table 4.2).

Month x Reserve

The mean recruitment density of *S. longicosta* showed a peak in recruitment in February 2003, followed by a gradual decline in recruit density through time (Fig. 4.2.1). There were periods with higher/lower recruit densities, but post-hoc tests showed no clear groupings except February 2003 when densities were especially high. Reserve and non-reserve sites showed almost identical patterns in the timing of recruitment, resulting in no significant interaction between month and reserve (Fig. 4.2.2). Non-reserves were greater than reserves in 19 months while reserves were greater than non-reserves in only 2 months.

Month x Site (Reserve)

Post-hoc tests on the interaction of month/site (reserve) effect revealed significant differences in the months showed by asterisks (Fig.4.2.3). Xhora showed especially high recruitment in 4 of the 5 months.

Month x Area (Reserve (Site))

There was a significant ($p < 0.05$) effect of area at Cwebe (Fig. 4.2.4).

4.3.2 Rarely exploited species

Cellana capensis

There were significant ($p < 0.05$) effects of site and area, including the interactions of month/site (reserve) and month/area (reserve (site)) (Table 4.1).

Month x Reserve

Recruit density was higher in four discrete periods: November 2002, February to May 2003, July to November 2003 and March to June 2004 (Fig. 4.3.1).

Although there was no significant effect of month, there were months with clear peaks in the mean recruitment density of *C. capensis*. These months included February, May, October 2003 and May 2004 (Fig. 4.3.1). In 14 months non-reserves had greater recruitment than reserves (Fig. 4.3.2). Reserve sites had greater recruit densities than non-reserve sites in 6 months (November 2002, July, October 2003, January, April and June 2004). There were also 2 months when the mean recruitment densities in reserves and non-reserves were almost identical (December 2002 and October 2003). The lowest mean recruit densities in reserves and non-reserves were 0.083 ± 0.062 and 0.267 ± 0.168 per m^2 (February 2004, respectively), while the highest mean recruit densities were 1.117 ± 0.721 and 1.383 ± 0.168 per m^2 (October 2003 and May 2004, respectively). Thus, the mean recruit densities of non-reserves were generally greater than reserves.

Month x Site (Reserve)

There appeared to be a north-south gradient in recruitment density with density increasing from south to north.

The overall mean recruit density of *C. capensis* (Fig. 4.3.3) among sites was, in descending order, Xhora (1.172 ± 0.053) > Cwebe (0.842 ± 0.053) > Nqabara (0.282 ± 0.053) > Dwesa (0.233 ± 0.053), although there was a month/site (reserve) interaction.

<u>Month x Area (Reserve (Site))</u>

There was a significant ($p < 0.05$) effect of area, which was nested within site and reserve, indicating high variability on scales of 100 m within sites, but this occurred only at Cwebe and Xhora (Fig. 4.3.4).

Scutellastra granularis

Four-way nested ANOVA tests showed that reserve, site and area as main factors had no significant ($p > 0.05$) effect but month and the interactions between month/site (reserve) and between month/area (reserve (site)) were significant (Table 4.4).

<u>Month x Reserve</u>

The mean recruit density of *S. granularis* showed two major peaks of recruitment in February and October 2003 (Fig. 4.4.1). Although there was no significant month/reserve interaction, in reserves, there was a pulse of recruitment in October 2003 while in non-reserves, the same pulse occurred a month later, in November and December 2003 (Fig. 4.4.2). In 8 months, mean recruit densities in reserves were greater than in non-reserves and non-reserves were also greater than reserves in 8 months (Fig. 4.4.2) The lowest mean recruit densities in reserves and non-reserves were 0.033 ± 0.277 and 0.033 ± 0.098 per m^2 (December/June 2003 and September 2003, respectively), while the highest mean recruit densities were 1.067 ± 0.098 and 0.700 ± 0.506 per m^2 (February 2003, respectively).

Month x Site (Reserve)

Post-hoc tests of the month/site interaction in the mean recruit density of *S. granularis* revealed significant differences in months showed by asterisks with no clear pattern (Fig. 4.4.3).

Month x Area (Reserve (Site))

Tukey HSD tests on the month/area interaction showed significant differences between areas within sites. As for *C. capensis* this occurred only at Cwebe and Xhora (Fig. 4.4.4).

4.4 DISCUSSION

The data consistently revealed significant effects of the month/site (reserve) interaction for all species. Although the area/month interactions were also significant in three out of the four species, there was a relatively small number of months with significant differences (i.e about 6 out of 160 comparisons). Those months with significant differences occurred mainly at Xhora and Cwebe. Reserve as a main factor had no significant effect for any species. Xhora often showed the highest mean recruit densities. Generally, recruitment densities were greater in non-reserve than reserve sites. A significant strong month/site (reserve) effect for all species, suggests high spatio-temporal variation in recruit density on scales of 10 km. There was a total of 16 months with significant differences out of 80 comparisons. Variations in mean recruit densities in reserves and non-reserves over time, from month to month and from year to year, suggest sporadic recruitment. Disturbance as a result of major climatic events such as storms and cold winters or small-scale physical damage may also have important effects (Shanks & Wright 1986; Christopher 2000).

Essentially the results indicated strong temporal effects, as expected, with similar patterns, but different timing among species. On the other hand, significant variability in recruit density sometimes occurred at the smallest spatial scale examined. The area effect for *C. capensis* and *S. granularis* (rarely exploited species) mainly occurred at Cwebe and Xhora (the two northern sites with high recruitment). However, there was no consistent ranking of areas at these sites, suggesting that this was actually an effect at the level of site.

There was evidence of strong significant month/site (reserve) effects for all 4 species and the hypothesis that recruit densities in commonly exploited species would be affected by reserve was not generally supported. The fact that there was a significant relationship between adult density and recruit density (Table 4.5) and that Xhora had the highest mean recruit density, indicates that recruitment is independent of protection. There are several possible effects that could cause a negative association between adults and recruits. Although these were not investigated in the present study, it could be that juvenile limpets may have different habitat preferences from those of adults or that adults may kill some recruits. For example, Underwood *et al*. (1983) reported that recruitment of *Cellana tramoserica* was negatively correlated with density of adult limpets. There was a general trend of increase in recruit density from south to north (i.e. Nqabara < Dwesa < Cwebe < Xhora) for all species which implies a geographic effect. Surface water currents on this coast are strongly affected by wind (Lutjeharms 2004) and south westerly winds predominate. Therefore, more larvae may be transported from southern to northern sites.

The significant differences in recruitment among sites may reflect food availability, which is known to influence recruitment among sites (Hindell & Quinn 2000). On scales of 10 to 100 km, spatial variability in recruitment has been suggested to be related to the regional larval pool (which is dependent on both number of eggs produced and larval survival) and regional physical transport processes (Gaines & Roughgarden 1985; Gaines & Bertness 1992; Rodriguez *et al*. 1993). Furthermore, the composition of intertidal communities is known to change across large spatial scales, often as a function of upwelling intensity and other oceanographic patterns, which are strong drivers of recruitment variability (Bustamante *et al*. 1995b; Menge *et al.* 1997; Connolly & Roughgarden 1998; Connolly *et al.* 2001; Menge 2000). This can therefore, explain why Xhora, despite being the most heavily exploited site, had the highest numbers of recruits for all species.

Most studies have shown recruitment to be spatially and temporally variable (Sousa 1984; Connolly *et al*. 2001; Broitman *et al.* 2005), and adjacent sites, which one would expect to receive recruits from the same potential pool (Denny & Shibata 1989), can have very different settlement patterns (Connell 1985; Porri *et al*. 2006). Such variations can be attributed to differences in settlement at this scale, which may be due to variation in potential recruit densities in the water column or differential delivery to the shore (Porri *et al*. 2006), coupled with other aspects such as localized, small scale variation in grazer densities on the shore resulting in an interaction between local and non-local processes (Underwood & Jernakoff 1984). On the other hand, in addition to the direct effects of removing adults from the population, exploitation may deplete breeding stocks to a level that affects recruitment (Foster & Hodgson 2000). Sustained productivity in the wild is therefore dependent on natural recruitment (Harris *et al*. 1998). This highlights the importance of connectivity and the physical scales at which these populations are open. Xhora has the lowest adult density but highest recruit density, implying these populations are open on scales of at least 40 km.

The observed recruitment variability on scales of 100 m (i.e. significant area effects) for all species may be caused by settlement processes, such as microhydrodynamics or availability of free-space for larvae (Shanks & Wright 1987, Minchinton & Scheibling 1993, Pineda 1994; Noda *et al.* 1998) and by post-settlement processes, such as predation and competition (Osman & Whitlatch 1995; Hunt & Scheibling 1997) or abiotically driven mortality. In addition, larvae require a damp place to settle (Lewis & Bowman 1975; Thompson 1980). Thus, variability in the availability of crevices, moist rocks or pools, which provide a more stable habitat for juveniles than the open rock (Branch 1975b; Delany *et al*. 1998), may play an important role. For example, *Patella vulgata* emigrates from pools as it grows; only utilizing the pool environment as a nursery ground, while *P. ulyssiponensis* is an obligate pool-dweller throughout its lifespan (Delany *et al*. 1998). *H. concolor* and *C. capensis* have been reported as being found in crevices, moist rock and on sand (Branch 1975a). *S. longicosta* juveniles (recruits) are found on other shells, particularly those of *Oxystele sinensis*, and have short costae and relatively high shells. As growth occurs, *S. longicosta* shifts to lithothamnion on a rocky substratum, and migrates considerably (i.e. it undergoes a comparable change of habitat during the life cycle). The transition from a substratum of other shells to lithothamnion occurs after 1 year of growth and is accompanied by heavy mortality (Branch 1975b). The shift to a flat rocky substratum leaves the animals very susceptible to predation and desiccation until their shells grow to fit the new substratum.

The lack of a significant reserve effect, suggests that larvae can be transported far from where they are released (Shanks 1998). For instance, *Littorina scutulata* larvae were found to spend more than 20 days in the plankton and are thus likely to settle at great distances from the adults (Rochette & Dill 2000). In contrast, larvae of *Lottia digitalis* (limpets) recruit directly into the adult habitat (Kay 2002). On a small scale in the water column near the conspecific adults, larvae of the limpet *Crepidula onyx* detect waterborne conspecific cues (Zhao & Qian 2002).

Local populations and associated assemblages are often strongly affected by recruitment variability, which reflects the amount of external larval supply into the local population (Connell 1985). The high recruitment density of *S. granularis* at Xhora and Cwebe could be a result of the association of this species with other species, especially barnacles (*pers. obs.*). These interactions may change from place to place and time to time in relation to other physical and biological processes such as storms. Some studies have found that limpet recruitment is enhanced by both mussels (Lewis & Bowman 1975; Ruiz Sebastian 2002) and barnacles (Lewis & Bowman 1975; Choat 1977). Lewis and Bowman (1975) suggested that many limpets settle on mussels but subsequently migrate onto the rock. Erlandsson and McQuaid (2004) noted that, for mussels, the association of recruits and adults may be due to larval choice during settlement and /or increased rates of survival for recruits settling among adults.

In summary, different species showed different timing of major recruitment events, though some had similar patterns. These events varied from sporadic (*C. capensis* and *S. longicosta*) to protracted (*H. concolor* and *S. granularis*) recruitment. The lack of a reserve effect indicates that recruitment is generally independent of whether the site is protected or not. Although the effects of site were non-significant, Xhora had the highest recruitment densities for all species. Therefore, reserves do not enhance recruitment directly, but that because these populations appear to be open on scales of 40 km, high limpet populations within reserves may enhance overall recruitment because they would have greater gamete output. Thus reserves should have an indirect effect on recruitment if not a direct one.

Table 4.1: Results of 4-way ANOVA based on mean recruitment density estimates of *H. concolor*. * denotes a significant effect at $p < 0.05$, ** = < 0.001 and *** = < 0.0001.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	50.283	19	2.646	4.539	< 0.001**
Reserve	3.840	1	3.840	0.580	0.534
Site (Reserve)	14.083	2	7.042	3.621	0.079
Area (Reserve (Site))	5.477	4	1.369	3.154	< 0.05*
Month x Reserve	11.077	19	0.582	0.578	0.899
Month x Site (Reserve)	38.350	38	1.009	2.324	< 0.001**
Month x Area (Reserve (Site))	32.990	76	0.434	1.143	0.189
Error	850.400	2240	0.379		

Table 4.2: Results of 4-way ANOVA based on mean recruit density estimates of *S. longicosta*. * denotes a significant effect at $p < 0.05$, ** = < 0.001 and *** = < 0.0001.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	406.058	19	21.371	10.623	< 0.0001***
Reserve	48.450	1	48.450	0.970	0.442
Site (Reserve)	107.451	2	53.725	4.257	0.060
Area (Reserve (Site))	36.778	4	9.195	3.885	< 0.05*
Month x Reserve	38.225	19	2.012	0.347	0.991
Month x Site (Reserve)	220.032	38	5.790	2.447	< 0.0001***
Month x Area (Reserve (Site))	179.855	76	2.3	1.951	< 0.0001***
Error	2716.667	2240	1.213		

Table 4.3: Results of 4-way ANOVA based on mean recruit density estimates of *C. capensis*. * denotes a significant effect at $p < 0.05$, ** = < 0.001 and *** = < 0.0001.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	116.0	19	6.109	1.656	0.140
Reserve	21.470	1	21.470	0.125	0.758
Site (Reserve)	348.651	2	174.325	13.853	< 0.001**
Area (Reserve (Site))	36.878	4	9.219	3.013	< 0.05*
Month x Reserve	70.105	19	3.689	0.574	0.901
Month x Site (Reserve)	244.066	38	6.422	2.099	< 0.05*
Month x Area (Reserve (Site))	232.488	76	3.059	1.959	< 0.0001***
Error	3498.40	2240	1.562		

Table 4.4: Results of 4-way ANOVA based on mean recruit density estimates of *S. granularis*. * denotes a significant effect at $p < 0.05$, ** = < 0.001 and *** = < 0.0001.

Source of variation	**SS**	**df**	**MS**	**F**	**p**
Month	78.741	19	4.144	2.754	< 0.05*
Reserve	0.920	1	0.920	0.062	0.828
Site (Reserve)	30.961	2	15.480	4.106	0.066
Area (Reserve (Site))	10.995	4	2.748	2.279	0.068
Month x Reserve	28.588	19	1.504	0.675	0.818
Month x Site (Reserve)	84.623	38	2.226	1.847	< 0.05*
Month x Area (Reserve (Site))	91.638	76	1.205	2.252	< 0.0001***
Error	1198.933	2240	0.535		

Table 4.5: Correlation analysis on the relationship between adult and recruit density of commonly exploited and rarely exploited species in each of the four study sites.

Commonly exploited species						
	H. concolor			***S. longicosta***		
Site	**n**	**r^2**	**p**	**n**	**r^2**	**p**
Dwesa	600	0.063	< 0.05	600	0.016	< 0.05
Cwebe	600	0.012	< 0.05	600	0.020	< 0.05
Nqabara	600	0.035	< 0.05	600	0.041	< 0.05
Xhora	600	0.007	< 0.05	600	0.009	< 0.05
Rarely exploited species						
	C. capensis			***S. granularis***		
Site	**n**	**r^2**	**p**	**n**	**r^2**	**p**
Dwesa	600	0.018	< 0.05	600	0.017	< 0.05
Cwebe	600	0.071	< 0.05	600	0.056	< 0.05
Nqabara	600	0.018	< 0.05	600	0.007	< 0.05
Xhora	600	0.171	< 0.05	600	0.020	< 0.05

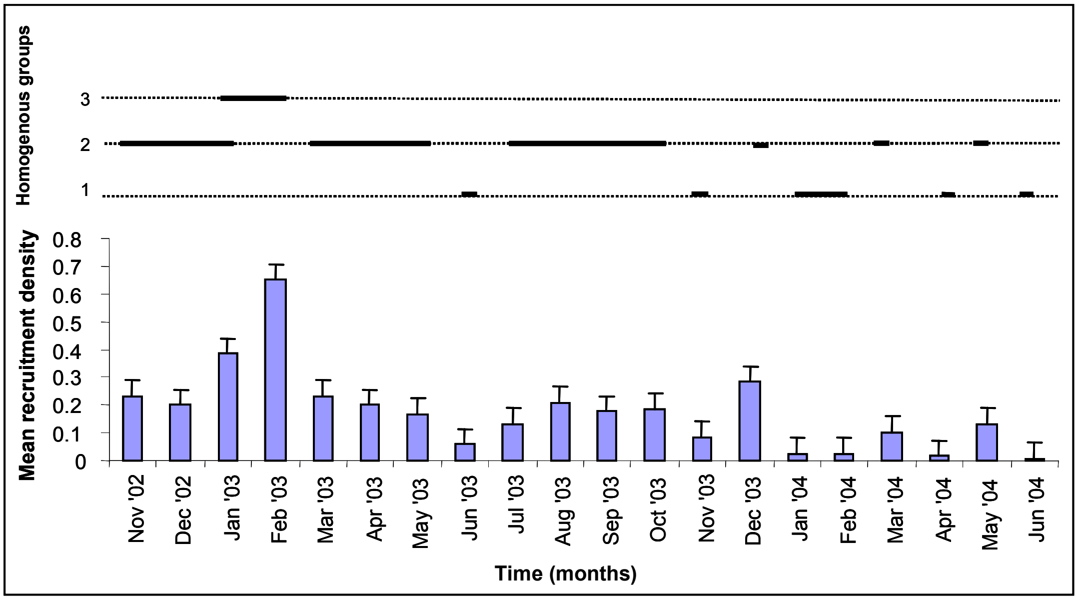


Fig. 4.1.1: Mean recruitment density (+SE) of *H. concolor* at all sites over time. Solid lines above the bar columns connect months that were not significantly ($p < 0.05$) different from each other (Tukey HSD test).

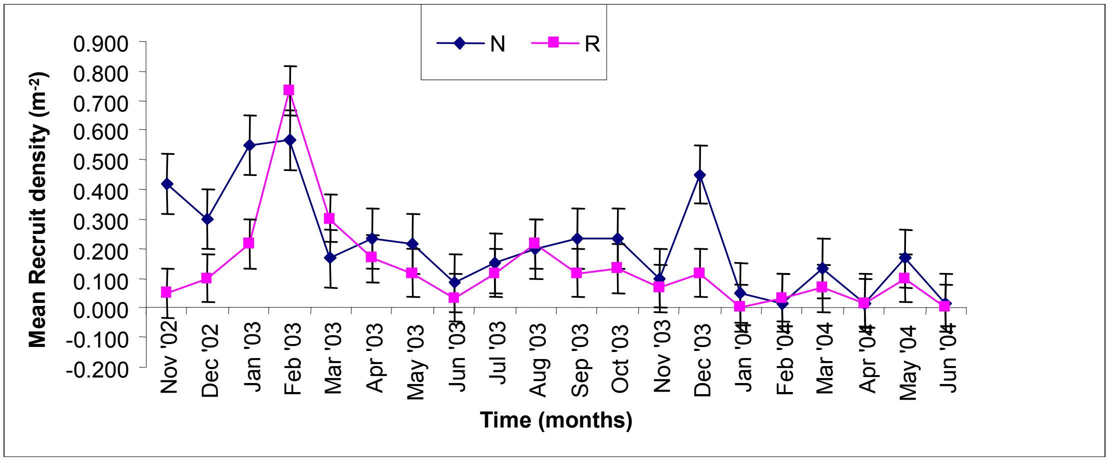


Fig. 4.1.2: Mean recruitment density (+SE) of *C. concolor* in reserve (R) and non-reserve (N) sites through sampling period.

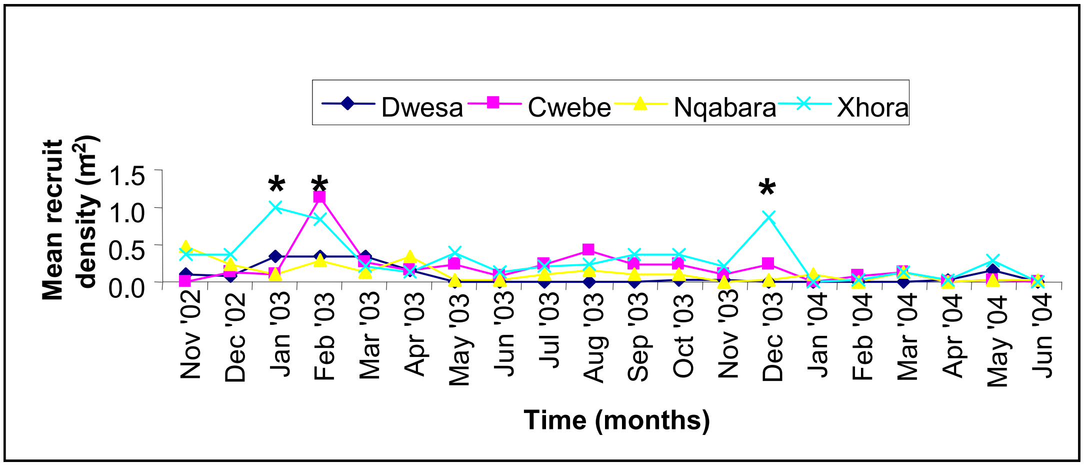


Fig. 4.1.3: Monthly mean recruit density (Standard errors (SE) were omitted for clarity) of *H. concolor* at each of the four study sites. * = significant difference ($p < 0.05$). D = Dwesa, C = Cwebe, N = Nqabara and X = Xhora. Post-hoc test results: Jan'03 X>D>C>N; Feb'03 C>X>D>N; Dec'03 X>C>D=N.

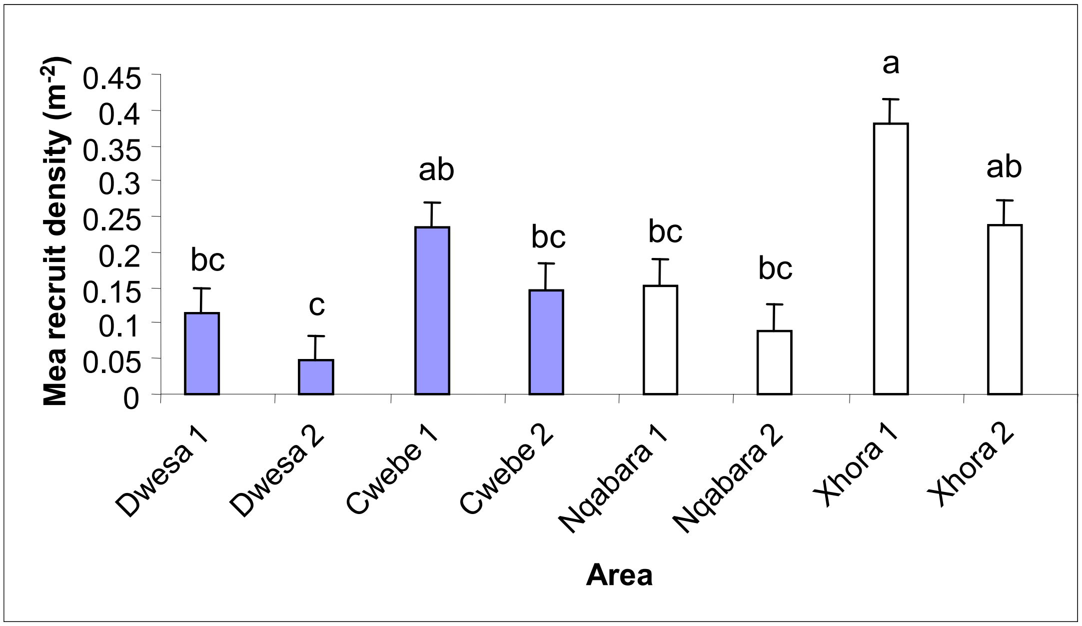


Fig. 4.1.4: Mean recruitment density (+SE) of *H. concolor* in areas within sites. Letters above the bars indicate homogenous groups.

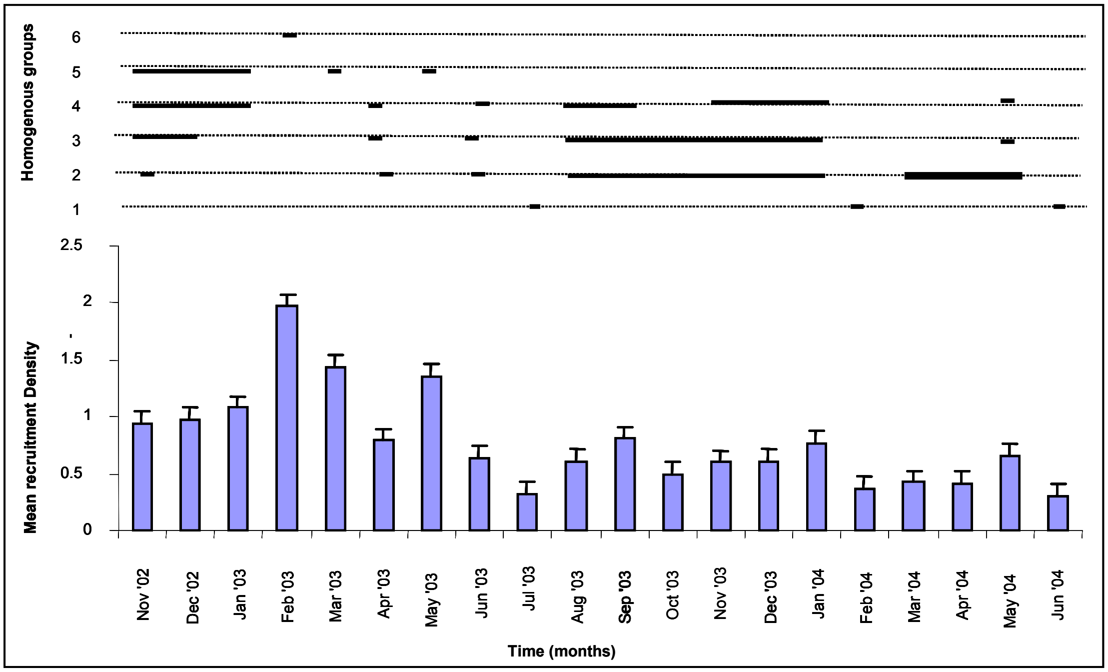


Fig. 4.2.1: Mean recruitment density (+SE) of *S. longicosta* at all sites over time. Solid lines above the bar columns connect months that were not significantly ($p < 0.05$) different from each other (Tukey HSD test).

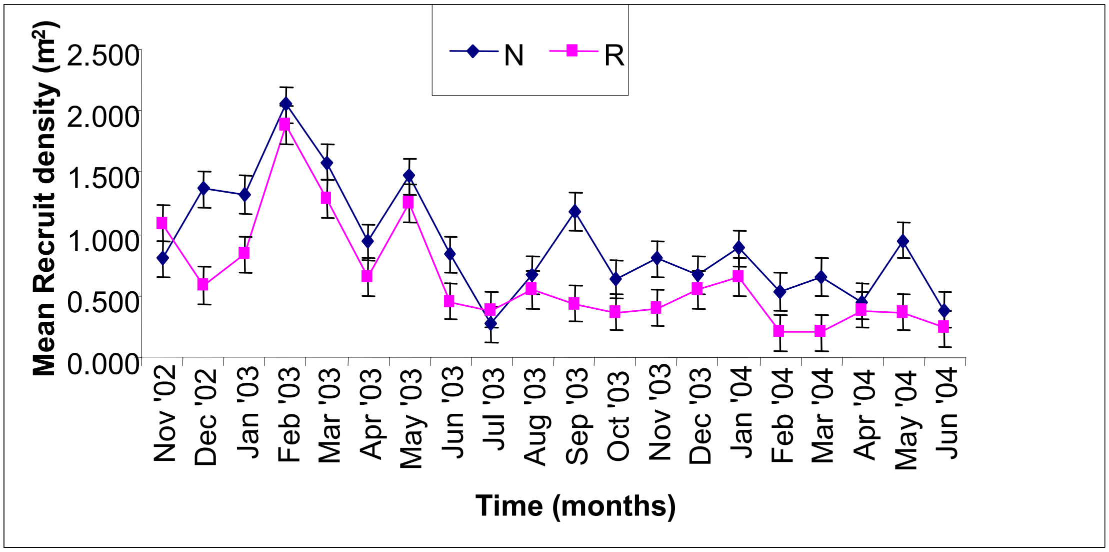


Fig. 4.2.2: Mean recruitment density (+SE) of *S. longicosta* in reserves (R) and non-reserve (N) sites through the sampling period.

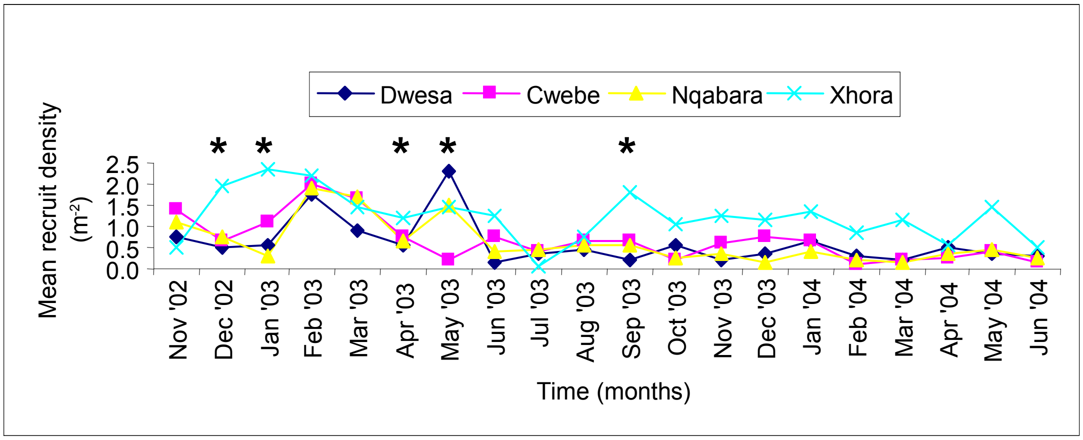


Fig. 4.2.3: Monthly mean recruit density (Standard errors (SE) were omitted for clarity) of *S. longicosta* at each of the four study sites. * = significant difference ($p < 0.05$). Post-hoc test results: Dec'02 X>N=C>D; Jan'03, Sep'03 X>C>D>N; Apr'03 X>C>N=D; May'03 D>X=N>C.

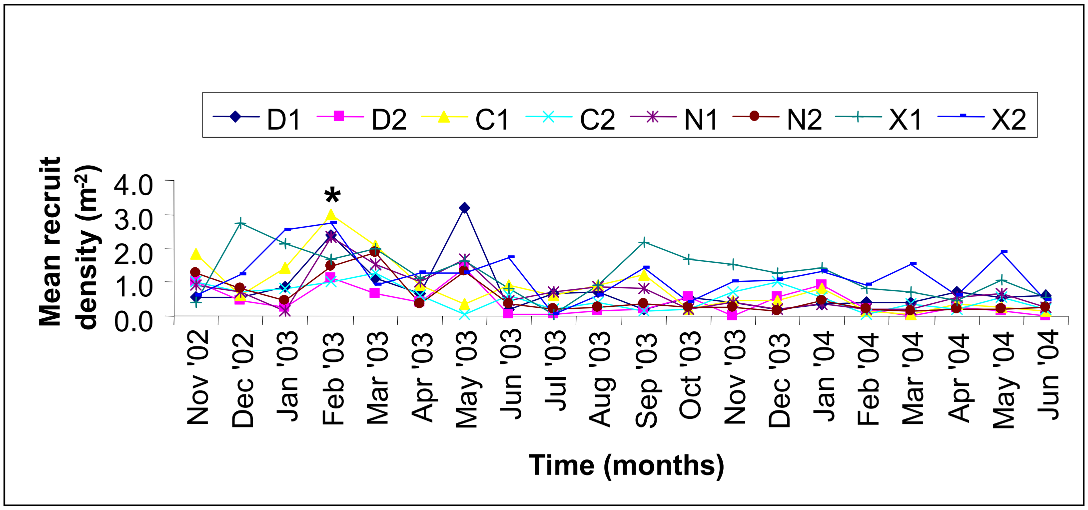


Fig. 4.2.4: Monthly mean density (Standard errors (SE) were omitted for clarity) of *S. longicosta* at each of the areas within sites. * = significant difference ($p < 0.05$). D1 = Dwesa 1, D2 = Dwesa 2, C1 = Cwebe 1, C2 = Cwebe 2, N1 = Nqabara 1, N2 = Nqabara 2, X1 = Xhora 1 and X2 = Xhora 2. Post-hoc test results: Feb'03 C1>C2.

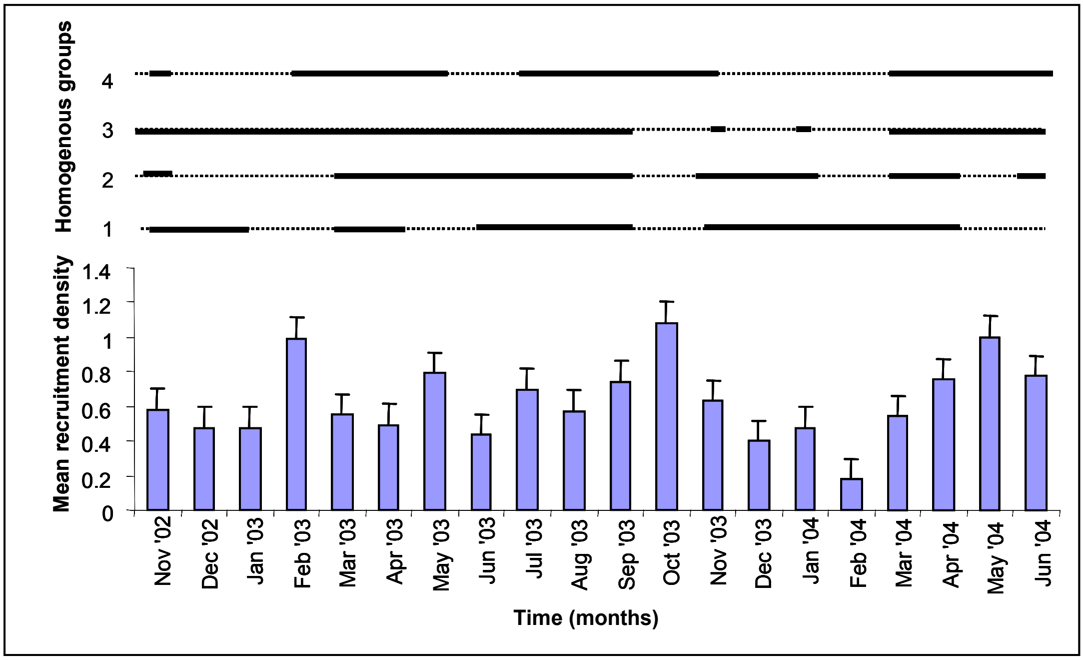


Fig. 4.3.1: Overall mean recruitment density (+SE) of *C. capensis* at all sites over time. Solid lines above the bar columns connect months that were not significantly ($p < 0.05$) different from each other (Tukey HSD test).

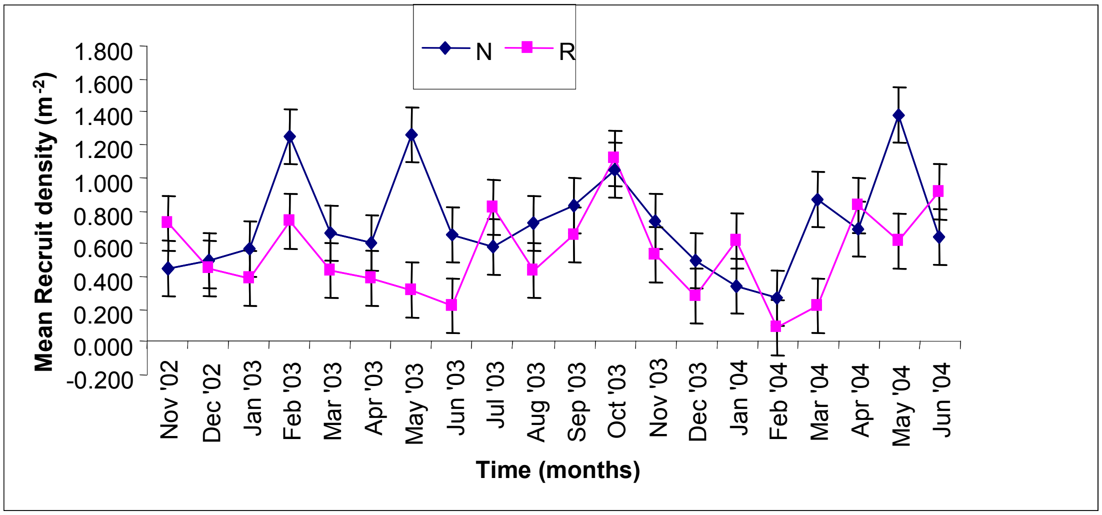


Fig. 4.3.2: Mean recruitment density (+SE) of *C. capensis* in reserve (R) and non-reserve (N) sites through the sampling period.

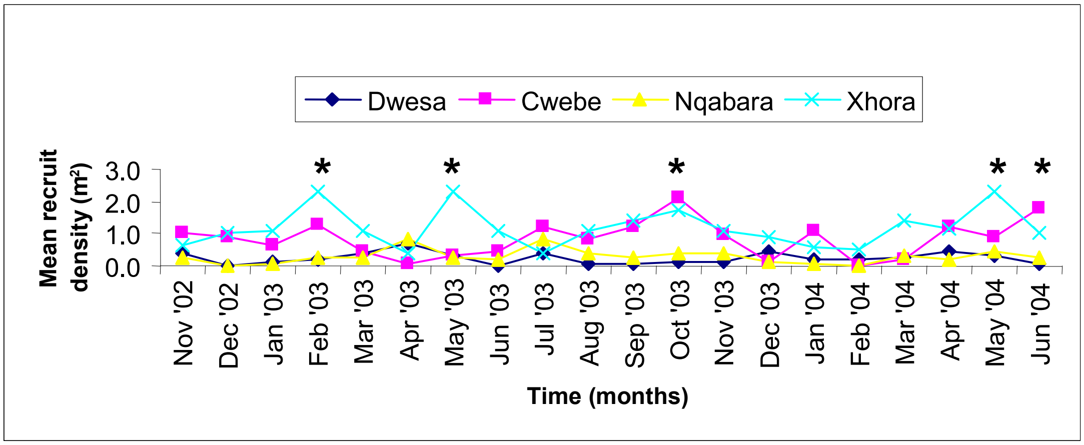


Fig. 4.3.3: Monthly mean recruit density (Standard errors (SE) were omitted for clarity) of *C. capensis* at each of the four study sites. * = significant difference ($p < 0.05$). Post-hoc test results: Feb'03, May'04 X>C>N=D; May'03 X>D=C=N; Oct'03, Jun'04 C>X>N>D.

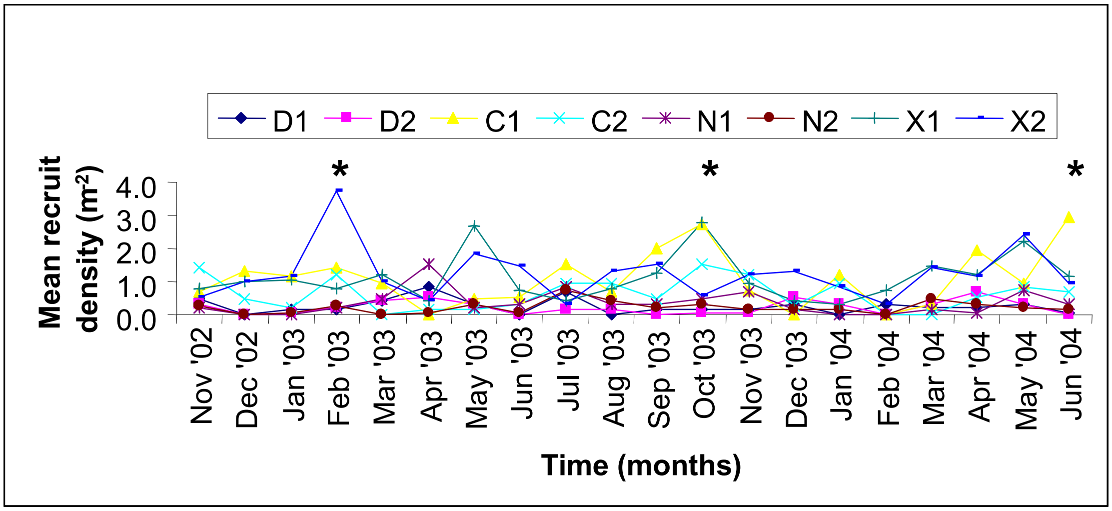


Fig. 4.3.4: Monthly mean density (Standard errors (SE) were omitted for clarity) of *C. capensis* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Feb'03 X2>X1; Oct'03 X1>X2; Jun'03 C1>C2.

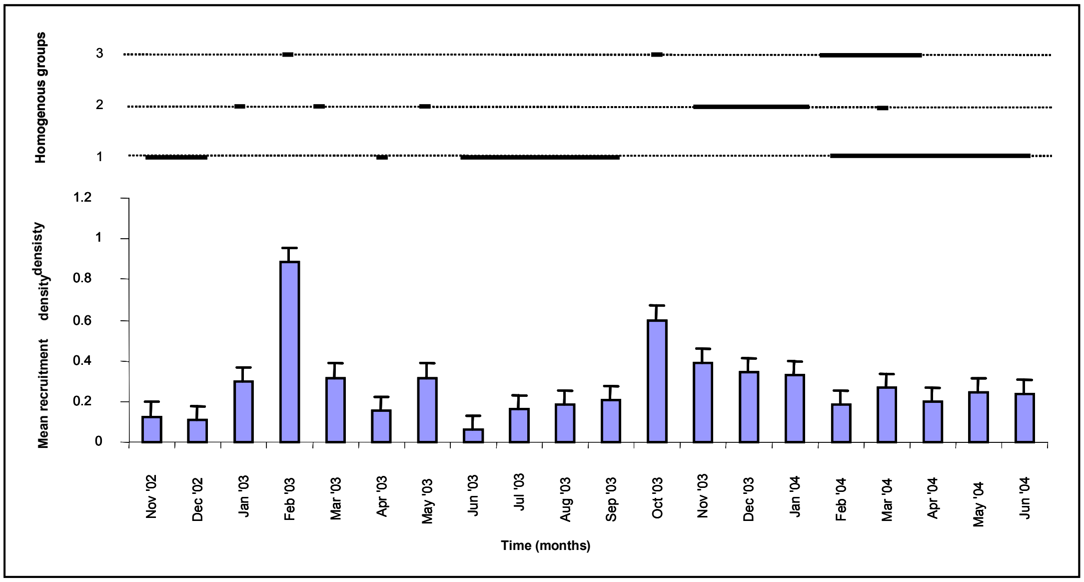


Fig. 4.4.1: Mean recruitment density (+SE) of *S. granularis* at all sites over time. Solid lines above the bar columns connect months that were not significantly ($p < 0.05$) different from each other (Tukey HSD test).

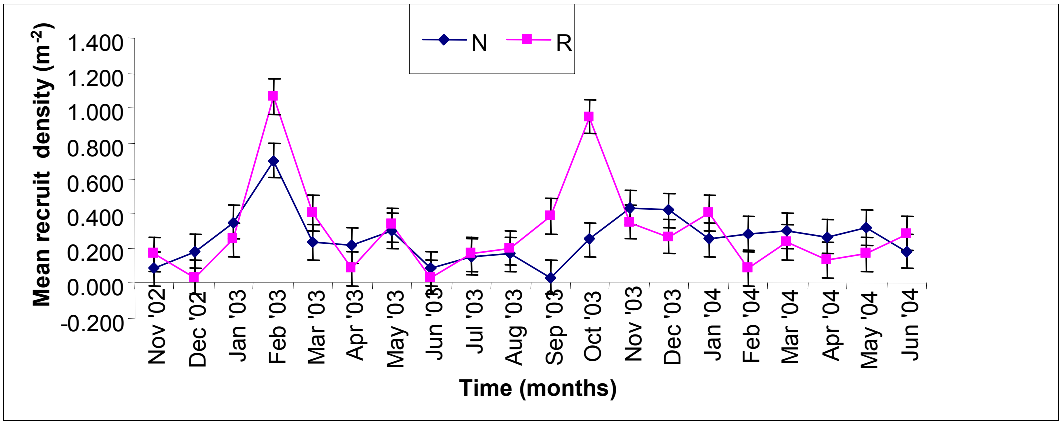


Fig. 4.4.2: Mean recruitment density (+SE) of *S. granularis* in reserve (R) and non-reserve (N) sites through sampling period.

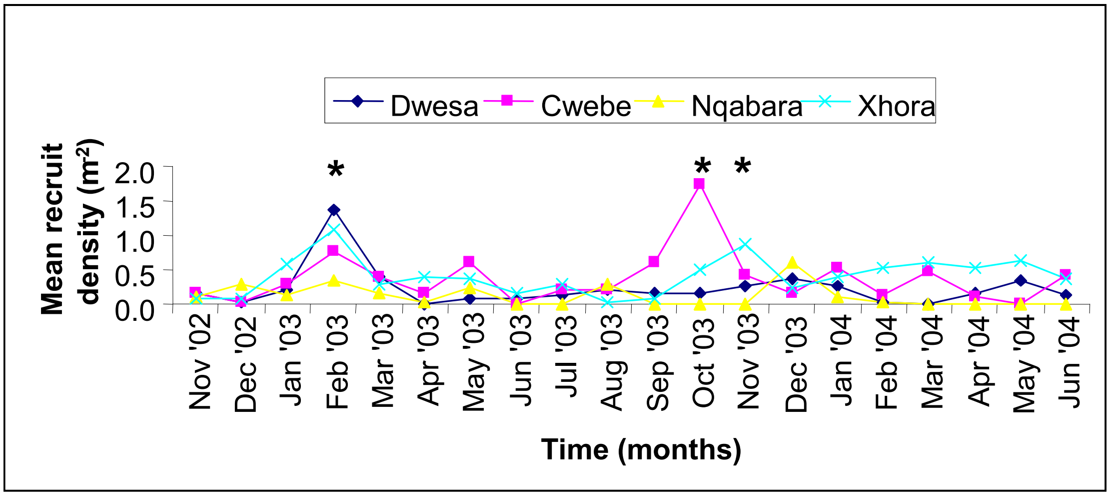


Fig. 4.4.3: Monthly mean recruit density (Standard errors (SE) were omitted for clarity) of *S. granularis* at each of the four study sites. * = significant difference ($p < 0.05$). Post-hoc test results: Feb'03 D>X>C>N; Oct'03 C>X>D>N; Nov'03 X>C>D>N.

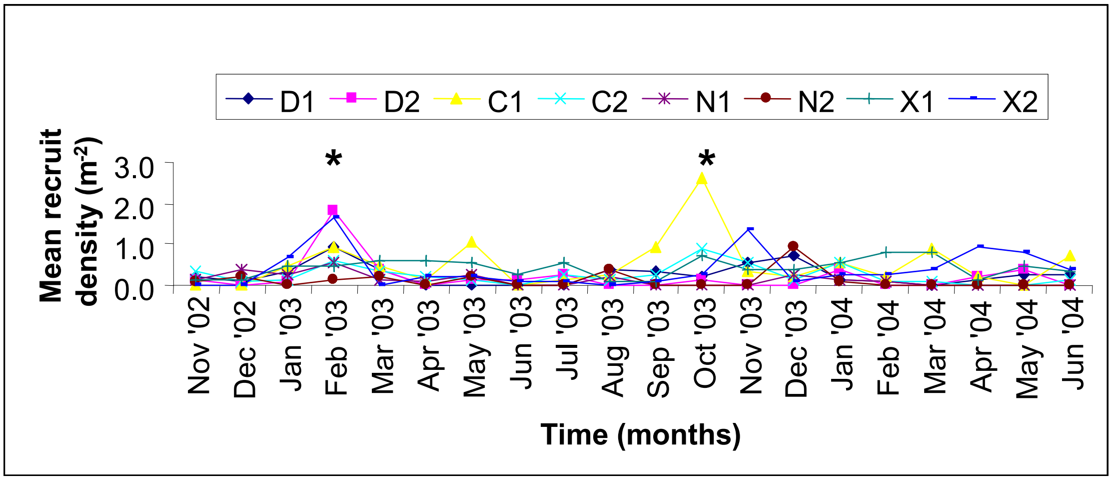


Fig. 4.4.4: Monthly mean density (Standard errors (SE) were omitted for clarity) of *S. granularis* at each of the areas within sites. * = significant difference ($p < 0.05$). Post-hoc test results: Feb'03 X2>X1; Oct'03 C1>C2.

CHAPTER 5

GROWTH RATES

5.1 INTRODUCTION

A knowledge of growth patterns is fundamental to understanding an organism's life-history. Overall, growth rate in particular is critical to the general population dynamics of a resource, while an understanding of seasonal growth rates provide additional insight into the ecological factors that determine growth (Clarke *et al.* 2004). Growth rates can influence fitness in several ways and are often used as a surrogate for fitness, especially in snails (Palmer 1983; Brown & Quinn 1988). For example, as fecundity is typically a positive function of size, faster growing snails have the potential to produce more offspring at any particular age (Trussell 2002). Growth can also play a major role in determining the amount of time a species is vulnerable to predation. For instance, in some snails, once a certain size is attained, mortality due to predation is reduced (Coleman *et al.* 1999).

Processes affecting growth, mortality and recruitment rates of exploited species determine the rate at which a species will replenish itself under particular environmental conditions. These parameters are required in order to develop management plans (Bruton *et al.* 1991). A huge variety of factors is known to affect growth rate. Apart from position on the shore, wave action, latitude, season and habitat-associated differences in food availability and seasonal fluctuations in temperature, age and shell shape of limpets (Branch 1981; Creese & Underwood 1982; Underwood 1984), these include competition for food (Branch 1976; Bosman & Hockey 1988; Lasiak 1993; Liu 1994; Bustamante *et al.* 1995a; Christopher 2000; Jenkins & Hartnoll 2001), pollution (Tablado *et al.* (1994), the presence of predators (Akester & Martel 2000), shell damage/erosion (Day *et al.* 2000), genetic differentiation, relative density, quality of food, foraging efficiency and/or energy allocation to other needs such as maintenance and reproduction (Etter 1996; Trussell 2002).

The two most important determinants of fitness and population growth are the age and size of an organism at maturity. As a consequence, these two determinants have been the focus of intense empirical and theoretical investigation (Sebens 1982; Abrams & Rowe 1996) as they influence population growth. Intraspecific competition at increased densities (e.g. in reserves) has been shown to affect greatly the growth and mortality of limpet species (Underwood 1978; Creese & Underwood 1982; Espinosa *et al*. 2006). Growth reduction in dense stocks has also been observed in bivalves (Beukema *et al*. 2001). Comparisons of growth parameters have been reported as useful in determining whether differences in growth of a species occur under different ecological conditions (Hernandez-Llamas & Ratkowsky 2004).

Modern approaches to management require that information from monitoring be nested within a modeling framework, in which the monitoring is used to evaluate the validity of predictions (from models) of the consequences of management actions (Kendall *et al*. 2004). Various studies have used different methods to estimate growth. These include captive rearing (Trussell 2002; Navarro *et al*. 2006), mark-recapture techniques (Rao 1976; Roberts & Hughes 1980; Takada 1995; Kido & Murray 2003; Griffiths & Attwood 2005; Riascos *et al*. 2007), investigation of annual growth rings (Richardson 2001; Branch & Odendaal 2003; Steffani & Branch 2003a; Gilman 2007), fluorochrome calcium markers (Clarke *et al.* 2004), and length-frequency analysis (Fournier *et al*. 1990; Fournier *et al*. 1998; Thieltges *et al.* 2004).

The objective of this chapter was to test three *a priori* hypotheses, based on the assumption that intraspecific competition for food is important. In the earlier chapter on mean density (Chapter 2), reserve effects were stronger for commonly exploited species and weaker for rarely exploited species (i.e. reserve effects were evident in one out of two species). However, some studies have shown that homing limpets defend their territory or maintain dominance (Branch 1975b; Iwasaki 1995; Lindberg 2007) and reduce intraspecific competition (Mackay & Underwood 1977; Iwasaki 1995). The established territory varies in size with the size of the limpet and thus, under normal conditions and at natural densities, growth rates in territorial limpets are influenced by size not density. Thus, the three hypotheses were: 1) growth rates of rarely exploited species will be the same inside and outside reserves as a result of the effects of natural processes, 2) growth rates of commonly exploited territorial species will be the same inside and outside reserves, and 3) growth rates of exploited non-territorial species will be higher outside reserves than inside reserves due to relaxed intraspecific competition. Direct (individual tagging) and indirect (size frequency distribution) analytical approaches were used.

5.2 MATERIALS AND METHODS

5.2.1 Individual tagging

Approximately 100 individuals of each species at each site (50 from each area) were marked with non-toxic paint (colour coded to give a specific number) and tagged using bee tags (Opalithplattchen, Germany), which were embedded in rapidly setting epoxy glue (Lohse 1993; Jenkins & Hartnoll 2001). Individuals were randomly chosen from a wide size range and the smallest size that could be effectively tagged. Prior to the placement of glue, shells were careful cleaned using a scalpel to remove epibionts including encrusting coralline and lichens.

Each limpet was double-tagged to provide insurance against tag loss by attaching two numbered bee tags to the dry shell of each individual and coating each tag with clear epoxy for protection from abrasion due to wave action.

Subsequently measurements were taken without removing the limpets from the substratum and thus manipulation stress was avoided. Individuals were re-measured with a pair of dividers at approximately monthly intervals from February 2003 to June 2004. This method of measuring limpets has proven successful and allowes for rapid *in situ* measurement of many limpets during a low-tide period (Liu 1994; Tablado *et al.* 1994; Clarke *et al*. 2004). Measurements were later read to the nearest millimeter, a precision confirmed by direct measurements of limpets with Vernier calipers. Tags of marked individuals were shed after some months and recovery rates varied with species. Limpets that had lost their tags were individually identifiable (from a residual glue mark left on the shell from the previous tag) such that the data series could be maintained.

Estimation of growth parameters from tagged limpets

Annual growth rates in each of the limpet populations were calculated from all individuals recaptured. Growth was estimated from mean monthly growth increments by fitting a modified Von Bertalanffy growth equation.

Using mark-recapture data for estimating growth rates requires the following assumptions about the tagging procedures and data collection procedures:

1. Tagging does not retard growth,

2. The tagged limpets are uniquely and correctly recorded at release and recapture,
3. The lengths of limpets are measured without bias at release and recapture, and
4. A wide range of limpet sizes is represented within the recaptures.

Growth in length as a function of time t (L_t) was modeled using the Von Bertalanffy growth equation (VBGE) of the form:

$$L_t = L_\infty(1 - e^{-kt}),$$

where L_∞ is the length that limpets grow to asymptotically and k is the rate at which L_t approaches L_∞.

The VBGE is derived from the differential equation $\frac{dL}{dt} = k\ (L_\infty - \bar{L})$, where $\bar{L}$ is the mean length. Therefore, both dL and dt were obtained from the growth measurements and time at liberty. The maximum likelihood estimates of L_∞ and k were obtained by minimizing a negated, natural logarithm-transformed Normal likelihood of the form:

$$-\ln L_{sp} = \frac{n^{sp}}{2}\ln\sum_{i=1}^{n^{sp}}\frac{dL_i^{sp}}{dt_i^{sp}} - k^{sp} - \left(L^{sp} - \bar{L}^{sp}\right) + \frac{n^{sp}}{2}$$

where s and p denote the number of recaptures per species per population.

All analyses were conducted using AD Model Builder (Otter Research Ltd.) with parameter variability calculated from the inverse Hessian matrix.

The null hypotheses that L_∞ and k were equal across populations of each species were tested using a Likelihood Ratio Test (Hearn & Polacheck 2002). The data for each species were pooled for reserve and non-reserve sites. The null hypotheses that L_∞ and k were equal for reserves and non-reserves were also tested using a Likelihood Ratio Test.

The likelihood ratio test is the ratio of the likelihoods of the reduced and fully parameterized models. The full (saturated) model has all calculated parameters and the reduced model has a subset of the parameters from the full model such that:

$$\Lambda = -2 \ln \lambda = -2 \ln \left(\frac{L_{reduced}}{L_{full}} \right) = -2 \left(\ln L_{reduced} - \ln L_{full} \right)$$

This ratio is considered to be asymptotically chi-square distributed with the degrees of freedom (ν) being equal to the difference in parameters between the two models such that $\Lambda \sim \chi^2$ ($\nu = p_{full} - p_{reduced}$). The null hypotheses that parameter estimates are equal between models were tested by estimating common parameters of the different reduced models and then comparing their likelihoods against the full model.

5.2.2 Length-frequency analysis

Monthly sampling to determine the cohorts from size-frequency distribution of target species was conducted at the same sites as in the previous chapters. Quadrats of 0.5 x 0.5 m were thrown haphazardly and repeatedly in each zone of each species occurrence until about 200 limpets had been measured. The sizes of the cohorts from each limpet population were analysed to estimate growth. Growth rates were then estimated from the monthly change in the mean size of each cohort (McQuaid 1981; Lasiak 1993; Liu 1994) using the MULTIFAN method (Fournier *et al.* 1990; Fournier & Sibert 1991). To allow for comparison of results with the tagging method, areas were pooled.

The approach is statistically robust as it allows the analysis of multiple 'length-frequency data' sets and the simultaneous analysis of several length frequency data sets within a likelihood framework. It has several advantages such as the estimation of the important parameters other than growth, for example, size selectivity of the first age class, parameters associated to a dependency of standard deviation on mean size, relative year class strengths and mortality (Fournier *et al.* 1990). The model details are outlined in Fournier *et al.* (1991). It was assumed that there was a maximum of 7 cohorts for all species. This is the minimum life-span (i.e. 7 years) recorded for these limpets (Branch 1974b; 1975a) All analyses were conducted using AD Model Builder (Otter Research Ltd.) with parameter variability calculated from the inverse Hessian matrix.

5.3 RESULTS

The overall patterns of growth in reserves and non-reserves generally differed between the two methods of growth estimation. The growth rates not only differed among species but also among sites. The growth rate always decreased with an increase in mean shell length in all the species.

5.3.1 Individual tagging

As a result of low recovery of tagged individuals, the data from areas within sites were pooled for each species. Although the coefficients of determination were often extremely low, and sample size small in two instances, annual growth rates decreased significantly ($p < 0.05$) with an increase in mean shell length at all sites and in all species (Figs. 5.1 & 5.2). The annual increment of mean shell growth in limpets was, however, highly variable among sites as well as among species. This reflected the fact that the fastest and lowest annual mean shell growth based on slopes for *Helcion concolor* were found at Xhora and Dwesa, while for *Scutellastra longicosta*, they were found at Dwesa and Nqabara, respectively (Fig. 5.1). In the case of rarely exploited species, the lowest mean annual growth rates for *Cellana capensis* and *Scutellastra granularis* were both obtained at Cwebe, while the highest annual mean shell growths were found at Nqabara and Xhora, respectively (Table 5.3.1, Fig. 5.3). The annual increment of mean shell length at Nqabara was significantly ($p < 0.05$) greater than at Xhora for *C. capensis* while opposite was found for *S. granularis* (Table 5.3.1, Fig. 5.3). Although the annual increment of mean shell length at Dwesa was slightly greater than at Cwebe for both *C. capensis* and *S.granularis*, the differences were statistically insignificant.

The growth curves showed significant differences ($p < 0.05$) between reserves and non-reserves (Table 5.3.2, Fig. 5.4). Except for *S. longicosta* and *H. concolor*, the results from individual tagging showed faster growth rates in non-reserve than reserve sites only for young (< 4-6 years) limpets. The significant differences between reserves and non-reserves ($p < 0.05$) in the growth rate were remarkably clear and maintained throughout the life span for *H. concolor*. In rarely exploited species, the non-reserve sites supported initially greater growth than reserve sites before subsequently approaching asymptotic length of 32 and 33 mm in the 5th and 6th year of age for *C. capensis* and *S. granularis*, respectively (Fig. 5.4).

5.3.1.1 Commonly exploited species

Helcion concolor

The annual growth rate decreased significantly ($p < 0.05$) with an increase in mean shell length in all sites for *Helcion concolor* (Fig. 5.1). The growth rates of *H. concolor* were highest at Xhora and lowest at Dwesa.

The Von Bertalanffy growth equations (VBGE) for *H. concolor* obtained from tagging revealed identical growth rates for Xhora and Nqabara, reaching an asymptotic length of 42 mm in the 3rd year of age (Fig. 5.3). After the second year of age, however, the growth rate at Cwebe became constant while at Dwesa it showed a gradual decrease. While growth at Dwesa was greater than at Cwebe, overall the results showed significantly faster growth rates in non-reserve than reserve sites (Fig. 5.4). The highest and lowest maximum sizes of 43 and 29 mm for *H. concolor* were obtained at Xhora and Cwebe, respectively (Table 5.3.1, Fig. 5.3). The Von Bertalanffy growth equation based on tagging showed that, at first year of age, *H. concolor* was 34 mm at Xhora and 24 mm at Cwebe. The overall mean shell lengths at first year of age of *H concolor* in different sites were, in decreasing order: Xhora (34 mm) ≥ Nqabara (34 mm) > Cwebe (24 mm) > Dwesa (19 mm).

There were significant differences ($p < 0.05$) between reserves and non-reserves in the growth rate of *H. concolor* (Table 5.3.2, Fig. 5.4). This indicated that growth in non-reserves was greater than reserves. The Von Bertalanffy growth equations based on tagging showed that at first year of age, *H. concolor* in non-reserves and reserves was 21 and 17 mm, respectively.

Scutellastra longicosta

There was a significant ($p < 0.05$) negative correlation between between the mean shell length and the growth rate of *S. longicosta* at all sites (Fig. 5.1). The highest and lowest growth rates of *S. longicosta* were obtained at Dwesa and Nqabara, respectively.

The growth rate at Nqabara was significantly lower ($p < 0.05$) than that at Dwesa but no other significant differences were revealed (Table 5.3.1). Although reserves had greater growth rates than non-reserves (Table 5.3.2, Fig. 5.4), the difference was not significant. The mean shell lengths for 1 year old animals were 17 and 12 mm for reserves and non-reserves, respectively.

The curvature parameter, *k* for *S. longicosta* was significantly ($p < 0.05$) affected by site, being highest at Dwesa and lowest at Nqabara (Table 5.3.1, Fig. 5.3). This suggests that the growth rate was fastest at Dwesa and slowest at Nqabara. Thus, individuals of similar lengths were substantially younger at Dwesa than at Nqabara. But the growth parameter, L_∞ value was highest at Nqabara and lowest at Xhora. The highest and lowest maximum sizes of 64 and 41 mm were obtained at Nqabara and Xhora, respectively (Table 5.3.1).

The VBGE based on tagging showed that *S. longicosta* growth increment was almost twice as large at Dwesa (20 $mm.yr^{-1}$), Xhora (17 $mm.yr^{-1}$) and Cwebe (16 $mm.yr^{-1}$) as at Nqabara (9 $mm.yr^{-1}$) (Fig. 5.3). Thus, individuals of similar lengths were substantially younger at Dwesa than at Nqabara.

5.3.1.2 Rarely exploited species

Cellana capensis

Growth rates decreased with an increase in mean length of *C. capensis* at all sites (Fig. 5.2). There were significant differences ($p < 0.05$) among sites in the growth rate of *C. capensis* (Table 5.3.1, Fig. 5.3), the highest and lowest growth rates were found at Nqabara and Xhora, respectively. The growth rates of *C. capensis* were in decreasing order: Nqabara > Xhora > Dwesa > Cwebe (Fig. 5.3).

L_∞ values for *C. capensis* were significantly ($p < 0.05$) greater in reserves than in the non-reserves (Table 5.3.2), with asymptotic lengths of 54 and 38 mm in reserves and non-reserves, respectively. The L_∞ values of 26 and 34 mm for Xhora and Nqabara were reached in the third and fourth year while Dwesa and Cwebe showed a progressive increase. The VBGC revealed that at 1 year of age, *C. capensis* was almost one and half times as long at Nqabara (16 mm), as at Cwebe (9 mm). Thus individuals of similar lengths were younger at Nqabara than at Cwebe (Fig. 5.3). The growth parameter, *k* for *C. capensis* was significantly ($p < 0.05$) higher in non-reserves than reserves (Table 5.3.2, Fig. 5.4).

Scutellastra granularis

There was an inverse relationship between the growth rate and mean shell length of *S. granularis* in all sites (Fig. 5.2), with the fastest and lowest growth rates being found at Xhora and Nqabara, respectively. Growth rates also differed significantly ($p < 0.05$) between Cwebe and Xhora (Table 5.3.1), with no other significant difference among sites. At 1 year of age, growth rates for *S. granularis* were greatest at Xhora (13 mm) and lowest at Cwebe (8 mm) so that individuals of similar lengths were younger at Xhora than at Cwebe (Fig. 5.3). The overall growth rate for *S. granularis* was in decreasing order: Xhora > Nqabara > Dwesa > Cwebe. But this order was reversed in the 5th and 6th year as growth rates decreased at Xhora and Nqabara but increased at Dwesa and Cwebe. Thus asymptotic lengths were reached earlier at Nqabara and Xhora than at Dwesa and Cwebe. The highest and lowest maximum lengths of 38 and 33 mm were observed at Dwesa and Nqabara, respectively (Fig. 5.3). Although the growth rate was slightly greater at Dwesa than Cwebe, the difference was not significant.

The growth parameter, L_∞ for *S. granularis* was significantly ($p < 0.05$) higher in non-reserves than reserves (Table 5.3.2, Fig. 5.4). But this effect was true before the 6th year of age at a shell length of 33 mm. After that, the growth rate decreased and increased in non-reserves and reserves, respectively. The growth parameter k for *S. granularis* showed no significant differences between reserves and non-reserves (Table 5.3.2).

5.3.2 Length frequency analysis

Although cohorts were not easy to identify, for each species at all sites there were a few that could be traced from recruitment in November 2002 through to June 2004. The number of such cohorts ranged from 3 to 5 (Figs. 5.5.1 to 5.8.4). Except for *S. longicosta*, the von Bertalanffy growth equations obtained from cohort analysis showed a slight difference in growth rate in reserves for all species which revealed a more pronounced increase in reserves than non-reserves (Fig. 5.4). Reserves led to significant differences ($p < 0.05$) in the growth rates of *S. longicosta,* with growth in reserves being greater than in non-reserves (Fig. 5.4).

5.3.2.1 Commonly exploited species

Helcion concolor

The growth rates of *H. concolor* showed remarkable, significant differences among sites, with greatest and lowest growth rates at Dwesa and Xhora, respectively (Fig. 5.3). This reflected a decreasing order of Dwesa > Nqabara > Cwebe > Xhora. The Von Bertalanffy growth curves based on cohort analysis revealed that at 1 year of age, *H. concolor* was largest at Nqabara (9 mm) and smallest at Xhora (6 mm) (Fig. 5.3). There was a slight effect of reserve on the growth rate of *H. concolor*, with growth in reserves being greater than in non-reserves but the estimated first year shell length was 7 mm for both (Fig. 5.4) and the overall difference was not significant.

Scutellastra longicosta

There were significant differences ($p < 0.05$) in the growth rates of *S. longicosta* at different sites (Fig. 5.3). The fastest and slowest growth rates were observed at Cwebe and Xhora, respectively. The VBGE based on cohort analysis showed that *S. longicosta* had a growth rate that decreased in the order: Cwebe (9 $mm.yr^{-1}$) > Nqabara (8 $mm.yr^{-1}$) = Xhora (8 $mm.yr^{-1}$) > Dwesa (6 $mm.yr^{-1}$) (Fig. 5.3). Although rates were significantly greater in reserves than non-reserves, the estimated first year shell length was 8 mm for both and the overall difference was not significant (Fig. 5.4).

5.3.2.2 Rarely exploited species

Cellana capensis

There were marked differences in the growth rates of *C. capensis* at different sites (Fig. 5.3). The highest and lowest growth rates of *C. capensis* were found at Dwesa and Xhora, respectively and decreased in the order: Dwesa > Nqabara > Cwebe > Xhora (Fig. 5.3). The VBGE revealed that at 1 year of age, *C. capensis* at Dwesa was identical in length to those at Xhora (3 mm) but differed subsequently. The L_∞ of *C. capensis* were significantly greater in reserves than non-reserves, with the highest at Dwesa (28 mm) and lowest at Xhora (16 mm) (Fig. 5.3). Although the growth parameter, k was higher in non-reserves than reserves (Fig. 5.4), this difference was not significant.

Scutellastra granularis

There was a significant ($p < 0.05$) site effect on the growth rate of *S. granularis* (Fig. 5.3), with the highest and lowest growth rates at Nqabara and Xhora, respectively. There was no significant difference between Dwesa and Cwebe. The growth rates of *S. granularis* were, in decreasing order: Nqabara > Cwebe = Dwesa > Xhora (Fig. 5.3). The VBGE of *S. granularis* showed the highest and lowest growth rates of 5 and 4 $mm.yr^{-1}$ were found at Cwebe and Nqabara, respectively. This indicates that individuals of similar lengths were younger at Nqabara than at Xhora (Fig. 5.3). The growth parameter L_∞ showed no significant effect of reserve (Fig. 5.4). Although the growth parameter, k was higher in non-reserves than in the reserves, this difference was not significant (Fig. 5.4).

5.4 DISCUSSION

The two techniques to estimate growth rates of limpets revealed quite different results for reserve effects on the study limpets (Table 5.3.3). The main thrust of the discussion will focus mainly on tagging results rather than those from cohort analysis. The tagging results are more reliable than cohort analysis in that they are based on direct measurements of individuals unlike the cohort analysis which is based on indirect measurement. Moreover, it is not easy to identify cohorts (Clarke *et al*. 2004) as this requires a very large sample size (Grant *et al*. 1987). Growth curves constructed from cohort analysis represent differences in growth between length classes and one assumes that growth changes over time in a predictable way, causing each cohort to be older than the previous one by an amount consistent with the respective growth rates (Millstein & O'Clair 2001). However, growth rates can vary significantly between individuals of the same age, leading to length differences that need not reflect age differences. Secondly, small animals grow faster than adult animals (i.e. growth decreases with age). A further difficulty with cohort analysis is that comparisons based simply on the von Bertalanffy growth parameter k, can be misleading because of the influence of maximum size, L_∞ on k. For instance, it is likely that selective exploitation of larger individuals in non-reserve sites can have an effect on growth increment curves by decreasing the expected age of limpets in the larger length classes. A similar pattern was reported in mussels *Mytilus trossulus* (Millstein & O'Clair 2001). Individual tagging gave higher estimates of growth than cohort analysis for all species and this can be attributed not only to differences in the growth estimation techniques but also to low sample sizes in cohort analysis. Moreover, individual tagging gave a significant effect of reserves on L_∞ in 3 out of 4 species, while the cohort analysis this occurred in only 1 of 4. In contrast, McQuaid & Lindsay (2000) noted that cohort analysis produced higher estimates of growth rate of mussels than tagging but this was because the marking technique they used caused a temporary growth check. Therefore, this study has shown that the mark-recapture technique is a suitable and viable approach for determining growth rates in limpets.

The results revealed a general decrease in growth rate with an increase in the mean shell length for all species at all sites. Primarily, this is an effect of age. In most molluscs, shell deposition decreases with age, while body growth is at a maximum in early life and then decreases progressively (Branch 1974b). The decrease in the rate of shell deposition may be due to a number of factors, e.g. metabolism decreases with age and size. Thus growth rates are rarely constant during the developmental period of animals. Slow growth rates in large snails may also be related to senescence or a shift in energy allocation from growth to reproduction in older snails (Takada 1995; Alfaro & Carpenter 1999). Apart from ontogenetic effects, shell thickness can be important. For example, thick-shelled snails generally grow less in terms of shell length than thin-shelled snails of similar shape (Trussell & Nicklin 2002). In the present study, *Helcion concolor* has the thinnest shell compared to the other species and showed the fastest growth rate.

Other factors such as the substratum are also known to affect the growth rates of limpets. For instance, any given sizes of limpets on regular substrata have a higher growth increment than those on irregular substrata (Silva *et al*. 2003). Moreover, the frequency and duration with which patches are wetted can determine how much time animals living in each patch have available to feed. Therefore, patterns of wetting of the substratum may be more important in determining rates of growth and maximal size of gastropods living in different patches than the density of animals living there (Chapman 1994a). Other studies have examined differences in growth rates of gastropods with respect to tidal zone (Fletcher 1984a), and microalgal abundance (Underwood 1984). The variations in growth rates could be influenced by habitat use. Many organisms switch between two habitats to maximize fitness by trading-off reduced growth against a decreased mortality risk in the safer habitat (Gosselin & Qian 1997).

The observed differences among sites in the growth rates of the study limpets may be attributed to differences in food supply (Hindell & Quinn 2000). For instance, competition for food may lead to different growth rates as growth is affected by food intake (Bosman & Hockey 1988) and differences in growth rates have often been attributed to food availability (Creese and Underwood 1982; Underwood 1984; Bosman & Hockey 1988). Although seasonality in growth rates was not determined in this study, it has been found that epilithic algal production (in the form of *Chl* a) peaks during the winter months along the south east coast of South Africa (Bustamante *et al*. 1995b). Food availability is also related to the emersion duration of a given intertidal level (Cusson & Bourget 2005).

The effects of grazing gastropods on rocky shores are known to vary seasonally in relation to variation in recruitment of algae and/or in the foraging activity of herbivores (Hawkins 1981). Temporal and spatial variations in sediment loads can influence the grazing activity of limpets. Airoldi and Hawkins (2007) recently noted that a thin layer of sediment severely reduced the grazing activity of *Patella vulgata* in United Kingdom. Paine (1969) suggested that individuals of *Tugela* grew slowly at high levels on the shore but after reaching a certain adult size, moved down shore in response to increased food availability, and grew faster. Growth rate depends directly on foraging effort, and so optimal foraging behaviour necessarily influences growth and size at maturity (Johannesson *et al*. 1997; Tenhumberg *et al*. 2000). Growth rates of herbivorous molluscs are also affected by the palatability, cell wall toughness, digestibility and nutritional value of the algae they consume (Foster *et al*. 1999). Generally the results of the present study showed that small limpets grew faster than adult limpets in all species. The presence of adult limpets can have a negative impact on the growth of small limpets by bulldozing them when grazing (Boaventura *et al*. 2003).

The differences in the growth rates found among the limpet species in this study reflect the differences in the respective mean and maximum lengths of the individuals from each of the populations. There are other factors, both endogenous and exogenous, that can contribute to length differences between individuals e.g. genetics, fluctuations in temperature and salinity and food availability (Branch 1981). Branch (1974b) noted that migratory species such as *Scutellastra granularis, Cellana capensis* and *Helcion concolor* and other patellid limpets over-exploit their food supplies and have greater growth rates, high mortality and decreased longevity relative to non-migratory species.

An unexpected result was that the maximum theoretical length (L_∞) of *S. longicosta* was greater in non-reserves than reserves. An asymptotic size is probably set by extrinsic factors within the local environment such as energetic constraints (Sebens 1982), or mortality induced by hydromechanical forces generated by breaking waves (Denny *et al*. 1985). In mussels, the effect of wave action may be species-specific (McQuaid & Lindsay 2000), as an increase in wave exposure may lead to either increased (van Erkom Schurink & Griffiths 1993), or decreased (McQuaid *et al.* 2000) growth rates. Increasing flow speeds over limpets can result in lower growth rates, survival rates and fitness (Denny *et al*. 1985; Etter 1989). However, whether a population is limited physically by water motion depends both on the ability of an organism to adhere to the substratum, and on the magnitude and/or frequency of wave-generated forces impacting the organism (Denny & Blanchette 2000; Trussell 2002).

There was no reserve effect on the growth rate of *S. granularis* and that was expected as it is the least exploited species. The significant difference between reserves and non-reserves in maximum size may be explained in terms of the interaction of *S. granularis* with other species. Barnacles compete directly with *S. granularis* for space and food. Barnacles filter out food which would normally settle on the substratum and deposited food is often inaccessible because of irregular barnacle shape. Consequently, mean limpet size, growth and reproductive outputs are reduced as barnacle cover increases (Branch 1981). Consequently, dense barnacle populations depress growth of limpets (Lewis & Bowman 1975). This may apply here, as there are more barnacles in reserves than non-reserves (*pers. obs*.). Instances where growth rates are faster in non-reserves than in reserves may be attributed to suppressed growth in reserves due to intraspecific competition. This was true for *H. concolor*, which showed greater growth rates in non-reserve sites. It has been shown that growth rates of intertidal gastropods increase when densities are exceptionally reduced (Underwood 1976). Marshall and Keough (1994) also showed that there is strong intra size-class competition, with growth rates of individual limpets falling as their densities increased. The allocation of extra energy for reproduction and the lower growth rate of large snails could be related to reproductive activity (Takada 1995).

As predicted, the commonly exploited territorial species (*Scutellastra longicosta*) showed no reserve effects on growth rates. As this species feeds on *Ralfsia*, it establishes gardens and defends them (Branch 1974b). These gardens vary with the size of the limpet and are thus not affected by density under natural conditions. The hypothesis that the commonly exploited non-territorial species *H. concolor* is affected by intraspecific competition was supported. Interestingly, this study revealed no significant differences in asymptotic length of *H. concolor* between reserves and non-reserves, despite the fact that it is one of the most preferred species. This may support the suggestion that this species is often confused with *Cellana capensis*, as shown by interview surveys (Chapter 1), as one would expect a decrease in size in non-reserves due to intraspecific competition and especially harvesting.

Thus of the three hypotheses, two were supported and the third was partly supported. The first hypothesis that growth rates of rarely exploited species will be the same inside and outside reserves was supported for *S. granularis* but not for *C. capensis*. The unexpected existence of a reserve effect on the growth rate of *C. capensis* reflects its confusion with *H. concolor*. Secondly, the hypothesis that growth rates of commonly exploited territorial species (*S. longicosta*) will be the same inside and outside the reserves was supported. Thirdly and lastly, the hypothesis that growth rates of exploited non-territorial species (*H. concolor*) will be higher outside than inside the reserves was supported.

Table 5.3.1: Von Bertalanffy growth parameter estimates (±SE) based on tagging for the four limpet species sampled at four sites. Differences in model parameters, grouped by species, were determined using a likelihood ratio test. Estimates sharing common superscripts are homogenous groups (i.e. not significantly different ($p > 0.05$) from one another).

Species	**Site**	L_∞	***k***	**n**
H. concolor	Dwesa	$38.39^{b} \pm 2.47$	$0.67^{d} \pm 0.11$	8
	Cwebe	$29.05^{c} \pm 1.89$	$1.68^{b} \pm 0.24$	5
	Nqabara	$42.10^{a} \pm 3.07$	$0.85^{c} \pm 0.19$	12
	Xhora	$43.19^{ac} \pm 1.38$	$2.50^{ac} \pm 0.21$	4
S. longicosta	Dwesa	$42.89^{b} \pm 2.77$	$0.61^{a} \pm 0.11$	25
	Cwebe	$43.85^{b} \pm 5.32$	$0.40^{c} \pm 0.11$	41
	Nqabara	$63.67^{a} \pm 14.55$	$0.15^{d} \pm 0.06$	33
	Xhora	$41.26^{b} \pm 12.67$	$0.53^{bc} \pm 0.31$	32
C. capensis	Dwesa	$49.64^{b} \pm 8.03$	$0.22^{cd} \pm 0.07$	105
	Cwebe	$53.50^{a} \pm 3.57$	$0.18^{d} \pm 0.17$	95
	Nqabara	$34.30^{c} \pm 2.51$	$0.61^{b} \pm 0.11$	100
	Xhora	$25.98^{d} \pm 3.66$	$0.73^{a} \pm 0.24$	76
S. granularis	Dwesa	$47.69^{a} \pm 14.71$	$0.20^{cd} \pm 0.11$	73
	Cwebe	$48.72^{a} \pm 20.46$	$0.19^{d} \pm 0.12$	40
	Nqabara	$34.34^{c} \pm 4.63$	$0.41^{b} \pm 0.11$	41
	Xhora	$36.26^{b} \pm 4.91$	$0.45^{a} \pm 0.11$	45

Table 5.3.2: Von Bertalanffy growth parameter estimates (±SE) based on tagging for the four limpet species sampled at four sites. Differences in model parameters, grouped by species, were determined using a likelihood ratio test. Estimates sharing common superscripts are homogenous groups (i.e. not significantly different ($p > 0.05$) from one another).

Species	**Site**	L_{∞}	***k***	**n**
H. concolor	Reserves	38.80^{a} ± 2.23	0.84^{b} ± 0.18	13
	Non-reserves	38.80^{a} ± 2.18	1.50^{a}± 0.20	16
S. longicosta	Reserves	44.11^{b} ± 4.05	0.45^{a} ± 0.11	66
	Non-reserves	49.35^{a} ± 13,61	0.34^{a} ± 0.19	65
C. capensis	Reserves	54.06^{a} ± 5.80	0.18^{b} ± 0.12	200
	Non-reserves	38.18^{b} ± 3.09	0.39^{a} ± 0.18	176
S. granularis	Reserves	38.54^{b} ± 17.59	0.30^{a} ± 0.12	113
	Non-reserves	44.04^{a} ± 4.77	0.30^{a} ± 0.11	86

Table 5.3.3: Summary of likelihood ratio tests results of reserve effects based on individual tagging and cohort analysis. s = significant difference at $p < 0.05$ and ns = non-significant difference at $p > 0.05$ between reserves (R) and non-reserves (N). L_∞ = asymptotic length and k = growth rate.

	Individual tagging			**Cohort analysis**	
Species	L_∞	***k***		L_∞	***k***
H. concolor	ns	s (N>R)		ns	ns
S. longicosta	s (R>N)	ns		ns	s (R>N)
C. capensis	s (R>N)	s (N>R)		s (R>N)	ns
S. granularis	s (N>R)	ns		ns	ns

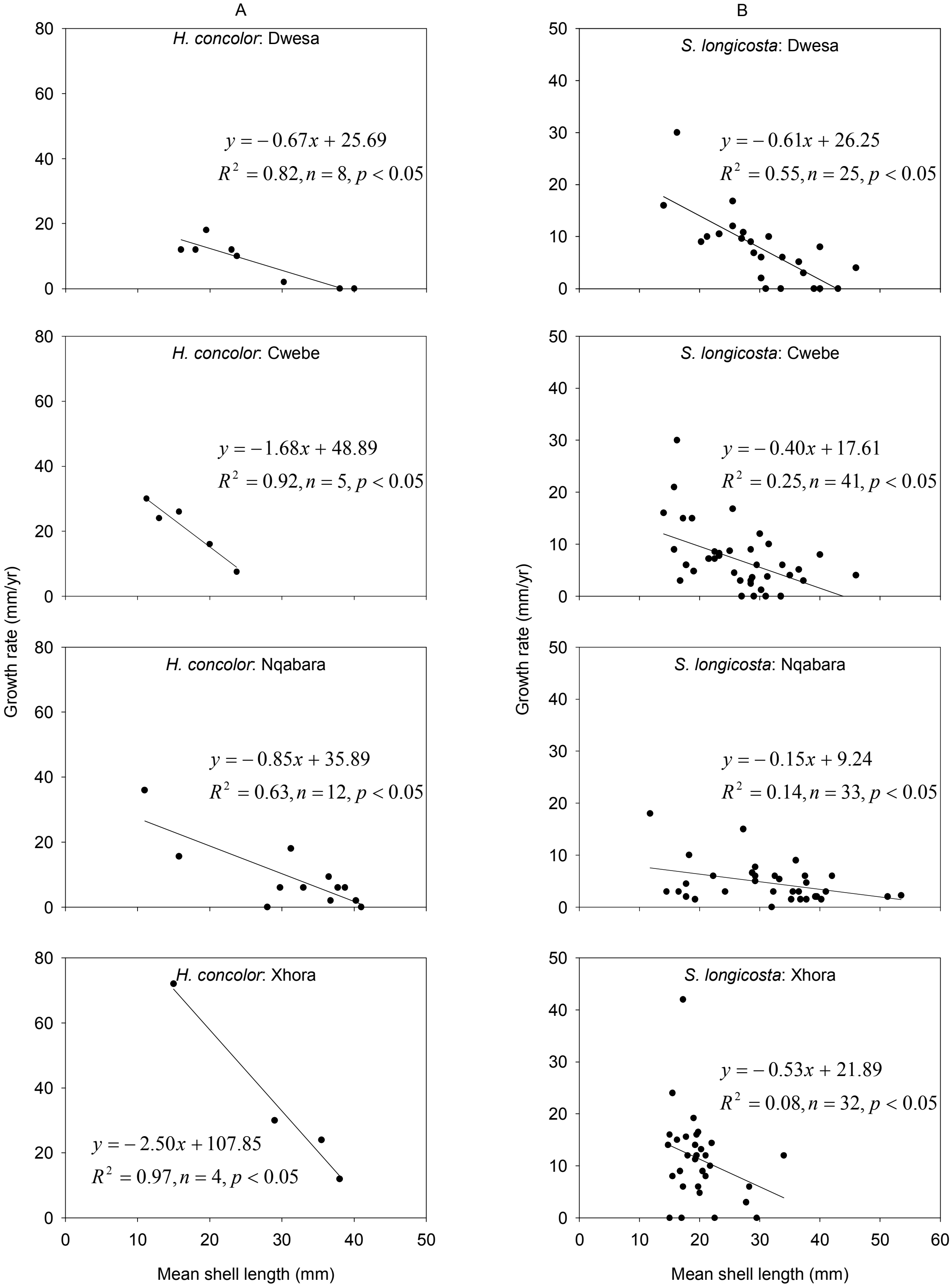


Fig. 5.1: Annual growth rate as a function of mean shell length of marked *H. concolor* (A) and *S. longicosta* (B) at the four study sites.

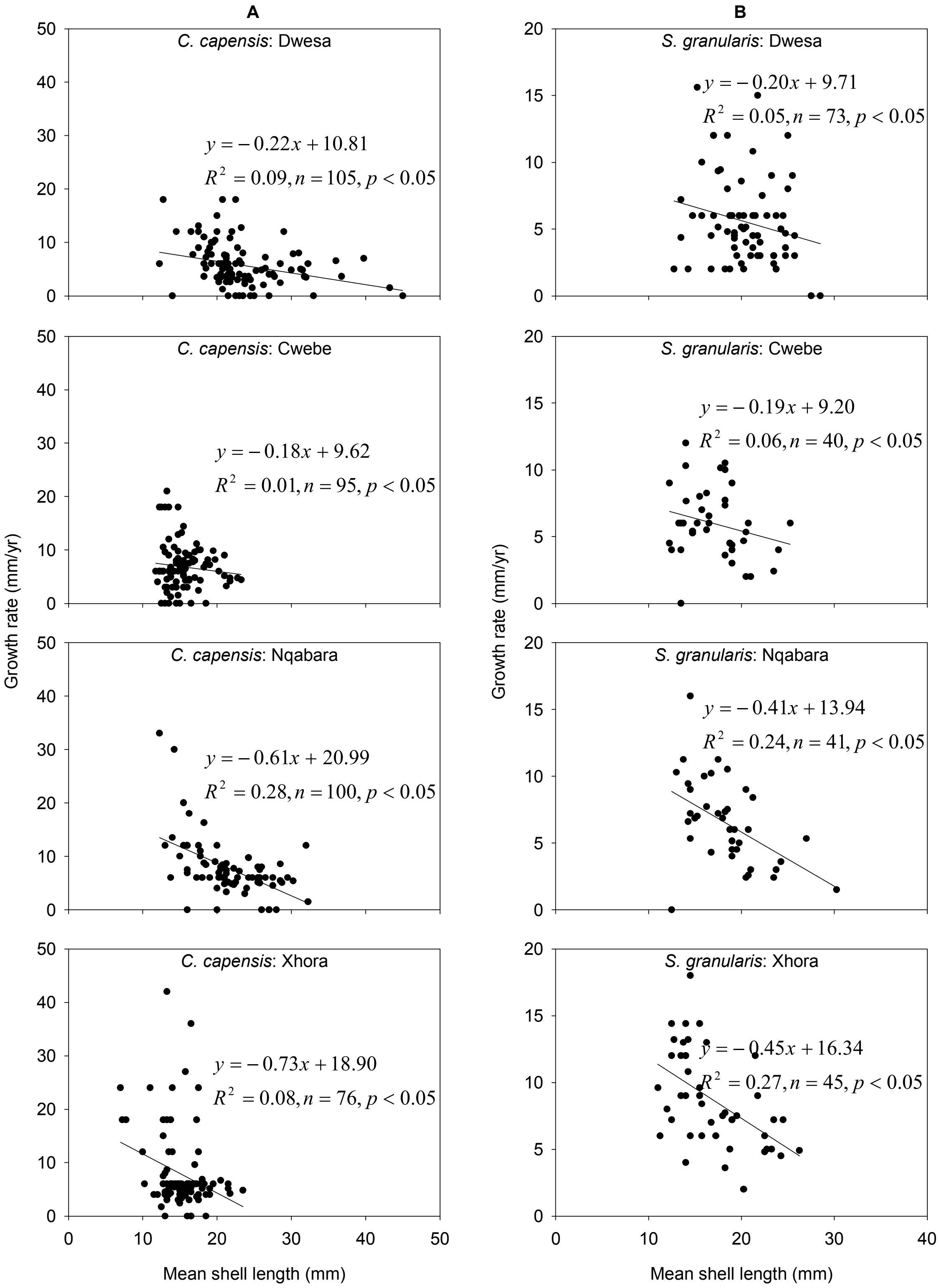


Fig. 5.2: Annual growth rate as a function of mean shell length of marked *C. capensis* (A) and *S. granularis* (B) at the four study sites.

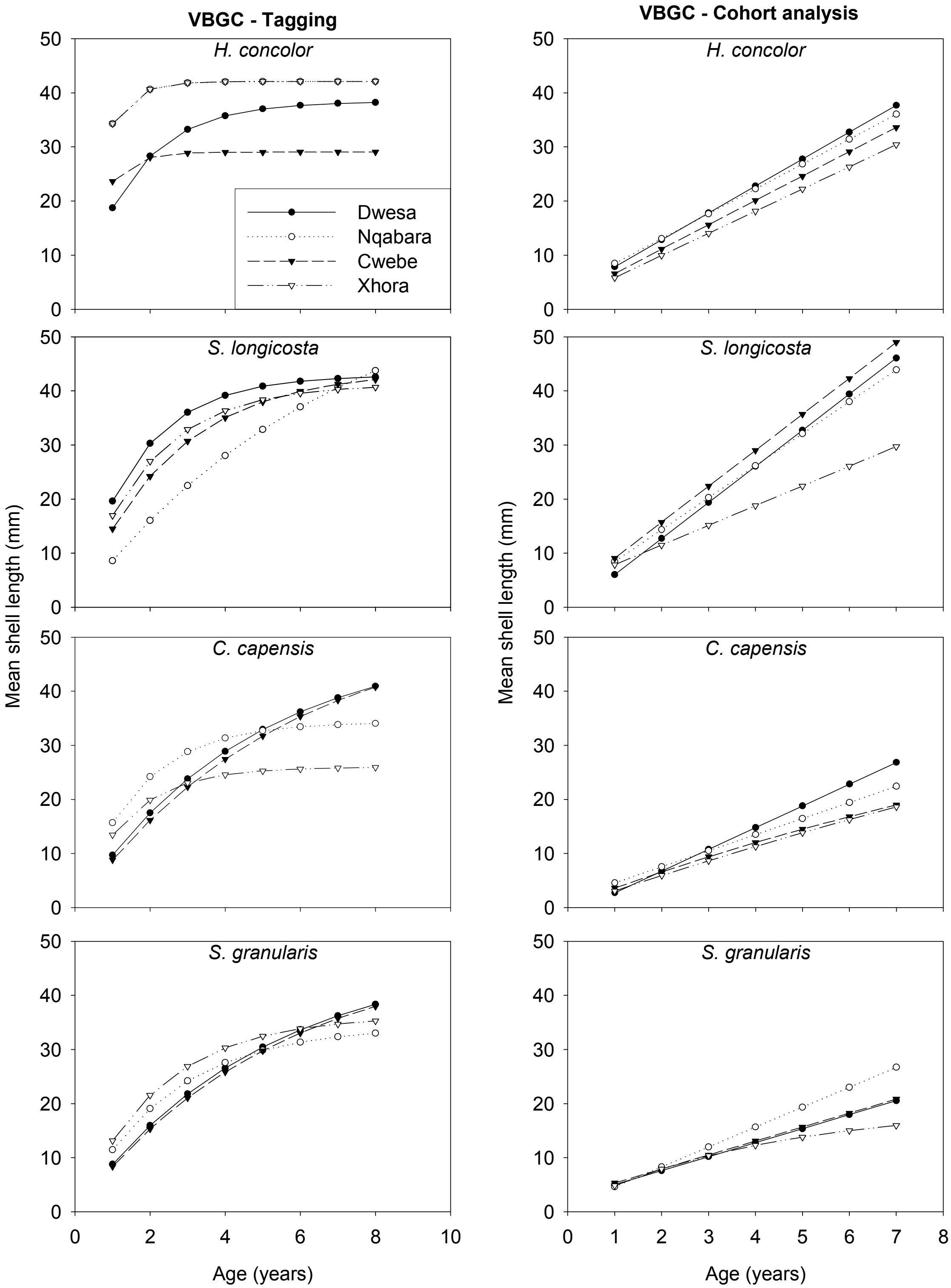


Fig. 5.3: Model predicted Von Bertalanffy growth curves of each species obtained from tagging and cohort analysis among the four sites.

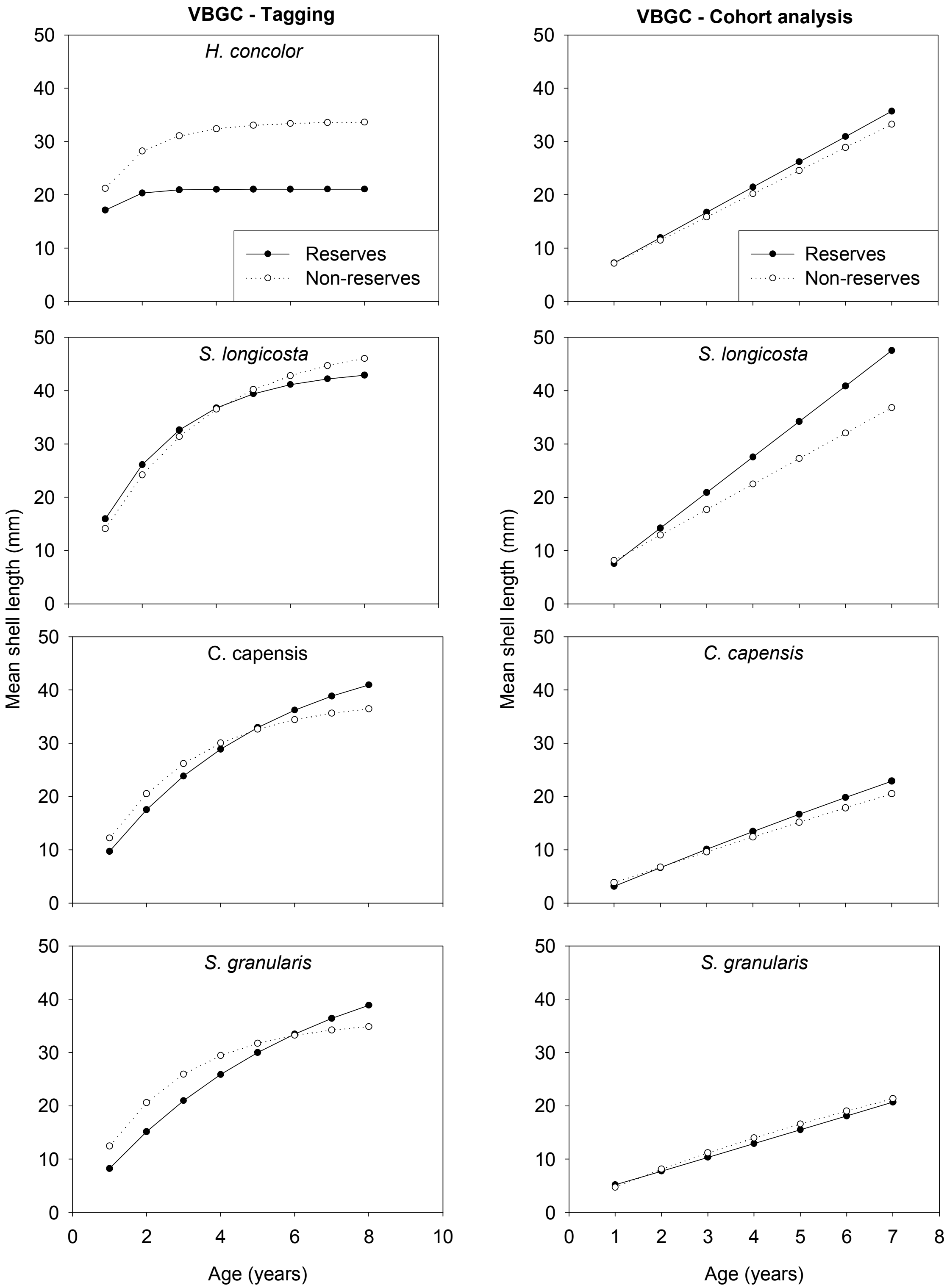


Fig. 5.4: Model predicted Von Bertalanffy growth curves of each species obtained from tagging and cohort analysis in reserve and non-reserve sites.

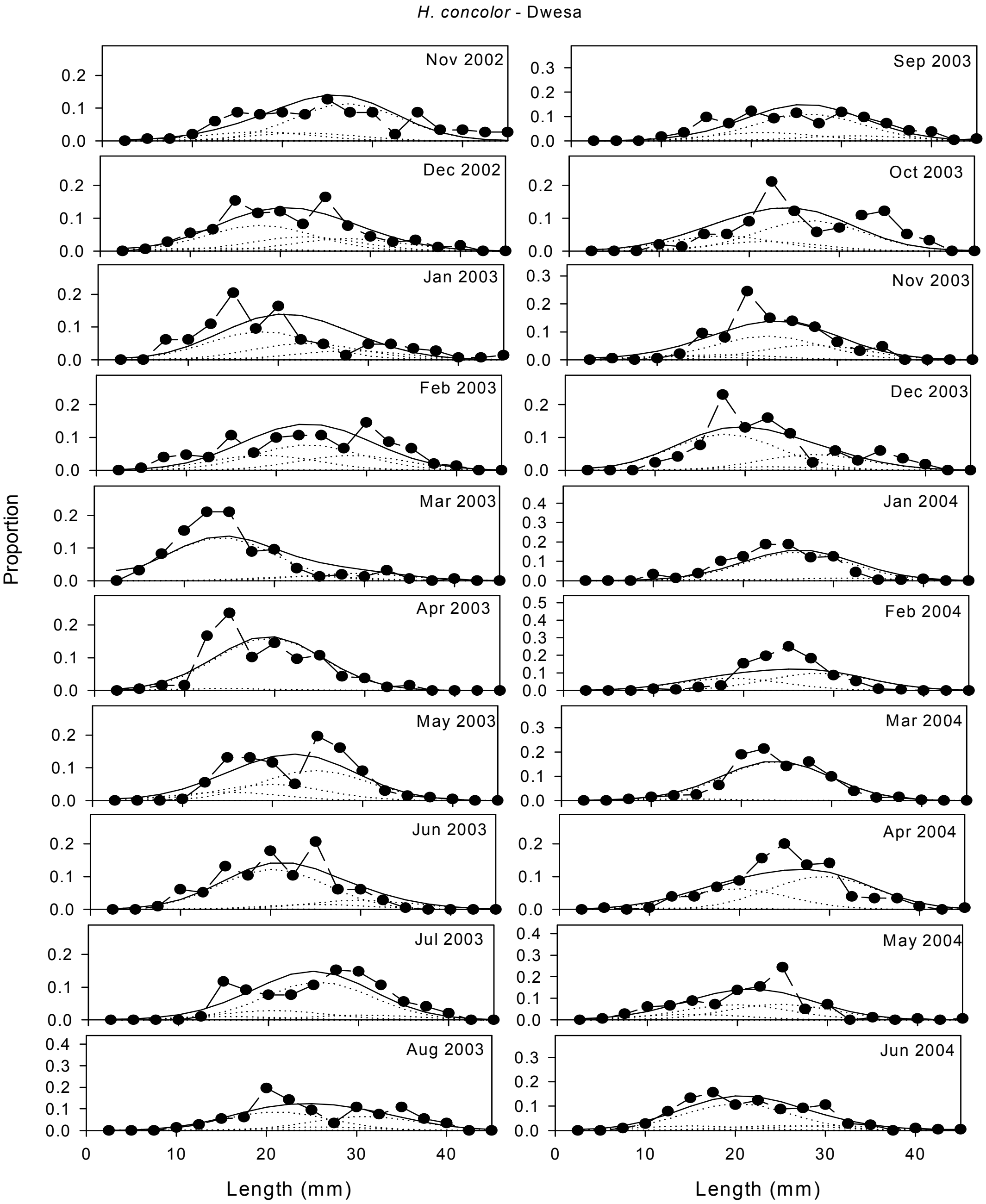


Fig. 5.5.1: Cohorts for *H. concolor* identified from size-frequency distribution from Dwesa. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

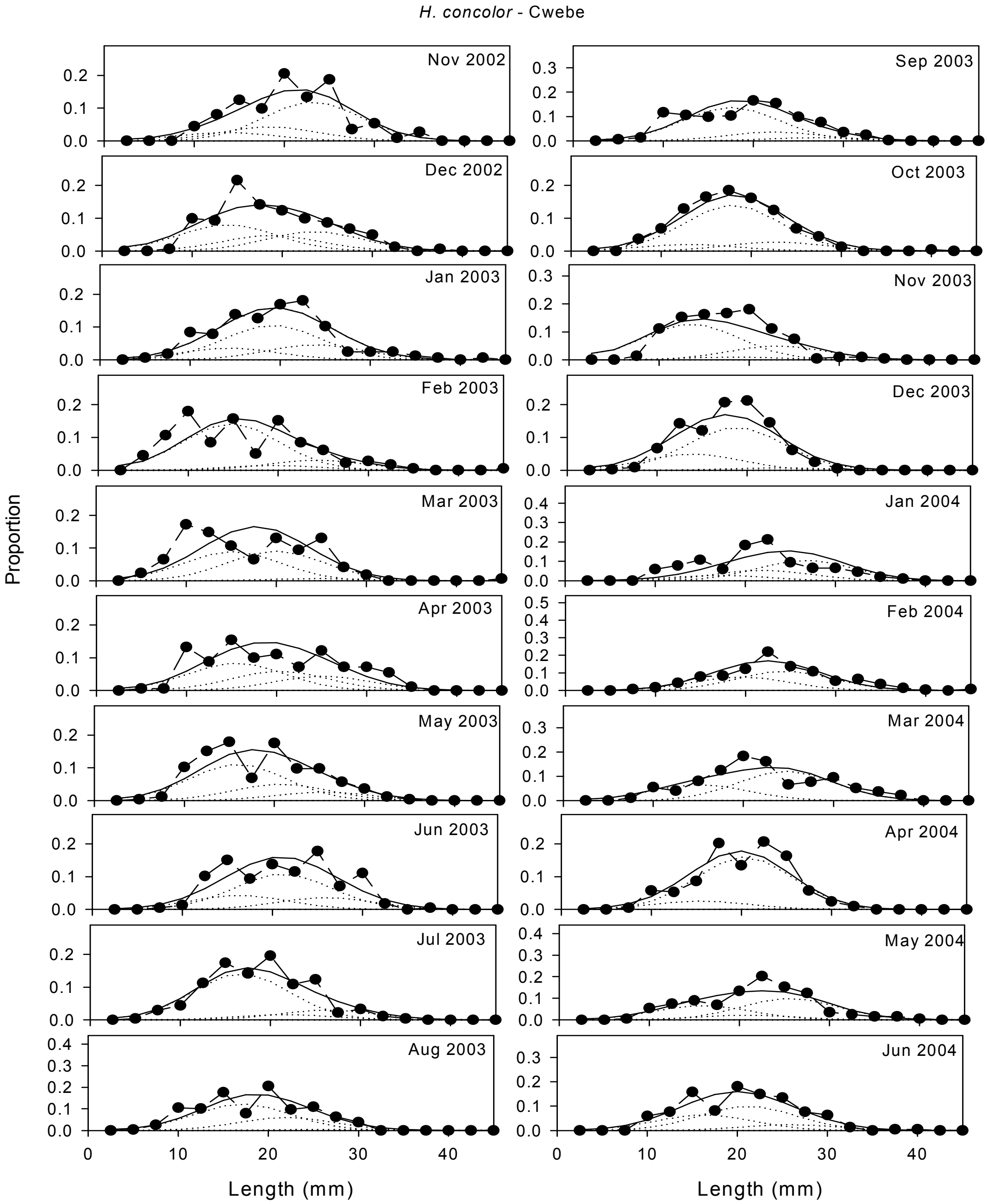


Fig. 5.5.2: Cohorts for *H. cocncolor* identified from size-frequency distribution from Cwebe. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

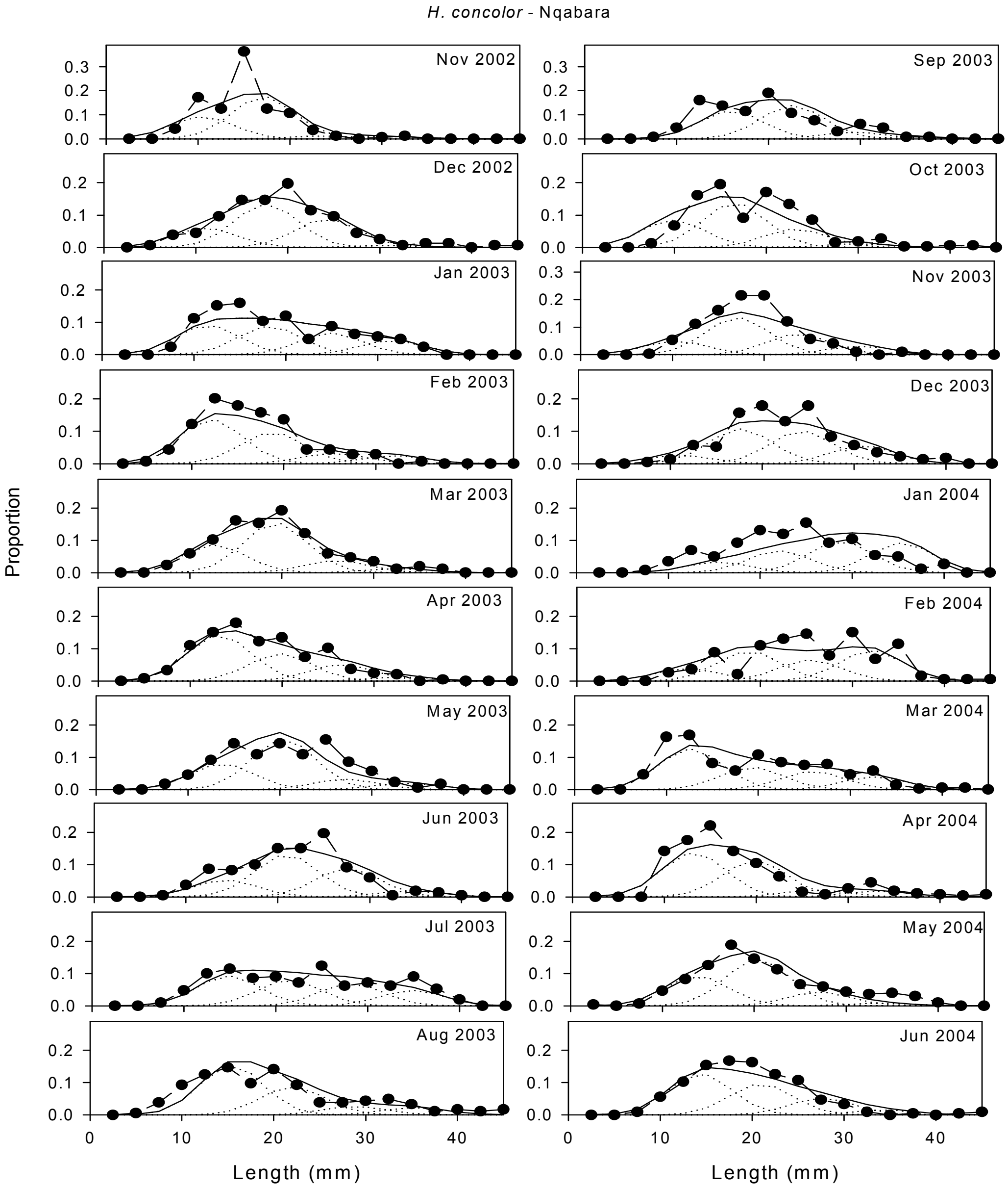


Fig. 5.5.3: Cohorts for *H. concolor* identified from size-frequency distribution from Nqabara. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

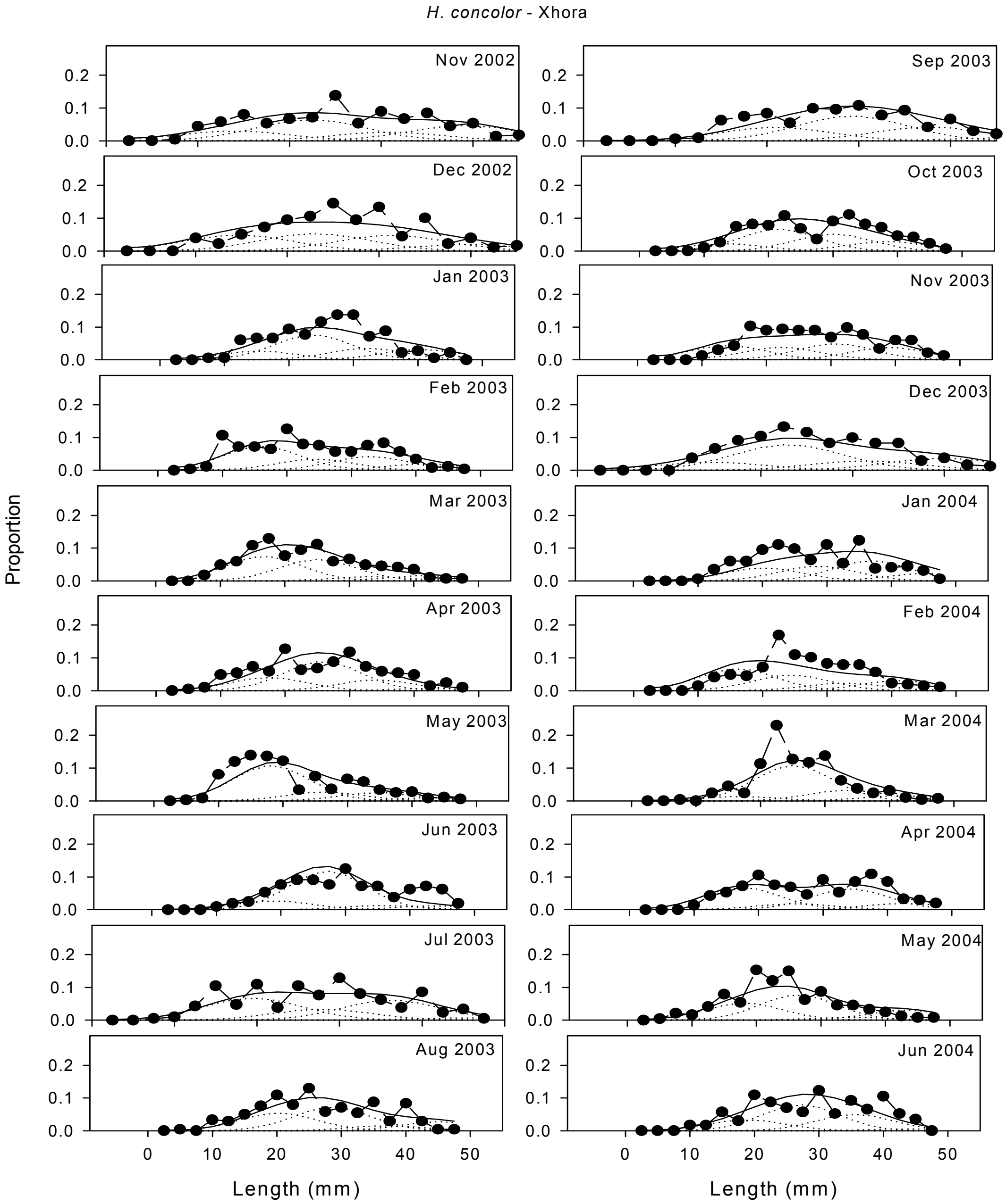


Fig. 5.5.4: Cohorts for *H. concolor* identified from size-frequency distribution from Xhora. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

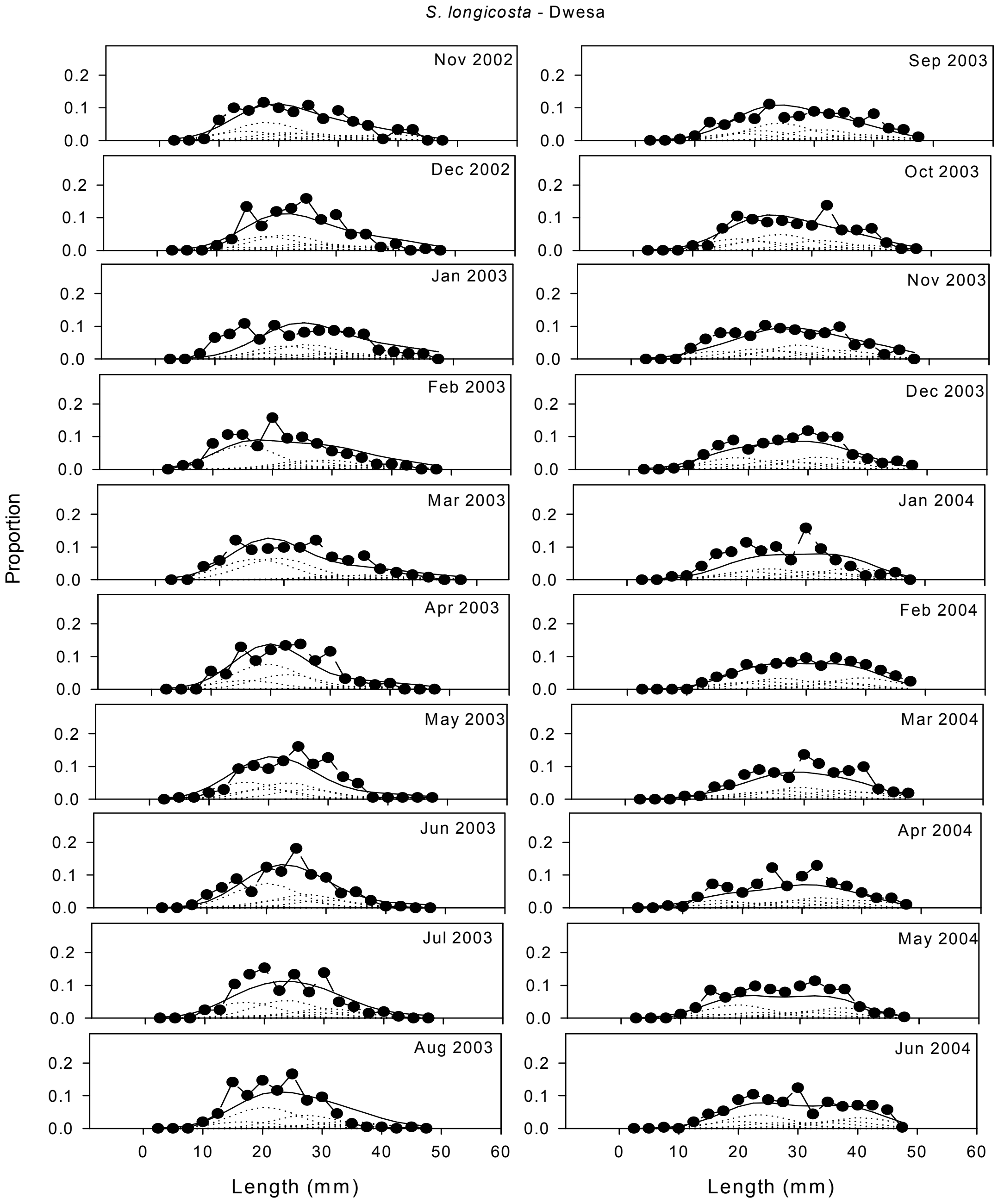


Fig. 5.6.1: Cohorts for *S. longicosta* identified from size-frequency distribution from Dwesa. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

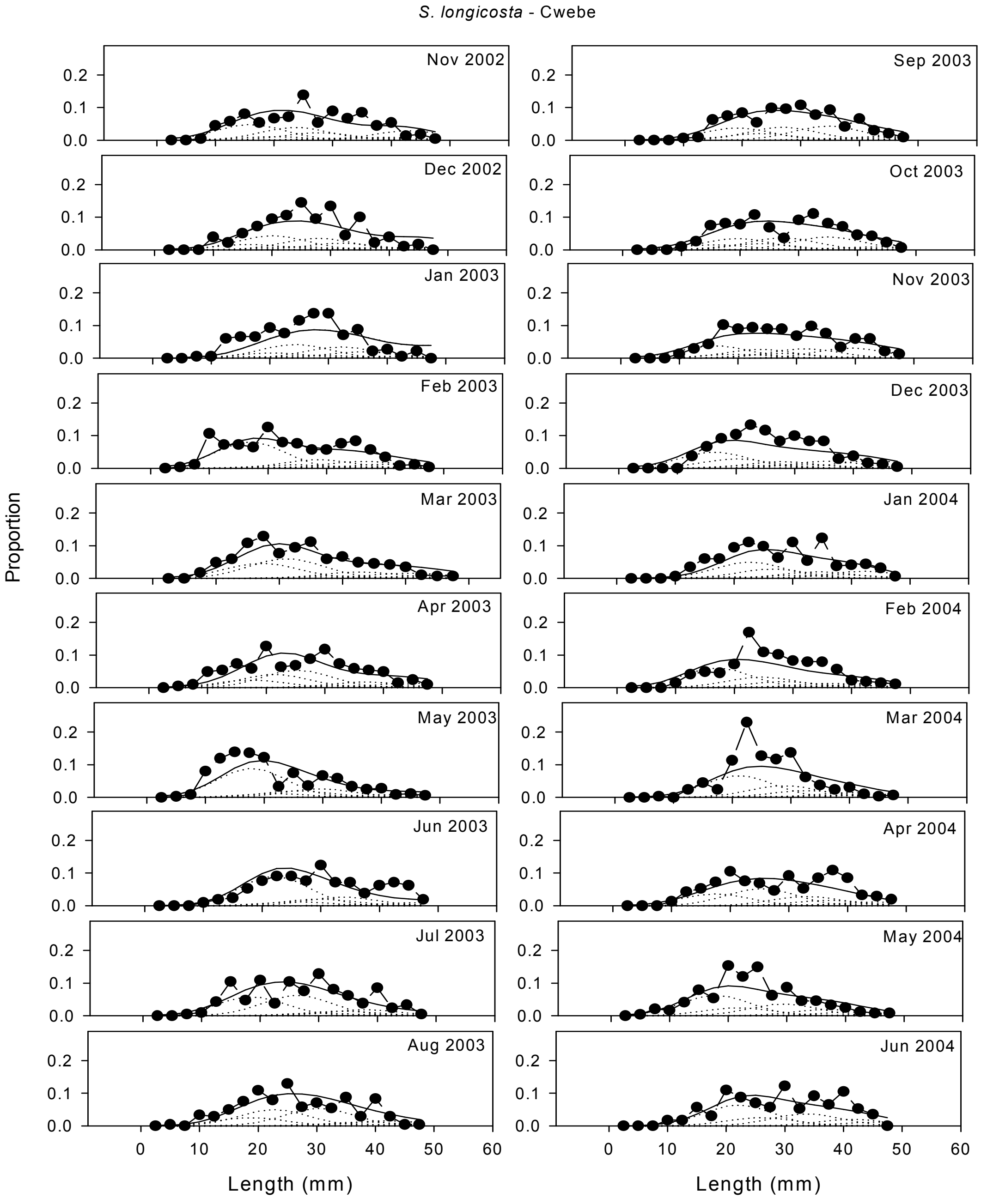


Fig. 5.6.2: Cohorts for *S. longicosta* identified from size-frequency distribution from Cwebe. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

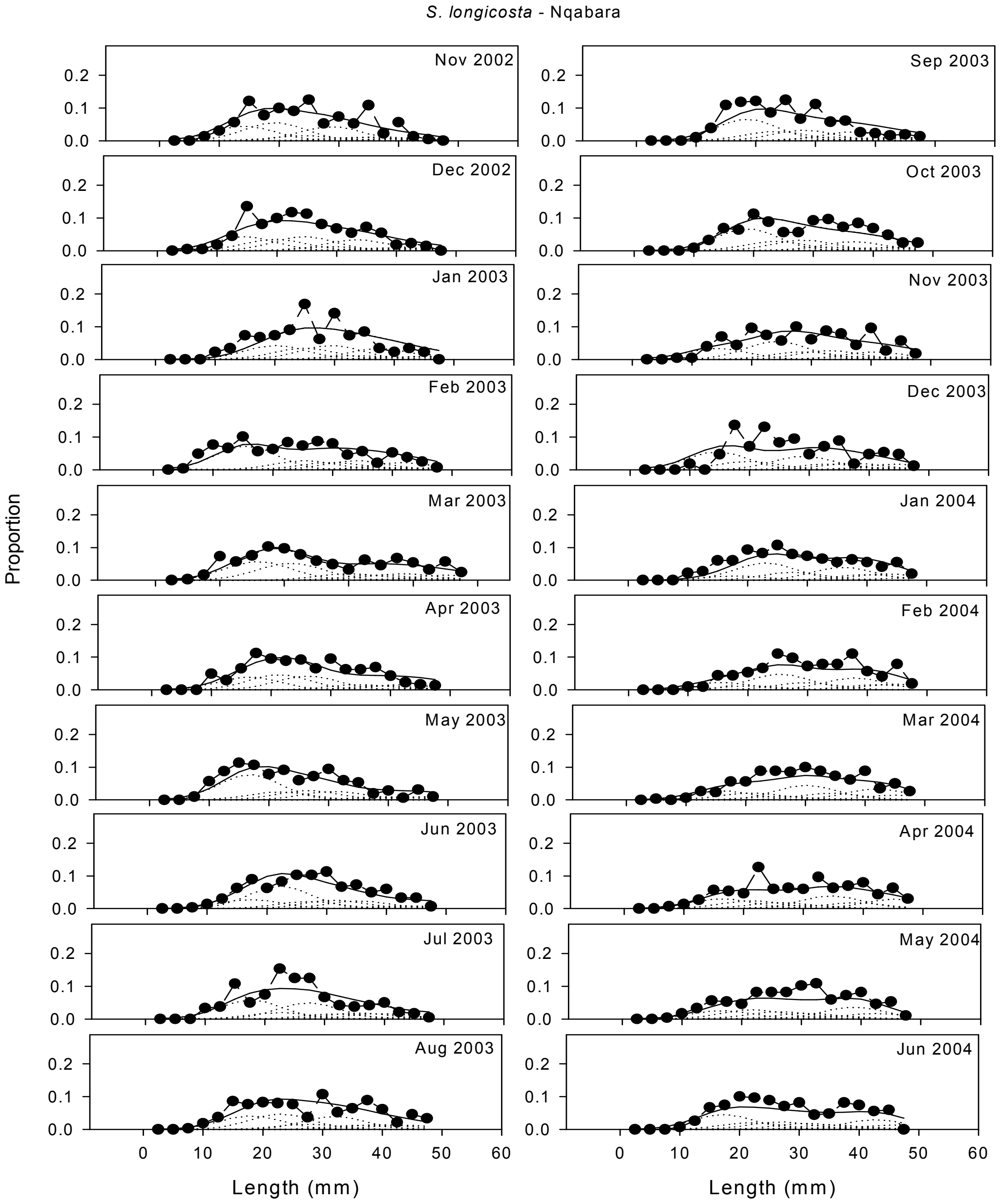


Fig. 5.6.3: Cohorts for *S. longicosta* identified from size-frequency distribution from Nqabara. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

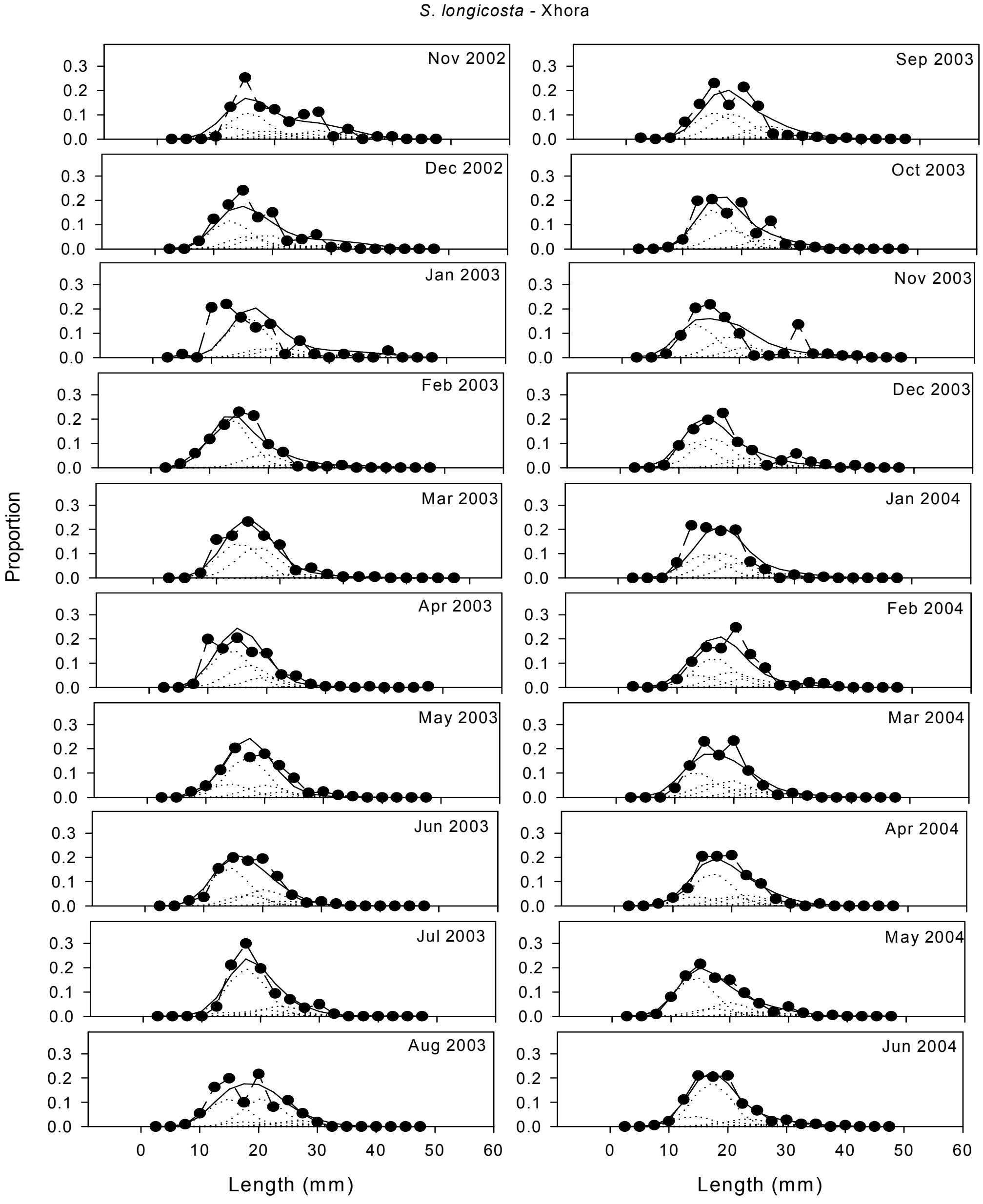


Fig. 5.6.4: Cohorts for *S. longicosta* identified from size-frequency distribution from Xhora. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

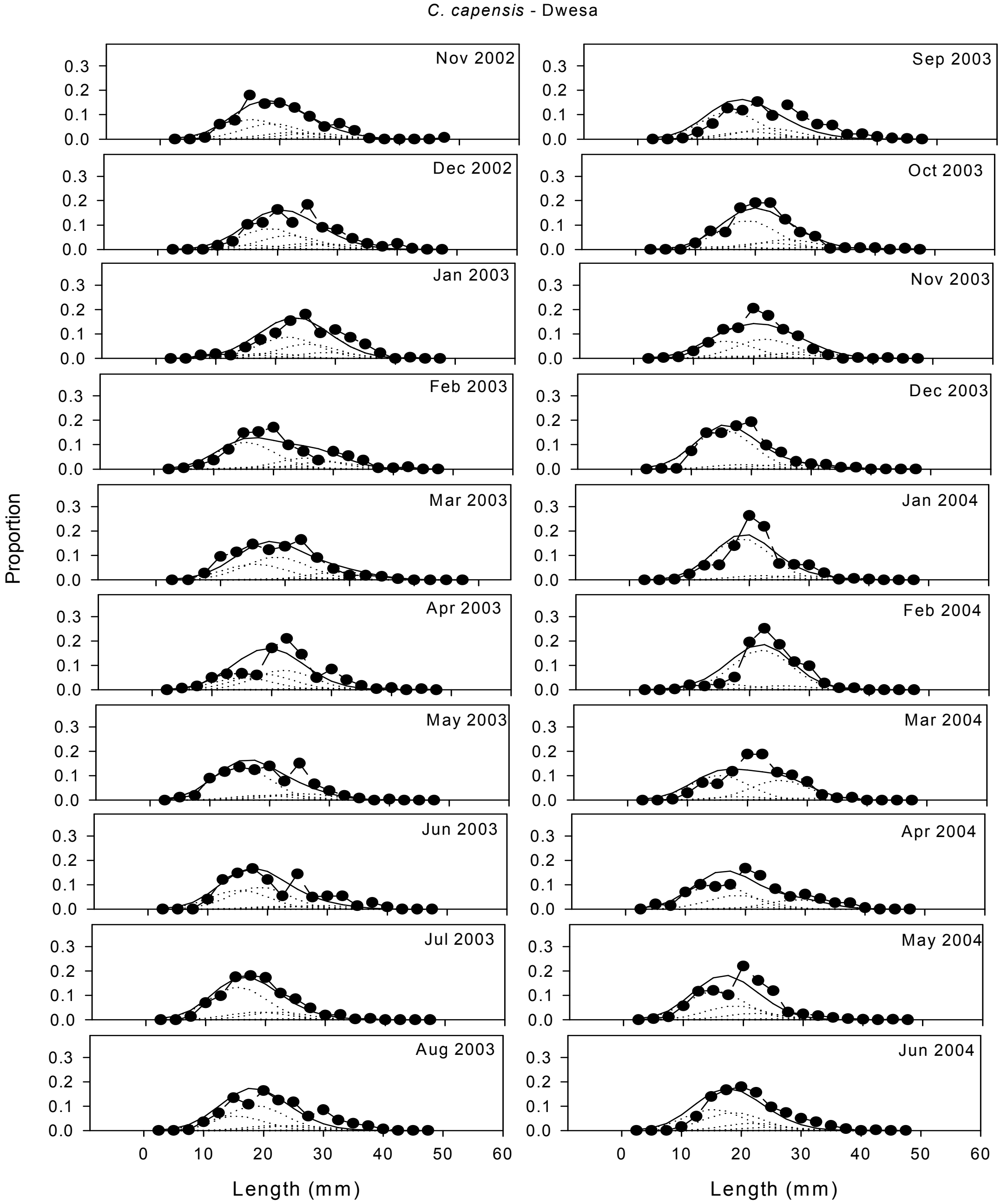


Fig. 5.7.1: Cohorts for *C. capensis* identified from size-frequency distribution from Dwesa. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

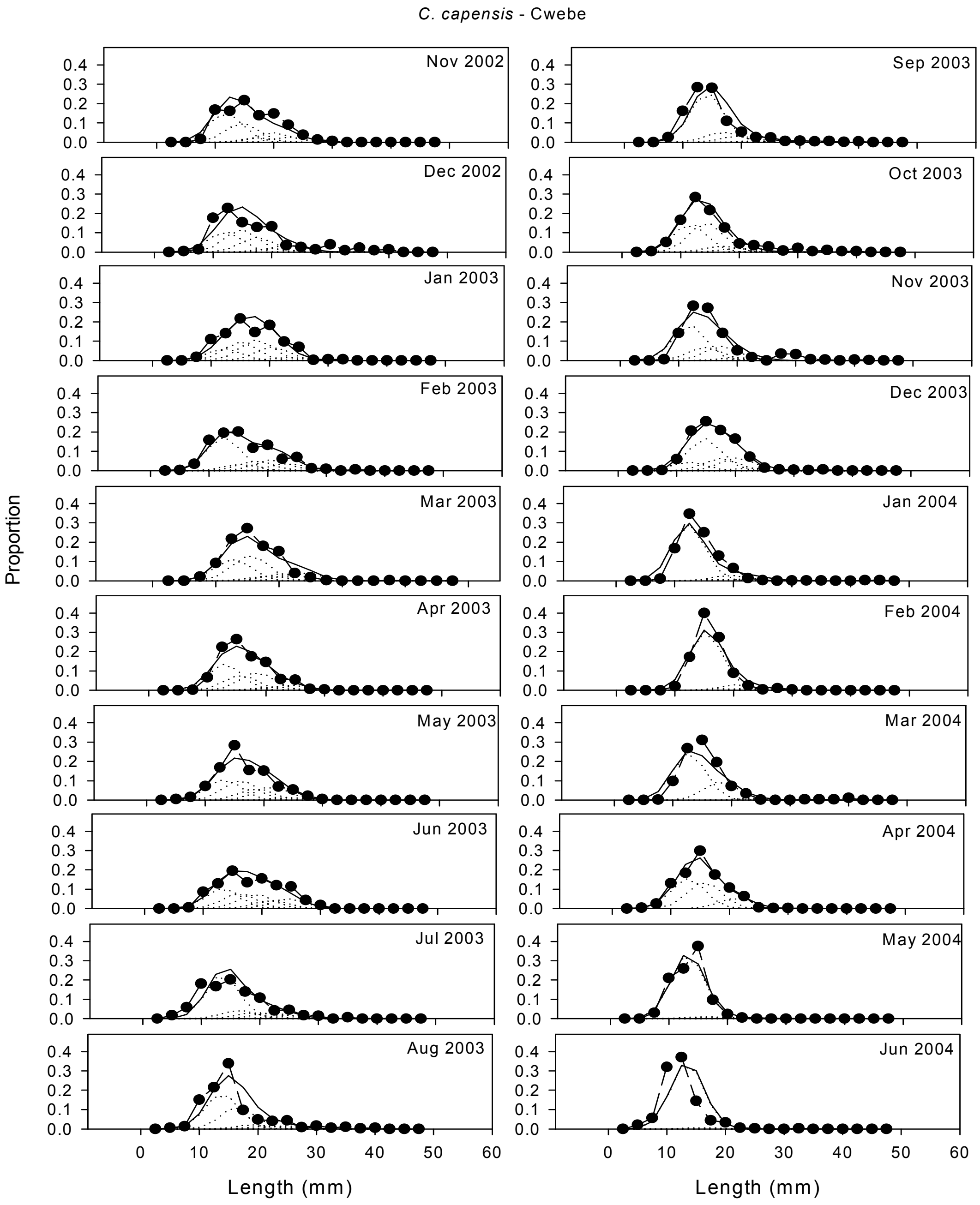


Fig. 5.7.2: Cohorts for *C. capensis* identified from size-frequency distribution from Cwebe. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

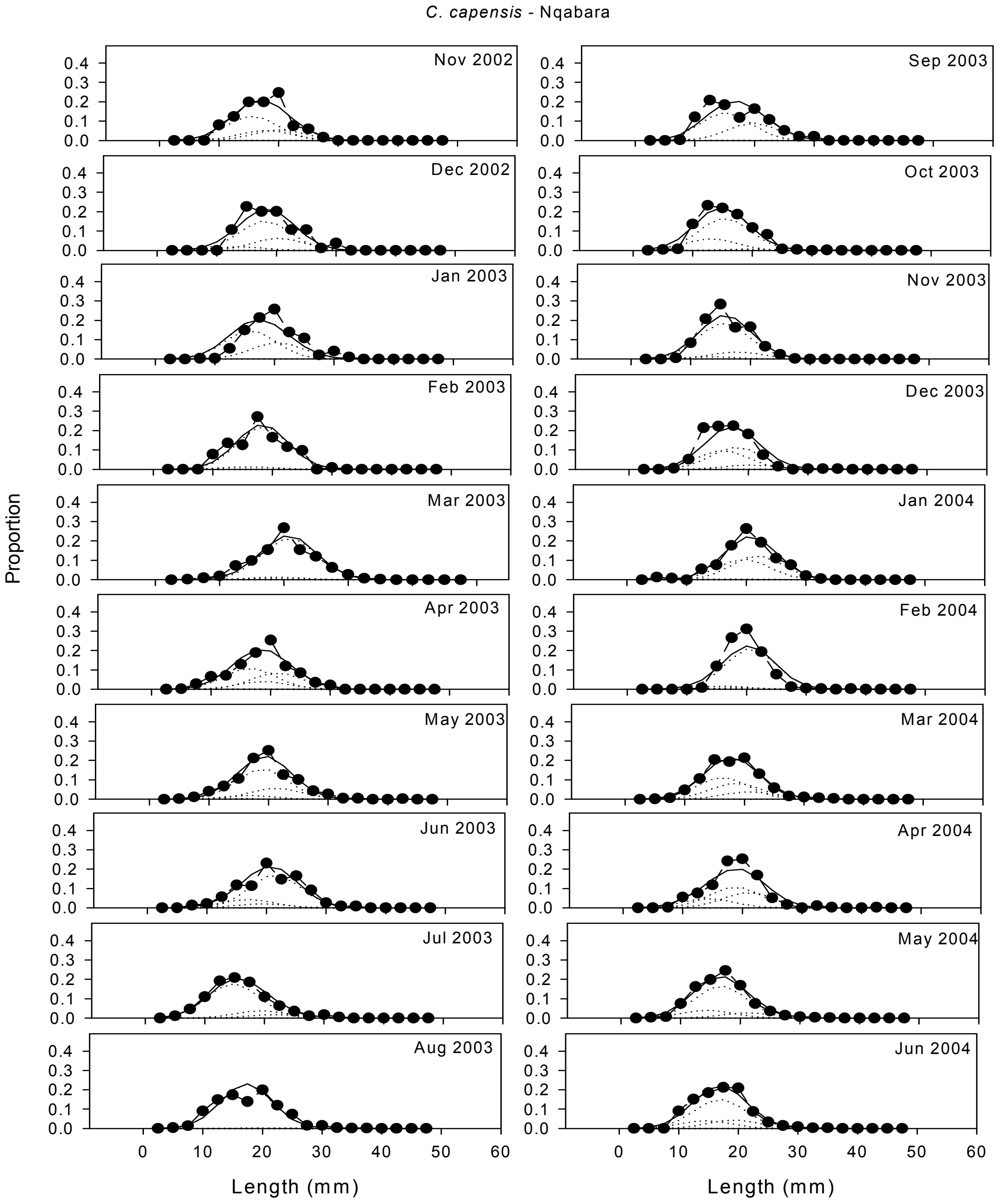


Fig. 5.7.3: Cohorts for *C. capensis* identified from size-frequency distribution from Nqabara. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

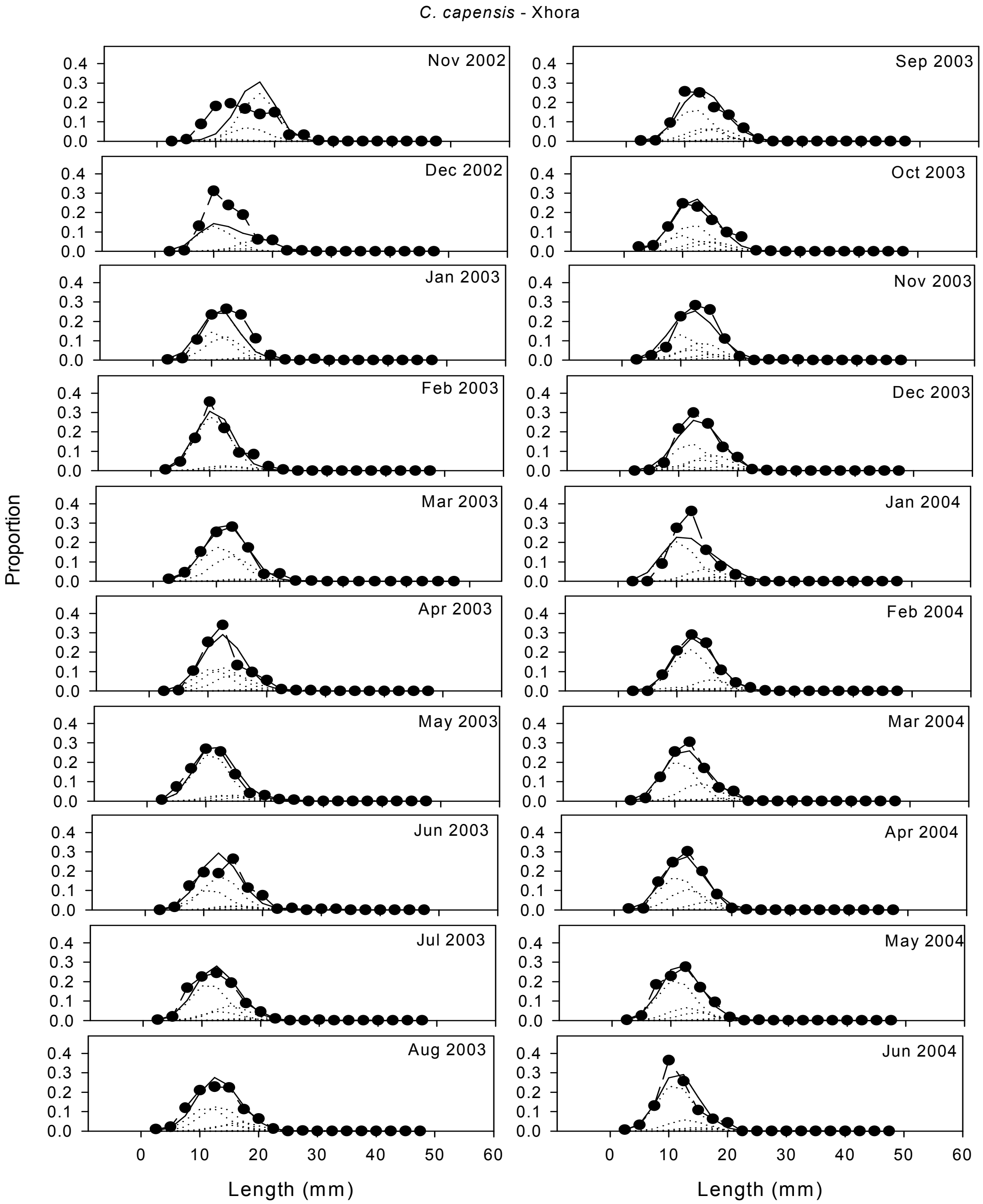


Fig. 5.7.4: Cohorts for *C. capensis* identified from size-frequency distribution from Xhora. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

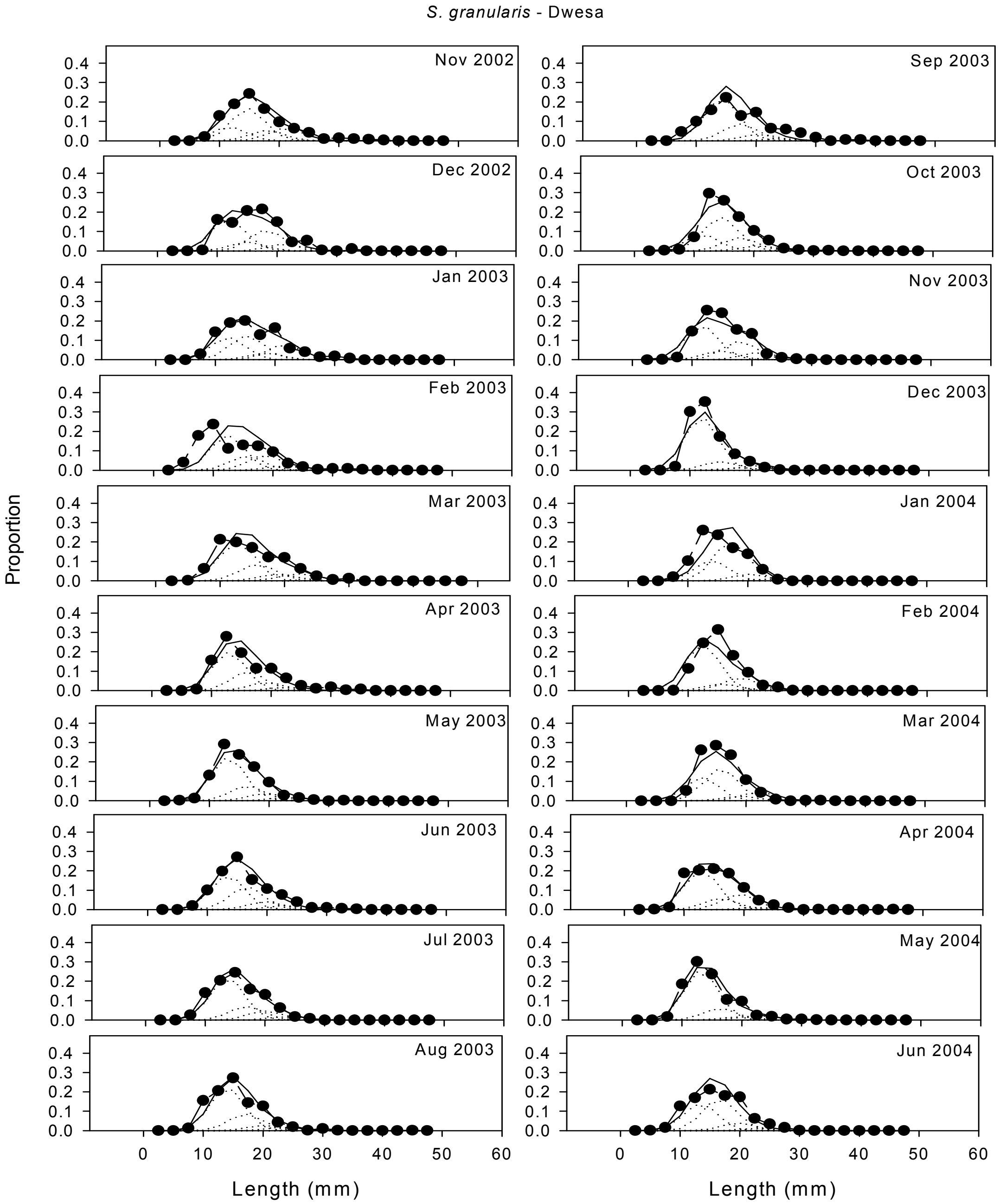


Fig. 5.8.1: Cohorts for *S. granularis* identified from size-frequency distribution from Dwesa. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

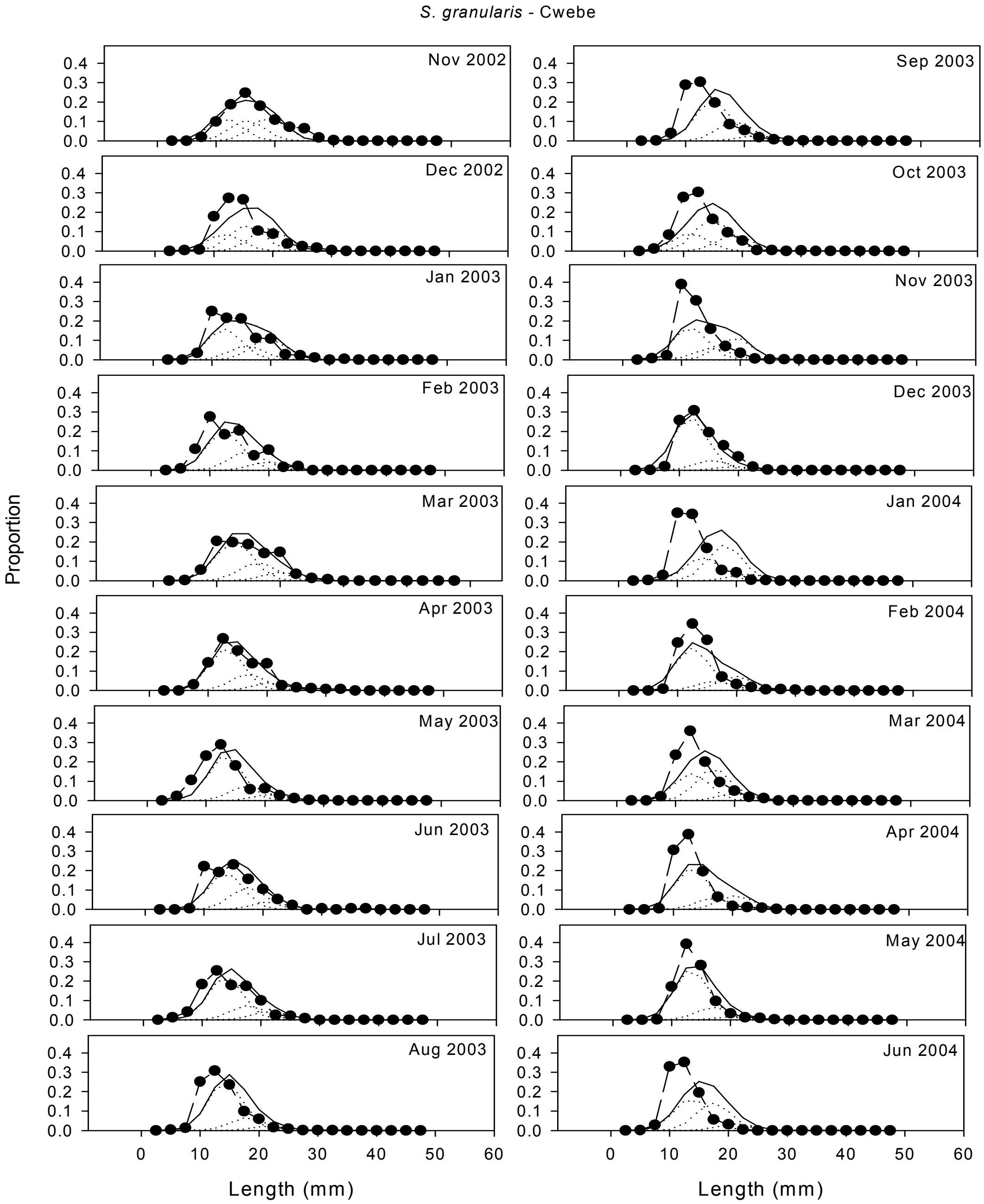


Fig. 5.8.2: Cohorts for *S. granularis* identified from size-frequency distribution from Cwebe. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

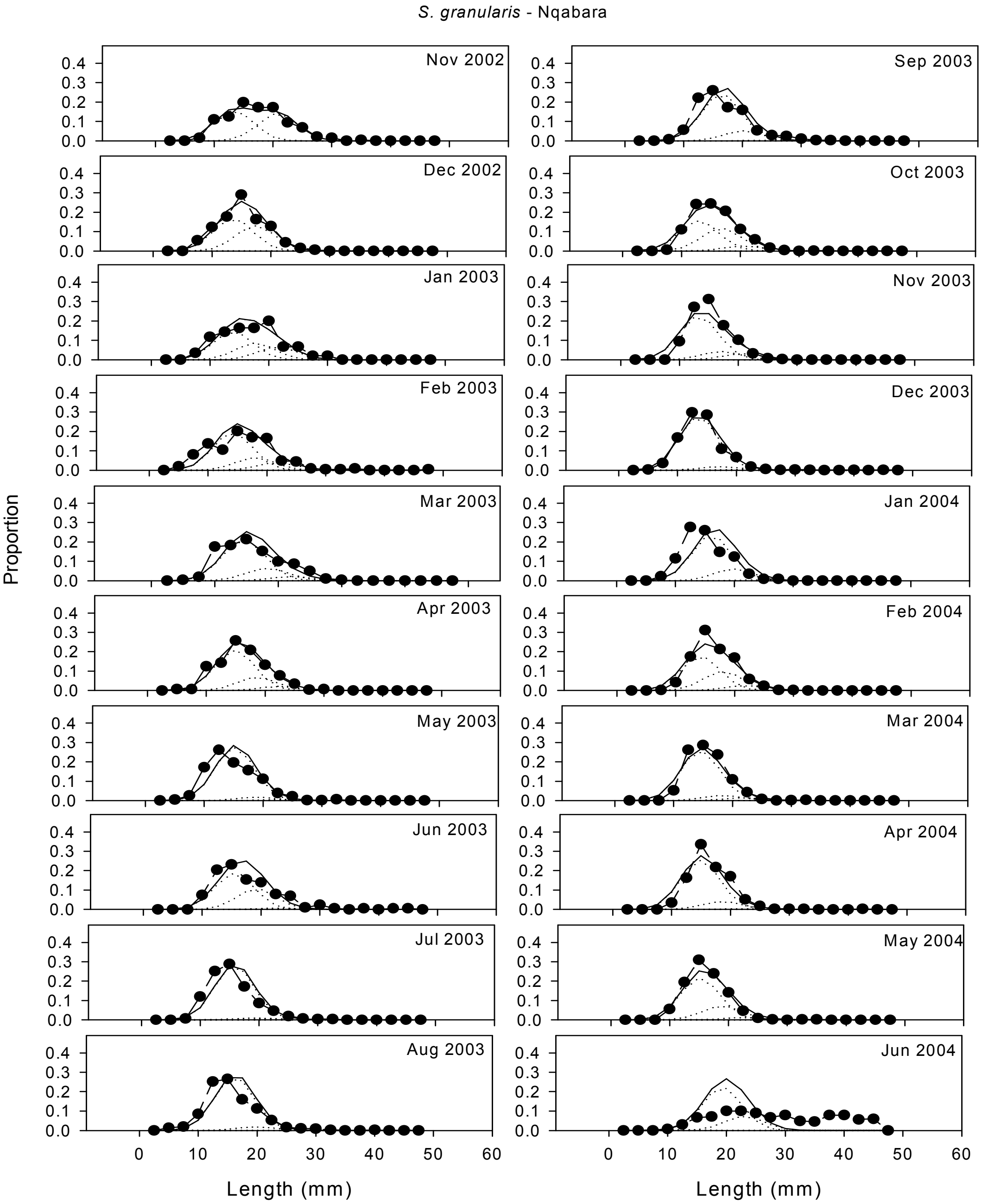


Fig. 5.8.3: Cohorts for *S. granularis* identified from size-frequency distribution from Nqabara. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

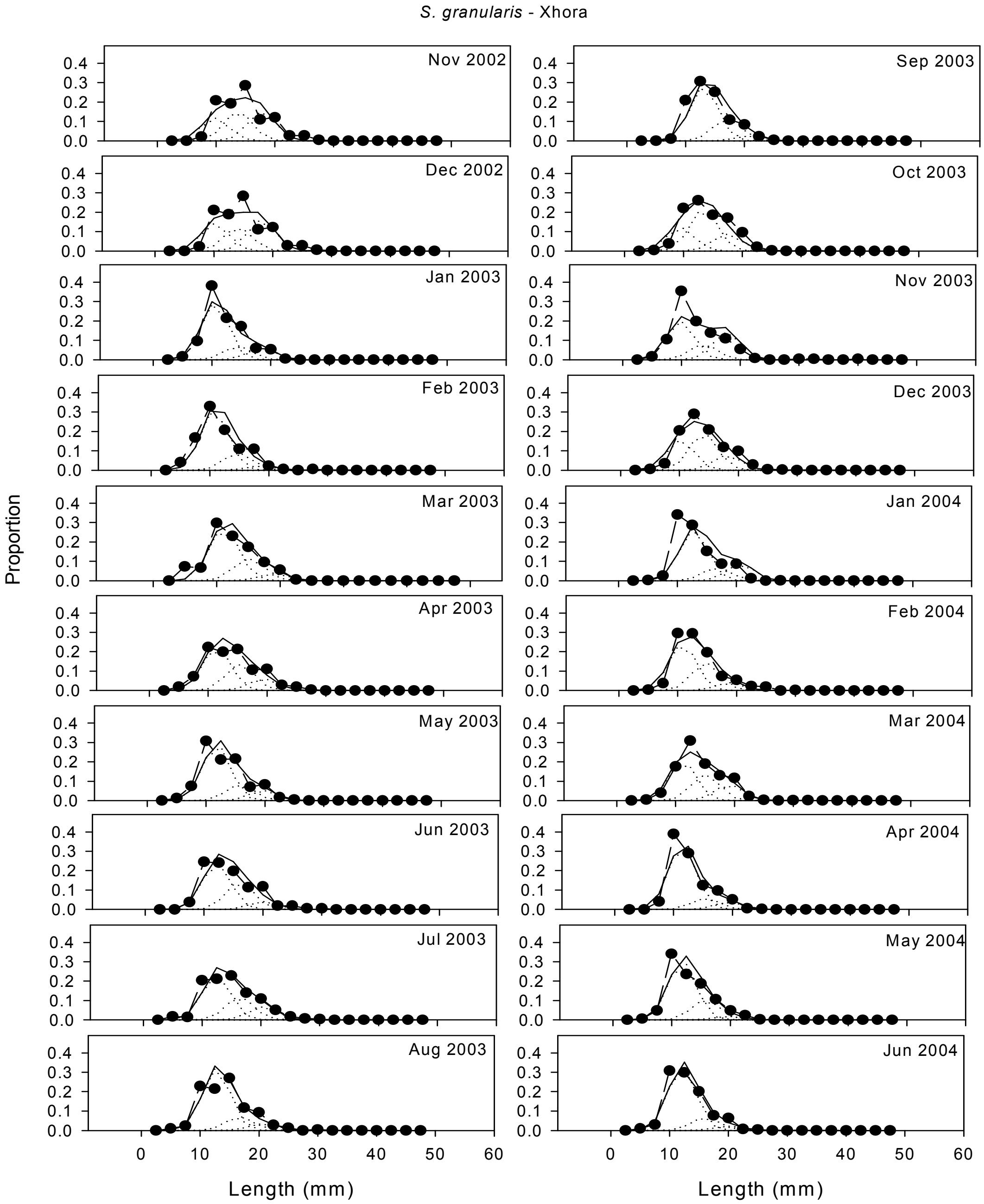


Fig. 5.8.4: Cohorts for *S. granularis* identified from size-frequency distribution from Xhora. Observed (dots), overall model predicted (solid lines) and model predicted cohorts (dotted lines). The overall model predicted proportions at each length are the summation of all cohorts for that month.

CHAPTER 6

REPRODUCTION

6.1 INTRODUCTION

Studies of intertidal invertebrates have investigated reproductive cycles to provide basic information on spawning times and fecundity (Rao 1973; Griffiths 1977; Branch 1974a; Fletcher 1984b; Lasiak 1990; Liu 1994; Morais *et al*. 2003; Pal & Hodgson 2004; Coleman *et al*. 2006a). This knowledge is useful when estimating the timing and magnitude of the arrival of recruits on the shore, age at sexual maturity, sex ratios of a population, and replenishment rate of individuals in a population (Dunmore & Schiel 2000). Previous studies have reported marked differences in reproductive biology and demography of molluscs both across and within habitat types (Lewis & Bowman 1975; Choat 1977). In protandrous limpet species, larger, older individuals are mostly female and harvesting or other sources of mortality that selectively concentrate on larger animals can alter male-female ratios and reproductive output of the population (Lindberg *et al.* 1987, 1998; Branch & Odendaal 2003; Kido & Murray 2003).

Some studies have linked spawning times with geographic position. Studies on the reproductive patterns of South African limpets have revealed that species on the cool temperate west coast tend to have a single spawning period, usually in winter (Branch 1974a). Limpets from warm waters (i.e. south & east coast) either have biannual spawning periodicity with the main reproductive period occurring in summer and autumn, or protracted spawning in which it is difficult to detect seasonality (Robson 1986; Lasiak 1987, 1990; Henninger & Hodgson 2001).

Biological factors can also affect reproduction. Parasitic infection by trematodes can have dramatic effects, for example by castrating females or affecting the maturation of the reproductive organs (Hughes & Answer 1982; Huxham *et al*. 1993; Calvo-Ugarteburu & McQuaid 1998). Likewise, predation can be responsible for earlier sexual maturity (Rochette *et al*. 2003). Patterns of predation are at least partly responsible for the scarcity of large adult snails in low-intertidal areas. Such a phenotypic response is predicted by life-history theory, which holds that under conditions of reduced adult survival, phenotypes are favoured that are capable of reproducing earlier, at a smaller size and with a greater reproductive effort (Stearns 1976). Morton (1991) showed that individuals can also be expected to regulate their reproductive effort and available resources, as determined by the environment, to maximize reproductive potential. The environment therefore, plays a crucial role in moulding not just individual size and population densities, through variations in recruitment, but also gametogenic allocation and thus, perceived variations in life-history characteristics. Through reductions in density and shifts toward smaller individuals, human exploitation also can decrease the reproductive output of intertidal invertebrate populations in which there is an increase in individual fecundity with body size (Branch 1974a, 1975a, Creese 1980; Levitan 1991; Tegner *et al.* 1996). This is especially true for broadcast spawners such as limpets and other intertidal species that depend on high gamete concentrations coupled with the simultaneous release of gametes by male and female individuals to increase the probability of successful fertilization (Linquist *et al.*1997; Levitan & Irvine 2001).

Many studies have shown that increased densities of competitors and the presence of sessile organisms can limit the reproductive output of various limpet species (Branch 1976; Choat 1977; Underwood *et al.* 1983; Boaventura *et al*. 2003). Intra-specific competition for food has been demonstrated to be an important factor in several grazing gastropod species (Branch 1975b; Underwood 1976, 1984; Creese & Underwood 1982; Boaventura *et al*. 2002b). This type of competition is more likely to occur and to have more profound consequences in populations exposed to extreme physical conditions and with aggregated spatial distribution (Morais *et al*. 2003). Intraspecific density can also have a profound influence on the probability of sex change.

In the present study, the following predictions were tested:

i) Limpets outside reserves will mature earlier than those inside reserves because of reductions in density.

ii) Population reproductive output will be higher inside than outside the reserve as a result of increased biomass

iii) The sex ratio of rarely exploited limpet species will be the same inside and outside reserves since they are all subjected to the same natural processes.

This is because differences in sex ratio between reserves and non-reserves would be expected only for sequential hermaphrodites and none of the study species are such hermaphrodites.

Several methods have been used to identify sexes in limpets. This study utilizes subjective grading of reproductive condition, which has been used extensively and is based on the visual appearance of the gonad, in terms of size, shape, colour and texture (Orton *et al.* 1956; Creese & Ballantine 1983; Creese *et al*. 1990; Morais *et al*. 2003; Kolbin 2006). Widespread use of this technique reflects the fact that it requires virtually no equipment and relatively little skill, it is also quick and easy to apply. This technique, coupled with the estimation of gonad indices has, in the past, been used to pinpoint accurately the spawning periods of several South African limpets (Branch 1974a; Lasiak 1990).

6.2 MATERIALS AND METHODS

For each of the four limpet species, about 30 animals selected haphazardly, but comprising a wide size ranges were collected monthly for 20 months from each site for gonad analysis. To avoid the confounding effects of different habitats, animals were collected from one fixed area (~ 1000 m^2) within each site, where the standing stocks of each species would sustain long-term sampling. Limpets were rejected if the shell was damaged in any way. Once collected, animals were preserved in 10% formalin in seawater for at least three weeks to allow the gonad to harden (Lasiak 1990).

6.2.1 Gonado Somatic Index (GSI)

Prior to dissection, the collected individuals were cleaned to remove sand particles. The gonad was dissected out and the dry weights of the gonad and the somatic tissue of each individual were determined and the ratio of gonad to somatic weight (g/s ratio) was calculated for each limpet. The gonado somatic index was calculated by dividing the dry gonad weight by the dry total body weight (excluding shell) and multiplying by 100.

$$i.e.\ GSI \quad = \quad \frac{Dry\ gonad\ weight}{Dry\ somatic\ weight}\ x\ 100$$

Dry weights were obtained to the nearest 0.01g after oven drying to a constant weight at 60^0C. The gonad indices of each sex at each site were plotted against month of sampling.

This procedure also allowed the determination of the gonad development status for each limpet population. The GSI was used to describe the annual cycle of gonad development.

The gonado-somatic indices for each sex at each site were plotted against month of sampling. The effects of reserves on the GSI were analysed separately for each species, using a four-way nested analysis of covariance (ANCOVA) to test the effects of month, reserve, site (nested in reserve) and sex. The factors reserve and sex were treated as fixed while month, site and area as a random factor and shell length as a covariate. Data conformed to the assumptions of normality and homogeneity of variance. This was tested using Kolmogorov-Smirnov and Cochran's tests, respectively (Zar 1996; Underwood 1997).

Post-hoc tests (Tukey HSD tests) were used to determine whether the GSI of males and females varied significantly over time and between reserve and non-reserve sites.

6.2.2 Size at sexual maturity

The size at sexual maturity was estimated by calculating the percentage of each species with mature gonads in 5 mm size classes. An animal was classified as being sexually mature if the gonad had developed gender-specific reproductive structures (Branch & Odendaal 2003; Rochette *et al*. 2003). The gonad was exposed by cutting the foot away from the visceral mass and displacing it anteriorly. The size at which 50% of the individuals in a given size class had mature gonads was taken to represent size at sexual maturity (Gray & Hodgson 2003; Pardo & Johnson 2005). The smallest individual of each of the limpet populations with a mature gonad was recorded to determine the minimum size at the onset of sexual maturity. The size at maturity for males and females was investigated through the categorization of each limpet as immature or a mature adult (i.e. greater than or equal to size at sexual maturity as estimated above).

6.2.3 Sex ratios

In the laboratory, the shell length of each animal was measured to the nearest 0.05 mm using Vernier calipers. Individuals greater than or equal to the size at sexual maturity were removed from their shells and the gonad dissected out and sexed to determine the sex ratio. The sex was determined by microscopic examination of spermatozoa and vitellogenic oocytes and by the gonad colour, the male gonad being creamish or whitish and the female brownish. This method has proven to be successful (Morais *et al.* 2003; Kolbin 2006; Le Quesne & Hawkins 2006). Sex ratios were calculated for each species at each site. The animals used in the comparison of sex ratios in this study were mature males and mature females. Sex ratio was determined from a total of 1573, 999, 1725 and 1920 for *Helcion concolor*, *Scutellastra longicosta*, *Cellana capensis* and *Scutellastra granularis*, respectively. Chi-square tests were used on the total samples to determine whether the sex ratio deviated significantly from 1:1.

6.3 RESULTS

6.3.1 Gonado Somatic Index (GSI)

All species showed rather regular maximum GSI in autumn/winter. Reserve as a main effect showed a significant effect for commonly exploited species but not for rarely exploited species. However, there were significant month/reserve interactions for all species, indicating that even for exploited species, the reserve effect was not consistent. Except for one (*Helcion concolor*) out of four species, site was always significant, indicating spatial variability on scales of 10 km. Similarly, the interaction of month/sex was only significant in one (*H. concolor*) out of four species. There was a significant effect of sex in only one of the exploited species (*Scutellastra longicosta*) and the unexploited *Cellana capensis*. Length as the covariate, month and the interaction of month/reserve were significant for all species.

6.3.1.1 Commonly exploited species

Helcion concolor

Site and sex had no significant ($p > 0.05$) effect on GSI in *H. concolor*. All other effects, including the interactions, were significant (Table 6.1).

Month x Reserve

There was an increase in GSI of *H. concolor* from November 2002 to June 2003 (summer to mid winter) (Fig. 6.1.1). This reached the highest peak in the latter month, suggesting an increase in gonadal development during this period. From July to September 2003 (winter to early spring), there was a decrease in GSI, indicating spawning during this period. This was followed by asynchronous or protracted/multiple spawning occurring from October 2003 until June 2004 (summer to winter). Thus, in both years there was a general increase from minimum GSI in summer to maximum in midwinter (June). In the first year (2002/2003), this increase was smooth/monotonic, in 2003/2004 there were sporadic spawning periods superimposed on the overall seasonal trend. The highest and lowest mean values of GSI for *H. concolor* were 31.6% and 10.1% attained in June 2003 and December 2002 respectively (Fig. 6.1.1). The GSI of *H. concolor* was generally greater in reserves than non-reserves.

Post-hoc tests (Tukey HSD tests) on the month/reserve interaction revealed significant ($p < 0.05$) differences between reserves and non-reserves in the mean GSI of *H. concolor* (see asterisks in Fig. 6.1.2). Reserves were significantly higher than non-reserves in 6 months, including the month of maximum GSI (June 2003). Mean GSI in reserves was non-significantly greater than in non-reserves for a further 7 months. Mean GSI in non-reserves was greater than reserves for 5 months but the differences were not significant. The highest and lowest mean values of GSI for *H. concolor* in reserves and non-reserves were 39.2% and 6.7% attained in June 2003 and November 2002 and 29.2% and 7.2% attained in August and January 2003, respectively (Fig. 6.1.2).

Month x Sex

Although there was a significant month/sex interaction, the two sexes were generally well synchronized, the curves of GSI against month were generally parallel, (i.e. males and females mature in synchrony as we would expect). Tukey HSD tests on the month/sex interaction indicated significant ($p < 0.05$) differences between sexes in the mean GSI of *H. concolor* (Fig. 6.1.3). In 5 months, the mean GSI in males was greater than in females but significant results existed in only 3 months (see asterisks in Fig. 6.1.3). The mean GSI for females was greater than for males for 7 months, however, significant differences were observed only in 4 months, as indicated by asterisks. There were 8 months when the mean GSI of *H. concolor* in males and females were almost identical.

The highest and lowest mean values of GSI for *H. concolor* in males and females were 34.2% and 8.3% recorded in June 2003 and November 2002 and 28.9% and 6.0% attained in June and January 2003, respectively (Fig. 6.1.3).

Site

There was no significant effect of site on the mean GSI of *H. concolor* ($p > 0.05$, Table 6.1).

Scutellastra longicosta

Reserve as a main effect and all other effects except for the interaction of month/sex, were significant ($p < 0.05$, Table 6.2).

Month x Reserve

Post-hoc tests were rather difficult to interpret here, but there was a clear increase from summer to winter in 2003 with maximum GSI in June and a suggestion of a second peak each December. There was an increase in the mean GSI of *S. longicosta* from November 2002 to January 2003, March to June 2003, September to December 2003 and February to June 2004 (Fig. 6.2.1), indicating gonadal development during these periods. But significant ($p < 0.05$) differences existed in June 2003, September to December 2003, and between March to June 2004 (Fig. 6.2.1). The highest and lowest mean GSI of *S. longicosta* were 16.8% and 5.1% attained in June and March 2003, respectively (Fig. 6.2.1).

Post-hoc tests on the month/reserve interaction revealed significant ($p < 0.05$) differences in the mean GSI of *S. longicosta* between reserves and non-reserves (Fig. 6.2.2). Although the mean GSI in reserves was greater than non-reserves for 4 months, significant results were observed only in 1 month. On the other hand, the mean GSI in non-reserves was greater than in reserves for 14 months with significant results in 4 months, as indicated by asterisks (Fig. 6.2.2). In 2 months (May 2003 and April 2004) the mean GSI of *S. longicosta* in reserves and non-reserves were almost identical.

The highest and lowest mean values of GSI for *S. longicosta* in reserves and non-reserves were 16.1% and 3.9% attained in March 2004 and February 2004 and 19.4% and 3.1% attained in June and January 2003, respectively (Fig. 6.2.2).

Month x Sex

The mean GSI of male and female *S. longicosta* showed relatively little variation in the first 7 months of sampling, but this was followed by high variability in the remaining months of sampling. Post-hoc tests on the month/sex interaction indicated significant ($p < 0.05$) differences in the mean GSI of male and female *S. longicosta* (Fig. 6.2.3).

The mean GSI for males was greater than for females for 15 months with significant differences in 8 months (see asterisk in Fig. 6.2.3). In the case of females, the mean GSI was greater than males for 3 months but the differences were not significant. There were 2 months (May and November 2003) when the mean GSI of *S. longicosta* in males and females were almost identical. The highest and lowest mean values of GSI for *S. longicosta* in males and females were 19.3% and 4.6% recorded in December and March

2003, and 15.3% and 3.2% attained in June 2003 and November 2002, respectively (Fig. 6.1.3).

Site (Reserve)

There was a significant ($p < 0.05$) site effect on the mean GSI of *S. longicosta* (Table 6.2). Tukey HSD tests indicated that the mean GSI at Xhora was significantly different from that at the other three sites, with the highest and lowest mean GSI 13.1% and 8.1% found at Xhora and Dwesa, respectively. The overall mean GSI of *S. longicosta* was, in decreasing order, Xhora (13.1%) > Cwebe (9.6%) ≥ Nqabara (8.8%) ≥ Dwesa (8.1%) (Fig. 6.2.4).

6.3.1.2 Rarely exploited species

Cellana capensis

Three-way ANCOVA showed no significant effect of reserve as a main factor or of the interaction of month/sex ($p > 0.05$), but all other effects were significant (Table 6.3).

Month x reserve

The mean GSI of *C. capensis* showed two peaks in April 2003 and March 2004 (Fig. 6.3.1), suggesting an increase in gonad over summer to a maximum in autumn (March/April) followed by spawning. There was a gradual decrease in the mean GSI of *C. capensis* from May to September 2003 and from April to June 2004, suggesting that trickle spawning occurred during this time. The highest and lowest mean values of GSI for *C. capensis* were 36.8% and 10.8% attained in April 2003 and September 2003, respectively.

Tukey HSD tests on the month/reserve interaction revealed that although the mean GSI in reserves was greater than in non-reserves for 6 months, significant in only 2 months (Fig. 6.3.2). The mean GSI in non-reserves was greater than reserves for 6 months but significant results were observed in only 1 month (December 2002). For 8 months the mean GSI of *C. capensis* in reserves and non-reserves was almost identical. The highest and lowest mean values of GSI for *C. capensis* in reserves and non-reserves were 37.4% and 8.3% attained in April 2003 and December 2002, and 36.2% and 10.1% attained in April and September 2003, respectively (Fig. 6.3.2).

Month x Sex

There was no significant ($p > 0.05$) month/sex effect on the mean GSI of *C.capensis* (Table 6.3).

Site (Reserve)

There was a significant ($p < 0.05$) site effect on GSI of *C. capensis* (Table 6.3). Post-hoc tests indicated that the mean GSI at Cwebe was significantly different from that of Xhora and Dwesa, which were grater than that at Nqabara. This reflected that the highest and lowest mean GSI of 23.2% and 18.3% attained at Cwebe and Nqabara, respectively (Fig. 6.3.3). The overall mean GSI of *C. capensis* was, in decreasing order, Cwebe (23.2%) > Xhora (22.2%) ≥ Dwesa (18.8%) > Nqabara (18.3%).

Scutellastra granularis

Reserve and sex as the main factors and the interaction of month/sex showed no significant ($p > 0.05$) effects but all other effects, were significant (Table 6.4).

<u>Month x Reserve</u>

There was an increase in mean GSI of *S. granularis* from November 2002 to July 2003 (Fig. 6.4.1), reaching the highest peak in the latter month, suggesting an increase in gonadal development during this period. *S. granularis* showed three peaks of mean GSI, these were recorded between March to August 2003, December 2003, and between March and June 2004. From July to September 2003, there was a decrease in GSI, indicating spawning during this period. This was followed by asynchronous or protracted/multiple spawning of *S. granularis*, from October 2003 until June 2004. The highest and lowest mean values of GSI for *S. granularis* were 20.7% and 3.7% attained in June 2004 and November 2002, respectively (Fig. 6.4.1).

Post-hoc tests on the month/reserve effect indicated significant ($p < 0.05$) differences between reserves and non-reserves in the mean GSI of *S. granularis* (Fig. 6.4.2). Although the mean GSI in reserves was greater than in non-reserves for 7 months, significant results existed in only 1 month (July 2003). Mean GSI in non-reserves was greater than in reserves for 10 months, but significant differences were observed in only 2 months (December 2002 and December 2003). There were 3 months (March, April, and November 2003) when the mean GSI of *S. granularis* in reserves and non-reserves were almost identical. The highest and lowest mean GSI values for *S. granularis* in reserves and non-reserves were 21.4% and 2.7% attained in June 2004 and November 2002, and 20.6% and 4.7% attained in March 2004 and November 2003, respectively (Fig. 6.4.2).

Month x Sex

There was no significant ($p > 0.05$) month/sex effect on the mean GSI of *S. granularis* (Table 6.4).

Site (Reserve)

There was a significant ($p < 0.05$) site effect on GSI of *S. granularis* (Table 6.4). Post-hoc tests indicated that the mean GSI at Cwebe was significantly different from that at Dwesa, Nqabara and Xhora. The overall mean GSI for *S. granularis* was, in decreasing order, Dwesa (14.6%) ≥ Nqabara (14.5%) ≥ Xhora (14.0%) > Cwebe (12.2%) (Fig. 6.4.3).

6.3.2 Sex ratio

The ratio of males to females ranged from 1.8:1 to 1:2.2 and differed significantly from 1:1 ($p < 0.05$) for all species except *S. granularis*. Three patterns emerged with regard to sex ratios:

1) *H. concolor*: males significantly more abundant than females

2) For *S. longicosta* and *C. capensis*, males were significantly fewer than females

3) *S. granularis*, no significant difference.

6.3.2.1 Commonly exploited species

H. concolor

Sites differed in the number of individuals used to determine sex ratios of *H. concolor* (Table 6.5.1). A total of 1573 individuals were used to examine the sex ratio. Of these, 934 were males, of which 483 and 451 were from reserve and non-reserve sites while 639 were females, 365 and 274 were from reserve and non-reserve sites. Chi-square results showed significant ($p < 0.05$) differences in male to female ratio both when sites were considered separately and when sites were grouped as reserves or non-reserves (Table 6.6.1).

S. longicosta

The number of individuals used to determine the sex ratio of *S. longicosta* differed among sites (Table 6.5.1), with a total of 999 individuals. Of these, 394 were males, from which 235 and 159 were from reserve and non-reserve sites while 605 were females from which 322 and 283 were from reserve and non-reserve sites.

Chi-square results revealed significant ($p < 0.05$) differences in male to female ratio both when sites were considered separately and when sites were grouped as reserves or non-reserves (Table 6.6.1).

6.3.2.2 Rarely exploited species

C. capensis

Sites varied in the number of individuals used to determine the sex ratio of *C. capensis* (Table 6.5.2). A total of 1725 individuals was used. Of these, 734 were males, of which

347 and 387 were from reserve and non-reserve sites, respectively while 991 were females of which 472 and 519 were from reserve and non-reserve sites. Chi-square results showed significant ($p < 0.05$) differences from 1:1 male to female ratio at all sites when considered separately sites or grouped as reserves and non-reserves (Table 6.6.3).

S. granularis

A total of 1920 individuals were used to determine sex ratios (Table 6.5.2). Of these, 930 were males, of which 458 and 472 were from reserve and non-reserve sites while 990 were females of which 544 and 446 were from reserve and non-reserve sites. Chi-square results revealed a significant ($p < 0.05$) difference from 1:1 only at Cwebe. This site-specific effect was so strong that it resulted in a significant effect for reserves as a whole (Table 6.6.4).

Summary

The ratio of male to female differed significantly ($p < 0.05$) from 1:1 for all species except *S. granularis*.

6.3.3 Size at sexual maturity

There was relatively little difference between male and female sizes at sexual maturity. For three species size at maturity was generally greater for males than females. But for *C. capensis* the reverse was true.

6.3.3.1 Commonly exploited species

H. concolor

There was a slight difference in the male and female size at sexual maturity. At 3 out of 4 sites, females matured at a larger size than males (Table 6.6.5).

S. longicosta

Except for Cwebe, all sites revealed that females of *S. longicosta* mature at a larger size than their male counterparts (Table 6.6.5).

6.3.3.2 Rarely exploited species

C. capensis

The smallest sizes for 50% sexual maturity of male and female *C. capensis* were 8 and 9 mm, both found at Xhora (Table 6.6.5). At all sites, males matured at a smaller size than females.

S. granularis

At all sites males showed 50% maturity at 8-9 mm and females at 8.5 – 9.5 (Table 6.6.5).

6.4 DISCUSSION

The present study revealed that, despite significant month/reserve interactions, there were overall clear effects of reserve on the GSI of exploited species. *Helcion concolor* and *Scutellastra longicosta* had clear effects of reserve, with GSI values in reserves generally being greater than in non-reserves in the former species and vice versa for the latter species. Site had a significant effect for all species except *H. concolor*, indicating a high spatial variability in GSI of these species on 10 km scales. There was also a significant sex effect for *S. longicosta* and *Cellana capensis*, with males having greater GSI values than females in both species. The month/sex interaction was not significant except for *H. concolor*, for which it was not strong.

The observed significant effect of reserve for *H. concolor* and *S. longicosta* but not for *C. capensis* and *S. granularis* was expected as variations in the mean GSI in both reserves and non-reserves over time, from month to month and from year to year, largely reflect the effects of intraspecific competition. Boaventura *et al*. (2003) reported that animals with a lower gonad index occurred in greater proportions at increased densities. Generally molluscs from the south and southeast coast of South Africa reproduce in spring/summer (McGwyne & van der Horst 1985, Lasiak 1986, 1987; Hennninger & Hodgson 2001), whereas those on the west coast are autumn and or winter breeders (Branch 1974a, Griffiths 1977). Similarly, the present study on the southeast coast has shown that most spawning in these limpet species occurred in autumn (*C. capensis*) or winter/spring for the remaining species.

The fact that effect of sex and month interaction as a factor was weak even when significant, indicates a high degree of synchrony on *C. capensis*. Similar results were reported for *Patella depressa* (Morais *et al*. 2003). The observed temporal variations in GSI of the limpet species among sites can also be attributed to food availability and other factors (Pardo & Johnson 2004). It is highly likely that, as limpets graze and remove microalgae/biofilms, small-scale variations in the abundance of food (Jenkins & Hartnoll 2001; Jenkins *et al*. 2001) may influence patterns of gonad development. Coleman *et al*. (2006a) suggest that the production of gametes is energetically costly and it would not be unreasonable to expect a strong correlation between food abundance and reproductive development, although this has not been tested in limpets. Moreover, limpet grazing activity was found to decrease in winter in Europe (Jenkins *et al*. 2001). Winter is the most stressful season in cool temperate areas whereas in warm temperate/tropical, such as the study area summer is more stressful.

Many studies have shown that increased densities of competitors and the presence of sessile organisms result in a reduction in tissue weight and thus limit the reproductive output of various patellid limpets (Branch 1976; Choat 1977; Underwood *et al*. 1983, Fletcher 1984b). Branch (1974a) noted that gonadal output in *S. granularis* was strongly density dependent, reaching a peak at about 100 limpets per m^2 and then decreasing progressively to zero at about 450 per m^2. Geller (1990) noted an increase in reproductive effort of molluscs as risks of mortality increase. That was attributed to the fact that limpets have a partial refuge in size from predatory shore crabs and reduce the risk of predation by postponing reproduction and putting more energy into rapid growth in order to attain a refuge in size. Limpets living in polluted waters have been shown to have a relatively high reproductive allocation (GSI) compared to their cleaner water counterparts (Liu & Morton 1998). Migratory species such as *S. granularis, C. capensis* and *H. concolor* and other patellid limpets are reported to have large gonads, unlike *S. longicosta* and *S. cochlear* which are territorial species and have relatively small gonads (Branch 1974a, 1975a).

Although statistical testing was not possible, it was clear that size at sexual maturity varied among sites for some species. Generally, males matured at an earlier size than females. These results are consistent with other studies on limpet reproduction (Boulding *et al*. 1993; Morais *et al.* 2003; Rochette *et al.* 2003). The earlier sexual maturity at Xhora may result from selection for high reproductive effort before the adults are taken away by harvesters or natural mortality. There was no effect of site on size at sexual maturity for *S. granularis* i.e. the effect of site differed among species and between genders. The lack of effect on *S. granularis* is interesting, as it is the least exploited species. In theory, reduction in population size through harvesting should result in lower intraspecific competition. Lower competition allows greater food intake per individual and thus faster growth. In turn, faster growth enables limpets to achieve maturity at a younger age. The larger size of females has been found to be advantageous as larger females would be able to produce a greater number of eggs which take up much more room and energy than spermatozoa (Hodgson 1999). Conversely, it may be disadvantageous to be a small female because it is energetically more expensive to produce eggs than sperm (Branch 1981). Various factors may be responsible for differences in size at sexual maturity and these include the effects of parasitism on growth and reproductive structures (Lafferty 1993).

In only one species, *S. granularis*, were there more males than females. This has advantages, such as a reduction in sperm limitation. Sperm limit is a consequence of dilution in sea water, and has been reported to be the most important factor in reducing fertilization success in broadcast spawning invertebrates (Levitan 2002; Metaxas *et al.* 2002). The probability of external fertilization success decreases with increased gamete dispersal (Levitan 1996). Thus, aggregation, combined with synchronization of spawning may increase fertilization rates, as the mass release of gametes creates a localized area of high sperm and egg concentration, giving a higher probability of a sperm and egg collision (Denny & Shibata 1989; Warner *et al*. 1996; Stoner & Ray-Culp 2000; Levitan 2002). Despite this, there is no evidence here of very strong synchrony in spawning. Synchrony generally decreases towards the tropics, presumably because of weaker spawning cues, rather than reduced advantages in synchronization. For *C. capensis* and *S. longicosta*, there were more females than males. This result is similar to a study of *Cellana grata* and *Patelloida pygmaea* by Liu (1994) who found more female than males. This was attributed to the fact that males put more effort into reproduction than females, which then results in a higher mortality of the former than the latter and leads to a female bias.

The fact that there were generally no significant effects of the month/sex interaction on GSI, except for *H. concolor,* indicates that both male and females had similar reproductive patterns. Others have reported similar results on the reproduction of limpets (Liu & Morton 1998; Morais *et al*. 2003). In contrast, Dunmore & Shiel (2000) reported contrasting results in reproductive studies of *Cellana ornata*. *H. concolor* and *S.*

longicosta had maximum GSI values in mid-winter while *S. granularis* had high GSI values over winter and *C. capensis* had its maximum GSI values in autumn. Therefore, they all have high GSI values in autumn/winter.

Although there were month/reserve effects on the GSI of all species, months with significant differences occurred more often in the commonly exploited species than the rarely exploited species. For instance, there were more months in which GSI was greater in reserves than in non-reserves for *H. concolor*. The reverse was true for *S. longicosta* while there were few months with significant differences for the other species.

In summary, site generally had a significant effect on the mean GSI for all species except *H. concolor*. There were three species (*H. concolor, S. longicosta* and *S. granularis*) which reached maximum GSI in winter and one (*C. capensis*) in autumn though seasonality was clearer in 2003 than in 2004. Sex ratios generally differed significantly from 1:1 and were relatively constant among sites, suggesting that sex ratios are likely to be set by the biology of the species, rather than whether it is exploited or not. Reserves generally did have significant effects on the reproductive biology of these species. Size at sexual maturity showed relatively little difference between male and female in all species. Except for *C. capensis*, the lack of consistency for size at 50% maturity in among either sites or species may imply that different species repond differently to natural processes.

Table 6.1: Results of a 4-way ANCOVA on GSI estimates of *H. concolor* over time. * denotes significant difference at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Source of variation	**SS**	**df**	**MS**	**F**	**P**
Length (co-variate)	10104.6	1	10104.62	40.427	< 0.0001***
Month	447926	19	2357.50	9.432	< 0.001**
Reserve	8354.1	1	8354.12	33.424	< 0.001**
Site (Reserve)	1105.4	2	552.69	2.211	0.110
Sex	101.3	1	101.27	0.405	0.525
Month x Reserve	20849.8	19	1097.36	4.390	< 0.001**
Month x Sex	8406.6	19	442.46	1.770	< 0.05*
Error	376664.8	1507	249.94		

Table 6.2: Results of a 4-way ANCOVA on GSI estimates of *S. longicosta* over time. * denotes significant difference at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Source of variation	**SS**	**df**	**MS**	**F**	**P**
Length (co-variate)	5264.15	1	5264.147	50.361	< 0.0001***
Month	8696.75	19	457.724	4.379	< 0.001**
Reserve	823.21	1	823.208	7.876	< 0.05*
Site (Reserve)	1664.64	2	832.307	7.963	< 0.001**
Sex	2084.25	1	2084.251	19.940	< 0.001*
Month x Reserve	4093.19	19	215.431	2.061	< 0.05*
Month x Sex	1763.91	19	92.837	0.888	0.598
Error	97837.84	936	104.528		

Table 6.3: Results of a 4-way ANCOVA on GSI estimates of *C. capensis* over time. * denotes significant difference at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Source of variation	**SS**	**df**	**MS**	**F**	**P**
Length (co-variate)	16169.7	1	16169.69	65.030	< 0.001***
Month	83998.6	19	4420.98	17.780	< 0.001**
Reserve	206.6	1	206.59	0.831	0.362
Site (Reserve)	6354.3	2	3177.16	12.778	< 0.001**
Sex	3287.8	1	3287.75	13.222	< 0.001**
Month x Reserve	17252.4	19	908.02	3.652	< 0.001**
Month x Sex	4382.7	19	230.67	0.928	0.548
Error	413256.1	1662	248.65		

Table 6.4: Results of a 4-way ANCOVA on GSI estimates of *S. granularis* over time. * denotes significant difference at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Source of variation	**SS**	**df**	**MS**	**F**	**P**
Length (co-variate)	1003.6	1	1003.642	10.033	< 0.05*
Month	29705.2	19	1563.431	15.629	< 0.001**
Reserve	324.5	1	324.541	3.244	0.072
Site (Reserve)	1325.0	2	662.483	6.623	< 0.001**
Sex	159.4	1	159.436	1.594	0.207
Month x Reserve	6787.1	19	357.217	3.571	< 0.001**
Month x Sex	2566.0	19	135.053	1.350	0.142
Error	185661.5	1856	100.033		

Table 6.5.1: Total number of males and females of each species in each site.

	Commonly exploited species							
	Helcion concolor				***Scutellastra longicosta***			
Site	**Male**	**Reserve**	**Female**	**Reserve**	**Male**	**Reserve**	**Female**	**Reserve**
Dwesa	239	483	171	365	123	235	164	322
Cwebe	244		194		112		158	
Nqabara	219	451	147	274	92	159	136	283
Xhora	232		127		67		147	
	934		**639**		**394**		**605**	

Table 6.5.2: Total number of males and females of each species in each site.

	Rarely exploited species							
	Cellana capensis				***Scutellastra granularis***			
Site	**Male**	**Reserve**	**Female**	**Reserve**	**Male**	**Reserve**	**Female**	**Reserve**
Dwesa	169	347	219	472	259	458	268	544
Cwebe	178		253		199		276	
Nqabara	184	387	264	519	275	472	248	446
Xhora	203		255		197		198	
	734		**991**		**930**		**990**	

Table 6.6.1: Chi-square results on sex ratios of *H. concolor*. * denotes significant difference at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$).

Site	**M**	**F**	**Total**	**Ratio**	**Chi-square**	**df**	**p-value**
Dwesa	239	171	410	1.4:1	11.278	1	< 0.001**
Cwebe	244	194	438	1.3:1	5.708	1	0.05*
Nqabara	219	147	366	1.5:1	14.164	1	< 0.0001***
Xhora	232	127	359	1.8:1	30.710	1	< 0.0001***
Reserve	483	365	816	1.3:1	9.064	1	< 0.05*
Non-reserve	451	274	757	1.6:1	57.703	1	< 0.001**

Table 6.6.2: Chi-square results on sex ratios of *S. longicosta*. * denotes significant difference at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Site	**M**	**F**	**Total**	**Ratio**	**Chi-square**	**df**	**p-value**
Dwesa	123	164	287	1:1.3	5.857	1	0.05*
Cwebe	112	158	270	1:1.4	7.837	1	0.05*
Nqabara	92	136	228	1:1.5	8.491	1	0.05*
Xhora	67	147	214	1:2.2	29.907	1	< 0.001**
Reserve	235	322	557	1:1.4	13.589	1	< 0.001**
Non-reserve	159	283	442	1:1.8	34.787	1	< 0.001**

Table 6.6.3: Chi-square results on sex ratios of *C. capensis*. * denotes significant difference at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Site	**M**	**F**	**Total**	**Ratio**	**Chi-square**	**df**	**p-value**
Dwesa	169	219	388	1:1.3	6.443	1	< 0.05*
Cwebe	178	253	431	1:1.4	13.051	1	< 0.001**
Nqabara	184	264	448	1:1.4	14.286	1	< 0.001**
Xhora	203	255	458	1:1.3	4.878	1	< 0.05*
Reserve	347	472	819	1:1.4	19.078	1	< 0.001**
Non-reserve	387	519	906	1:1.3	19.232	1	< 0.001**

Table 6.6.4: Chi-square results on sex ratios of *S. granularis*. * denotes significant difference at $p < 0.05$, ** = $p < 0.001$ and *** = $p < 0.0001$.

Site	**M**	**F**	**Total**	**Ratio**	**Chi-square**	**df**	**p-value**
Dwesa	259	268	527	1:1	0.154	1	0.695
Cwebe	199	276	475	1:1.4	12.482	1	< 0.001**
Nqabara	275	248	523	1.1:1	1.394	1	0.238
Xhora	197	198	395	1:1	0.003	1	0.960
Reserve	458	544	1002	1:1.2	7.381	1	< 0.05*
Non-reserve	472	446	918	1.1:1	0.736	1	0.391

Table 6.6.5: Size (in mm) at 50% sexual maturity of the four species at each site.

	Dwesa		**Cwebe**		**Nqabara**		**Xhora**	
	M	F	M	F	M	F	M	F
H. concolor	12	11.5	10	10.5	10	11.5	9.5	11
S. longicosta	18	15	14	17	19	13.5	19	17.5
C. capensis	11	14	11	10.5	12	13.5	8	9
S. granularis	8.5	8.5	9	9.5	8	9.5	9	8.5

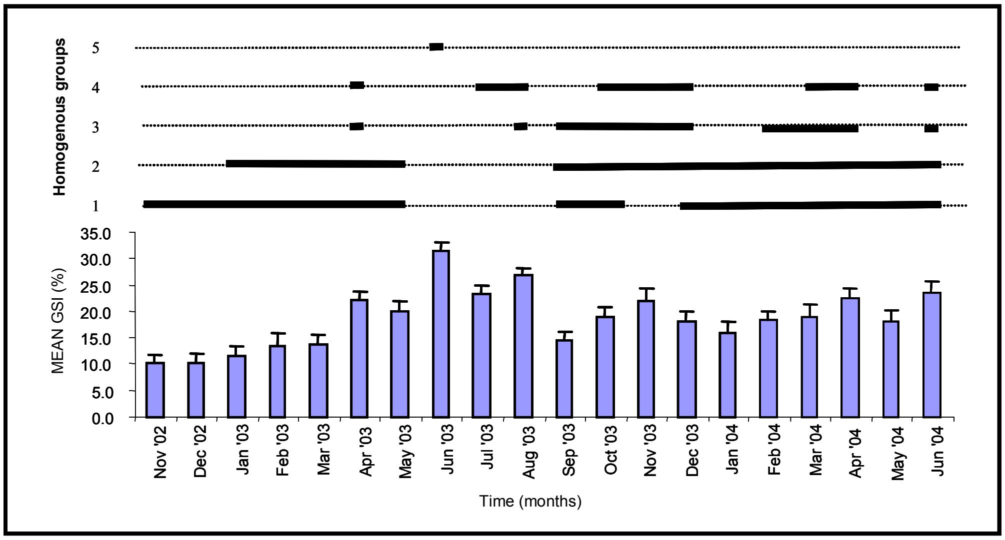


Fig. 6.1.1: Monthly mean (+SE) GSI of *H. concolor* through sampling period. Solid lines above the bar columns connect months that were not significantly ($p > 0.05$) different from each other (Tukey HSD test).

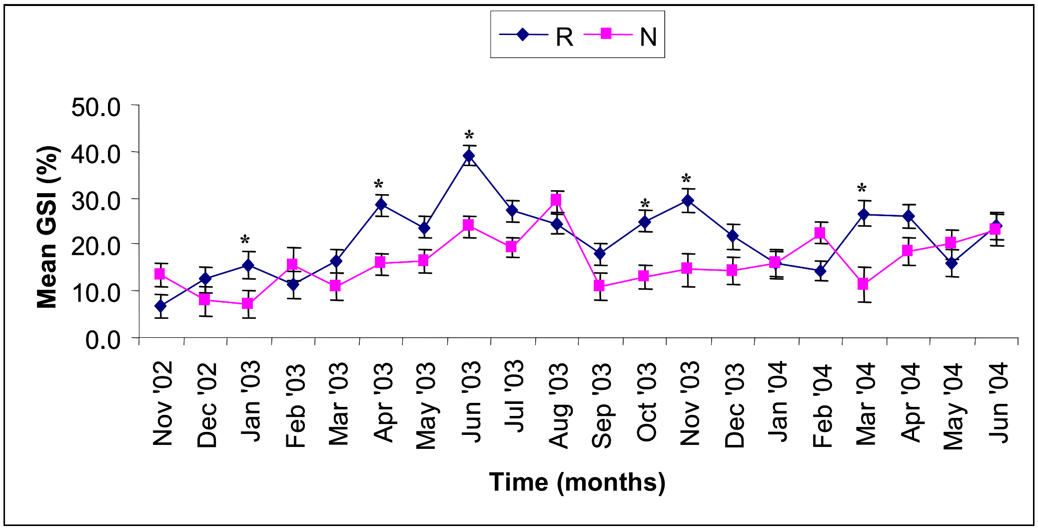


Fig. 6.1.2: Monthly mean (±SE) GSI of *H. concolor* in reserve (R) and non-reserve (N) sites through sampling period. * = significant difference between reserves and non-reserves in this month.

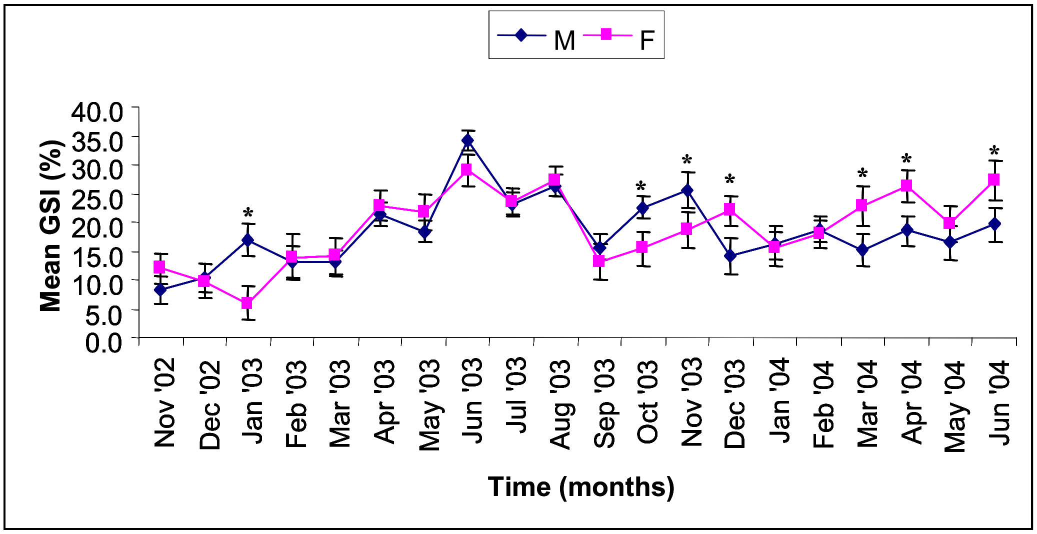


Fig. 6.1.3: Monthly mean (±SE) GSI of male and female *H. concolor* through sampling period. * = significant difference between males and females in this month.

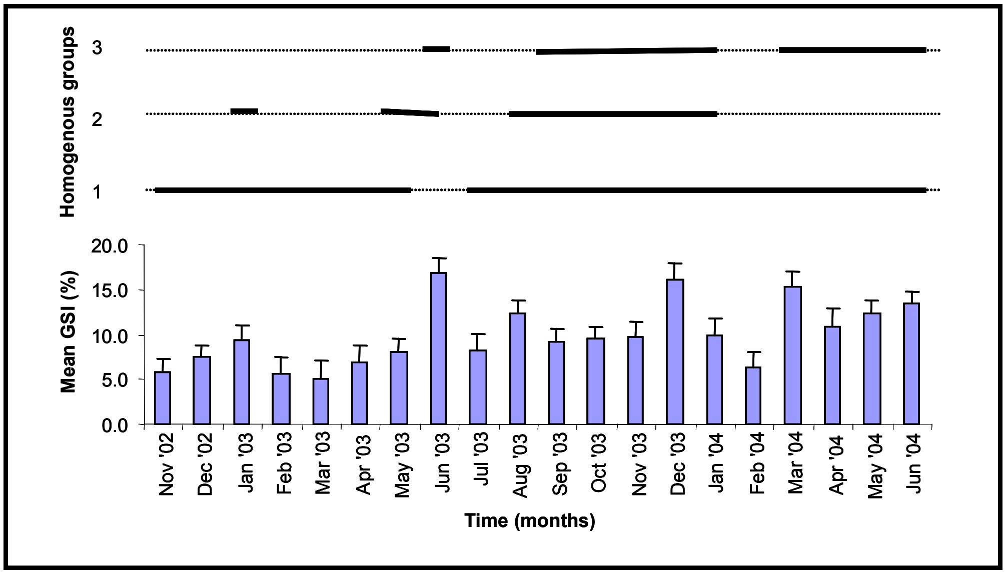


Fig. 6.2.1: Monthly mean (+SE) GSI of *S. longicosta* through sampling period. Solid lines above the bar columns connect months that were not significantly ($p > 0.05$) different from each other (Tukey HSD test).

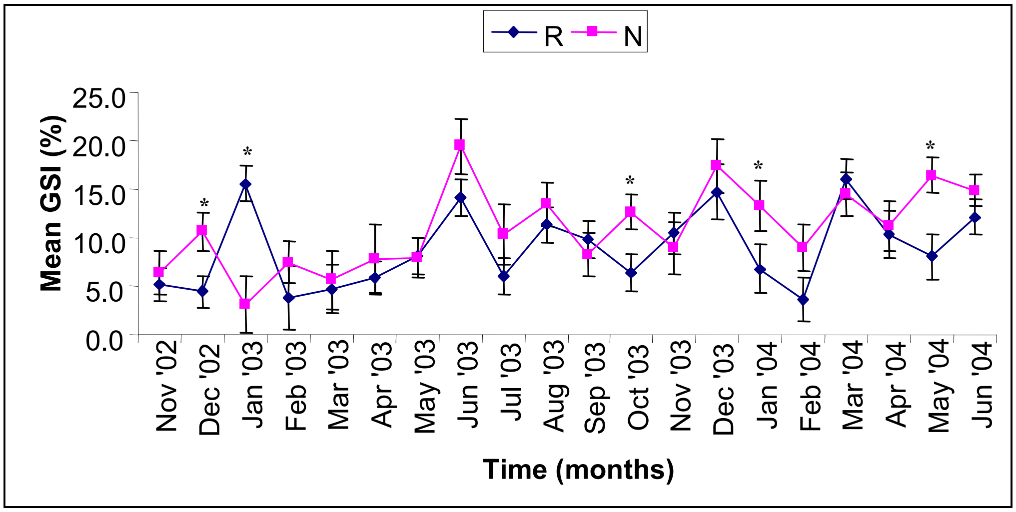


Fig. 6.2.2: Monthly mean (±SE) GSI of *S. longicosta* in reserve and non-reserve sites through sampling period. * = significant difference between reserves and non-reserves in this month.

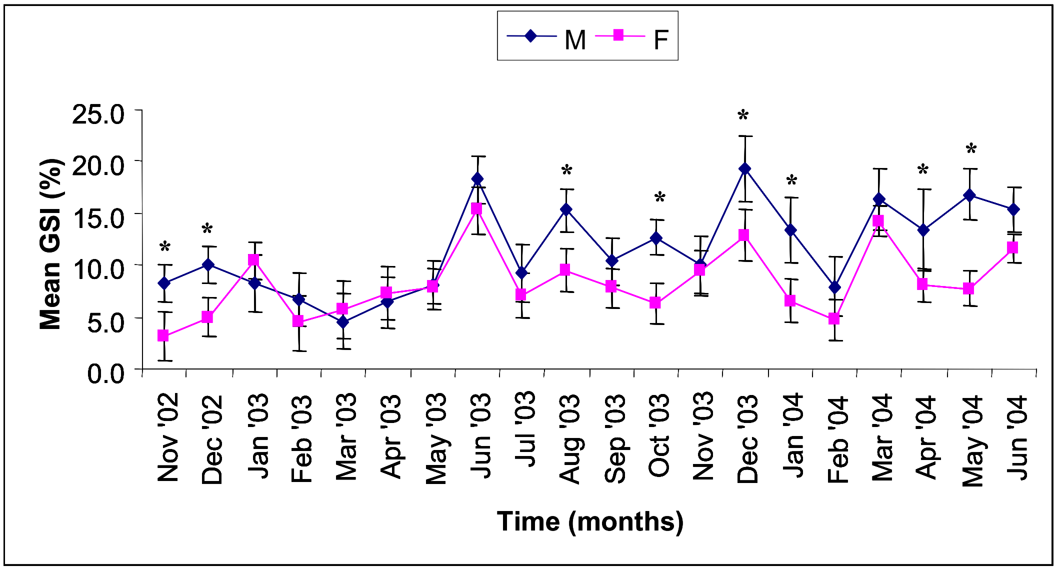


Fig. 6.2.3: Monthly mean (±SE) GSI of male and female *S. longicosta* through sampling period. * = significant difference between males and females in this month.

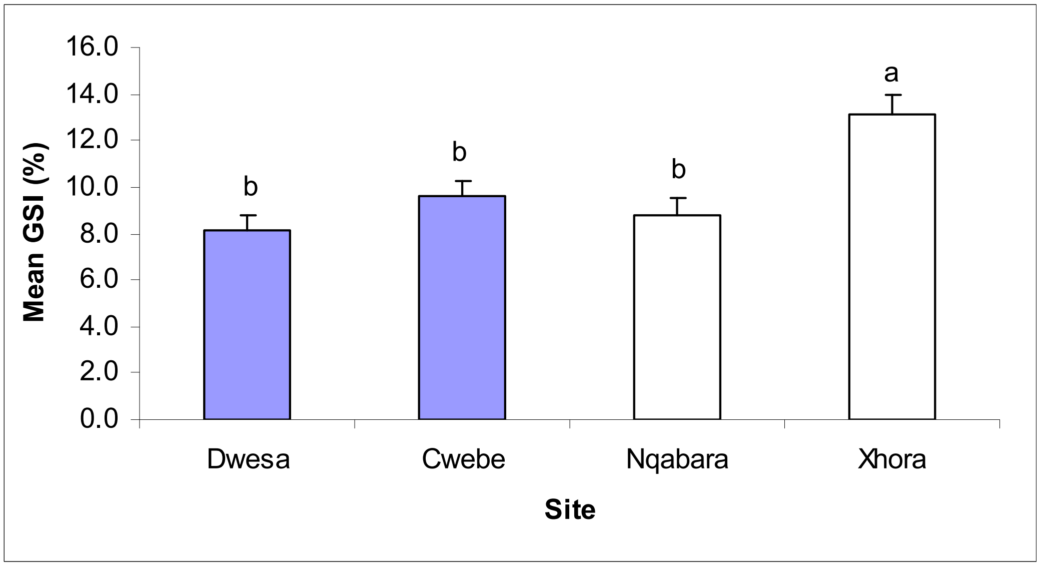


Fig. 6.2.4: Mean (+SE) GSI of *S. longicosta* at the four study sites. Letters above the bars indicate homogenous groups.

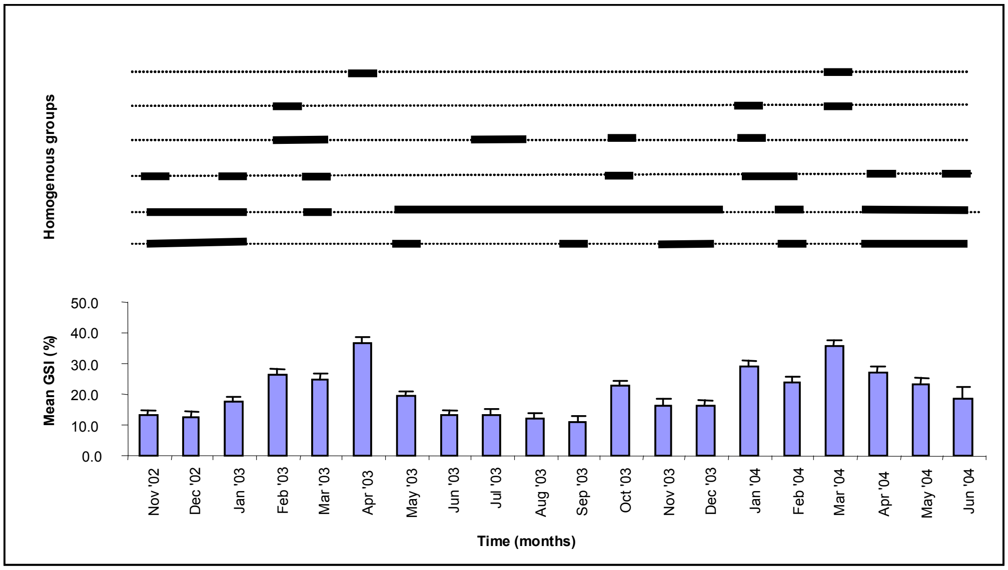


Fig. 6.3.1: Monthly mean (+SE) GSI of *C. capensis* through sampling period. Solid lines above the bar columns connect months that were not significantly (p > 0.05) different from each other (Tukey HSD test).

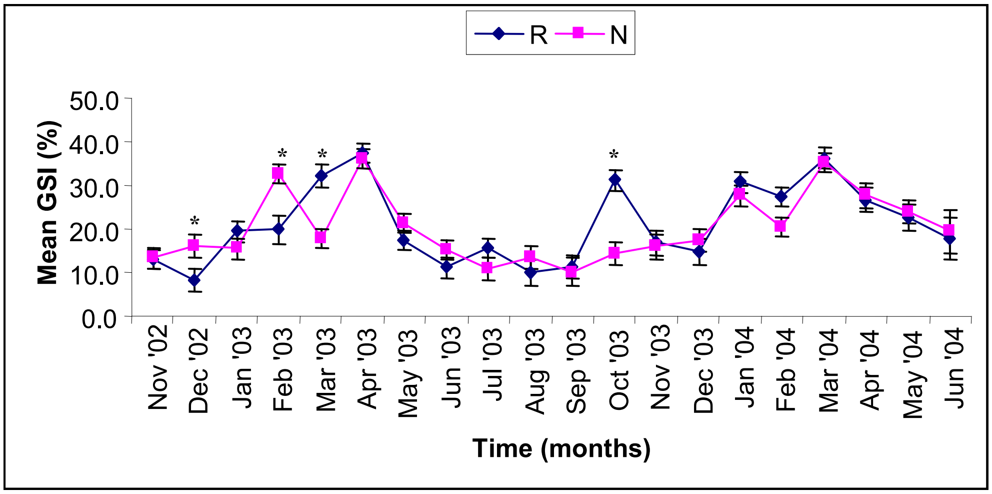


Fig. 6.3.2: Monthly mean (±SE) GSI of *C. capensis* in reserves (R) and non-reserve (N) sites through sampling period. * = significant difference between reserves and non-reserves in this month.

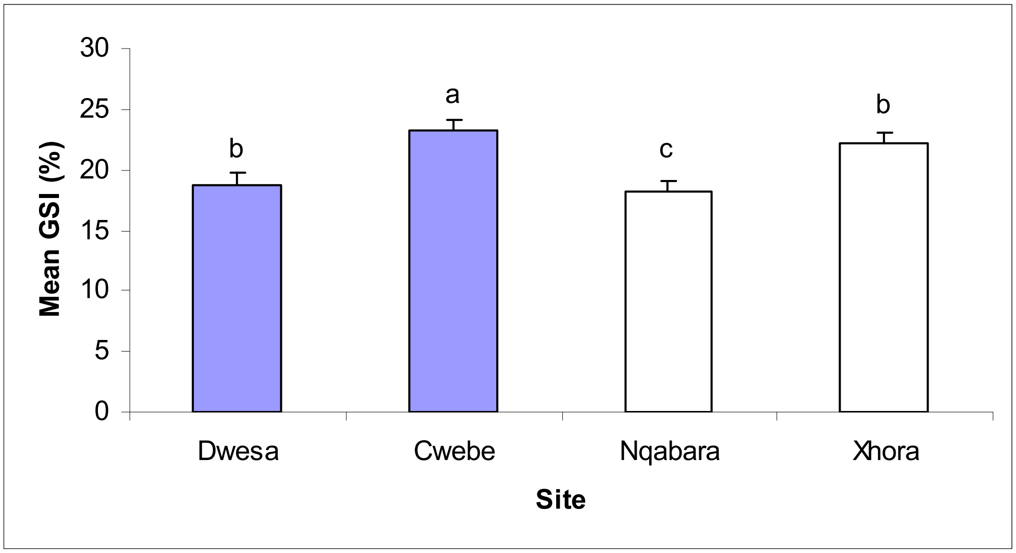


Fig. 6.3.3: Mean (+SE) GSI of *C. capensis* at the four study sites. Letters above the bars indicate homogenous groups.

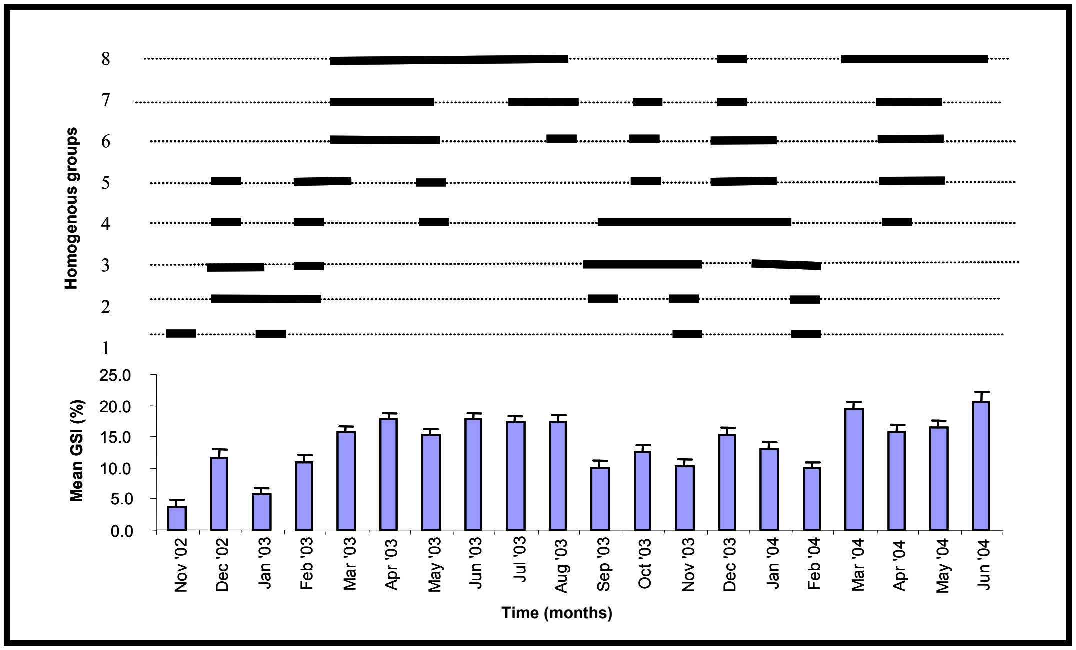


Fig. 6.4.1: Monthly mean (+SE) GSI of *S. granularis* through sampling period. Solid lines above the bar columns connect months that were not significantly ($p > 0.05$) different from each other (Tukey HSD test).

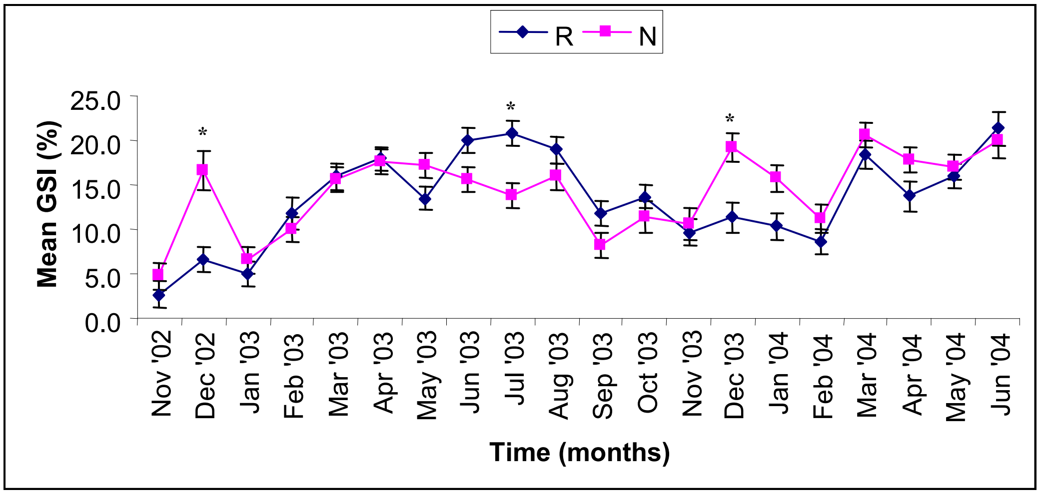


Fig. 6.4.2: Monthly mean (±SE) GSI of *S. granularis* in reserves and non-reserve sites through sampling period. * = significant difference between reserves and non-reserves in this month.

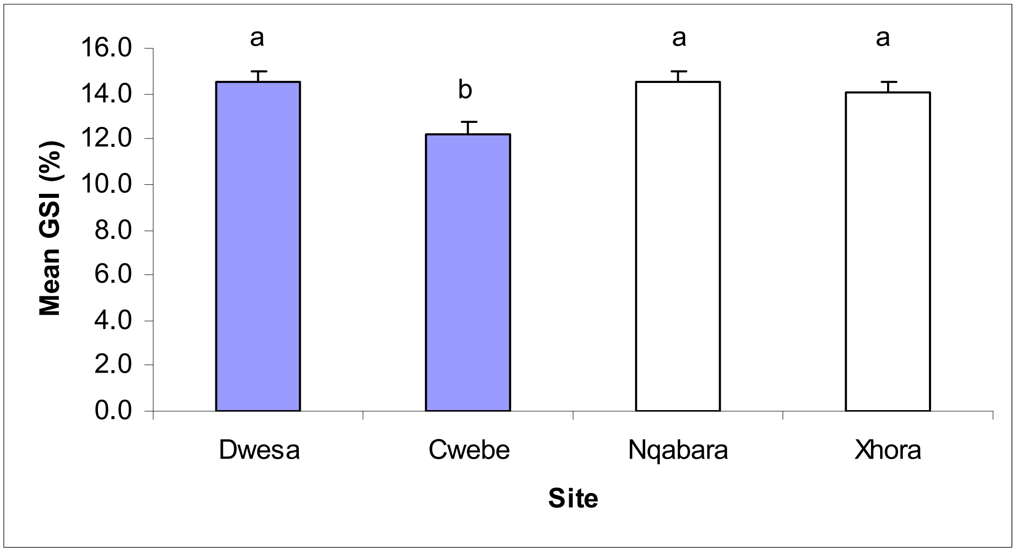


Fig. 6.4.3: Mean (+SE) GSI of *S. granularis* at the four study sites. Letters above the bars indicate homogenous groups.

CHAPTER 7

A MARK-RECAPTURE APPROACH TO THE ESTIMATION OF MORTALITY RATES IN COMMONLY AND RARELY EXPLOITED LIMPET SPECIES

7.1 INTRODUCTION

Predation is an important evolutionary and ecological factor that affects the composition and structure of communities by altering activity, behavioural patterns, and demographic characteristics (Lima & Dill 1990). The generalized life history of an organism is characterized by juvenile and adult stages, and a predator can prey on either one or both stages. Mortality has been shown to vary considerably depending on environmental conditions. These are biotic (e.g. food, predators) and/or abiotic (e.g. heat stress and desiccation) conditions that can in turn, also vary markedly with intertidal height, causing conspicuous zonation patterns of plants and animals (Rochette & Dill 2000).

Predation may be responsible for the distributional limits of prey, decreases in prey abundance, changes in age and size-structure of prey communities, morphological adaptations of prey, alteration of prey behaviour and changes in competitive interactions among prey and so helps to shape intertidal assemblages (ap Rheinallt 1986; Stachowicz & Hay 1999; Hamilton 2000).

Limpets have various means of defence against predation, including large size (Frank 1982; Marsh 1987; Bosman *et al*. 1989; Wootton 1992) and crypsis. Crypsis may occur through the growth of foliose algae on the shells of limpets (Bosman *et al*. 1989) or changes in shell colouration making visual detection by predators more difficult (Sorensen & Lindberg 1991). The most successful means of predation avoidance by limpets is to utilize substrata inaccessible to predators (Lewis & Bowman 1975; Frank 1982; Wootton 1992). Some limpets adapt their behavioural patterns by retreating to refuges like cracks and crevices (Williams & Morritt 1995), sealing their shells with mucus (Garrity 1984) and positioning their shells to minimize exposure to insolation and maximize evaporative cooling (Garrity 1984; Williams & Morritt 1995). Limpets that use refugia can desiccate and die if prevented from returning to home sites after foraging (Garrity 1984; Williams & Morritt 1995). Limpets also exhibit a wide range of behavioural rhythms with some species foraging while submerged or immersed during the day or night and returning to a fixed scar, while other species select suitable non-permanent resting sites (Branch 1981; Little 1989; Hodgson 1999; Nakai *et al*. 2006).

There are numerous factors that affect mortality of limpets. Reported sources include predation by oystercatchers (Marsh 1987; Bosman *et al*. 1989; Coleman *et al*. 1999), crabs (Cannicci *et al*. 2002; Silva *et al*. 2004), fish (Lechanteur & Prochazka 2001), predation by wrasses (Parry 1982), interspecific competition (Petraitis 1989), parasitic trematodes (Calvo-Ugarteburu 1998), endolithic cynobacteria (Kaehler 1999; Kaehler & McQuaid 1999), wave action (Underwood & McFadgen 1983; Denny *et al.* 1985), habitat disturbance (Brey & Gage 1997) and food availability (Tenhumberg 2000).

Mortality rates can be estimated directly by monitoring the disappearance of tagged animals (Takada 1995; Clarke *et al*. 2004) or indirectly from the reduction in density of cohorts over time (Fournier & Sibert 1991; McQuaid & Lindsay 2000). Capture-recapture methods with tagged animals are a primary means of estimating the abundance and survival of animal populations (Williams *et al.* 2001). These methods have received considerable attention over the last century from biologists and statisticians interested in developing applied statistical models to estimate animal abundance (Pollock *et al*. 1991) and mortality rates (Brownie *et al*. 1985; Nichols *et al*. 1992; Hoenig *et al*. 1998; Nichols *et al*. 2000).

The main aim of the present study is to test the two hypotheses that: 1) commonly exploited species will show higher mortality rates outside reserves than inside reserves due to the combined effects of natural and human predation, and 2) rarely exploited species will show no differences in mortality rates inside and outside the reserves as natural mortality rates will be similar inside and outside reserves.

7.2 MATERIALS AND METHODS

7.2.1 Capture-recapture experiments

A series of capture-recapture experiments was conducted over a period of 15 months. About 100 individuals of each species at each of the four sites (Chapter 1, Fig. 1.1) were marked with non-toxic paint (colour coded to give individual numbers) and tagged using bee tags (Opalithplattchen from Germany), which were embedded in rapidly setting epoxy glue (Lohse 1993; Jenkins & Hartnoll 2001). Individuals were randomly chosen from a wide size range down to the smallest size that could be effectively tagged. On each sampling occasion, *i*, captured limpets were marked with uniquely numbered tags and released. On subsequent sampling occasions, if a limpet was recaptured, its tag information was recorded and it was released.

At the end of each experiment, the capture history of each animal was constructed. For each sampling occasion, each limpet was given a "1" if it was captured and a "0" otherwise. For instance, in a 3-sample experiment, a limpet with a capture history of "101" denotes that it was captured, tagged and released at time 1, not observed at time 2, and recaptured and released at time 3.

7.2.2 Cormack-Jolly-Seber model

The Cormack-Jolly-Seber (CJS) model (Pollock *et al*. 1990) was chosen to estimate the probability of capture and the probability of survival for each sampling occasion for each limpet individual. One important biological issue is that only apparent survival probability (ϕ), can be estimated in open capture recapture studies. That is $1-\phi$ represents both animals that either died or that merely left the population through emigration.

Assumptions of the model are that:

1. All animals present at time i have the same probability of being captured.
2. All animals present immediately following sample time i have the same probability of surviving to sample time $i + 1$.
3. No tags are lost and all tags are correctly identified.
4. Sampling occurs instantaneously and animals are released immediately.
5. Emigration from the sample area is permanent, such that emigration is indistinguishable from death.

6. The survival and capture of an animal is independent of the survival and capture of all other animals.

Maximum likelihood estimates of the probability that a limpet is captured at time j, p_j, and the probability that a limpet alive at time j survives to time $j+1$, ϕ_j, were obtained by maximizing the multinomial likelihood of the form:

$$LL = \prod_{i=1}^{n_\omega} \chi(l_i) \prod_{j=f_i}^{l_i - 1} \phi_j \prod_{j=f_i+1}^{l_i} p_j^{\omega_{ij}} \left(1 - p_j\right)^{1-\omega_{ij}}$$

where

f_i is the first time limpet i was observed,

l_i is the last time limpet i was observed,

n_ω is all capture histories,

ω_{ij} is an indicator variable given a "1" if limpet i was captured at sampling occasion j and a "0" if the limpet was not captured, and

χ_j is the probability that a limpet is not observed after time j, given that it was alive at time j

such that: $\chi_j = (1 - \phi_j) + \phi_j \, (1 - p_{j+1})\chi_{j+1} \quad if \;\; j < k$

or $\chi_j = 1 \quad if \;\; j = k$

and k is the total number of sampling occasions.

Four modeling scenarios were compared for each of the four species and four study sites. These were based on the different combinations of temporally independent, denoted as $(\cdot)$, or temporally dependent, denoted as (t), capture (*p*) and survival (ϕ) probabilities.

The scenarios are therefore summarized as $p(\cdot)\phi(\cdot)$, $p(\cdot)\phi(t)$, $p(t)\phi(\cdot)$ and $p(t)\phi(t)$, respectively. Parameter redundancy was investigated for each model using the Hessian method advocated by Gimenez *et al*. (2004).

Model selection

The most parsimonious model, that model explaining the most variation with the fewest parameters, was chosen using Akaike's Information Criterion (Pollock *et al*. 1990) where $AIC = -2(LL + parameters)$. The model with the lowest AIC statistic was chosen as the most parsimonious model.

To assist with parameter comparison between species and sites, the temporally independent model is presented for all species. Likelihood ratio tests were conducted to test the null hypotheses that capture probabilities were equal for all populations within each species (Hearn & Polacheck 2002).

7.3 RESULTS

7.3.1 Capture-recapture experiments

There was good sampling coverage and many animals were recaptured often. This effect was stronger in the rarely exploited than the commonly exploited species. The lowest recaptures, hence the largest number of zeros in the capture histories were from *Helcion concolor*. In the rarely exploited species *Cellana capensis* and *Scutellastra granularis*, the model $p(\cdot)\phi(t)$ had the lowest AIC value and therefore was considered to be the most parsimonious. This pattern was true in all sites except Xhora for *S. granularis*.

The commonly exploited species showed highly variable capture-recapture probabilities, not only among sites but also between reserve and non-reserve sites. Reserve effects were evident in the survival probability of one exploited species, *Scutellastra longicosta* which is one of the most commonly exploited species. There were also reserve effects revealed in the capture probability but not the survival probability of the rarely exploited species, *Cellana capensis* and *S. granularis*.

7.3.1.1 Commonly exploited species

Helcion concolor

The model $p(\cdot)\phi(\cdot)$ which assumes constant capture and survival probabilities, was most parsimonious at two sites, Cwebe and Nqabara while the model $p(\cdot)\phi(t)$, assuming constant capture probability and time dependant survival was the one that best fitted data at Dwesa and no model could be fitted for Xhora due to lack of recaptures (Table 7.1).

Results from likelihood ratio tests indicated no significant differences ($p > 0.05$) among sites in either capture or survival probability (Table 7.3, Fig. 7.1). There were also no significant differences ($p > 0.05$) between reserves and non-reserves in either capture or survival probability (Table 7.3, Fig. 7.1).

Scutellastra longicosta

At three out of the four sites, the time dependent capture and survival model $p(t)\phi(t)$, was the most parsimonious (Table 7.1). The model $p(\cdot)\phi(t)$, was the most parsimonious for the Xhora population. The likelihood ratio test showed no significant differences (p >

0.05) among sites in the capture probability of *S. longicosta*. However, there were significant differences in the survival probabilities between Cwebe and Xhora as well as between Nqabara and Xhora (Table 7.2, Fig 7.1). This reflected the fact that the highest and lowest survival probabilities of 0.69.month^{-1} (CV (i.e. correlation coefficient) = 3.9%) and 0.56.month^{-1} (CV = 6.75%) were found at Cwebe and Xhora, respectively.

The likelihood ratio tests revealed significant differences ($p < 0.05$) between reserve and non-reserve sites in the survival probability of *S. longicosta* (Table 7.3, Fig. 7.1). This reflected the fact that the survival probability of *S. longicosta* in reserves was significantly greater in reserves than non-reserves. The survival probability ranged from 60-69% and 56-67% in reserves and non-reserves, respectively (Table 7.2). There were, however, no significant differences ($p > 0.05$) between reserves and non-reserves in the capture probability of *S. longicosta*.

7.3.1.2 Rarely exploited species

Cellana capensis

Out of the four models considered, model $p(\cdot)\phi(t)$ was the most parsimonious for *C. capensis* in all sites (Table 7.1, Fig. 7.1). There were no significant differences ($p > 0.05$) observed between the survival probabilities of the four *C. capensis* populations. Significant differences ($p < 0.05$) were however noted in the capture probabilities found between Dwesa and Nqabara as well as between Nqabara and Xhora. The highest and lowest capture probabilities of 0.93.month^{-1} (CV = 1.27) and 0.88.month^{-1} (CV = 1.9%) were found at the other sites and Nqabara, respectively.

The likelihood ratio tests showed significant differences ($p < 0.05$) between reserves and non-reserves in capture probability of *C. capensis* (Table 7.3, Fig. 7.1). This reflected the fact that the capture probability of *C. capensis* was significantly greater in reserves than non-reserves. The capture probability ranged from 92-93% and 88-93% in reserves and non-reserves, respectively (Table 7.2). There were, however, no significant differences ($p > 0.05$) between reserves and non-reserves in the survival probability of *C. capensis*.

Scutellastra granularis

For *S. granularis*, model $p(\cdot)\phi(t)$ was the most parsimonious for three sites, Dwesa, Cwebe and Nqabara, while time dependent capture and survival model $p(t)\phi(t)$ was the most suitable for the Xhora population (Table 7.1, Fig. 7.1). Significant differences ($p < 0.05$) in the capture probabilities of *S. granularis* were observed between Dwesa and Cwebe, Cwebe and Nqabara, as well as Cwebe and Xhora. This reflected the fact that the capture probabilities of *S. granularis* were, in descending order: Cwebe ($1.00.\text{month}^{-1}$ CV = 0.01%) > Dwesa ($0.96.\text{month}^{-1}$ CV = 1.25%) = Nqabara ($0.96.\text{month}^{-1}$ CV = 1.45%) > Xhora ($0.93.\text{month}^{-1}$ CV = 2.02%). There were no significant differences ($p > 0.05$) among sites in the survival probabilities of *S. granularis* (Table 7.2).

The likelihood ratio tests revealed significant differences ($p < 0.05$) between reserves and non-reserves in the capture probability of *S. granularis* (Table 7.3, Fig. 7.1). The capture probability of *S. granularis* was significantly greater in reserves than non-reserves. This reflected the fact that the capture probability ranged from 96-100% and 93-96% in reserves and non-reserves, respectively (Table 7.2). There were no significant differences

($p > 0.05$) showed between reserves and non-reserves in the survival probability of *S. granularis*.

7.4 DISCUSSION

This study revealed strong reserve effects in the survival probability of the most commonly exploited species, *Scutellastra longicosta*. This was expected because of high ranking of this species in terms of preference. The territorial nature of this species may also have played an important role. Homing in limpet species has been reported to reduce predation (Branch 1975b; Garitty & Levings 1983; Iwasaki 1993; Shanks 2002) and increase survival from wave action (Branch 1975b; Chelazzi *et al*. 1994; Gray & Hodgson 1998). There were however, unexpected reserve effects in the capture probability of the rarely exploited species (*Cellana capensis* and *S. granularis*). The unexpected result for *C. capensis* may be related to the fact that this species is occasionally exploited in the absence of the preferred species (Lasiak 1993). In the case of *S. granularis*, it was found earlier to show a reserve effect on mean density (Chapter 2). It is therefore possible that, as there are more barnacles in reserve than non-reserves (*pers. obs*.), the rugose surface of barnacles in reserves may offer protection.

The lack of significant reserve effects for *Helcion concolor* was, however, unexpected. The overall results suggest that there were variations in both the capture and survival probabilities among the limpet species and *H. concolor* had the lowest recapture probability of all species investigated. Thus, the absence of recaptures from Xhora, suggests high mortality from human predation. Moreover, this may be related to low tenacity and a small foot surface area, though this was not tested in the present study. Branch and Marsh (1978) noted that there was a relationship between tenacity and wave action in patellid limpets. They found that species on the low shore had high tenacity and experienced high wave action, while those occupying the high shore, such as *H. concolor*, had very low tenacity and experienced less wave action. It is also possible that some of this loss is due to natural predators (Coleman *et al*. 1999; Cannicci *et al*. 2002; Silva *et al*. 2004). Predation pressure generally varies across the shore (Johannesson 2003), and its effect on limpet populations depends both on the spatial variation of predation intensity (e.g. high/low zones) and variability in the vulnerability of individuals with different attributes like size and shell thickness. The destruction of habitat and human pressure when collecting were noted as the main causes for the endangered status of *Patella ferruginea* (Guerra-García *et al.* 2004).

On exposed shores dislodgement by waves (Denny & Blanchette 2000) is considered the major cause of mortality whereas on protected shores, predation by shore crabs and desiccation are thought to be more important (Boulding & LaBarbara 1986). The small size and proportionally large foot of gastropods from wave exposed shores are thought to be adaptations to resist dislodgement by waves (Underwood & McFadyen 1983; Denny *et al*. 1985). The large size and thick shell of protected shore gastropods are thought to resist predation by crabs and other mobile predators, crushing by stones, heat stress and desiccation (Branch 1981; Johannesson 2003). Moreover, preferences for thin-shelled mollusc species have been demonstrated in the shell-breaking crab *Hemigrapsus nudus* (Boulding 1984; Boulding & LaBarbera 1986). Larger snails can suffer lower mortality from shore birds with small gapes (Marsh 1987), fish with small mouths (Haldorson & Moser 1979), and other crabs with small claws (Boulding 1984). When dislodged, limpets cannot easily reattach or right themselves if overturned (Denny & Blanchette 2000).

The observed inconsistent reserve effects in capture and survival probabilities of these limpets may be due to variation in life-history characteristics among species (Bailey *et al*. 2004) or age or size (Tilley 1980) and could be the source of the slight lack-of-fit observed in goodness-of-fit tests. In littorrinid snails, variation in predation was suggested as one of the major factors creating life-history differences among individuals in different environments (Johannesson 2003; Rochette *et al*. 2003).

Heterogeneity in the spatial distribution of limpets of different size classes may also occur. As limpets age, specific size classes may become more or less likely to be captured relative to the rest of the population. In many limpet populations, different size classes occupy different habitats and have different tenacities (Branch & Marsh 1978). For example, small limpets are concentrated in crevices, while adult limpets are found more on flat/less irregular rocks. Crevices act as a refuge from wave activity, reducing the chances of a limpet being washed away by the incoming tide (Gray & Hodgson 2004). It has been shown previously that heterogeneity in capture probabilities can lead to bias in estimates of survival (Nichols 1992; Clobert 1995) and growth (Trites 1993). This cannot be true in the present study, as individuals from each site were thoroughly checked but the variations in the number of crevices in different sites may influence their survival hence observed variations in survival probabilities in different sites.

It is also important to note that the CJS model cannot separate between mortality and emigration and only estimates apparent mortality. The coefficients of variation (CV) of parameter estimates for capture and survival probabilities were higher in commonly exploited than in rarely exploited species, indicating a lower degree of precision in the former than the latter species. The capture and survival probabilities not only differed between commonly and rarely exploited species but also within commonly and rarely exploited species. But the overall results indicated consistent reserve effects on the capture probabilities of the rarely exploited species while inconsistent reserve effects were evident on the survival probabilities of the commonly exploited species (i.e. *S. longicosta* showed significant results and *H. concolor* insignificant results). These results have management implications as they suggest that different species respond differently to natural processes.

Table 7.1: Summary of AIC statistics and the number of estimated parameters in parenthesis. The most parsimonious model is both italised and underlined.

Species	Population	Model			
		$p(\cdot)\phi(\cdot)$	$p(\cdot)\phi(t)$	$p(t)\phi(\cdot)$	$p(t)\phi(t)$
H. concolor	Dwesa	78.48 (2)	*76.35* (4)	80.49 (3)	76.49 (5)
	Cwebe	*57.26* (2)	58.89 (5)	59.95 (4)	62.45 (7)
	Nqabara	*133.74* (2)	140.16 (10)	139.76 (9)	144.85 (17)
	Xhora	-	-	-	-
S. longicosta	Dwesa	250.2 (2)	243.66 (6)	254.21 (5)	*241.51* (9)
	Cwebe	551 (2)	534.07 (12)	547.1 (11)	*533.48* (21)
	Nqabara	389.38 (2)	350.49 (10)	380.53 (9)	*349.1* (17)
	Xhora	316.89 (2)	*303.54* (8)	320.2 (7)	309.72 (13)
C. capensis	Dwesa	815.36 (2)	*782.18* (12)	811.78 (11)	783.7 (21)
	Cwebe	783.7 (2)	*764.04* (13)	791.79 (12)	772.83 (23)
	Nqabara	745.7 (2)	*738.2* (14)	753.94 (13)	745.91 (25)
	Xhora	754.19 (2)	*706.5* (13)	744.4 (12)	707.9 (23)
S. granularis	Dwesa	524.11 (2)	*490.69* (14)	535.79 (13)	499.72 (25)
	Cwebe	316.61 (2)	*301.91* (14)	337.84 (13)	323.82 (25)
	Nqabara	430.8 (2)	*358.93* (11)	427.99 (10)	366.61 (19)
	Xhora	423.09 (2)	348.27 (11)	418.01 (10)	*348.20* (19)

Table 7.2: Temporally independent monthly estimates of capture and survival probabilities obtained from CJS model for both commonly and rarely exploited species at each site. A = not possible to estimate parameters as there were no recaptures and correlation coefficient (CV) in parenthesis. Superscripts denote homogenous groups.

	Commonly exploited species								
	Helcion concolor					*Scutellastra longicosta*			
	Reserves		**Non-reserves**			**Reserves**		**Non-reserves**	
	Dwesa	Cwebe	Nqabara	Xhora		Dwesa	Cwebe	Nqabara	Xhora
$p(\cdot)$	0.53^{a} (33.89%)	0.27^{c} (54.5%)	0.44^{b} (24.02%)	A		0.67^{a} (9.68%)	0.71^{a} (5.38%)	0.74^{a} (5.99%)	0.75^{a} (7.60%)
$\phi(\cdot)$	0.43^{a} (23.39%)	0.52^{a} (28.13%)	0.51^{a} (13.32%)	A		0.60^{b} (6.94%)	0.69^{a} (3.9%)	0.67^{a} (4.75%)	0.56^{b} (6.75%)
	Rarely exploited species								
	Cellana capensis					*Scutellastra granularis*			
	Reserves		**Non-reserves**			**Reserves**		**Non-reserves**	
	Dwesa	Cwebe	Nqabara	Xhora		Dwesa	Cwebe	Nqabara	Xhora
$p(\cdot)$	0.93^{a} (1.27%)	0.92^{a} (1.44%)	0.88^{b} (1.9%)	0.93^{a} (1.33%)		0.96^{b} (1.25%)	1.00^{a} (0.01%)	0.96^{b} (1.45%)	0.93^{c} (2.02%)
$\phi(\cdot)$	0.83^{a} (1.75%)	0.86^{a} (1.65%)	0.85^{a} (1.77%)	0.82^{a} (1.89%)		0.80^{a} (2.43%)	0.78^{a} (3.06%)	0.76^{a} (3.06%)	0.79^{a} (2.88%)

Table 7.3: Summary of likelihood ratio tests results on estimates of capture (p) and survival (ϕ) probabilities obtained from CJS model for both commonly and rarely exploited species. * = significant difference at $p < 0.05$ and ns = non-significant difference between reserves (R) and non-reserves (N) at $p > 0.05$.

Species		**(p)**	**(ϕ)**
Commonly exploited species	*Helcion concolor*	ns (R > N)	ns (R > N)
	Scutellastra longicosta	ns (N > R)	* (R > N)
Rarely exploited species	*Cellana capensis*	* (R > N)	ns (N > R)
	Scutellastra granularis	* (R > N)	ns (R > N)

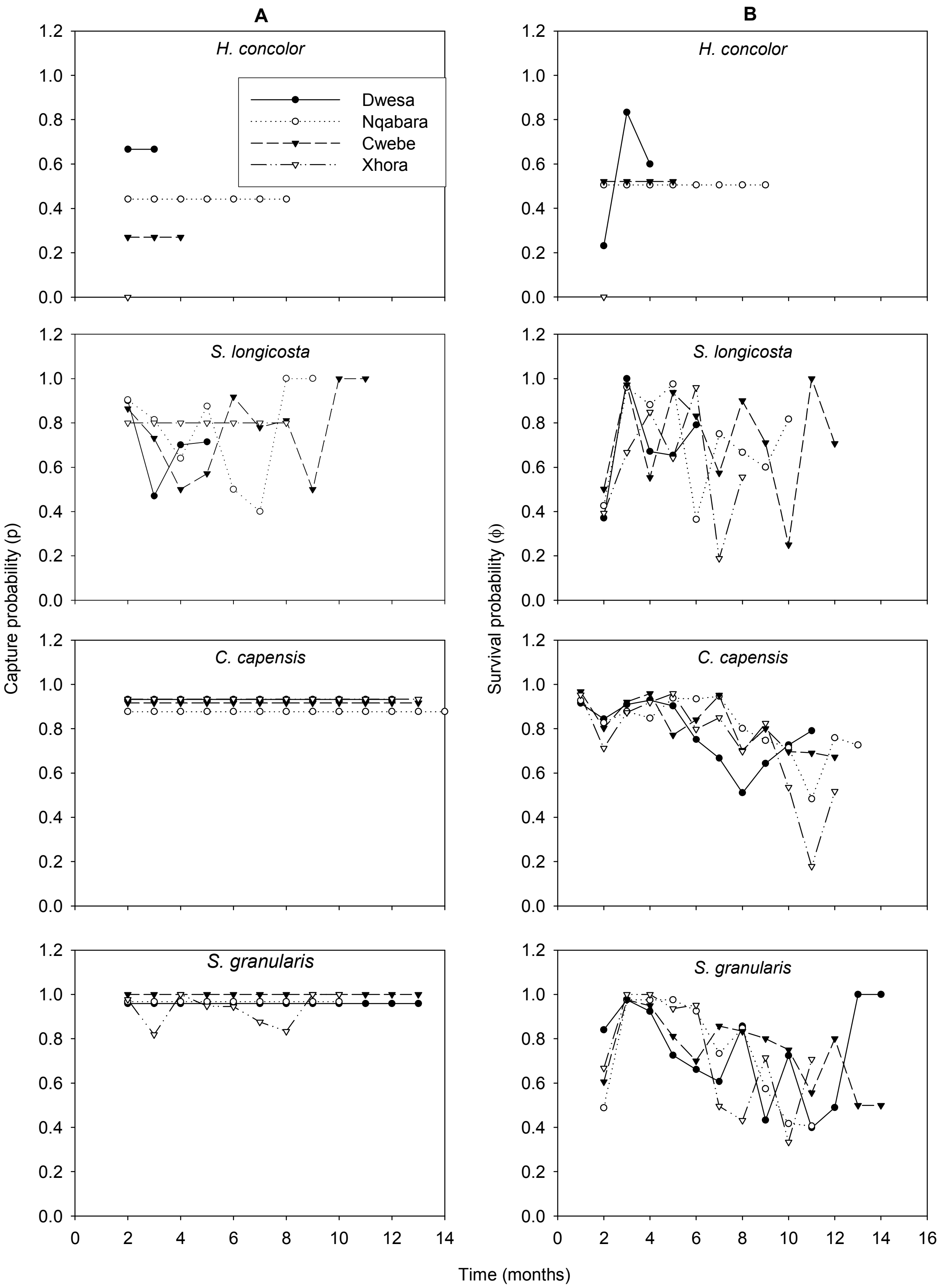


Fig. 7.1: Estimated monthly capture (A) and survival (B) probabilities of each species among sites throughout the sampling period.

CHAPTER 8

GENERAL DISCUSSION

8.1 DISCUSSION

Marine reserves are an important conservation management tool. They protect natural populations from fishing and are used as a means of determining the impact of fishing on marine ecosystems (Sala *et al*. 1998; Tegner & Dayton 2000). Many studies report that protection from fishing leads to rapid and dramatic changes in populations in reserves (Roberts & Hawkins 1999; Halpern & Warner 2002; Sagarin *et al*. 2007). There is much evidence that protection from fishing leads to rapid buildup of abundances and biomass of populations of exploited species, increases species diversity, fosters habitat recovery from fishing disturbances, increases average body size, and extends population age structure (Bennett & Attwood 1993; Russ & Alcala 1996; Edgar & Barrett 1999; Kelly *et al*. 2000; McClanahan & Mangi 2000; Willis *et al*. 2003). The present study revealed that the above-mentioned characteristics do not apply to all the study limpets but depend on the exploitation status of the species (i.e. whether it is commonly exploited of rarely exploited). Therefore, the said characteristics are true for the most commonly exploited species *Scutellastra longicosta* and not true for the least exploited species *S. granularis*.

Marine protected areas are affected by human activities that lie outside their boundaries, ranging from marine transportation and fishing to land-based sources of marine pollution e.g. agriculture, urban runoff, and industry. In many, if not most cases, these exogenous sources have far greater effects on resources of the marine protected area than activities within the protected area (Jones 2002). Connectivity is low across biogeographic boundaries and is further reduced by habitat fragmentation and overfishing. The size of a reserve is also influential in that larger reserves maximize the probability of selfrecruitment within reserves for short-distance dispersers, while for long-distance dispersers, smaller reserves spaced at broader intervals may have greater connectivity (Kramer & Chapman 1999).

The Climatic-envelope hypothesis assumes that populations near the margins of their range will show both relatively low abundances and relatively depressed organism condition as reflected in reproductive output, growth, stress or other performance measures (Sagarin *et al*. 2006). For example, highly skewed or multi-modal size structure at range edges relative to sites within the range can indicate dispersal, rather than temperature-mediated range boundaries. Zacherl *et al*. (2003), for instance, combined size-structure data, abundance data and data on physical factors related to propagule transport to separate the roles of larval transport from climate warming in an analysis of the recent range expansion of the marine snail *Kelletia kelletii*. Physiological responses to climate are likely to be important drivers of population-abundance patterns (Sagarin *et al*. 2006), but Clarke (2003) argued that we still lack a clear model linking physiology, climate and macroecology.

Environmental stress is another factor that affects intertidal community structure (Menge & Branch 2001). Environmental stress models assume that community structure results from species interactions and disturbances and how these are modified by underlying gradients of environmental stress (where stress is a consequence of environmental conditions such as temperature, moisture and salinity). At the community level, interspecific interactions can alter predicted responses to climate change drastically

(Davis *et al*. 1998) and affect populations and demographics differently across the species' range of distribution (Garcia *et al*. 2000). Alternatively, community composition is likely to be altered dramatically when a key element of the community is affected by climate or other factors. On the Pacific coast of North America, the keystone predator *Pisaster ochraceus* (the ochre starfish), showed depressed feeding rates under upwelling conditions (Sanford 1999), which are heterogeneous across latitude.

Since most exploited marine species, including the limpets of the present study have pelagic eggs or larval stages (Branch 1971; Hodgson 1999), the offspring of protected animals can be dispersed widely from reserves to re-supply non-reserves. Larvae that settle relatively indiscriminately are likely to settle soon after becoming competent, while those using very specific settlement cues are likely to spend longer in the planktonic before encountering the appropriate cue (Krug 2001; Toonen & Pawlik 2001). Any variation in settlement behaviour may, therefore, result in variation in dispersal potential of larvae (Krug 2001; Toonen & Pawlik 2001). The maximum planktonic period of non-feeding larvae is determined by energetic reserves (Lucas *et al.* 1979; Wendt 2000). Reported disadvantages of producing larger larvae include the fact that increased energetic costs and increases in the size of off-spring are likely to result in decreases in their numbers (Vance 1973). Larger larvae that spend more time in the plankton and settle later are more vulnerable to predation and advection away from suitable habitats (Stanwell-Smith *et al*. 1999), although chemical defenses in larvae can mitigate such effects (Lindquist & Hay 1996). The production of larger larvae seems riskier, but does allow for increased dispersal and/or settlement in better quality habitats. Contrary to planktonic vulnerability to predation, recent studies on corals showed that planktonic larvae suffer little or no predation by planktonic predators (Johnson & Shanks 2003). Johnson and Shanks (2003) attributed their findings to either predators being inefficient at capturing prey or larvae having an effective escape response. Traditionally, models of optimal egg/larval size in marine invertebrates assume that an increase in per-offspring investment will shorten the planktonic period, thereby reducing planktonic mortality (Vance 1973; Podolsky & Strathmann 1996).

As stocks build up in reserves, there is predicted to be movement of juveniles and adults from protected areas to non-reserves, so-called “spillover” (McClanahan & Mangi 2000). Potential scales of spillover vary across species and ecosystems. Fish tagging and movement data from coral reefs, estuaries, rocky reefs and continental shelves suggest spillover extending from hundreds of meters to hundreds of kilometers from reserves (Gell & Roberts 2003; Russ & Alcala 2004). In contrast, rocky intertidal limpets are not that highly mobile and in the present study, reserve as the main factor showed no significant effects on recruitment for any species on scales of 5 to 10 km. But there were month/reserve interactions with more months showing more recruits in reserves than non-reserves for the rarely exploited species and vice versa for the commonly exploited species. This suggests that a population of these limpets in this region, recruit from distant sources and such connectivity among habitats has implications for the conservation of these limpet species. Thus, their recruitment variations did not correspond to the reproduction or distribution of local adult populations.

Biological communities in rocky shores tend to exhibit particular variability or discontinuities due to a combination of biotic, abiotic and anthropogenic factors, the interactions between which are increased by connectivity within the marine environment (Jones 2004). Therefore, populations may rise and fall in a relatively unpredictable and non-attributable manner due to complex interactions among the ecological dynamics of different communities. Such variations also occur in response to variations in the physical environment, such as changes in currents, terrestrial run-off and coastal geomorphology (Menge 2000). Human activities often also affect inshore communities, and the connectivity of a marine environment means that such activities may occur a considerable distance from the marine protected area, but can still have a significant impact on inshore communities (Jones 2002).

At the broadest scale, reserve networks protect ecological processes essential for ecosystem functioning (Roberts *et al*. 2003). Conserving the functioning of an ecosystem, (i.e. maintaining the ecological processes of that system) requires attention not only to species but also to functional groups of species. In a species-poor ecosystem, each primary process (primary production, decomposition, nitrogen fixation, capture of water, habitat creation, recycling of nutrients etc) may be provided by many fewer species than in a species-rich ecosystem. In a species rich system, many species are likely to coexist with others that perform similar roles (Roberts 1995; Orians 2000). Therefore, in species rich systems, removal of any particular species may not result in serious disruption of the process because other functionally similar species may be able to compensate for the lost species. However, species loss in a low-diversity system may lead to complete loss of a process.

An analysis of species composition from the west to the east coasts of South Africa recognized three types of communities defined by their exposure to wave action (sheltered, semi-exposed and exposed). These communities were found to be more similar if they shared similar levels of wave action than if they came from adjacent localities with different wave action (Emanuel *et al*. 1992; Dye *et al*. 1994). Omission of any one of these communities from a system of reserves would leave unprotected a significantly "different" community. Similarly, locations within the same biogeographic region will be much more likely to interact than locations in adjacent regions. Although the study sites (Chapter 1, Figs. 1.1 & 1.2) are located in the same biogeographic region, they are in a transition area between two biogeographic provinces (Emanuel *et al*. 1992) and may thus be affected by biogeographic edge effects. Of the four species, *Scutellastra granularis* is the only one that occurs in all four of the main biogeographic regions found in South Africa, while *S. longicosta* and the other two species *Cellana capensis* and *Helcion concolor* occur in just two.

Strong gradients of nutrient levels and intertidal productivity exist around the coast of South Africa, from high on the west to low on the east coast (Bustamante & Branch 1996). In parallel with this, the average biomass of grazers and filter feeders declines from west to east. Variations in oceanographic factors (currents, upwelling, nutrients, rates of particle flux) are associated with different magnitudes of algal and/or phytoplankton abundance, availability of particulate food and rates of recruitment (Menge 1999; Benedetti-Cecchi *et al*. 2001; Forde & Doak 2004).

Top-down and bottom-up processes (Menge 2000) can be important joint determinants of community structure in rocky shores. Oceanographers working in a three-dimensional environment have stressed the roles of productivity, nutrients and both horizontal and vertical transport called “bottom-up” processes (Seitz & Lipcius 2001), as determinants of community pattern. In contrast, marine rocky intertidal ecologists, working in a largely two-dimensional, space-limited environment have historically regarded “bottom-up” factors as less important sources of community differences than “top-down” factors such as predation or grazing. In the rocky intertidal, community structure and dynamics depend, in part, on bottom-up effects driven by phytoplankton. Specifically, differences in filter-feeder growth rates and abundance, trophic interactions, and perhaps prey recruitment rates (through increased survival of larvae or recruits with more food) may depend on consistently different phytoplankton concentrations (Menge *et al.* 1997). More phytoplankton means more food for filter feeders and thus faster growth. Moreover, high phytoplankton concentration could increase recruitment by increasing the survival of larvae or recruits that are more resistant to physical stresses. For example, Duggins *et al*. (1989) indicated that subtidal kelps, by generating organic detritus, may accelerate the growth of filter feeding, intertidal mussels and barnacles. Bustamante *et al*. (1995b) working at both 100 km and 100 m spatial scales on the coast of South Africa, found that nutrients, microalgal productivity and invertebrate grazer abundance were positively correlated. Their work suggests that detritus subsidies from kelp beds adjacent to intertidal areas control limpet density and biomass.

Though the reproductive cycles of the study limpets were broadly synchronized, asynchronies between reproductive activity and suitable environmental conditions could lead to individual reproductive failure as a result of sperm limitation, variation in the availability of food for larvae, unpredictable nearshore oceanographic features, and larval predation. Each of these factors may have dramatic consequences on recruitment success and may lead to reproductive failure by a significant fraction of the adult population (Caley *et al*. 1996). This study showed that there were reserve effects on the reproductive output of the commonly exploited species and none for the rarely exploited species. The mean GSI values of commonly exploited species were greater in reserves than non-reserves.

As a consequence of free spawning in the unpredictable nearshore environment, marine species with large fecundities and high pre-reproductive mortality may be subject to extreme variability in reproductive success (Flowers *et al*. 2002). When pre-reproductive stages (e.g. planktonic larvae) experience high rates of mortality, selection favours allocating proportionately more resources to growth and maintenance at the expense of reproduction (Branch 1974b). This switch in resource allocation increases the probability of reproductive success by distributing reproductive efforts over many years (i.e. bet-hedging). Thus, environments that predictably facilitate high pre-reproductive survival and low variance in reproductive success favour short life, whereas unpredictable environments with low pre-reproductive survival and high variance in reproductive success favour long life (Flowers *et al*. 2002).

The majority of marine populations are demographically open, their replenishment is largely or exclusively dependent on a supply of juveniles from the plankton (Caley *et al*. 1996; Gosselin & Qian 1996). The irregular nature of coastlines, particularly the presence of bays and estuaries, generates substantial regional variation in coastal transport that generates correspondingly large variation in recruitment to marine populations (Gaines & Bertness 1992). Models of open population dynamics demonstrate that local populations may fluctuate around an equilibrium level due to regulation by recruitment, even in the absence of density-dependent mortality (Bence & Nisbet 1989; Karlson & Levitan 1989). Even minor variation in rates of mortality of adults will decouple the relationship between recruitment and population size (Holm 1990; Robertson 1998), and where recruitment is inhibited by adults as is the case for limpets (Boaventura *et al.* 2003), cyclical variations in local population size can result from the time lag between recruitment and adulthood (Roughgarden *et al*. 1985; Bence & Nisbet 1989; Hyder *et al*. 1998). For example, competition can result in wide fluctuations in numbers that might easily be mistaken for the result of peaks and troughs of recruitment.

For most benthic invertebrates and demersal fishes, the local production of offspring has little or no direct role in setting local population size because larval recruitment from elsewhere provides the only substantial input of new individuals. If recruitment fails, the local population will decline to extinction, regardless of local fecundity (Caley *et al*.

1996). Conversely, the local population will persist as long as recruitment continues, even if these adults produce no viable offspring. As a result, a local population cannot be regulated by its own fecundity, even if density-dependent effects on local reproductive output are evident (Colegrave 1993).

Species differ markedly in early post-settlement mortality rates (Doherty & Sale 1985; Sale & Ferrell 1988), which may alter patterns of relative abundance established at settlement (Caley 1993; Carr & Hixon 1995). For example, the rarely exploited species (*C. capensis* and *S. granularis*) showed a very similar long-term trend of increasing densities with time, indicating an increase in recruitment. The commonly exploited, territorial species *S. longicosta* revealed a long-term trend with density in reserves being greater than non-reserves, though the two showed parallel patterns over time, suggesting a similar balance between recruitment and mortality rates. Although densities of *H. concolor* in reserves and non-reserves were generally stable, reserves showed an initial decline, indicating an imbalance between recruitment and post-settlement mortality rates. The presence of marine reserves to protect such populations may help replenish non-protected areas through larval export. The present study revealed significant effects of reserves on the survival probability of the most commonly exploited species, *S. longicosta* and the capture probability of the rarely exploited species.

The commonly exploited species showed clear reserve effects on reproduction. Since all four study limpets are broadcast spawners, they require high densities of fertile individuals to optimize reproduction. There were no significant reserve effects on densities for any of the species. However, there were strong, significant month/site (reserve) for all of them, with mean densities in reserves generally being greater than in non-reserves for commonly exploited species. Increases in animal abundances and size in marine reserves translate into increased reproductive potential (Gell & Roberts 2003). There were inconsistent reserve effects on growth rates for both commonly exploited and rarely exploited species, suggesting the influence of different life-history characteristics. Reserve effects on growth rates were found in the commonly exploited, non-territorial species *H. concolor* and in one rarely exploited species *C. capensis*. But there were no reserve effects on the growth rates of the commonly exploited territorial species *S. longicosta*, suggesting that growth rate depends on the status of the species in terms of territoriality and exploitation.

Apart from sex ratios, capture probabilities etc, this thesis tested four main hypotheses on limpet density, size, growth and reproduction with the predictions that for exploited species density and size would be greater within reserves, while growth and reproduction would both be reduced. For non-exploited species the predictions were of no effect of reserves on these parameters. The results were not clear-cut as there were generally interactions between month and site (reserve). The results also highlight the importance of detail. Very crudely the findings were as follows: *S. longicosta* conformed to 3 predictions after adjustment of the hypothesis on growth to allow for territoriality. *H. concolor* did not conform to the prediction on reproduction for unknown reasons. *S. granularis* conformed to all predictions except that on density, possibly due to either or both of two effects: barnacle interaction, with more barnacles inside than outside reserves and the effects of trampling with more human traffic outside than inside reserves. *C. capensis* was the most problematic as it is occasionally mistaken for *H. concolor* and harvested. Although there were no reserve effects on density, however, it showed greater size and slower growth in reserves. This could be explained by the removal of large individuals outside reserves leading to relaxed intraspecific competition without a significant effect on density.

In conclusion, reserve effects on the biology of the study limpets were inconsistent, suggesting that the different life-history characteristics in these limpets influence the efficacy of reserves. The overall results generally indicate a gradient of species exploitation from the most commonly exploited species, *S. longicosta*, to the least exploited species, *S. granularis*. However, also emerging from this study was a gradient of exploitation between non-reserve sites and also between reserve sites. Xhora was found to be heavily exploited while Nqabara was a moderately exploited non-reserve site. For the reserve sites, Cwebe was found to have more poachers than Dwesa. Thus, studies of population density, size structure, recruitment, growth, reproduction and mortality have provided great insight into many interactions that occur within reserves and non-reserves as well as among the various species. Future studies are required to investigate the effects of reserves on the genetic diversity of populations of exploited limpets and their ability to maintain resilience in view of changing conditions in terms of climatic change and human impacts.

REFERENCES

ABRAMS, P.A. & ROWE, L. 1996. The effects of predation on the age and size of maturity of prey. *Evolution* 50(3): 1052-1061.

ADDESSI, L. 1994. Human disturbance and long-term changes on a rocky intertidal community. *Ecol. Applic*. 4: 786-797.

AIROLDI, L. & HAWKINS, S.J. 2007. Negative effects of sediment deposition on grazing activity and survival of the limpet *Patella vulgata*. *Mar. Ecol. Prog. Ser*. 332: 235-240.

AKESTER, R.J. & MARTEL, A.L. 2000. Shell shape, dysodont tooth morphology, and hinge-ligament thickness in the bay mussel *Mytilus trossulus* correlate with wave exposure. *Can. J. Zool*. 78(2): 240-253.

ALFARO, A.C. & CARPENTER, R.C. 1999. Physical and biological processes influencing zonation patterns of a subtidal population of the marine snail, *Astraea* (*Lithopoma*) *undosa* Wood 1828. *J. Exp. Mar. Biol. Ecol.* 240: 259-283.

ap RHEINALLT, T. 1986. Size selection by the crab *Liocarcinus puber* feeding on mussels *Mytilus edulis* and on shore crabs *Carcinus maenas*: the importance of mechanical factors. *Mar. Ecol. Prog. Ser*. 29: 45-53.

ATTWOOD, C.G., MANN, B.Q., BEAUMONT, J. & HARRIS, J.M. 1997. Review of the state of marine protected areas in South Africa. *S. Afr. J. Mar. Sci*. 18: 341-367.

BAILEY, L.L., SIMONS, T.R. & POLLOCK, K.H. 2004. Estimating detection probability parameters for Plethodon salamanders using the robust capture-recapture design. *J. Wildl. Manage*. 68(1): 1-13.

BENCE, J.R. & NISBET, R.M. 1989. Space-limited recruitment in open systems: the importance of time delays. *Ecology* 70: 1434-1441.

BENEDETTI-CECCHI, L., BULLERI, F., ACUNTO, S. & CINELLI, F. 2001. Scales of variation in the effects of limpets on rocky shores in the northwest Mediterranean. *Mar. Ecol. Prog. Ser*. 209: 131-141.

BENNETT, B.A. & ATTWOOD, C.G. 1993. Shore-angling catches in the De Hoop Reserve and further evidence for protective value of marine reserves. *S. Afr. J. Mar. Sci*. 13: 213-222.

BERLOW, E.L. & NAVARRETE, S.A. 1997. Spatial and temporal variation in rocky intertidal community organization: lessons from repeating field experiments. *J. Exp. Mar. Biol. Ecol.* 214: 195-229.

BEUKEMA, J.J., DEKKER, R., ESSINK, K. & MICHAELIS, H. 2001. Synchronized reproductive success of the main bivalve species in the Wadden Sea: causes and consequences. *Mar. Ecol. Prog. Ser*. 211: 143-155.

BILGALKE, E.H. 1973. The exploitation of shellfish by coastal tribesmen of Transkei. *Ann. Cape Prov. Mus., Nat. Hist.* 9: 159-175.

BOAVENTURA, D., Da FONSECA, L.C. & HAWKINS, S.J. 2002a. Analysis of competitive interactions between the limpets *Patella depressa* Pennant and *Patella vulgata* L. on the northern coast of Portugal. *J. Exp. Mar. Biol. Ecol*. 271: 171-188.

BOAVENTURA, D., ALEXANDER, M., SANTINA, P.D., SMITH, N.D., RÉ, P., Da FONSECA, L.C. & HAWKINS, S.J. 2002b. The effects of grazing on the distribution and composition of low-shore algal communities on the central coast of Portugal and on the southern coast of Britain. *J. Exp. Mar. Biol. Ecol*. 267: 185-206.

BOAVENTURA, D., Da FONSECA, L.C. & HAWKINS, S.J. 2003. Size matters: competition within populations of the limpet *Patella depressa*. *J. Anim. Ecol.* 72: 435-446.

BOSMAN, A.L. & HOCKEY, P.A.R. 1988. Life-history patterns of populations of the limpet *Patella granularis*: the dominant roles of food supply and mortality rate. *Oecologia* 75: 412-419.

BOSMAN, A.L., HOCKEY, P.A.R. & SIEGFRIED, W.R. 1988. Patterns and correlates of shellfish exploitation by coastal people in Transkei: an enigma of protein production. *J. Appl. Ecol.* 25: 353-363.

BOSMAN, A.L., HOCKEY, P.A.R. & UNDERHILL, L.G. 1989. Oystercatcher predation and limpet mortality: the importance of refuges in enhancing the reproductive output of prey populations. *Veliger* 32 (2): 120-129.

BOULDING, E.G. 1984. Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *J. Exp. Mar. Biol. Ecol*. 76: 201-223.

BOULDING, E.G. & LaBARBARA, M. 1986. Fatigue damage: repeated loading enables crabs to open larger bivalves. *Biol. Bull.* (Woods Hole) 171: 538-547.

BOULDING, E.G. & VAN ALSTYNE, K.L. 1993. Mechanisms of differential survival and growth of two species of *Littorina* on wave-exposed and on protected shores. *J. Exp. Mar. Biol. Ecol*. 169: 139-166.

BOULDING, E.G., BUCKLAND-NICKS, J. & VAN ALSTYNE, K.L. 1993. Morphological and allozyme variation in *Littorina sitkana*. *J. Shellfish Res.* 20(1): 402-409.

BOULDING, E.G., HOLST, M. & PILON, V. 1999. Changes in selection on gastropod shell size and thickness with wave-exposure on Northern Pacific shores. *J. Exp. Mar. Biol. Ecol*. 232: 217-239.

BRANCH, G.M. 1971. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. I. Zonation, movements and feeding. *Zool. Afr*. 6: 1-38.

BRANCH, G.M. 1974a. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. II. Reproductive cycles. *Trans. Roy. Soc. S. Afr*. 41 (2): 111-160.

BRANCH, G.M. 1974b. The ecology of *Patella* Linnaeus from the Cape Peninsula, South Africa. III. Growth rates. *Trans. Roy. Soc. S. Afr*. 41 (2): 161-193.

BRANCH, G.M. 1975a. Notes on the ecology of *Patella concolor* and *Cellana capensis* and the effect of human consumption on limpet populations. *Zool. Afr*. 10: 75-85.

BRANCH, G.M. 1975b. Mechanisms reducing intraspecific competition in *Patella* spp.: migration, differentiation and territorial behaviour. *J. Anim. Ecol*. 44: 575-600.

BRANCH, G.M. 1976. Interspecific competition experienced by South African *Patella* species. *J. Anim. Ecol*. 45: 507-529.

BRANCH, G.M. 1981. The biology of limpets: physical factors, energy flow and ecological interactions. *Oceanogr. Mar. Biol. Annu. Rev.* 19: 235-380.

BRANCH, G.M. 1985. Limpets: their role in littoral and sublittoral community dynamics. In: *The Ecology of Rocky Shores*, (*edn*.) P.G. Moore & Seed. Hodder & Stroughton, London.

BRANCH, G.M. & MARSH, A.C. 1978. Tenacity and shell shape in six *Patella* species: adaptive features. *J. Exp. Mar. Biol. Ecol.* 34: 111-130.

BRANCH, G.M. & ODENDAAL, F. 2003. The effects of marine protected areas on the population dynamics of a South African limpet, *Cymbula oculus*, relative to the influence of wave action. *Biol. Conserv.* 114: 255-269.

BRANCH, G.M. & STEFFANI, C.N. 2004. Can we predict the effects of alien species? A case-history of the invasion of South Africa by *Mytilus galloprovincialis* (Lamarck). *J. Exp. Mar. Biol. Ecol.* 300: 189-215.

BRANCH, G.M., GRIFFITHS, C.L., BRANCH, M.L. & BECKLEY, L.E. 2002. *Two oceans: a guide to the marine life of southern Africa*, 5th *edn*. David Phillip Publishers, Cape Town.

BREEN, P.A. 1972. Seasonal migration and population regulation in the limpet *Acmaea (Collisella) digitalis*. *Veliger* 15: 133-141.

BREY, T. & CAGE, J.D. 1997. Interactions of growth and mortality in benthic inverterbrate populations: empirical evidence for a mortality-growth continuum. *Arch. Fish. Mar. Res*. 45(1): 45-59.

BROITMAN, B. R., BLANCHETTE, C.A. & GAINES, S.D. 2005. Recruitment of intertidal invertebrates and oceanographic variability at Santa Cruz Island, California. *Limnol. Oceanogr*. 50(5): 1473-1479.

BROWN, K.M. & QUINN, J.F. 1988. The effect of wave action on growth in three species of intertidal gastropods. *Oecologia* 75: 420-425.

BROWNIE, C., ANDERSON, D.R., BURNHAM, K.P. & ROBSON, D.S. 1985. *Statistical inference from band recovery data – a handbook*, 2nd *edn*. U.S. Fish and Wildlife. Service, Resource Publication 156, Washington, DC.

BRUTON, J., BAID, D. & COETZEE, P.S. 1991. Population structure and yield-per-recruit analysis of the giant periwinkle *Turbo sarmaticus* in the Cape St Francis region, South Africa. *S. Afr. J. Mar. Sci*. 11: 345-356.

BURKE, R.D. 1983. The induction of metamorphosis of marine invertebrate larvae: stimulus and response. *Can. J. Zool*. 61: 1701-1719.

BUSTAMANTE, R.H. & CASTILLA, J.C. 1987. The shellfishery in Chile: an analysis of 26 years of landings (1960-1985). *Biologia Pesquera* 16: 79-97.

BUSTAMANTE, R.H. & BRANCH, G.M. 1996. Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. *J. Biogeogr.* 23: 339-351.

BUSTAMANTE, R.H., BRANCH, G.M. & EEKHOUT, S. 1995a. Maintenance of an exceptional grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology* 76: 2314-2329.

BUSTAMANTE, R.H., BRANCH, G.M., EEKHOUT, S., ROBERTSON, B., ZOUTENDYK, P. SCHLEYER, M., DYE, A., HANEKOM, N., KEATS, D., JURD, M. & McQUAID, C.D. 1995b. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* 102: 189-201.

BUTMAN, C.A. 1987. Larval settlement of soft sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamic processes. *Oceanogr. Mar. Biol. Annu. Rev*. 25: 113-165.

CADEË, G.C. 1999. Shell damage and shell repair in the Antarctic limpet *Nacella concinna* from King George Island. *J. Sea. Res.* 41: 149-161.

CAFFEY, H.M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecol. Monogr*. 55: 313-332.

CALEY, M.J. 1993. Predation, recruitment and the dynamics of communities of coral-reef fishes. *Mar. Biol*. 117: 33-43.

CALEY, M.J., CARR, M.H., HIXON, M.A., HUGHES, T.P., JONES, G.P. & MENGE, B.A. 1996. Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst*. 27: 477-500.

CALVO-UGARTEBURU, G. & McQUAID, C.D. 1998. Parasitism and invasive species: effects of digenetic trematodes on mussels. *Mar. Ecol. Prog. Ser*. 169: 149-163.

CANNICCI, S., GOMEI, M., BODDI, B. & VANNINI, M. 2002. Feeding habits and natural diet of the intertidal crab *Pachygrapsus marmoratus*: opportunistic browser or selective feeder? *Est. Coast. shelf Sci.* 54: 983-1001.

CARR, M.H. & HIXON, M.A. 1995. Predation effects on early post-settlement survivorship of coral-reef fishes. *Mar. Ecol. Prog. Ser*. 124: 31-42.

CASTILLA, J.C. & DURÁN, L.R. 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects of *Concholepas concholepas* (Gastropoda). *Oikos* 45: 391-399.

CHAPMAN, M.R. & KRAMER, D.L. 1999. Gradients of coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Mar. Ecol. Prog. Ser*. 181: 81-96.

CHAPMAN, M.G. 1994a. Small- and broad-scale patterns of distribution of the upper-shore littorinid *Nodilittorina pyramidalis* in New South Wales. *Aust. J. Ecol*. 19: 83-95.

CHAPMAN, M.G. 1994b. Small-scale patterns of distribution and size-structure of the intertidal littorinid *Littorina unifasciata* (Gastropoda: Littorinidae) in New South Wales. *Aust. J. Mar. Freshw. Res*. 45: 635-652.

CHAPMAN, M.G. & UNDERWOOD, A.J. 1996. Influences of tidal conditions, temperature and desiccation on patterns of aggregation of the high shore periwinkle, *Littorina unifasciata*, in New South Wales, Australia. *J. Exp. Mar. Biol. Ecol*. 196: 213-237.

CHAPMAN, M.G. & UNDERWOOD, A.J. 1998. Inconcistency and variation in the development of rocky intertidal algal assemblages. *J. Exp. Mar. Biol. Ecol*. 224: 265-289.

CHELAZZI, G., DELLA SANTINA, P. & SANTINI, G. 1994. Rhythmical timing and spatial scattering of foraging in a homing limpet (*Patella rustica*). *Behav. Ecol*. 5: 288-292.

CHOAT, J.H. 1977. The influence of sessile organisms on the population biology of three species of acmaeid limpets. *J. Exp. Mar. Biol. Ecol*. 26: 1-26.

CHOW, V. 1975. The importance of size in the intertidal distribution of *Littorina scutulata*. *Veliger* 18: 69-78.

CHRISTOPHER, H. 2000. Effects of winter light limitation and herbivory on high intertidal community. *Oecologia* 123(3): 406-417.

CLARKE, A. 2003. Costs and consequences of evolutionary temperature adaptation. *Trends Ecol. Evol*. 18: 573-581.

CLARKE, K.R. & GREEN, R.H. 1988. Statistical design and analysis for a “biological effects” study. *Mar. Ecol. Prog. Ser*. 46: 213-226.

CLARKE, A., PROTHERO-THOMAS, E., BEAUMONT, J.C., CHAPMAN, A.L. & BREY, T. 2004. Growth in the limpet *Nacella concinna* from contrasting sites in Antarctica. *Polar Biol.* 28: 62-71

CLOBERT, J. 1995. Capture-recapture and evolutionary ecology: a difficult wedding? *J. Appl. Statist.* 22: 989-1008.

COLEGRAVE, N. 1993. Does larval competition affect fecundity independently of its effect on adult weight? *Ecol. Entomol*. 18(3): 275-277.

COLEMAN, M.A. 2002. Small-scale spatial variability in intertidal and subtidal turfing algal assemblages and the temporal generality of these patterns. *J. Exp. Mar. Biol. Ecol*. 267: 53-74.

COLEMAN, M.A, UNDERWOOD, A.J. & CHAPMAN, M.G. 2004. Absence of costs of foraging excurtions in relation to limpet aggregation. *J. Anim. Ecol.* 73: 577-584.

COLEMAN, R.A., HAWKINS, S.J. & WOOD, H.L. 2006a. Testing the reproductive benefits of aggregation: the limpet *Patella vulgata* shows no evidence of synchrony in gonad development. *Mar. Ecol. Prog. Ser*. 306: 201-207.

COLEMAN, R.A., GOSS-CUSTARD, J.D. Dit DURELL, S.E.A. LeV. & HAWKINS, S.J. 1999. Limpet *Patella* spp. consumption by oystercatchers *Haematopus ostralegus*: a preference for solitary prey items. *Mar. Ecol. Prog. Ser*. 183: 253-261.

COLEMAN, M.A, UNDERWOOD, A.J., BENEDETTI-CECCHI, L., ARRONTES, J., CASTRO, J., HARTNOLL, R.G., JENKINS, S.R., PAULA, J., SANTINA, P.D. & HAWKINS, S.J. 2006b. A continental scale evaluation of the role of limpet grazing on rocky shores. *Oecologia* 147: 556-564.

CONNELL, J.H. 1985. The consequences of variation in initial settlement vs post-settlement mortality in rocky intertidal communities. *J. Exp. Mar. Biol. Ecol*. 93: 11-45.

CONNOLLY, S.R. & ROUGHGARDEN, J. 1998. A latitudinal gradient in intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. *Am. Nat*. 151: 311-326.

CONNOLLY, S.R., MENGE, B.A. & ROUGHGARDEN, J. 2001. A latitudinal gradient in recruitment of intertidal invertebrates in the northeast Pacific Ocean. *Ecology* 82: 1799-1813.

CORPUZ, G.C. 1981. Settlement and emergence in a supratidal Hawaiian limpet, *Cellana exarata* Reeve (Prosobranchia: Patellidae). *Pac. Sci*. 35: 265-266.

CREESE, R.G. 1980. Reproductive cycles and fecundities of four common eastern Australian Archaeogastropod limpets (Mollusca: Gastropoda). *Aust. J. Mar. Freshw. Res*. 31: 49-59.

CREESE, R.G. 1982. Distribution and abundance of the acmaeid limpet, *Patelloid latistrigata*, and its interaction with barnacles. *Oecologia* 52: 85-96.

CREESE, R.G. & UNDERWOOD, A.J. 1982. Analysis of inter-and intra-specific competition amongst intertidal limpets with different methods of feeding. *Oecologia* 53: 337-346.

CREESE, R.G. & BALLANTINE, W.J. 1983. An assessment of breeding in the intertidal limpet, *Cellana radians* (Gmelin). *J. Exp. Mar. Biol. Ecol*. 67: 43-59.

CREESE, R.G., SCHIEL, D.R. & KINGSFORD, M.J. 1990. Sex change in a giant endemic limpet, *Patella kermadecensis*, from the Kermadec Islands. *Mar. Biol*. 104: 419-426.

CUSSON, M. & BOURGET, E. 2005. Small-scale variations in mussel (*Mytilus* spp.) dynamics and local production. *J. Sea Res*. 53: 255-268.

DAVIES, A.J., JOHNSON, M.P. & MAGGS, C.A. 2007. Limpet grazing and loss of *Ascophyllum nodosum* canopies on decadal time scales. *Mar. Ecol. Prog. Ser*. 339: 131-141.

DAVIS, A.J., LAWTON, J.H., SHORROCKS, B. & JENKINSON, L.S. 1998. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *J. Anim. Ecol*. 67: 600-612.

DAY, G.E., BRANCH, G.M. & VILJOEN, C. 2000. How costly is molluscan shell erosion? A comparison of two patellid limpets with contrasting shell structures. *J. Exp. Mar. Biol. Ecol*. 243: 185-208.

DAYTON, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilisation of space in a rocky intertidal community. *Ecol. Monogr*. 41: 351-388.

DELANY, J., MYERS, A.A. & McGRATH, D. 1998. Recruitment, immigration and population structure of two coexisting limpet species in mid-shore tidepools, on the west coast of Ireland. *J. Exp. Mar. Biol. Ecol*. 221: 221-230.

DENNY, M.W. & SHIBATA, M.F. 1989. Consequences of surf-zone turbulence for settlement and external fertilization. *Am. Naturalist* 134(6): 859-889.

DENNY, M.W. & BLANCHETTE, C.A. 2000. Hydrodynamics, shell shape, behavior and survivorship in the owl limpet *Lottia gigantea*. *J. Exp. Biol.* 203: 2623-2639.

DENNY, M.N., DANIEL, T.L., & KOEHL, M.A.R. 1985. Mechanical limits to size in wave-swept organisms. *Ecol. Monogr.* 55: 69-102.

DOHERTY, P.J. & SALE, P.F. 1985. Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs.* 4: 225-234.

DUGAN, J.E. & DAVIS, G.E. 1993. Applications of marine refugia to coastal fisheries management. *Can. J. Fish. Aquat. Sci*. 50: 2029-2042.

DUGGINS, D.O., SIMENSTAD, C.A. & ESTES, T.A. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245: 170-173.

DULVY, N.K., SADOVY, Y. & REYNOLDS, J.D. 2003. Extinction vulnerability in marine populations. *Fish Fish.* 4: 25-64.

DUNMORE, R.A. & SCHIEL, D.R. 2000. Reproduction in the intertidal limpet *Cellana ornata* in southern New Zealand. *N. Z. J. Mar. Freshw. Res.* 34: 653-660.

DUNMORE, R.A. & SCHIEL, D.R. 2003. Demography, competitive interactions and grazing effects of intertidal limpets in southern New Zealand. *J. Exp. Mar. Biol. Ecol.* 288: 17-38.

DURÁN, L.R. & CASTILLA, J.C. 1989. Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Mar. Biol.* 103: 555-562.

DYE, A.H. 1993. Recolonisation of intertidal macroalgae in relation to gap size and molluscan herbivory on a rocky shore on the east coast of South Africa. *Mar. Ecol. Prog. Ser.* 95: 263-271.

DYE, A.H. 1995. The effects of excluding limpets from the lower balanoid zone of rocky shores in Transkei, South Africa. *S. Afr. J. Mar. Sci.* 15: 9-15.

DYE, A.H. 1998. Dynamics of rocky intertidal communities: analyses of long time series from South African shores. *Est. Coast. Shelf Sci.* 46: 287-305.

DYE, A.H., BRANCH, G.M., CASTILLA, J.C. & BENNETT, B.A. 1994. Biological options for the management of the exploitation of intertidal and subtidal resources. In: Siegfried W.R. (edn.) *Ecological studies - rocky shores: exploitation in Chile and South Africa*. Springer-Verlag, Berlin, pp. 131-154.

EDGAR, G.J. & BARRETT, N.S. 1999. Effects of the declaration of marine reserves on Tasmanian reef fish, invertebrates and plants. *J. Exp. Mar. Biol. Ecol*. 242: 107-144.

EDGAR, G.J., BUSTAMANTE, R.H., FARIÑA, J.M., CALVOPIÑA, M., MARTÍNEZ, C. & TORAL-GRANDA, M.V. 2004. Bias in evaluating the effects of marine protected areas: the importance of baseline data for the Galapagos Marine Reserve. *Environ. Conserv*. 31(3): 212-218.

EEKHOUT, S., RAUBENHEIMER, C.M., BRANCH, G.M., BOSMAN, A.L. & BERGH, M.O. 1992. A holistic approach to the exploitation of intertidal stocks: limpets as a case study. *S. J. Mar. Sci*. 12: 1017-1029.

EMANUEL, B.P., BUSTAMANTE, R.H., BRANCH, G.M., EEKHOUT, S. & ODENDAAL, F.J. 1992. A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *S. Afr. J. Mar. Sci.* 12: 341-354.

ERLANDSSON, J. & McQUAID, C.D. 2004. Spatial structure of recruitment in the mussel *Perna perna* at local scales: effects of adults, algae and recruitment size. *Mar. Ecol. Prog. Ser.* 267: 173-185.

ESPINOSA, F., GUERRA-GARCíA, J.M. FA, D. & CARLOS GARCíA-GÓMEZ, J. 2006. Effects of competition on an endangered limpet *Patella ferruginea* (Gastropoda: Patellidae): Implications for conservation. *J. Exp. Mar. Biol. Ecol.* 330: 482-492.

ETTER, R.J. 1989. Life history variation in the intertidal snail *Nucella lapillus* across a wave-exposure gradient. *Ecology* 70: 1857-1876.

ETTER, R.J. 1996. The effect of wave action, prey type, and foraging time on growth of the predatory snail *Nucella lapillus* (L.). *J. Exp. Mar. Biol. Ecol.* 196: 341-356.

FAIRWEATHER, P.G. & UNDERWOOD, A.J. 1991. Experimental removals of a rocky intertidal predator: variations within two habitats in the effects on prey. *J. Exp. Mar. Biol. Ecol.* 154: 29-75.

FENBERG, P.B. & ROY, K. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Mol. Ecol*. 17: 209-220.

FIELDING, P.J., ROBERTSON, W.D., DYE, A.H., TOMALIN, B.J., VAN DER ELST, R.P., BECKLEY, L.E., MANN, B.Q., BIRNIE, S., SCHLEYER, M.H. & LASIAK, T.A. 1994. *Transkei Coastal Fisheries Resources*. Special Publication No.3. Oceanographic Research Institute, Durban.

FLETCHER, W.J. 1984a. Intraspecific variation in the population dynamics and growth of the limpet, *Cellana tramoserica*. *Oceologia* 63: 110-121.

FLETCHER, W.J. 1984b. Variability in the reproductive effort of the limpet, *Cellana tramoserica*. *Oecologia* 61: 259-264.

FLOWERS, J.M., SCHROETER, S.C. & BURTON, R.S. 2002. The recruitment sweepstakes has many winners: genetic evidence from the sea urchin *Strongylocentrotus purpuratus*. *Evolution* 56(7): 1445-1453.

FORDE, E.S. & DOAK, D.F. 2004. Multitrophic interactions mediate recruitment variability in a rocky intertidal community. *Mar. Ecol. Prog. Ser.* 275: 33-45.

FORDE, S.E. & RAIMONDI, P.T. 2004. An experimental test of the effects of variation in recruitment intensity on intertidal community composition. *J. Exp. Mar. Biol. Ecol.* 301: 1-14.

FORSTER, M.S., NIGG, E.W., KIGUCHI, L.M., HARDIN, D.D. & PEARSE, J.S. 2003. Temporal variation and succession in an algal-dominated high intertidal assemblage. *J. Exp. Mar. Biol. Ecol.* 289: 15-39.

FOSTER, G.G. & HODGSON, A.N. 2000. Intertidal population structure of the edible mollusc *Turbo sarmaticus* (Vetigastropoda) at unexploited and exploited sites along the coast of the Eastern Cape Province, South Africa. *Afr. Zool.* 35: 173-183.

FOSTER, G.G., HODGSON, A.N. & BALARIN, M. 1999. Effect of diet on growth rate and reproductive fitness of *Turbo sarmaticus* (Mollusca: Vetigastropoda: Turbinidae). *Mar. Biol.* 134: 307-315.

FOURNIER, D.A. & SIBERT, J.R. 1991. Analysis of length frequency samples with relative abundance data for the Gulf of Maine Northern shrimp (*Pandalus borealis*) by the MULTIFAN method. *Can. J. Fish. Aquat. Sci.* 48: 591-598.

FOURNIER, D.A., HAMPTON, J. & SIBERT, J.R. 1998. MULTIFAN-CL: a length-based, age-structured model for fisheries stock assessment, with application to South Pacific albacore, *Thunnus alalunga*. *Can. J. Fish. Aquat. Sci.* 55: 2105-2116.

FOURNIER, D.A., SIBERT, J.R, MAJKOWSKI, J. & HAMPTON, J. 1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from length frequency data sets illustrated using data for southern bluefin tuna (*Thunnus maccoyii*). *Can. J. Fish. Aquat. Sci.* 47: 301-317.

FRANK, P.W. 1982. Effects of winter feeding on limpets by black oystercatchers (*Haematopus bachmani*). *Ecology* 63: 1352-1362.

GAINES, S.D. & BERTNESS, M.D. 1992. Dispersal of juveniles and variable recruitment in sessile marine species. *Nature* 360: 579-580.

GAINES, S.D. & ROUGHGARDEN, J. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. Natl. Acad. Sci*. USA 2: 3707-3711.

GARCIA, D., ZAMORA, R., GÓMEZ, J.M. & HÓDAR, J.A. 2000. Geographical variation in seed production, predation and abortion in *Juniperus communis* throughout its range in Europe. *J. Ecol*. 88: 436-446.

GARRITY, S.D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* 65: 559-574.

GARRITY, S.D. & LEVINGS, S.C. 1983. Homing to scars as a defense against predators in the pulmonate limpet *Siphonaria gigas* (Gastropoda). *Mar. Biol*. 72: 319-324.

GASCOIGNE, J. & LIPCIUS, R.N. 2004. Allee effects in marine systems. *Mar. Ecol Prog. Ser*. 269: 49-59.

GELLER, J.B. 1990. Reproductive responses to shell damage by the gastropod *Nucella emarginata* (Deshayes). *J. Exp. Mar. Biol. Ecol*. 136: 77-87.

GELL, F.R. & ROBERTS, C.M. 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.* 18: 448-455.

GILMAN, S.E. 2007. Shell microstructure of the Patellid Gastropod *Collisella scabra* (Gould): ecological and phylogenetic implications. *Veliger* 48(4): 235-242.

GIMENEZ, O., VIALLEFONT, A., CATCHPOLE, E.A. CHOQUET, R. & MORGAN, B.J.T. 2004. Methods for investigating parameter redundancy. *Anim. Biodivers. Conserv***.** 27: 1-12.

GOSSELIN, L. & QIAN, P.Y. 1996. Early post-settlement mortality of an intertidal barnacle: a critical period for survival. *Mar. Ecol Prog. Ser*. 135: 69-75.

GOSSELIN, L. & QIAN, P.Y. 1997. Juvenile mortality in benthic marine invertebrates. *Mar. Ecol Prog. Ser*. 146: 265-282.

GRAY, D.R. & HODGSON, A.N. 1997. Temporal variation in foraging behaviour of *Patella granularis* (Patellogastropoda) and *Siphonaria concinna* (Basommatophora) on a South African shore. *J. Moll. Stud.* 63: 121-130.

GRAY, D.R. & HODGSON, A.N. 1998. Foraging and homing behaviour in the high-shore, crevice-dwelling limpet *Helcion pectunculus* (Prosobranchia: Patellidae). *Mar. Biol*. 132: 283-294.

GRAY, D.R. & HODGSON, A.N. 2003. Growth and reproduction in the high-shore South African limpet *Helcion pectunculus* (Mollusca: Patellogastropoda). *Afr. Zool*. 38(2): 371-386.

GRAY, D.R. & HODGSON, A.N. 2004. The importance of a crevice environment to the limpet *Helcion pectunculus* (Patellidae). *J. Moll. Stud*. 70: 67-72.

GRANT, A., MORGAN, P.J. & OLIVE, P.J.W. 1987. Use made in marine ecology of methods for estimating demographic parameters from size/frequency data. *Mar. Biol*. 95: 201-208.

GRIFFITHS, R.J. 1977. Reproductive cycles in littoral populations of *Choromytilus meridionalis* (Kr.) and *Aulacomya ater* (Molina) with a quantitative assessment of gamete production in the former. *J. Exp. Mar. Biol. Ecol*. 30: 53-71.

GRIFFITHS, C.L. & BRANCH, G.M. 1997. The exploitation of coastal invertebrates and seaweeds in South Africa: historical trends, ecological impacts and implications for management. *Trans. Roy. Soc. S. Afr*. 52: 121-148.

GRIFFITHS, C.L. & ATTWOOD, C.G. 2005. Do dart tags suppress growth of dusky kob *Argyrosomus japonicus*? *Afr. J. Mar. Sci*. 27(2): 505-508.

GUERRA-GARCÍA, J.M., CORZO, J., ESPINOSA, F. & GARCÍA-GÓMEZ, J.C. 2004. Assessing habitat use of the endangered marine mollusc *Patella ferruginea* (Gastropoda, Patellidae) in northern Africa: preliminary results and implications for conservation. *Biol. Conserv*. 116: 319-326.

HALPERN, B.S. 2003. The impact of marine reserves: do reserves work and does size matter? *Ecol. Applic.* 13: S117-S137.

HALDORSON, L. & MOSER, M. 1979. Geographic patterns of prey utilization in two species of surfperch (Embiotocidae). *Copeia* 1979: 567-572.

HALPERN, B.S. & WARNER, R.R. 2002. Marine reserves have rapid and lasting effects. *Ecol. Lett.* 5:361-366.

HAMILTON, D. 2000. Direct and indirect effects of predation by common eiders and abiotic disturbance in an intertidal community**.** *Ecol. Monogr.* 70: 21-43.

HARLEY, C.D.G. & ROGERS-BENNET, L. 2004. The potential synergistic effects of climate change and fishing pressure on exploited invertebrates on rocky intertidal shores. *CalCOFI Rep.* 45: 98-110.

HARLEY, C.D.G., HUGHES, A.R., HULTGREN, K.M., MINER, B.G., SORTE, C.J.B., THOMBER, C.S., RODRIGUEZ, L.F., TOMANEK, L. & WILLIAMS, S.L. 2006. The impacts of climate change in coastal marine systems. *Ecol. Lett*. 9: 228-241.

HARRIS, J.M., BRANCH, G.M., ELLIOT, B.L., CURRIE, B., DYE, A.H., McQUAID, C.D., TOMALIN, B.J. & VELASQUEZ, C. 1998. Spatial and temporal variability in recruitment of intertidal mussels around the coast of southern Africa. *S. Afr. J. Zool*. 33: 1-11.

HAWKINS, S.J. 1981. The influence of *Patella* grazing on the fucoid/barnacle mosaic on moderately exposed rocky shores. *Kiel. Meeresforsch* 5: 537-543.

HAWKINS, S.J. & HARTNOLL, R.G. 1983. Grazing of intertidal algae by marine invertebrates. *Oceanogr. Mar. Biol. Annu. Rev*. 21: 195-282.

HEARN, W.S. & POLACHECK, T. 2002. Estimating long-term growth-rate changes of southern bluefin tuna (*Thunnus maccoyii*) from two periods of tag-return data. *Fish Bull*. 101:58-74.

HENNINGER, T.O. & HODGSON, A. N. 2001. The reproductive cycle of *Helcion prunoisus* (Patellogastropoda) on two South African boulder shores. *J. Moll. Stud.* 67: 385-394.

HERBERT, R.J.H., SOUTHWARD, A.J., SHEADER, M. & HAWKINS, S.J. 2007. Influence of recruitment and temperature on distribution of intertidal barnacles in the English Channel. *J. Mar. Biol. Ass. U.K.* 87: 487-499.

HERNANDEZ-LLAMAS, A. & RATKOWSKY, D.A. 2004. Growth of fishes, crustaceans and mollusks: estimation of the von Bertalanffy, Logistic, Gompertz and Richards curves and a new growth model. *Mar. Ecol. Prog. Ser*. 282: 237-244.

HINDELL, J.S. & QUINN, G.P. 2000. Effects of sewage effluent on the population structure of *Brachidontes rostratus* (Mytilidae) on a temperate intertidal rocky shore. *Mar. Freshw. Res.* 51: 543-551.

HOBDAY, A. 1995. Body-size variation exhibited by an intertidal limpet: influence of wave exposure, tidal height and migratory behavior. *J. Exp. Mar. Biol. Ecol.* 189: 29-45.

HOCKEY, P.A.R. 1987. Influence of coastal utilization by man on the presumed extinction of the Canarian black oystercatcher *Haematopus meadewaldoi* Bannerman. *Biol. Conserv.* 39: 49-62.

HOCKEY, P.A.R. & BOSMAN, A.L. 1986. Man as an intertidal predator in Transkei: disturbance, community convergence and management of natural food resource. *Oikos* 46: 3-14.

HOCKEY, P.A.R., BOSMAN, A.L. & SIEGFRIED, R.W. 1988. Patterns and correlates of shellfish exploitation by coastal people in Transkei: an enigma of protein production. *J. Appl. Ecol.* 25: 353-364.

HODGSON, A.N. 1999. The biology of siphonariid limpets (Gastropoda: Pulmonata). *Oceanogr. Mar. Biol. Annu. Rev.* 37: 245-314.

HOENIG, J.M., BARROWMAN, N.J., POLLOCK, K.H., BROOKS, E.N., HEARN, W.S. & POLACHECK, T. 1998. Models for tagging data that allow for incomplete mixing of newly tagged animals. *Can. J. Fish. Aquat. Sci.* 55:1477-1483.

HOLM, E.R. 1990. Effects of density-dependent mortality on the relationship between recruitment and larval settlement. *Mar. Ecol. Prog. Ser.* 60: 141-146.

HUGHES, R.N. & ANSWER, P. 1982. Growth, spawning and trematode infection of *Littorina littorea* (L) from an exposed shore on north Wales. *J. Moll. Stud*. 48: 321-330.

HUNT, H.L. & SCHEIBLING, R.E. 1997. Role of early-post settlement mortality in recruitment of benthic marine invertebrates. *Mar. Ecol. Prog. Ser*. 155: 269-301.

HUTCHINSON, N & WILLIAMS, G.A. 2001. Spatio-temporal variation in recruitment on a seasonal, tropical rocky shore: the importance of local versus non-local processes. *Mar. Ecol. Prog. Ser*. 215: 57-68.

HUXHAM, M., RAFFAELLI, D. & PIKE, A. 1993. The influence of *Cryptocotyle lingua* (Digenea: Platyhelminthes) infections on the survival and fecundity of *Littorina littorea* (Gastropoda: Prosobranchia); an ecological approach. *J. Exp. Mar. Biol. Ecol*. 168: 223-238.

HYDER, K., JOHNSON, M.P., HAWKINS, S.J. & GURNEY, W.S.C. 1998. Barnacle demography: evidence for existing model and spatial scales of variation. *Mar. Ecol. Prog. Ser*. 174: 89-99.

IWASAKI, K. 1993. Analysis of limpet defense and predator offense in the field. *Mar. Biol*. 116: 277-289.

IWASAKI, K. 1995. Foraging and spawning rhythms of the pulmonate limpet *Siphonaria Sirius* (Pilsbry): switching of activity period by a diurnal forager. *J. Moll. Stud*. 61: 275-288.

JENKINS, S.R. & HARTNOLL, R.G. 2001. Food supply, grazing activity and growth rate in the limpet *Patella vulgata* L.: a comparison between exposed and sheltered shores. *J. Exp. Mar. Biol. Ecol.* 258: 123-139.

JENKINS, S.R., ABERG, P., CERVIN, G. COLEMAN, R.A., DELANY, J., HAWKINS, S.J., HYDER, K., MYERS, A.A., PAULA, J., POWER, A.M., RANGE, P. & HARTNOLL, R.G. 2001. Population dynamics of the intertidal barnacle Selibalanis balanoides at three European locations: spatial scales of variability. *Mar. Ecol. Prog. Ser*. 217: 207-217.

JENKINS, S.R., COLEMAN, R.A., DELLA SANTINA, P., HAWKINS, S.J., BURROWS, M.T. & HARTNOLL, R.G. 2005. Regional scale differences in the determinism of grazing effects in the rocky intertidal. *Mar. Ecol. Prog. Ser*. 287: 77-86.

JENKINS, R.G., KAIM, A. & HIKIDA, Y. 2007. Antiquity of the substrate choice among acmaeid limpets from Late Cretaceous chemosynthesis-based communities. *Acta Palaeontol. Pol*. 52(2): 369-373.

JOHANNESSON, K. 2003. Evolution in *Littorina*: ecology matters. *J. Sea Res*. 49: 107-117.

JOHANNESSON, K., ROLÁN-ALVAREZ, E. & ERLANDSSON, J. 1997. Growth rate differences between upper and lower shore ecotypes of the marine snail *Littorina saxatilis* (Olivi) (Gastropoda). *Biol. J. Linn. Soc*. 61: 267-279.

JOHNSON, M.P., BURROWS, M.T., HARTNOLL, R.G. & HAWKINS, S.J. 1997. Spatial structure on moderately exposed rocky shores: patch scales and the interactions between limpets and algae. *Mar. Ecol. Prog. Ser*. 160: 209-215.

JOHNSON, D.R. FUNICELLI, N.A. & BOHNSACK, J.A. 1999. Effectiveness of an existing estuarine no-take fish sanctuary within the Kennedy Space Center, Florida. *N. Am. J. Fish. Manage*. 19: 436-453.

JOHNSON, K.B. & SHANKS, A.L. 2003. Low rates of predation on planktonic marine invertebrate larvae. *Mar. Ecol. Prog. Ser*. 248: 125-133.

JONES, P.J.S. 2002. Marine protected area strategies: issues, divergences and the search for middle ground. *Rev. Fish. Biol. Fish.* 11: 197-216.

JONES, P.J.S. 2004. Marine protected area strategies: issues, divergences and the search for middle ground. *Rev. Fish. Biol. Fish*. 11(3): 197-216.

KAEHLER, S. 1999. Incidence and distribution of phototrophic shell degrading endoliths of the brown mussel *Perna perna* (L.). *Mar. Biol*. 135: 505-514.

KAEHLER, S. & McQUAID, C.D. 1999. Use of fluorochrome calcein as an in situ growth marker in the brown mussel *Perna perna*. *Mar. Biol*. 133: 455-460.

KARLSON, R.H. & LEVITAN, D.R. 1989. Recruitment-limitation in open populations of *Diadema antillarum*: an evaluation. *Oecologia* 82: 40-44.

KAY, M.C. 2002. Recruitment in the intertidal limpet *Lottia digitalis* (Patellogastropoda: Lottidae) may be driven by settlement cues associated with adult habitat. *Mar. Biol.* 141: 467-477.

KELLY, S., SCOTT, D., MAcDIARMID, A.B. & BABCOCK, R.C. 2000. Spiny lobster, *Jasus edwardsii*, recovery in New Zealand marine reserves. *Biol. Conserv*. 92: 359-369.

KENDALL, W.L., SAUER, J.R., NICHOLS, J.D., PRADEL, R. & HINES, J.E. 2004. On the use of capture-recapture models in mist-net studies. *Stud. Avian Biol*. 29: 173-181.

KEOUGH, M.J. & DOWNES, B.J. 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* 54: 348-352.

KEOUGH, M.J. & QUINN, G.P. 1998. Effects of periodic disturbances from trampling on rocky intertidal algal beds. *Ecol. Appl*. 8: 141-161.

KEOUGH, M.J., QUINN, G.P. & KING, A. 1993. Correlations between human collecting and internal mollusc populations on rocky shores. *Conserv. Biol.* 7(2): 378-390.

KEOUGH, M.J., QUINN, G.P. & BATHGATE, R. 1997. Geographic variation in interactions between size classes of the limpet *Cellana tramoserica*. *J. Exp. Mar. Biol. Ecol.* 215: 19-34.

KIDO, J.S. & MURRAY, S.N. 2003. Variation in owl limpet *Lottia gigantea* population structures, growth rates, and gonadal production on southern California rocky shores. *Mar. Ecol. Prog. Ser.* 257: 111-124.

KILBURN, R. & RIPPEY, E. 1982. *Sea shells of southern Africa*. Macmillan Publishers, Johannesburg.

KINGSFORD, M.J., UNDERWOOD, A.J. KENNELLY, S.J. 1991. Humans as predators on rocky reefs in New South Wales, Australia. *Mar. Ecol. Prog. Ser.* 72: 1-14.

KOHN, A.J. 1980. Populations of tropical intertidal gastropods before and after a typhoon. *Micronesica* 16: 215-228.

KOLBIN, K.G. 2006. Reproduction and development of the limpet *Limalepeta lima* (Dall, 1918) (Gastropoda: Lepetidae) from Peter the Great Bay, Sea of Japan. *Russ. J. Mar. Biol.* 32(4): 265-267.

KRAMER, G. & CHAPMAN, M.R. 1999. Implications of fish home range size and relocation for marine reserve function. *Environ. Biol. Fish.* 55: 65-79.

KRUG, P.J. 2001. Bet-hedging dispersal strategy of a specialist marine herbivore: a settlement dimorphism among sibling larvae of *Adalaria modesta*. *Mar. Ecol. Prog. Ser.* 213: 177-192.

KURIHARA, T. 2002. Spatial and temporal fluctuation in the density of the intertidal limpet, *Patelloida striata* Quoy & Gaimard, on subtropical cobbled shores. *J. Moll. Stud*. 68: 79-86.

KYLE, R., PEARSON, B., FIELDING, P.J., ROBERTSON, W.D. & BIRNIE, S.L. 1997. Subsistence shellfish harvesting in the Maputoland Marine Reserve in northern KwaZulu-Natal, South Africa: rocky shore organisms. *Biol. Conserv*. 2:183-192.

LAFFERTY, K.D. 1993. The marine snail, *Cerithidea california*, matures at smaller sizes where parasitism is high. *Oikos* 68: 3-11.

LASIAK, T.A. 1986. The reproductive cycle of the intertidal gastropod *Turbo coronatus* Gmelin, 1791, on the Transkei coast. *S. Afr. J. Zool*. 21: 153-155.

LASIAK, T.A. 1987. Observations on the reproductive cycles of *Cellana capensis* (Gmelin, 1991) & *Patella concolor* Krauss, 1848 (Gastropoda: Patellidae). *J. Moll. Stud*. 56: 69-81.

LASIAK, T.A. 1990. Asynchronous reproductive activity in the broadcast spawner *Cellana capensis* (Gmelin, 1791) (Gastropoda: Patellidae). *J. Moll. Stud*. 56: 69-81.

LASIAK, T.A. 1991a. Is there evidence of over-exploitation of mussel stocks on the Transkei coast? *S. Afr. J. Mar .Sci*. 10: 299-302.

LASIAK, T.A. 1991b. The susceptibility and/or resilience of rocky littoral molluscs to stock depletion by indigenous coastal people of Transkei, Southern Africa. *Biol. Conserv*. 56: 245-264.

LASIAK, T.A. 1992. Contemporary shellfish gathering practices of indigenous coastal people in Transkei: Some implications for interpretation of the archaeological record. *S. Afr. J. Sci.* 88: 19-28.

LASIAK, T.A. 1993. Temporal and spatial variations in exploited and non-exploited populations of the intertidal limpet *Cellana capensis*. *J. Moll. Stud.* 59: 295-307.

LASIAK, T.A. 1997. Temporal and spatial variations in the pattern of shoreline utilization in a region subject to subsistence exploitation. *Intern. J. Environ. Stud*. 52: 21-46.

LASIAK, T.A. 1998. Multivariate comparisons of rocky infratidal macrofaunal assemblages from replicate exploited and non-exploited localities on the Transkei coast of South Africa. *Mar. Ecol. Prog. Ser*. 167: 15-23.

LASIAK, T.A. 2006. Spatial variation in density and biomass of patellid limpets inside and outside a marine protected area. *J. Moll. Stud.* 72: 137-142.

LASIAK, T.A. & DYE, A. 1989. The ecology of the brown mussel *Perna perna* in Transkei, Southern Africa: implications for the management of a traditional food resource. *Biol. Conserv*. 47:0245-257.

LASIAK. T.A. & WHITE, D.R.A. 1993. Microalgal food resources and competitive interactions among the intertidal limpets *Cellana capensis* (Gmelin, 1791) and *Siphonaria concina* Sommerby, 1824. *S. Afr. Mar. Sci.* 13: 97-108.

LASIAK. T.A. & FIELD, J.G. 1995. Community-level attributes of exploited and non-exploited rocky infratidal macrofaunal assemblages in Transkei. *J. Exp. Mar. Biol. Ecol*. 185: 33-53.

LAWRIE, S.M. & McQUAID, C.D. 2001. Scales of mussel bed complexity: structure, associated biota and recruitment. *J. Exp. Mar. Biol. Ecol*. 257: 135-161.

LECHANTEUR, Y.A.R.G. & PROCHAZKA, K. 2001. Feeding biology of the giant clingsfish *Chorisochismus dentex* – implications for limpet populations. *Afr. Zool*. 36: 79-86.

Le QUESNE, W.J.F. & HAWKINS, S.J. 2006. Direct observations of protandrous sex change in the patellid limpet *Patella vulgata*. *J. Mar. Biol. Ass. U.K*. 86: 161-162.

LEVITAN, D.R. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biol. Bull.* (Woods Hole). 181: 261-268.

LEVITAN, D.R. 1996. Effects of gamete traits on fertilization in the sea and the evolution of sexual dimorphism. *Nature* 382: 153-155.

LEVITAN, D.R. 2002. Density-dependent selection on gamete traits in three congeneric sea urchins. *Ecology* 83: 464-479.

LEVITAN, D.R. & IRVINE, S.D. 2001. Fertilization selection on egg and jelly-coat size in the sand dollar *Dendraster excentricus*. *Evolution* 55(12): 2479-2483.

LEWIS, J.R. & BOWMAN, R.S. 1975. Local habitat-induced variations in the population dynamics of *Patella vulgata* L. *J. Exp. Mar. Biol. Ecol*. 17: 165-203.

LIMA, S.L. & DILL, L.M. 1990. Behavioural decisions made under risk of predation: A review and prospectus. *Can. J. Zool*. 68: 619-640.

LINDBERG, D.R. 2007. Reproduction, ecology, and evolution of the Indo-Pacific limpet *Scutellastra flexuosa*. *Bull. Mar. Sci.* 81(2): 219-234.

LINDBERG, D.R., WARHEIT, K.I. & ESTES, J.A. 1987. Prey preference and seasonal predation by oystercatchers on limpets at San Nicolas Island, California, USA. *Mar. Ecol. Prog. Ser*. 39: 105-113.

LINDBERG, D.R., ESTES, J.A. & WARHEIT, K.I. 1998. Human influences on trophic cascades along rocky shores. *Ecol. Applic*. 8(3): 880-890.

LINDQUIST, N. & HAY, M.E. 1996. Palatability and chemical defense of marine invertebrate larvae. *Ecol. Monogr*. 66: 431-449.

LINDQUIST, N., BOLSER, R. & LAING, K. 1997. Timing of larval release by two Caribbean demosponges. *Mar. Ecol. Prog. Ser*. 155: 309-313.

LINDSAY, T.L. & McQUAID, C.D. 2000. Effect of wave exposure on growth and mortality rates of the mussel *Perna perna*: bottom-up regulation of intertidal populations. *Mar. Ecol. Prog. Ser*. 206: 147-154.

LIPCIUS, R.N. & STOCKHAUSEN, W.T. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. *Mar. Ecol. Prog. Ser*. 266: 45-61.

LITTLE, C. 1989. Factors governing patterns of foraging activity in littoral marine herbivorous mollusks. *J. Moll. Stud*. 55: 273-284.

LITTLER, M.M. & MURRAY, S.N. 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. *Mar. Biol*. 30: 277-291.

LIU, J.H. 1994. The ecology of the Hong Kong limpets *Cellana grata* (Gould 1859) and *Patelloida pygmaea* (Dunker 1860): reproductive biology. *J. Moll. Stud*. 60: 97-111.

LIU, J.H. & MORTON, B. 1998. The impacts of pollution on the growth, reproduction and population structure of Hong Kong limpets. *Mar. Pollut. Bull.* 36(2): 152-158.

LOHSE, D.P. 1993. The effects of substratum type on the population dynamics of three common intertidal animals. *J. Exp. Mar. Biol. Ecol*. 173: 133-154.

LUBCHENCO, J. & MENGE, B.A. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr*. 48: 67-94.

LUBCHENCO, J., PALUMBI, S.R., GAINES, S.D. & ANDELMAN, S. 2003. Plugging a hole in the ocean: the energy science of marine reserves. *Ecol. Appl*. 13(1): S3-S7.

LUCAS, M.I., WALKER, G., HOLLAND, D.L. & CRISP, D.J. 1979. An energy-budget for the free-swimming and metamorphosing larvae of *Balanus balanoides* (Crustacea: cirrepedia). *Mar. Biol*. 55: 221-229.

LUTJEHARMS, J.R.E. 2004. The coastal oceans of Southern-Eastern Africa. In: A.R. Robinson and K.H. Brink, eds. *The global coastal ocean: multiscale interdisciplinary processes (The Sea: idea and observations on progress in the study of seas)*. Harvard University Press.

MACKAY, D.A. & UNDERWOOD, A.J. 1977. Experimental studies on homing in the intertidal patellid limpet *Cellana tramoserica* (Sowerby). *Oecologia* 30: 215-237.

MANRÍQUEZ, P.H. & CASTILLA, J.C. 2001. Significance of marine protected areas in central Chile as seeding grounds for the gastropod *Concholepas concholepas*. *Mar. Ecol. Prog. Ser*. 215: 201-211.

MARSH, C.P. 1987. Impact of avian predation on interdial limpet populations. *J. Exp. Mar. Biol. Ecol.* 104: 185-201.

MARSHALL, P.G. & KEOUGH, M.J. 1994. Asymmetry in intraspecific competition in the limpet *Cellana tramoserica* Sowerby. *J. Exp. Mar. Biol. Ecol*. 177: 121-138.

MARSHALL, D.J. & KEOUGH, M.J. 2003a. Effects of settler size and density on early post-settlement survival of *Ciona intestinalis* in the field. *Mar. Ecol. Prog. Ser*. 259: 139-144.

MARSHALL, D.J. & KEOUGH, M.J. 2003b. Variation in the dispersal potential of non-feeding invertebrate larvae: the desperate larva hypothesis and larval size. *Mar. Ecol. Prog. Ser*. 255: 145-153.

MARSHALL, D.J. & KEOUGH, M.J. 2004. When the going gets rough: effect of maternal size manipulation on larval quality. *Mar. Ecol. Prog. Ser.* 272: 301-305.

MARTINS, G.M., HAWKINS, S.J., THOMPSON, R.C. & JENKINS, S.R. 2007. Community structure and functioning in intertidal rock pools: effects of pool size and shore height at different successional stages. *Mar. Ecol. Prog. Ser*. 329: 43-55.

McCLANAHAN, T.R. & MANGI, S. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol. Applic*.10: 1792-1805.

McCLANAHAN, T.R., MUTHIGA, A., KAMUKURU, H. MACHANO, H. & KIAMBO, R.W. 1999. The effects of marine parks and fishing on coral reefs of northern Tanzania. *Biol. Conserv*. 89: 161-182.

McCORMACK, S.M.D. 1982. The maintenance of shore-level size gradients in an intertidal snail (*Littorina sitkana*). *Oecologia* 54: 177-183.

McGRATH, D. 1992. Recruitment and growth of the blue-rayed limpet, *Helcion pellucidum* (L.) in South East Ireland. *J. Moll. Stud*. 58: 425-431.

McGWYNNE, L.E. & VAN DER HORST, G. 1985. Patterns of reproduction in three sandy beach whelks of the genus *Bullia* Griffith. *J. Moll. Stud*. 51: 190-197.

McLACHLAN, A. & LOMBARD, H.W. 1981. Growth and production in exploited and unexploited populations of a rocky shore gastropod, *Turbo sarmaticus*. *Veliger* 23: 221-229.

McQUAID, C.D. 1981. Population dynamics of *Littorina Africana knysnaensis* (Philippi) on an exposed rocky shore. *J. Exp. Mar. Biol. Ecol*. 54: 65-75.

McQUAID, C.D. & PAYNE, A.I.L. 1998. Regionalism in marine biology: the convergence of ecology, economics and politics in South Africa. *S. Afr. J. Sci*. 94(9): 433-436.

McQUAID, C.D. & LINDSAY, T.L. 2000. Effect of wave exposure on growth and mortality rates of the mussel *Perna perna*: bottom-up regulation of intertidal populations. *Mar. Ecol. Prog. Ser*. 206: 147-154.

McQUAID, C.D., LINDSAY, J.R. & LINDSAY, T.L. 2000. Interactive effects of wave exposure and tidal height on population structure of the mussel *Perna perna*. *Mar. Biol*. 137: 925-932.

MENGE, B.A. 2000. Recruitment vs. postrecruitment processes as determinants of barnacle population abundance. *Ecol. Monogr*. 70: 265-288.

MENGE, B.A. & BRANCH, G.M. 2001. Rocky intertidal communities. In: Gaines, S.D. & Hay, M.E. (edn.). *Marine community ecology*: 162-166 Sinauer Associates, USA.

MENGE, B.A., BERLOW, E.L. BLANCHETTE, C.A., NAVARRETE, S.A. & YAMADA, S.B. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol. Monogr*. 64(3): 249-286.

MENGE, B.A., DALEY, B.A., WHEELER, P.A., DAHLHOFF, E. SANFORD, E. & STRUB, P.T. 1997. Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? *Proc. Natl. Acad. Sci.* 94:14530-14535.

MENGE, B.A., DALEY, B.A., LUBCHENCO, J., SANFORD, E., DAHLHOFF, E., HALPIN, P.M., HUDSON, G. & BURNAFORD, J.J. (1999). Top-down and bottom-up regulation of New Zealand rocky intertidal communities, *Ecol. Monogr*. 69: 297-330.

METAXAS, A., SCHEIBLING, R.E. & YOUNG, C.M. 2002. Estimating fertilization success in marine benthic invertebrates: a case study with the tropical sea star *Oreaster reticulatus*. *Mar. Ecol. Prog. Ser*. 226: 87-101.

MILLSTEIN, J. & O'CLAIR, C.E. 2001. Comparison of age-length and growth increment general growth models of the Schnute type in the Pacific blue mussel, *Mytilus trossulus* Gould. *J. Exp Mar. Biol. Ecol.* 262: 155-176.

MINCHINTON, T.W. & SCHEIBLING, R.W. 1993. Free space availability and larval substratum selection as determinants of barnacle population structure in a developing rocky intertidal community. *Mar. Ecol. Prog. Ser*. 95: 233-244.

MONTEIRO, S.M., CHAPMAN, M.G. & UNDERWOOD, A.J. 2002. Patches of the ascidian *Pyura stolonifera* (Heller, 1878): Structure of habitat and associated intertidal assemblages. *J. Exp. Mar. Biol. Ecol*. 270: 171-189.

MOORE, P., HAWKINS, S.J. & THOMPSON, R.C. 2007. Role of biological habitat amelioration in altering the relative responses of congeneric species to climate change. *Mar. Ecol. Prog. Ser*. 334: 11-19.

MORAIS, S., BOAVENTURA, D., NARCISO, L., R.É., P. & HAWKINS, S.J. 2003. Gonad development and fatty acid composition of *Patella depressa* Pennant (Gastropoda: Prosobranchia) populations with different patterns of spatial distribution, in exposed and sheltered sites. *J. Exp Mar. Biol. Ecol.* 294: 61-80.

MORENO, C.A., SUTHERLAND, J.P &. JARA, H.F. 1984. Man as a predator in the intertidal zone of southern Chile. *Oikos* 42: 155-160.

MORENO, C.A., LUNECKE, K.M. & LEPEZ, M.I. 1986. The response of an intertidal *Concholepas concholepas* (Gastropoda) population to protection from man in southern Chile and the effects on benthic sessile assemblages. *Oikos* 46: 359-364.

MORRISEY, D.J., HOWITT, L., UNDERWOOD, A.J. & STARK, J.S. 1992. Spatial variation in soft-sediment benthos. *Mar. Ecol. Prog. Ser.* 81: 197-204.

MORTON, B. 1991. Do the Bivalvia demonstrate environment-specific sexual strategies? A Hong Kong model. *J. Zool.* 223: 131-142.

MOURITSEN, K.N. & POULIN, R. 2005. Parasitism can influence the intertidal zonation of non-host organisms. *Mar. Biol*. 148: 1-11.

MURRAY, S.N., DENIS, T.G., KIDO, J.S. & SMITH, J.R. 1999. Human visitation and the frequency and potential effects of collecting on rocky intertidal populations in southern California Marine Reserves. *CalCoFi Rep*. 40: 100-106.

NAKAI, S., MIURA, O., MAKI, M. & CHIBA, S. 2006. Morphological and habitat divergence in the intertidal limpet *Patelloida pygmaea*. *Mar. Biol.* 149: 515-523.

NAVARRO, J.M., URRUTIA, G.X. & CARRASCO, C. 2006. Scope for growth versus actual growth in the juvenile predatory gastropod *Chorus giganteus*. *J. Exp Mar. Biol. Ecol.* 86: 1423-1428.

NG, T.Y.T., & KEOUGH, M.J. 2003. Delayed effects of larval exposure to Cu in the bryozoan *Watersipora subtorquata*. *Mar. Ecol. Prog. Ser*. 257: 77-85.

NICHOLS, J.D. 1992. Capture-recapture models: using marked animals to study population dynamics. *Bioscience* 42: 94-102.

NICHOLS, J.D., SAUER, J.R., POLLOCK, K.H. & HESTBECK, J.B. 1992. Estimating transition probabilities for stage-based population projection matrices using capture-recapture data. *Ecology* 73: 306-312.

NICHOLS, J.D., HINES, J.E., LEBRETON, J.D. & PRADEL, R. 2000. Estimation of contributions to population growth: a reverse-time capture-recapture approach. *Ecology* 81: 3362-3376.

NODA, T. 2004. Large-scale variability in recruitment of the barnacle *Semibalanus cariosus*: its cause and effects on the population density and predator. *Mar. Ecol. Prog. Ser*. 278: 241-252.

NODA, T. & NAKAO, S. 1996. Multi-scale spatial patterns of recruitment in the barnacles *Semibalanus cariosus* at fishing ports on the Kameda Peninsula, southern Hokkaido, Japan. *Hydrobiologia* 324: 125-130.

NODA, T., FUKUSHIMA, K. & MORI, T. 1998. Daily settlement variability of the barnacle *Semibalanus cariosus*: importance of physical factors and density-dependent processes. *Mar. Ecol. Prog. Ser*. 169: 289-293.

OLABARRIA, C. & CHAPMAN, G.M. 2001. Habiatat-associated variability in survival and growth of three species of microgastropods. *J. Mar. Biol. Ass. U.K*. 81: 961-966.

OLIVA, D. & CASTILLA, J.C. 1986. The effects of human exclusion on the population structure of keyhole limpets *Fissurella crassa* and *F. limbata* on the coast of central Chile. *PSZN 1 Mar. Ecol*. 7: 201-207.

ORIANS, G.H. 2000. Biodiversity and ecosystem processes in tropical ecosystems. *Rev. Biol. Trop*. 48: 297-303.

ORTEGA, S. 1985. Competitive interactions among tropical intertidal limpets. *J. Exp. Mar. Biol. Ecol.* 90: 11-25.

ORTEGA, S. 1987. The effects of human predation on the size distribution of *Siphonaria gigas* (Molluscan: Pulmonata) on the Pacific coast of Costa Rica. *J. Exp. Mar. Biol. Ecol.* 29: 251-255.

ORTON, J.H., SOUTHWARD, A.J. & DODD, J.M. 1956. Studies on the biology of limpets: II the breeding of *Patella vulgata* L. in Britain. *J. Mar. Biol. Ass. U.K.* 35: 149-179.

O'RIORDAN, R.M., ARENAS, F., ARRONTES, J., CASTRO, J.J., CRUZ, T., DELANY, J., MARTINEZ, B., FERNANDEZ, C. HAWKINS, S.J., McGRATH, D., MYERS, A.A., OLIVEROS, J., PANNACCUILLI, F.G., POWER, A.M., RELINI, G., RICO, J.M. & SILVA, T. 2004. Spatial variation in the recruitment of the intertidal barnacles *Chthamalus montagui* Southward and *Chthamalus stellatus* (Poli) (Crustacea: Cirripedia) over a European scale. *J. Exp. Mar. Biol. Ecol.* 304: 243-264.

OSMAN, R.W. & WHITLATCH, R.B. 1995. Predation on early ontogenic life stages and its effect on recruitment into a marine epifaunal community. *Mar. Ecol. Prog. Ser.* 177: 111-126.

OSMAN, R.W. & WHITLATCH, R.B. 1996. Processes affecting newly-settled juveniles and the consequences to subsequent community development. *Invertebr. Reprod. Dev.* 30: 217-225.

PAINE, R.T. 1969. A note on trophic complexity and species diversity. *Am. Nat.* 100: 65-75.

PAL, P. & HODGSON, A.N. 2004. Reproductive seasonality and simultaneous hermaphroditism in two species of *Siphonaria* (Gastropoda: Pulmonata) from the southeast coast of South Africa. *J. Moll. Stud*. 71: 33-40.

PALMER, A.R. 1983. Growth rates as a measure of food value in thaidid gastropods: assumptions and implications for prey morphology and distribution. *J. Exp. Mar. Biol. Ecol*. 73: 95-124.

PARDO, L.M. & JOHNSON, L.E. 2004. Activity and shelter use of an intertidal snail: effects of sex, reproductive condition and tidal cycle. *J. Exp. Mar. Biol. Ecol*. 301: 175-191.

PARDO, L.M. & JOHNSON, L.E. 2005. Explaining variation in life-history traits: growth rate, size, and fecundity in a marine snail across an environmental gradient lacking predators. *Mar. Ecol. Prog. Ser*. 296: 229-239.

PARRY, G.D. 1982. Reproductive effort in four species of intertidal limpets. *Mar. Biol*. 67: 267-282.

PENRITH, M.L. & KENSLEY, B.F. 1970. The constitution of the intertidal fauna of rocky shores of South West Africa. Part II. Rocky Point. *Cimbebasia* 1: 191-239.

PETRAITIS, P.S. 1989. Effects of the periwinkle *Littorina littorea* (L.) and of intraspecific competition on growth and survivorship of the limpet *Notoacmea testudinalis* (Muller). *J. Exp. Mar. Biol. Ecol*. 125: 99-115.

PFISTER, C.A. & PEACOR, S.D. 2003. Variable performance of individuals: the role of population density and endogenously formed landscape heterogeneity. *J. Anim. Ecol.* 72: 725-735.

PILLANS, S. PILLANS, R.D., JOHNSTONE, R.W., KRAFT, P.G., HAYWOOD, M.D.E. & POSSINGHAM, H.P. 2005. Effects of marine reserve protection on the mud crab *Scylla serrata* in a sex-biased fishery in subtropical Australia. *Mar. Ecol. Prog. Ser*. 295: 201-213.

PINEDA, J. 1994. Spatial and temporal patterns in barnacle settlement rate along a southern California rocky shore. *Mar. Ecol. Prog. Ser*. 107: 125-138.

PODOLSKY, R.D. & STRATHMANN, R.R. 1996. Evolution of egg size in free-spawner: consequences of the fertilization-fecundity trade-off. *Am. Ndt*. 148: 160-173.

POLLOCK, K.H., NICHOLS, A.D., BROWNIE, C. & HINES, J.E. 1990. Statistical inference for capture-recapture experiments. *Wildl. Monogr.* 107: 1-97.

POLLOCK, K.H., HOENIG, J.M. & JONES, C.M. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. *Amer. Fish. Soc. Symp*. 12: 423-434.

POMBO, O.A. & ESCOFET, A. 1996. Effect of exploitation on the limpet *Lottia gigantea*: a field study in Baja California (Mexico) and California (U.S.A.). *Pac. Sci*. 50: 393-403.

PORRI, F., McQUAID, C.D. & RADLOFF, S. 2006. Spatio-temporal variability of larval abundance and settlement of *Perna perna*: differential delivery of mussels. *Mar. Ecol. Prog. Ser.* 315: 141-150.

POVEY, A. & KEOUGH, M.J. 1991. Effects of trampling on plant and animal populations on rocky shores. *Oikos* 61: 355-368.

RAFFAELLI, D.G. 1978. The relationship between shell injuries, shell thickness and habitat characteristics of the intertidal snail, *Littorina rudis* Maton. *J. Moll. Stud.* 44: 166-170.

RAFFAELLI, D.G. & HUGHES, R.N. 1978. The effects of crevice size and availability on *Littorina rudis* and *Littorina neritoides*. *J. Anim. Ecol*. 47: 71-83.

RAIMONDI, P.T. 1988. Rock type effects settlement, recruitment, and zonation of the barnacle *Chthamalus anisopoma* Pilsbury. *J. Exp. Mar. Biol. Ecol*. 123: 253-267.

RAIMONDI, P.T. 1990. Patterns, mechanisms, consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecol. Monogr*. 60: 283-309.

RAKITIN, A. & KRAMER, D.L. 1996. Effects of marine reserve on the distribution of coral reef fishes in Barbados. *Mar. Ecol. Prog. Ser*. 131: 97-113.

RAO, M.B. 1973. Sex phenomenon and reproductive cycle in the limpet *Cellana radiata* (Born) (Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol*. 12: 263-278.

RAO, M.B. 1976. Studies on the growth of the limpet *Cellana tramoserica* (Born) (Gastropoda: Prosobranchia). *J. Moll. Stud*. 42: 136-144.

RIASCOS, J. GUZMAN, N., LAUDIEN, J., HEILMAYER, O. & OLIVA, M. 2007. Suitability of three stains to mark shells of *Concholepas concholepas* (Gastropoda) and *Mesodesma donacium* (Bivalvia). *J. Shellfish Res.* 26(1): 43-49.

RICHARDSON, C.A. 2001. Molluscs as archives of environmental change. *Oceanogr. Mar. Biol. Ann. Rev*. 39: 103-164.

RIDGWAY, T.M., STEWART, B.A., BRANCH, G.M. & HODGSON, A.N. 1998. Morphological and genetic differentiation of *Patella granularis* (Gastropoda: Patellidae): recognition of two sibling species along the coast of southern Africa. *J. Zool. Lond*. 245: 317-333.

ROBERTS, C.M. 1995. Effects of fishing on the ecosystem structure of coral reefs. *Conserv. Biol.* 9: 988-995.

ROBERTS, D.J. & HAWKINS, J.P. 1999. Extinction risk in the sea. *Trends Ecol. Evol*. 14(6): 241-246.

ROBERTS, D.J. & HUGHES, R.N. 1980. Growth and reproductive rates of *Littorina rudis* from three contrasted shores in North Wales, UK. 58: *Mar. Biol.* 47-54.

ROBERTS, C.M., BRANCH, G., BUSTAMANTE, R.H., CASTILLA, J.C., DUGAN, J., HALPERN, B.S., LAFFERTY, K.D., LESLIE, H. LUBCHENCO, J. McARDLE, D., RUCKELSHAUS, M. & WARNER, R.R. 2003. Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecol. Applic.* 13(1): S215-S228.

ROBERTSON, D.R. 1998. Implications of body size for interspecific interactions and assemblage organization among coral-reef fishes. *Austral Ecol*. 23: 252-257.

ROBLES, C.D. 1997. Changing recruitment in constant species assemblages: implications for predation theory in intertidal communities. *Ecology* 78: 1400-1414.

ROBLES, C.D. & DESHARNAIS, R. 2002. History and current development of a paradigm of predation in rocky intertidal communities. *Ecology* 83: 1521-1536.

ROBSON, G. 1986. A new species of South African limpet, *Patella aphenes* (Mollusca: Gastropoda: Patellidae), with a discussion of *P. obtecta* Kraus, 1848. *Durban Mus. Novit*. 13: 305-320.

ROCHETTE, R. & DILL, L.M. 2000. Mortality, behavior and the effects of predators on the intertidal distribution of littorinid gastropods. *J. Exp. Mar. Biol. Ecol*. 253: 165-191.

ROCHETTE, R., DUNMALL, K. & DILL, L.M. 2003. The effect of life-history variation on the population size structure of a rocky intertidal snail (*Littorina sitkana*). *J. Sea. Res.* 49: 119-132.

RODRIGUEZ, S.R., OJEDA, F.P. & INESTROSA, N.C. 1993. Settlement of benthic marine invertebrates. *Mar. Ecol. Prog. Ser*. 97: 193-207.

ROUGHGARDEN, J., IWASA, Y. & BAXTER, C. 1985. Demographic theory for an open marine population with space-limited recruitment. *Ecology* 66: 54-67.

ROUGHGARDEN, J., GAINES, S. & POSSINGHAM, H. 1988. Recruitment dynamics in complex life cycles. *Science* 241: 1460-1466.

ROY, K., COLLINS, A.G., BECKER, B.J. BEGOVIC, E. & ENGLE, J.M. 2003. Anthropogenic impacts and historical declines in body size of rocky intertidal gastropods in southern California. *Ecol. Lett*. 6: 1-7.

RUIZ SEBASTIAN, C., STEFFANI, C.N. & BRANCH, G.M. 2002. Homing and movement patterns of a South African limpet *Scutellastra argenvillei* in an area invaded by an alien mussel *Mytilus galloprovincialis*. *Mar. Ecol. Prog. Ser*. 243: 111-122.

RUSS, G.R. & ALCALA, A.C. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Mar. Ecol. Prog. Ser*. 132:1-9.

RUSS, G.R. & ALCALA, A.C. 1998. Natural fishing experiments in marine reserves, 1983-1993: community and trophic responses. *Coral Reefs*. 17: 383-397.

RUSS, G.R. & ALCALA, A.C. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* 138: 622-627.

SAGARIN, R.D., GAINES, S.D. & GAYLORD, B. 2006. Moving beyond assumptions to understand abundance distributions across the ranges of species. *Trends Ecol. Evol*. 21(9): 524-530.

SAGARIN, R.D., AMBROSE, R.F., BECKER, B.J., ENGLE, J.M., KIDO, J., LEE, S.F., MINER, C.M., MURRAY, S.N., RAIMONDI, P.T., RICHARDS, D.V. & ROE, C. 2007. Ecological impacts on the limpet *Lottia gigantea* populations: human pressure over a broad scale on island and mainland intertidal zones. *Mar. Biol*. 150: 399-413.

SALA, E., RIBES, M., HEREU, B., ZABALA, M., ALVA, V., COMA, R. & GARRABOU, J. 1998. Temporal variability in abundance of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* in the northwestern Mediterranean: comparison between a marine reserve and an unprotected area. *Mar. Ecol. Prog. Ser*. 168: 135-145.

SALE, P.F. & FERRELL, D.J. 1988. Early survivorship of juvenile coral reef fishes. *Coral Reefs*. 7: 117-124.

SANFORD, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283(5410): 2095-2097.

SANTINA, P.D., SANTINI, G. & CHELAZZI, G. 1995. Factors affecting variability of foraging excursions in a population of the limpet *Patella vulgata* (Mollusca, Gastropoda). *Mar. Biol*. 122: 265-270.

SCHEIBLING, R.E., EVANS, T., MULVAY, P., LEBEL, T., WILIAMSON, D. & HOLLAND, S. 1990. Commensalism between an epizoic limpet, *Patelloida nigrosulcata*, and its gastropod hosts, *Haliotis roei* and *Patella laticostata*, on intertidal platforms off Perth, Western Australia. *Aus. J. Mar. Freshw. Res*. 41: 647-655.

SEBENS, K.P. 1982. The limits to indeterminate growth: an optimal size model applied to passive suspension feeders. *Ecology* 63: 209-222.

SEITZ, R.D. & LIPCIUS, R.N. Variation in top-down and bottom-up control of marine bivalves at differing spatial scales. *J. Mar. Sci*. 58: 689-699.

SHANKS, A.L. 1998. Apparent oceanographic triggers to spawning of the limpet *Lottia digitalis* (Rathke). *J. Exp. Mar. Biol. Ecol*. 222: 31-41.

SHANKS, A.L. 2000. Previous agonistic experience determines both foraging behaviour and territoriality in the limpet *Lottia gigantea* (Sowerby). *Behav. Ecol*. 13: 467-471.

SHANKS, A.L. & WRIGHT, W.G. 1986. Adding teeth to wave action: the destructive effects of wave-borne rocks on intertidal organisms. *Oecologia* 69: 420-428.

SHANKS, A.L. & WRIGHT, W.G. 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae, and gamiarids and correlated longshore differences in the settling rate of intertidal barnacles. *J. Exp. Mar. Biol. Ecol*. 114: 1-13.

SIEGFRIED, W.R., HOCKEY, P.A.R. & CROWE, A.A. 1985. Exploitation and conservation of brown mussel stocks by coastal people of Transkei. *Environ. Conserv*. 12: 303-307.

SIEGFRIED, W.R., HOCKEY, P.A.R. & BRANCH, G.M. 1994. The exploitation of intertidal and subtidal biotic resources of rocky shores in Chile and South Africa – an overview. In: *Rocky Shores: Exploitation in Chile and South Africa*, (*edn*.) W.R. Siegfried, pp. 1-13. Springer-Verlag, Berlin Heildeberg.

SILVA, A., BOAVENTURA, D. & RÉ, P. 2003. Population structure, recruitment and distribution patterns of *Patella depressa* Pennant, 1777 on the central Portuguese coast. *Bol. Inst. Esp. Oceanogr*. 19(1-4): 461-471.

SILVA, A., BOAVENTURA, D., FLORES, A., Re' P. & HAWKINS, S.J. 2004. Rare predation by the intertidal crab *Pachygrapsus marmoratus* on the limpet *Patella depressa*. *J. Mar. Biol. Ass. U.K.* 84: 367-370.

SORENSEN, F.E. & LINDBERG, D.R. 1991. Preferential predation by American black oystercatchers on transitional ecopheno-types of the limpet *Lottia pelta* Rathke. *J. Exp. Mar. Biol. Ecol*. 154: 123-136.

SOUSA, W.P. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. *Ecology* 65: 1918-1935

STACHOWICZ, J.J. & HAY, M. 1999. Reduced mobility is associated with compensatory feeding and increased diet breadth of marine crabs. *Mar. Ecol. Prog. Ser*. 188: 169-178.

STANWELL-SMITH, D.; PECK, L.S., CLARKE, A.; MURRAY, A.W.A. & TODD, C.D. 1999. The distribution, abundance and seasonality of pelagic marine invertebrate larvae in the maritime Antarctic. *Biol. Sci*. 354: 471-484.

STEARNS, S.C. 1976. Life history tactics: a review of the ideas. *Q. Rev. Biol*. 51: 3-47.

STEFFANI, C.N. & BRANCH, G.M. 2003a. Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: responses to wave exposure. *Mar. Ecol. Prog. Ser*. 246: 197-209.

STEFFANI, C.N. & BRANCH, G.M. 2003b. Spatial comparisons of populations of an indigenous limpet *Scutellastra argenvillei* and an alien mussel *Mytilus galloprovincialis* along a gradient of wave energy. *Afr. J. Mar. Sci*. 25: 195-212.

STONER, A.W. & RAY-CULP, M. 2000. Evidence for Allee effects in an over-harvested marine gastropod: density-dependent mating and egg production. *Mar. Ecol. Prog. Ser*. 202: 297-302.

TABLADO, A., LOPEZ GAPPA, J.J. & MAGALDI, N.H. 1994. Growth of the pulmonate limpet *Siphonaria lessoni* (Blainville) in a rocky intertidal area affected by sewage pollution. *J. Exp. Mar. Biol. Eco*l. 175: 211-226.

TAKADA, Y. 1995. Variation of growth rate with tidal level in the gastropod *Monodonata labio* on a boulder shore. *Mar. Ecol. Prog. Ser*. 117: 103-110.

TANNER, J.E. 1997. The effects of density on the zoanthid *Palythoa caesia*. *J. Anim. Ecol.* 66: 793-810.

TEGNER, M.J. & DAYTON, P.K. 2000. Ecosystem effects of fishing in kelp forest communities. *ICES J. Mar. Sci.* 57: 579-589.

TEGNER, M.J., BASCH, L.V. & DAYTON, P.K. 1996. Near extinction of an exploited marine invertebrate. *Trends Ecol. Evol*. 11: 278-280.

TENHUMBERG, B., TYRE, A.J. & ROITBERG, B. 2000. Stochastic variation in food availability influences weight and age at maturity. *J. Theor. Biol*. 202: 257-272.

THACKERY, J.F. 1988. Molluscan fauna from Klasies River, South Africa. *S. Afr. Archaeol. Bull.* 43: 27-32.

THIELTGES, D.W., STRASSER, M., VAN BEUSEKOM, J.E.E. & REISE, K. 2004. Too cold to prosper – winter mortality prevents population increase of the introduced American slipper limpet *Crepidula fornicata* in northern Europe. *J. Exp. Mar. Biol. Ecol.* 311: 375-391.

THOMPSON, G.B. 1980. Distribution and population dynamics of the *Patella vulgata* L. in Bantry Bay. *J. Exp. Mar. Biol. Ecol*. 45: 173-217.

THOMPSON, R.C., CROWE, T.P. & HAWKINS, S.J. 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environ. Conserv*. 29: 168-191.

TILLEY, S.G. 1980. Life histories and comparative demography of two salamander populations. *Copeia* 1980: 806-821.

TOONEN, R.J. & PAWLIK, J.R. 2001. Foundations of gregariousness: a dispersal polymorphism among the planktonic larvae of a marine invertebrate. *Evolution* 55: 2439-2454.

TRITES, A.W. 1993. Biased estimates of fur seal pup mass: origins and implications. *J. Zool*. 229: 515-525.

TRUSSELL, G.C. 2002. Evidence of countergradient variation in the growth of an intertidal snail in response to water velocity. *Mar. Ecol. Prog. Ser*. 243: 123-131.

TRUSSELL, G.C. & NICKLIN, M.O. 2002. Cue sensitivity, inducible defense, and trade-offs in a marine snail. *Ecology* 83: 1635-1647.

UNDERWOOD, A.J. 1976. Food competition between age-classes in the intertidal neritacean *Nerita atramentosa* Reeve (Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol*. 23: 145-154.

UNDERWOOD, A.J. 1978. An experimental evaluation of competition between three species of intertidal Prosobranch Gastropods. *Oecologia* 33: 185-202.

UNDERWOOD, A.J. 1980. The effects of grazing by gastropods and physical factors on the upper limits of intertidal macroalgae. *Oecoogia* 46: 201-231.

UNDERWOOD, A.J. 1984. Vertical and seasonal patterns in competition for microalgae between intertidal gastropods. *Oecologia* 64: 211-222.

UNDERWOOD, A.J. 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge.

UNDERWOOD, A.J. 2000. Experimental ecology of rocky intertidal habitats: what are we learning? *J. Exp. Mar. Biol. Ecol*. 250: 51-76.

UNDERWOOD, A.J. & McFADYEN, K.E. 1983. The ecology of the intertidal snail *Littorina acutispira* Smith. *J. Exp. Mar. Biol. Ecol*. 66: 169-197.

UNDERWOOD, A.J. & JERNAKOFF, P. 1984. Effects of tidal height, wave exposure, seasonality and rock-pools on grazing and the disturbance on intertidal macroalgae in New South Wales, Australia. *J. Exp. Mar. Biol. Ecol*. 75: 71-96.

UNDERWOOD, A.J. & CHAPMAN, M.G. 1989. Experimental analyses of the influences of topography of the substratum on movements and density of an intertidal snail, *Littorina unifasciata*. *J. Exp. Mar. Biol. Ecol*. 134: 175-196.

UNDERWOOD, A.J. & KENNELLY, S.J. 1990. Pilot studies for designs of surveys of human disturbance of intertidal habitats in New South Wales. *Aust. J. Mar. Freshw. Res*. 41: 165-173.

UNDERWOOD, A.J. & CHAPMAN, M.G. 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107: 212-224.

UNDERWOOD, A.J. & CHAPMAN, M.G. 1998. A method for analyzing spatial scales of variation in composition assemblages. *Oecologia* 107: 570-578.

UNDERWOOD, A.J. & CHAPMAN, M.G. 2000. Variation in abundances of intertidal populations: consequences of extremities of environment. *Hydrobiologia*. 426: 25–36.

UNDERWOOD, A.J., DENLEY, E.J. & MORAN, M.J. 1983. Experimental analysis of the structure and dynamics of mid-shore rocky intertidal communities in New Wales. *Oecologia* 56: 202-219.

VANCE, R.R. 1973. On reproductive strategies of marine invertebrates. *Am. Nat*. 107: 339-352.

VAN ERKOM SCHURINK, C. & GRIFFITHS, C.L. 1990. Marine mussels of southern Africa: their distribution patterns, standing stocks, exploitation and culture. *J. Shellfish Res*. 9: 75-85.

VAN ERKOM SCHURINK, C. & GRIFFITHS, C.L. 1993. Factors affecting relative rates of growth in four South African mussel species. *Aquaculture* 109: 257-273.

VAN HERWERDEN, L., GRIFFITHS, C.L., BLAINE, M. & du PLESSIS, C. 1989. Patterns of shore utilization in a metropolitan area: the Cape Peninsula, South Africa. *Ocean. Shoreline Mgmt*. 12: 331-346.

VERMEIJ, G.J. 1972. Intraspecific shore-level size gradients in intertidal molluscs. *Ecol*ogy 53(4): 693-700.

WALTERS, C.J. & HOLLING, C.S. 1990. Large-scale management experiments and learning by doing. *Ecology* 71: 2060-2068.

WARNER, R.R., FITCH, D.L. & STANDISH, J.D. 1996. Social control of sex change in the shelf limpet, *Crepidula norrisiarum*: size-specific responses to local group composition. *J. Exp. Mar. Biol. Ecol*. 204: 155-167.

WENDT, D.E. 2000. Energetics of larval swimming and metamorphosis in four species of *Bugula* (Bryozoa). *Biol. Bull*. 198: 346-356.

WILLIAMS, G.A. & MORRITT, D. 1995. Habitat partitioning and thermal tolerance in a tropical limpet, *Cellana grata. Mar. Ecol. Prog. Ser*. 124: 89-103.

WILLIAMS, B.K., NICHOLS, J.D. & CONROY, M.J. 2001. *Analysis and management of animal populations*: *Modeling, estimation and decision making.* Academic Press: San Diego. pp. 817.

WILLIAMSON, D.H., RUSS, G.R. & AYLING, A.M. 2004. No-take marine reserves increase abundance and biomass of reef fish on inshore fringing reefs of the Great Barrier Reef. *Environ. Conserv*. 31(2): 149-159.

WILLIS, T.J., MILLAR, R.B. & BABCOCK, R.C. 2003. Protection of exploited fish in temperate regions: high density and biomass of snapper *Pagrus auratus* (Sparidae) in northern New Zealand marine reserves. *J. Appl. Ecol*. 40: 214-227.

WOLCOTT, T.G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*). A critical look at “Limiting Factors”. *Biol. Bull*. 145: 389-422.

WOOTTON, J.T. 1992. Indirect effects, prey susceptibility and habitat selection: impact of birds on limpets and algae. *Ecology* 73: 981-991.

ZABIN, C.J. & ALTIERI, A. 2007. A Hawaiian limpet facilitates recruitment of a competitively dominant invasive barnacle. *Mar. Ecol. Prog. Ser*. 337: 175-185.

ZACHERL, D., GAINES, S.D. & LONHART, S.I. 2003. The limits to biogeographical distributions: insights from the northward range extension of marine snail, *Kelletia kelletia* (Forbes, 1852). *J. Biogeogr*. 30: 913-924.

ZAR, J.H. 1996. *Biostatistical analysis*, 3rd edn. Prentice Hall, New York.

ZHAO, B. & QIAN, P.Y. 2002. Larval settlement and metamorphosis in the slipper limpet *Crepidula onyx* (Sowerby) in response to conspecific cues and the cues from biofilm. *J. Exp. Mar. Biol. Ecol*. 269: 39-51.

APPENDIX

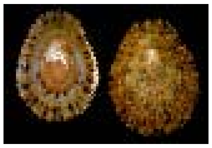
A.1: A questionare for interviewing shellfish collectors

i. Site …………..

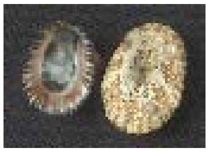
ii. Date ………….

iii. The 4 limpets are shown:

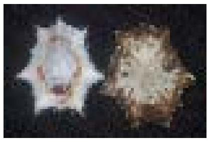
1 = *Cellana capensis*



2 = *Helcion concolor*



3 = *Scutellastra granularis*



4 = *Scutellastra* longicosta

iv. Do you eat these limpets? …………………

v. If YES and NO, which ones? ………………

vi. If ALL, rank in order of preference:

Name of person	Age	Sex	Code	Code	Code	Code

vii. How often do you collect them?

viii. How many do you collect? (i.e. quantity: < 10, 50, 100 > 100 etc) ……