POPULATION STRUCTURE, GROWTH AND RECRUITMENT OF TWO EXPLOITED INFRALITTORAL MOLLUSCS (*HALIOTIS MIDAE* AND *TURBO SARMATICUS*) ALONG THE SOUTH EAST COAST, SOUTH AFRICA.

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ABSTRACT

The two most frequently exploited species along the south east coast of South Africa are the gastropods, *Haliotis midae* (abalone) and *Turbo sarmaticus* (alikreukel). *H. midae* is a high valued commercial species, and suffers intense levels of illegal fishing. *T. sarmaticus* however, has no commercial value but is the preferred food item for impoverished subsistence communities. Owing to the fact that no legal commercial fishery exists for either species along the south coast, very few studies have been undertaken, especially in the heavily exploited infralittoral.

Infralittoral size frequency distributions for both species revealed significant variation in density and size among sites of varying exploitation pressure. Densities ranged between 0 – 2.23 m^{-2} (*H.* midae) and 0.03 – 4.93 m^{-2} (*T.* sarmaticus) and maximum shell lengths ranged from 49.4 – 153.5 mm (*H. midae*) and 28.3 – 104.4 mm (*T. sarmaticus*). Relatively high densities and large sizes were found in marine reserves and secluded areas, and low densities and small sizes at sites near to large population centres and within the former Ciskei homeland region. Mean size of the largest 10% of the population, total density and sexually mature density were significantly related to exploitation predictors for both species. In addition, densities of *H. midae* juveniles were significantly related to exploitation predictors, suggesting that recruitment may be suppressed at the most exploited sites. Exploitation of *T. sarmaticus* tended to be localized with refuge and subtidal populations persisting. *H. midae* exploitation was however, far more extensive and intense.

Growth of *H. midae* was investigated using three methods; mark-recapture, cohort analysis and growth banding analysis at Kowie Rocks, Port Alfred. The most useful of these methods for determining growth was a new technique described for growth banding analysis; which was validated using cohort analysis and measurements of shells of known age. This technique was less time consuming and labour intensive than previously described methods. Abalone growth was best described by the Schnute (1981) growth function. Systematic geographic variation in

growth was observed for 10 sites along the South African coastline. Significant differences in growth among sites existed for animals between 0-4 years ($P < 0.0001$) and 4-6 years ($P < 0.0001$), and in the mean maximum sizes attained ($P < 0.001$). In general, abalone from the south east/east coast were found to have faster growth rates, smaller mean maximum sizes and attained sexual maturity earlier than those along the south west/ west coast.

Haliotis midae recruit and juvenile densities were found to differ significantly among sites of varying exploitation pressure ($P < 0.0001$) and among months for recruit densities ($P < 0.001$). Exploited sites had low recruit and juvenile densities compared to unexploited sites and peak recruitment occurred during October/ November 2005. Recruit densities were significantly related to infralittoral adult densities during two of the three sampling months ($P<0.05$), when recruitment was low. No relationship was observed during the period of high recruitment, with all sites receiving high recruit densities. It was concluded that variation in recruit densities was the result of a combination of both density-dependent relationships (i.e. local spawner density and temporal variability in recruitment intensity) and the possible dispersal capabilities of *H. midae*. In addition, it was concluded that at present recruitment overfishing was not occurring along the south east coast. Post-recruitment mortality rates were variable but relatively constant, with hypothetical percentage survival and density curves revealing high rates and similar mortality curves among sites. Variation in juvenile densities was consequently a result of initial recruit densities and not variation in post-recruitment mortality.

T. sarmaticus populations were found to be regionally sustainable and persisted along the south east coast due to adjacent intertidal and subtidal refuge populations. However, *H. midae* populations are becoming decimated along the south east coast. From the information obtained in this study new management proposals were suggested and discussed, such as closed areas and region-based management fisheries together with stock enhancement. These suggestions may prove to be feasible alternatives to present management strategies.

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CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

1.1 General Background

More than 5000 species of molluscs are represented in Southern Africa (Branch *et al.* 2002). Among world-wide invertebrate fisheries, marine molluscs are one of the most important with just under 5 metric tonnes being taken in 2004 (FAO 2004) of this, gastropods comprised approximately 291 metric tonnes of total wild-stock mollusc takes (FAO 2004). Many exploited gastropod species have a high economic value in international markets and/or play important roles in smaller-scale artisanal/ subsistence fisheries (Hobday *et al.* 2001; Leiva and Castilla 2002; Ward and Davis 2002). A number of these fisheries have now collapsed as a result of over-exploitation (Alstatt *et al.* 1996; Leiva and Castilla 2002), with man being considered a 'keystone' predator in the structure and dynamics of rocky intertidal and subtidal invertebrate communities (Durán *et al.* 1987). Over-exploited marine gastropod fisheries include; abalone (*Haliotis* spp.), strombid conchs (*Strombus* spp.), the muricid "loco" *Concholepas concholepas*, the horned turban snail *Turbo truncates*, the periwinkle *Littorina littorea* and the whelk *Buccinum undatum* (Leiva and Castilla 2002). Declines and /or closures of these fisheries have been a result of either the effects of long-term overfishing or short-term overfishing (Jamieson 1993). Long-term overfishing is the result of the exploitation of a species for centuries, initially by the subsistence sector and then due to market expansion by the commercial sector, for example the queen conch, *Strombus gigas* (Jamieson 1993). Short-term overfishing is the result of either the development of a new fishery where ineffective management has been initiated due to insufficient information, for example the South American loco and many abalone species, or else a sudden unanticipated increase in the effective fishing effort, perhaps due to the introduction of a new harvest technology, for example coral fishing (Jamieson 1993).

In South Africa, marine molluscs have been exploited for subsistence purposes for thousands of years (Volman 1978; Griffiths and Branch 1997). On the west coast, archaeological records

have shown changes in the intensity of subsistence collection over time (Griffiths and Branch 1997). Harvesting of marine resources was found to have occurred at a low level between 7700 – 4400 years B.P. (Before the Present), harvesting then intensified between 2900 - 2100 years B.P. and subsequently declined dramatically at approximately 2100 B.P. with the appearance of pastoralism (Siegfried *et al.* 1994; Griffiths and Branch 1997). Archaeological records of harvesting on the south and east coasts are not as detailed but tend to be similar to the west coast, with records showing that in the early centuries of the first millennium human populations along these coasts lacked livestock and showed a strong reliance on shellfish as a source of protein (Siegfried *et al.* 1994; Griffiths and Branch 1997). Harvesting by subsistence collectors during these early periods focused predominantly on easily accessible intertidal species such as limpets and mussels (Siegfried 1994). Over the past 100 years, however, there has been a development of commercial fisheries targeting selected abundant, high value species concentrated on the south west and west coasts such as whitefish, rock lobster, squid and abalone (Griffiths and Branch 1997; Payne 2000). The development of commercial fisheries led to technological advances, allowing for previously inaccessible species to be targeted (Griffiths and Branch 1997). In addition, recreational as well as illegal fisheries have developed which tend to compete with either the subsistence or commercial sectors (Griffiths and Branch 1997). Subsistence, recreational and illegal fisheries are more difficult to control than commercial fisheries, and over the past few decades the intensity of exploitation by these sectors has increased dramatically as a result of organisms attaining high value, rapid human population growth, high poverty and a concentration of people into coastal areas (Griffiths and Branch 1997; Foster and Hodgson 2000).

The increased intensity of harvesting by the various fisheries sectors in recent decades has had an effect on both intertidal and subtidal communities (Griffiths and Branch 1997). Impacts on these communities may either be direct or indirect. Direct impacts affect the target species themselves and exploitation has been shown to have noticeable effects on the densities, population structures and mean maximum sizes of harvested marine invertebrates (Branch 1975; Lasiak and Dye 1989; Branch and Moreno 1994; Branch and Odendaal 2003). The removal of exploited species may also have profound indirect effects on the community; for example the removal of a prominent grazer, filter feeder or predator can effect the species assemblage and

structure of a community (Dye 1992; Branch and Moreno 1994; Lasiak and Field 1995; Griffiths and Branch 1997).

The south east coast of South Africa is characterized by the warm, south moving Agulhas Current, whereas the west coast is characterized by the distinctive cold and productive Benguela Current (Lubke 1998). As a result, there are marked differences in the distribution and composition of intertidal fauna and flora from the west to east coast (Branch and Branch 1981; Emanuel *et al.* 1992). This environment is also highly dynamic due to the characteristic ocean currents and water movement from the prevailing winds (Lutjeharms 1998). Along the South African coastline, there are also clear gradients in the use of resources and participation in subsistence fisheries (Cockcroft *et al.* 2002) as well as the natural abundance of many target species (Bustamante *et al.* 1995). There is very little commercial exploitation of grazers on the south east and east coasts as few species have large populations, these resources are however heavily utilised as a source of protein by subsistence fishers (Branch and Moreno 1994). While exploitation tends to be highest along the east coast, natural densities of target species are inclined to be higher along the more productive west coast (Bustamante *et al.* 1995; Cockcroft *et al.* 2002) and this disparity in resource abundance and utilization makes sustainability difficult. There tends also to be an increase in the diversity of resources used from west to east, with some 35 species being harvested along the South African coastline; predominantly mussels, limpets and winkles (Griffiths and Branch 1997; Cockcroft *et al.* 2002). In addition there is a clear distinction in poverty levels, with increasing poverty levels from west to east which is a reflection of the past history of the country (Cockcroft *et al.* 2002). In the early 1960's the politically motivated establishment of "Bantu homelands" resulted in large parts of the black African population being concentrated into three main coastal areas along the south and east coasts, these were the Ciskei along the south east coast, the Transkei and KwaZulu both along the east coasts (Siegfried *et al.* 1994). The resulting increase in population densities in coastal areas had severe impacts on shellfish resources (Siegfried *et al.* 1994). In the Transkei, subsistence resource utilization has been shown to be intense, with many exploited populations barely persisting at existing levels of exploitation (Hockey and Bosman 1986; Hockey *et al.* 1988; Lasiak and Dye 1989; Lasiak 1991; Cockcroft *et al.* 2002). Unlike the Transkei, which has received much attention (see above references), there is very little known about the extent of

marine resource utilization along the south-east coast and the former Ciskei region. The south east coast, from Cape St Francis to Kei River (Lubke 1998), makes for an ideal study area, as there are clear distinctions in resource utilization between previous homelands such as the Ciskei (with large numbers of subsistence fishers) and wealthier coastal settlements were resource utilization is primarily recreational. Surveys conducted between Port Alfred and East London identified two gastropod species as being the most frequently collected. These were *Haliotis midae* (abalone) and *Turbo sarmaticus* (alikreukel) (Kaehler 2003, Fig. 1.1).

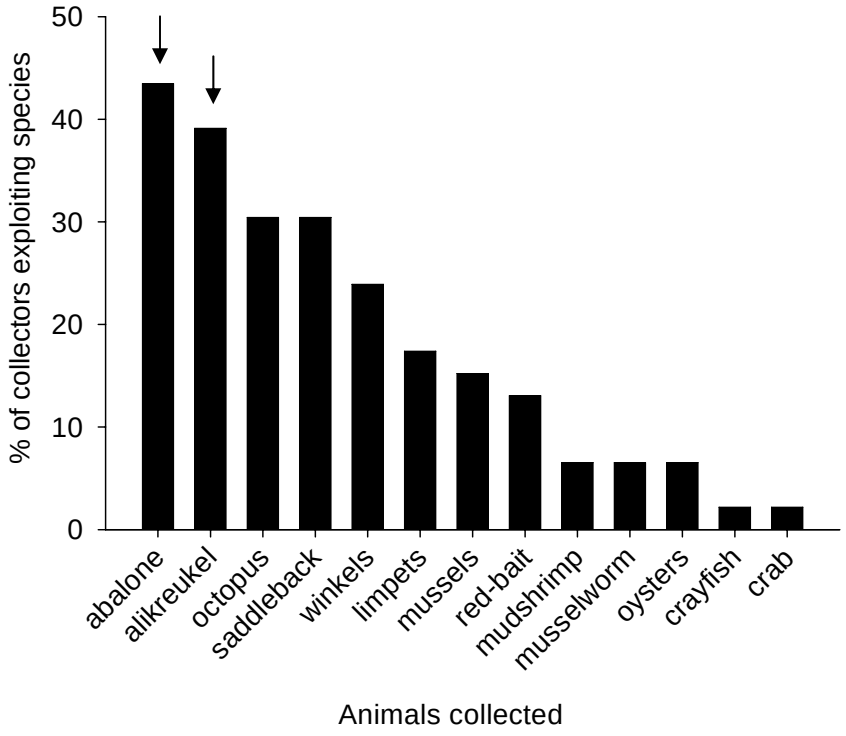


Fig. 1.1 Percentage of collectors exploiting common marine resources along the south coast (Kaehler 2003).

1.2 Introduction to species

1.2.1 *Haliotis midae*

Haliotis midae is one of approximately 70 abalone species of the genus *Haliotis* (Lindberg 1992). Members of the genus are distributed globally, from as far north as the Icy Strait, Alaska (*H. kamtschatkana*) to New Zealand (*H. rubra*) (Muller 1984; Lindberg 1992; Wood 1993). More typically, however, *Haliotis* species are found in temperate and tropical waters, inhabiting the intertidal and subtidal depths to approximately 400 m (Lindberg 1992; Wood 1993). Fisheries for abalone exist globally, with approximately 14 species being of commercial importance (Lindberg 1992; Godfrey 2003). The demand for the flesh of the well developed muscular foot in the Far East has lead to an increase in the exploitation of this genus both commercially and recreationally (Tarr 1993; Godfrey 2003). Early investigations into abalone fisheries by Heath (1925) suggested that stocks of the red abalone *Haliotis rufescens* in California were inexhaustible, as abalone live at great depths (35 m), are abundant in quantity along the coast, and have habits and methods of propagation that are such that the spawn will immediately repopulate. More recently, however, it has been realised that globally, abalone fisheries have declined substantially, causing growing concern for the fishery as a whole (Miller and Lawrenz-Miller 1993; Alstatt *et al.* 1996; Shepherd *et al.* 1998; Daniels and Florens 1998; Hobday *et al.* 2001; Rogers-Bennett and Butler 2002; Godfrey 2003). As a result, over the last 40 years, a number of studies have been initiated that investigated aspects of Haliotid biology such as population structure, reproduction, diet, age and growth, mortality, recruitment, habitat requirements, larval development and the feasibility of stock enhancement of hatchery reared juveniles into the wild in response to increased fishing effort (Leighton and Booloottian 1963; Hayashi 1980; Sainsbury 1982a; Prince *et al.* 1988a, 1988b, 1988c; McShane *et al.* 1988a, 1988b; Keesing and Wells 1989; Shepherd 1990; Schiel and Breen 1991; Moss and Tong 1992; McCormick *et al.* 1994; McShane 1995; Shepherd and Partington 1995; Rogers-Bennett and Pearse 1998). This knowledge thus procured was then applied to both the management and the culture of abalone (Wood 1993).

In South Africa, *H. midae* (abalone/perlemoen) is one of five endemic *Haliotis* species (Lindberg 1992; Branch *et al.* 2002). It has a wide distributional range, from St Helena Bay on the west coast to just north of Port St Johns on the east coast (Fig. 1.1) and is found on rocky reefs between the intertidal and subtidal zones, down to a depth of approximately 10 m (Barkai and Griffiths 1986; Branch *et al.* 2002).

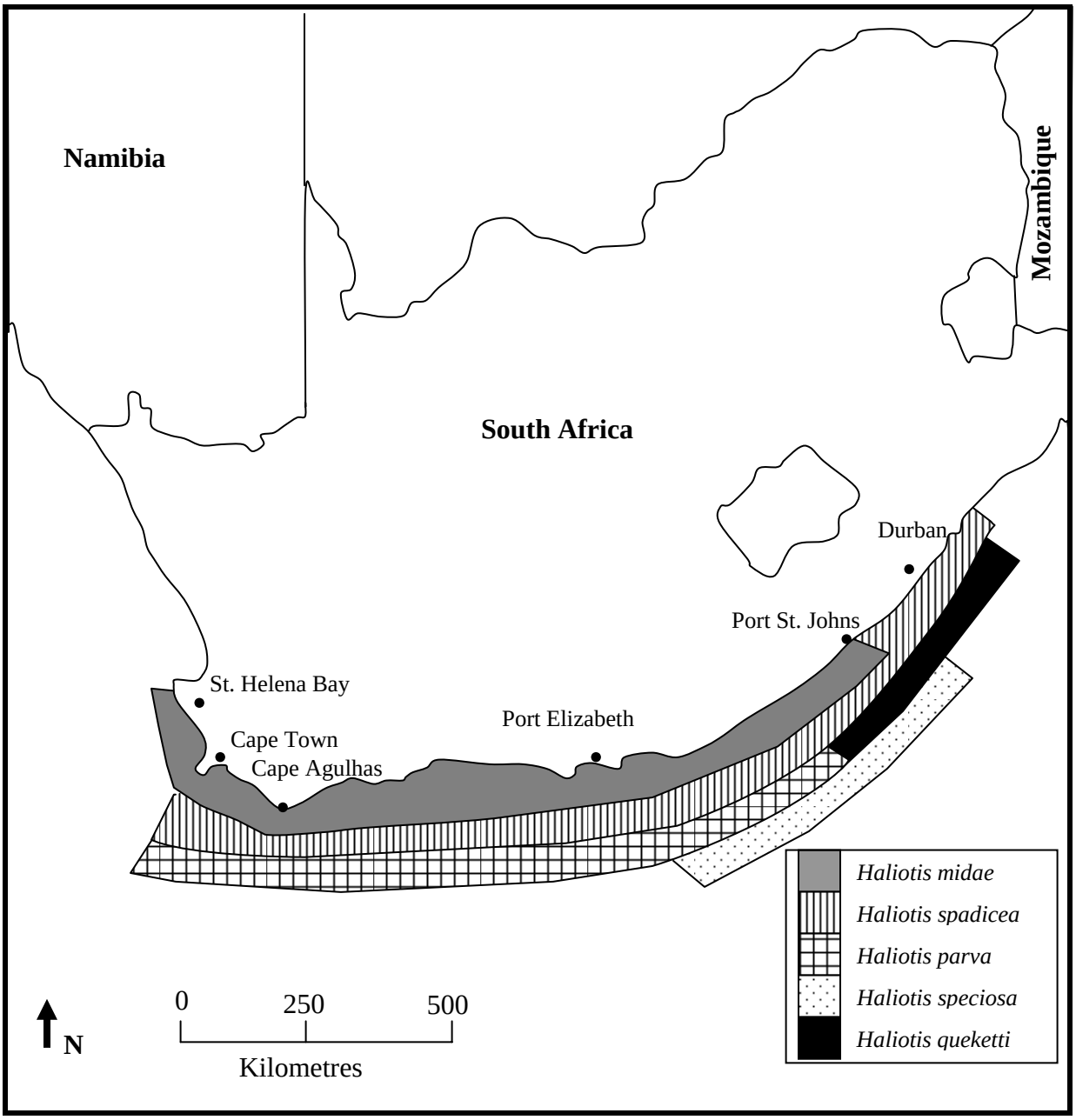


Fig 1.1 Distribution of *Haliotis* spp. along the South African coastline (Lindberg 1992)

Haliotis midae is the largest of the abalone species in South Africa and is also the most abundant, especially between St Helena Bay and Cape Agulhas (Newman 1969; Barkai and Griffiths 1986; Branch *et al.* 2002). It is an herbivorous, dioecious broadcast spawner and is thought to attain sexual maturity between 8-10 years and to reach a maximum age of 30 years on the west coast (Newman 1968; Branch *et al.* 2002).

The abalone industry in South Africa is reliant on *Haliotis midae* only, with the fishery (over 55 years old) extending over approximately 580 km of coastline from Cape Columbine to Quoin Point (Fielding 1995; Dichmont *et al.* 2000; Plagányi *et al.* 2001). Up until the 1990's, this fishery was almost completely commercial with only a small recreational component (Fielding 1995; Hauck and Sweijd 1999; Dichmont *et al.* 2000; Plagányi *et al.* 2001). The sought-after flesh of the foot and the decorative nature of the shell have made it one of the most profitable fisheries in South Africa (in terms of unit value), with a minimum annual gross value of approximately R70 million (Tarr 1993; Hauck and Sweijd 1999; Godfrey 2003). In addition to the commercial fishery along the south west and west coasts, a small experimental fishery was initiated in 1992 in Hamburg in the former Ciskei region with a Total Allowable Catch (TAC) of 3 tons (Wood 1993; Godfrey 2003). However at the end of 2003, the fishery was dropped due to the extent of illegal harvesting in the area (Godfrey 2003). As with other abalone fisheries around the world, dramatic declines in the catch of *H. midae* have been noted, with the TAC of 640 tons in 1986 being reduced to a TAC of 430 tons whole weight/year for 2002/2003 (Hauck and Sweijd 1999; Dichmont *et al.* 2000; Godfrey 2003). Decreases in catch have been attributed largely to the illegal sector (Hauck and Sweijd 1999; Tarr 2000; Hauck 2000; Plagányi *et al.* 2001; Levey 2002; Godfrey 2003), with concern growing as to the large volumes taken (as much as half that taken by the commercial sector) and many animals being below the minimum legal size (MLS) of 114 mm shell width or 144 mm shell length (Wood 1993; Tarr 2000). The high financial value and ease of accessibility of the intertidal and shallow subtidal zones have made abalone a target for illegal exploitation; especially along the south west coast (Hauck and Sweijd 1999). Recently, however, poaching of abalone has become increasingly more widespread along the South African coastline due to the fact that populations on the west coast are diminishing as a result of poaching (Godfrey 2003). In addition to the large poaching syndicates, the recreational sector is also thought to have contributed to the decline in catches, with estimated annual catches

of between 400-550 tons being approximately equal to the yield of the commercial fishery (Tarr 2000; Godfrey 2003). As a result, since 10/10/2003 tighter restrictions have been stipulated by the Department of Environmental Affairs, with the collection of abalone by the recreational and subsistence sectors being banned. A zero tolerance attitude has also been adopted towards poaching by the Department of Environmental Affairs, with fines increasing from R40 000 to R800 000 and confiscations of cars, boats, equipment etc. being initiated.

Past scientific work on natural populations of *Haliotis midae* (as opposed to in aquaculture) have focused primarily on the south-west and western Cape commercial fishing grounds, with the first studies detailing movement, reproduction, growth, differences in productivity and distribution of *H. midae* all originating on the west coast (Newman 1966, 1967a, 1968, 1969). A review of the state of abalone research in South Africa was published by Newman (1967b). The dietary intake, consumption, absorption efficiency, respiration and excretion of *H. midae* as well as a calculated energy budget were subsequently undertaken (Barkai and Griffiths 1986, 1987, 1988). A review of the fishery history, status and prospects was given by Tarr (1992), which was followed by a stock assessment of *H. midae* along the south west and west coasts in the commercial fishing grounds (Tarr 1993). In addition, other aspects such as growth and movement were described for populations along this stretch of coastline (Tarr 1993, 1995). Tarr (1993) described far more limited movement and faster growth rates of *H. midae* than Newman (1966, 1968) for populations on the west coast. Other studies include the associations between juvenile *H. midae* and the sea urchin *Parechinus angulosus* (Day and Branch 2000, 2002a, 2002b), the link between the influx of the rock lobster (*Jasus lalandii*) into commercial fishing grounds and the decrease in juvenile *H. midae* densities (Mayfield and Branch 2000), seeding of hatchery reared juveniles into the wild (Sweijd *et al.* 1998; De Waal and Cook 2001; De Waal *et al.* 2003) and the modelling of *H. midae* abundance (Dichmont *et al.* 2000).

Owing to the fact that no extensive commercial fishery existed along the south and east coasts, and little exploitation was assumed to be occurring (Newman 1969, Fig. 1.3A) very few studies were conducted along the south and east coastlines. Studies on natural populations of *Haliotis midae* along this stretch of the coast are limited to a few studies. Wood (1993) investigated aspects of the biology and ecology of *H. midae* (Wood and Buxton 1996a, 1996b).

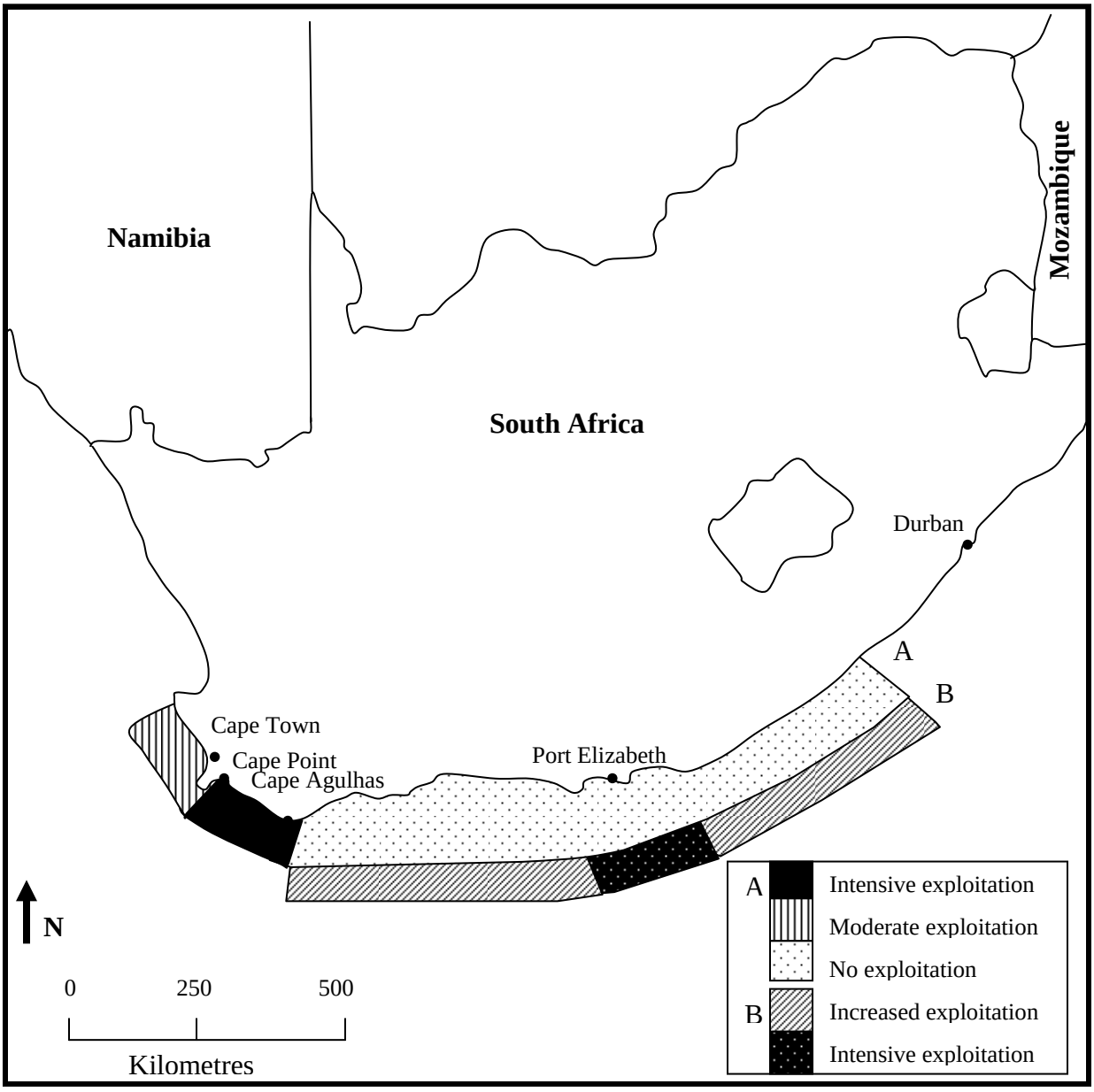


Fig. 1.3 Exploitation of *Haliotis midae* along the South African coastline **A)** estimated by Newman (1969) and **B)** Godfrey (2003) and Hauck and Sweijd (1999)

Wood (1993) determined faster growth rates for *Haliotis midae* and sexual maturity at smaller sizes at sites along the east coast than those described by Newman (1969) for the west coast, attributing this to differences in temperature regime and productivity between the coasts. Wood

also noted that the distribution of *H. midae* was largely patchy along this coastline due to the patchy availability of suitable habitats. Tarr (1993, 1995) studied an isolated population of abalone at Bird Island in the Eastern Cape, however he found that, in contrast to previous suggestions by Newman (1968, 1969), similar growth rates were obtained to those along the south west coast and that biannual spawnings occurred in *H. midae* populations. Fielding (1995) concluded from yield and egg-per-recruit modelling analysis that stocks in the Transkei had limited exploitation potential. Godfrey (2003) addressed the extent of poaching in the Port Elizabeth area and assessed the potential for stock enhancement as well as the economic feasibility of seeding into the area. Godfrey (2003) also commented that, even though no commercial fishery exists in the area, the intensity of poaching had spread eastwards, as was also mentioned by Hauck and Sweijd (1999), and that poaching in the Eastern Cape Province, especially in the Port Elizabeth municipal area, was escalating to scales similar to those in the south-western Cape (Fig. 1.3B). Crime intelligence reports estimated that between 5-10% of illegal harvesting was intercepted by compliance operations, and Godfrey (2003) equated this to be approximately 120 tons whole weight of abalone poached in the Eastern Cape in 2001 alone. It was also noted that, in contrast to the south-western Cape, large rural communities exist in most parts of the Eastern Cape Province, living by traditional subsistence agriculture and resource harvesting with shallow-water marine resources being utilized for food and income (Godfrey, 2003). The increase in organized poaching has made abalone a favoured target not only to organized poaching syndicates but to these subsistence fishers too; harvesting of marine resources by this group is however limited to spring low tides as many are unable to dive (Godfrey 2003). To date however, most studies on *H. midae* have been focused on emergent populations subtidally, at a limited number of sites along both the south east/ east and south west/ west coasts, or have been focused on the culture of abalone (Newman 1966, Newman 1968; Tarr 1993; Britz and Sales 2001), while investigations on intertidal populations, juvenile and recruit variation and growth are limited.

1.2.2 *Turbo sarmaticus*

Turbo sarmaticus belongs to the family Turbinidae (turban shells); species in this family are characterized by a hard calcareous operculum (Foster 1997; Branch *et al.* 2002). As with the Haliotidae, the Turbinidae have a world wide distribution, inhabiting both the intertidal and

subtidal zones, but being primarily restricted to hard substrata (Joll 1980; Worthington and Fairweather 1989; Ompi 1994; Pulfrich and Branch 2002; Ward and Davis 2002). The Turbinidae tend to be most conspicuous and abundant in temperate and tropical waters (Pulfrich and Branch 2002). Turban shells are harvested for their meat, but have remained a small fishery component, and although they are a common component of intertidal and subtidal invertebrate communities world-wide, the Turbinidae have not been extensively studied (Bruton *et al.* 1991; Ward and Davis 2002). However, aspects such as reproduction, growth, spawning, seeding and population dynamics have been investigated (Joll 1980; Worthington and Fairweather 1989; Klumpp and Pulfrich 1989; Bruton *et al.* 1991; Davidson and Chadderton 1994; Ompi 1994; Dichmont *et al.* 2000; Dwiono *et al.* 2001; Ward and Davis 2002; Misra and Kundu 2005).

Turbo sarmaticus (Alikreukel or Giant periwinkle) is one of four endemic *Turbo* species commonly found in South Africa, with a distribution range from False Bay to the Transkei (Fig. 1.4). It is however most abundant along the south and east coasts (Bruton *et al.* 1991; Foster and Hodgson 2000; Branch *et al.* 2002). *T. sarmaticus* inhabits the lower littoral and shallow sublittoral regions, to a depth of approximately 8 m, and is the largest Turbinid found on the rocky shore in South Africa (Yssel 1989; Bruton *et al.* 1991; Branch *et al.* 2002). This herbivorous, dioecious broadcast spawner, can attain shell lengths of 120 mm and reaches its Minimum Legal Size (MLS) at 3-4 years of age (Foster and Hodgson 2000; Branch *et al.* 2002). At present, a limit of 5/person/day may be collected, at a MLS of 63.5 mm shell diameter or 73.7 mm shell length (Bruton *et al*. 1991).

Unlike *Haliotis midae, Turbo sarmaticus* is not exploited commercially; instead it is collected primarily by the subsistence sector for food and to a lesser extent by the recreational sector for bait (McLachlan and Lombard 1981; Yssel 1989; Bruton *et al.* 1991; Griffiths and Branch 1997). From archaeological records and shell middens, it has been found that the harvesting of *T. sarmaticus* by indigenous coastal people has been occurring since prehistoric times, in large numbers and at unknown rates (Lasiak 1991; Pulfrich and Branch 2002).

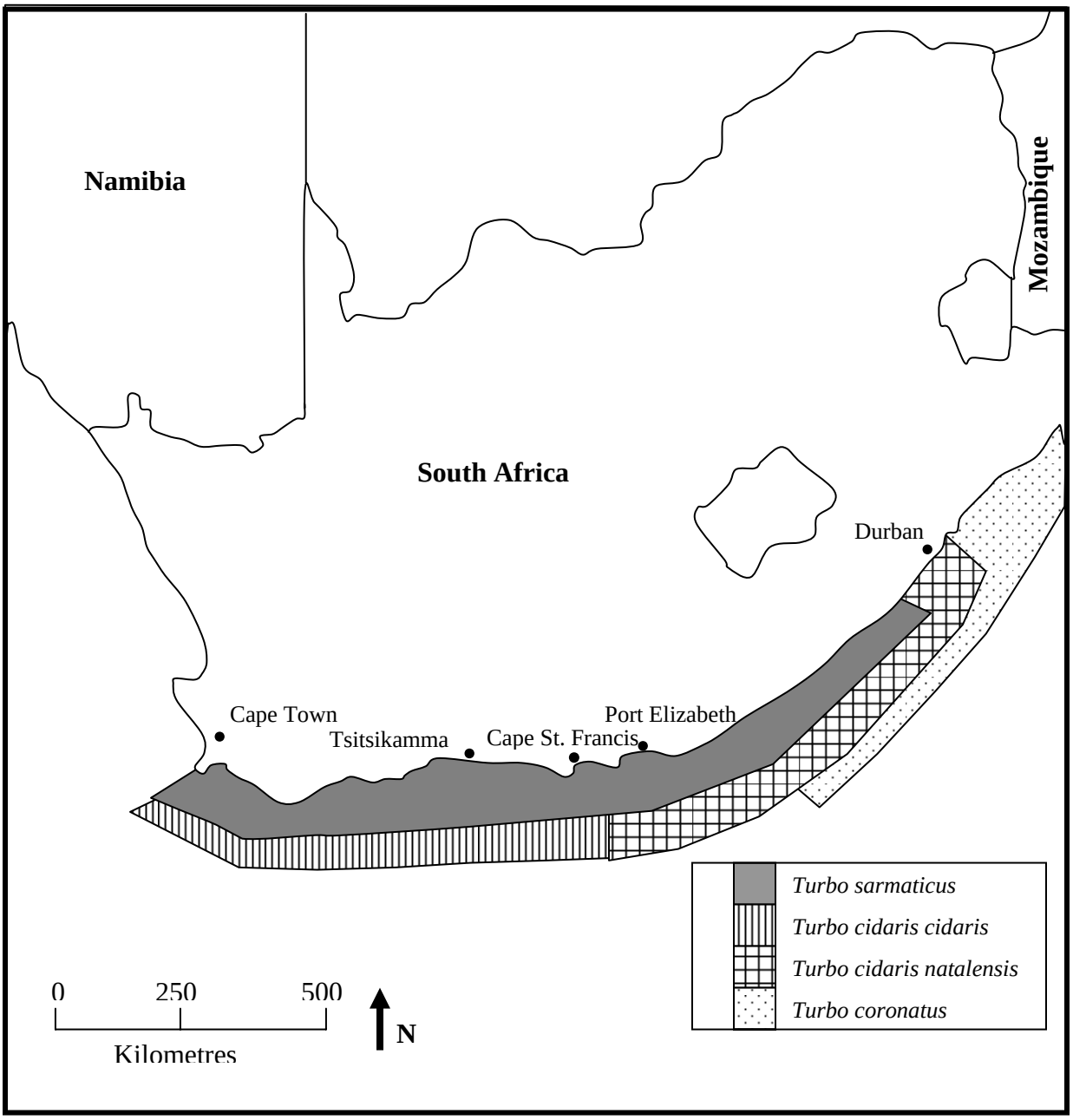


Fig. 1.4 Distribution of *Turbo* spp. along the South African Coastline (Foster 1997)

For many impoverished coastal communities, *Turbo sarmaticus* is a preferred food item (Lasiak 1991; Griffiths and Branch 1997; Foster and Hodgson 2000) and as mentioned previously, with high human population densities along the coast and high poverty rates, the intensity of gathering has increased (Griffiths and Branch 1997). This has resulted in the species becoming highly

exploited (Griffiths and Branch 1997; Foster and Hodgson 2000), with marked differences in size and standing crops being noted between exploited and unexploited sites (McLachlan and Lombard 1981; Yssel 1989; Branch and Moreno 1994; Foster and Hodgson 2000). Accessibility of the lower littoral region to subsistence fishers has allowed this species to become an easy target for exploitation.

Turbo sarmaticus is a common component of littoral and sublittoral communities on the rocky shore (22-36% of shore biomass according to McLachlan *et al.* 1981), is a prominent macroalgal grazer and its exploitation seems to be increasing, yet very few studies have been conducted on *T. sarmaticus* in South Africa. Studies on *T. sarmaticus* have covered energetics, biochemical composition, growth and production for populations in the Port Elizabeth area (Lombard 1977; McLachlan and Lombard 1980, McLachlan and Lombard 1981). Analysis of long term trends in the population structure of *T. sarmaticus* at Tsitsikamma Coastal National Park were undertaken by Yssel (1989) and population dynamics, potential yield and yield-per-recruit analysis have been discussed by Bruton *et al* (1991) and Pulfrich and Branch (2002). In these studies it was concluded that harvesting of *T. sarmaticus* was sustainable at the present MLS in the Cape St Francis region and that commercial harvesting would not be sustainable along the south west coast. Foster (1997) examined intertidal population structures and standing stocks along the south coast between Port Alfred and Cape Recife (Foster and Hodgson 2000), as well as growth, feeding biology, reproduction, consumption rate and digestibility of intertidal macroalgae (Foster and Hodgson 1998; Foster *et al.* 1999). Although most studies have occurred along the south coast, they have been limited in their spatial extent, with most work being concentrated between Port Alfred and Tsitsikamma (Fig. 1.4). In addition, knowledge on the extent to which the species is being exploited along the south east coast (where coastal rural communities are prevalent), is very limited.

Both *Haliotis midae* and *Turbo sarmaticus* are potentially susceptible to over-exploitation. They are sedentary animals, are restricted in their distribution to favourable reefs, inhabit easily accessible zones on the shore (intertidal and shallow subtidal), tend to be slow growing and long-lived, have a discontinuous distribution along the south and east coasts and like other haliotids or turbinids they may have irregular recruitment (Newman 1968; Yssel 1989; Bruton *et al.* 1991;

Tarr 1993; Wood 1993; McShane 1995; Foster 1997; Hobday *et al.* 2001). All of these characteristics make them prone to over-exploitation. *H. midae* in particular is highly susceptible to unsustainable harvesting due to its high economic value (Hobday *et al.* 2001).

The south east coast of South Africa is densely populated by impoverished rural communities. Exploitation of both abalone and alikreukel has become a concern in this region due to the increase in numbers of subsistence fishers that are utilizing the target species both for food and / or financial gain. In particular, for the subsistence sector, it is the infralittoral areas of the shore that are extensively exploited, as few rural collectors will harvest below a shallow snorkelling depth. Several lines of evidence now suggest that the regional exploitation of both *Haliotis mida*e and *Turbo sarmaticus* is becoming increasingly unsustainable (Foster 1997; Godfrey 2003).

The general aims of this study were to investigate aspects of the target species exploitation biology. In more detail, it was attempted to:

1. Determine the state of current exploitation patterns and of target species densities and to relate them to previous investigations (Chapter 2). *(Proudfoot et al. 2006 partially in press in the South African Journal of Science).*
2. Investigate variation in growth rates of the main 'problem' species (*Haliotis midae*) along the South African coast with a view to assessing the effectiveness of current national management strategies (Chapter 3).
3. Investigate the effects of over-exploitation on recruitment and survivorship of *H.midae* with a view to determining if fisheries recruitment failure is occurring (Chapter 4)
4. Evaluate and discuss regional information on the target species in light of existing management strategies and to suggest possible revisions thereof (Chapter 5).

CHAPTER 2

EXPLOITATION AND INFRALITTORAL POPULATION STRUCTURE OF *HALIOTIS MIDAE* AND *TURBO SARMATICUS* ALONG THE SOUTH EAST COAST

2.1 Introduction

Many species harvested by subsistence fishers have not been studied or monitored extensively and hence the information available on these organisms is scarce (Harris *et al.* 2002). Research on and monitoring of target organisms, for example *Haliotis midae* and *Turbo sarmaticus*, is essential, as subsistence fishers are dependant on the healthy status of the stocks they utilize (Harris *et al.* 2002). The Subsistence Fisheries Task Group (SFTG), appointed by Marine and Coastal Management (MCM), has identified that most true subsistence fisheries occur along the east and south coasts of the country, where the focus is primarily on invertebrate species in the intertidal zone and in estuaries (Cockcroft *et al.* 2002). To a large extent, however, our understanding of both exploitation patterns and their effects on resources is based on a few localized investigations (see references below), with large stretches of the coastline as yet unstudied. There is a need therefore, for the stocks of targeted species to be monitored, especially along the south coast where information on abundances of these marine invertebrates is restricted.

In the past, indirect indices, such as catch per unit effort (CPUE), has been used to determine relative stock abundances of species and in so doing monitor the health of many fisheries (Tarr 1993). However the use of CPUE have been shown to be an unreliable indicator of stock abundance, particularly for abalone, because they have patchy distributions, they are cryptic until they reach maturity, they aggregate and the fact that the handling time of divers catching abalone changes over time. All these factors make reliable estimates difficult (Breen 1992; Prince 1992; McShane 1996; Gorfine *et al.* 1998). Useful estimates of density, however, can be obtained using direct measurements such as transect surveys, by which a thin strip of reef is sampled with

contiguous quadrats (McShane 1994). These surveys provide a standard sampling unit which can be used for comparison and are not biased by diver effort or diver effort over time, but they do depend on atypically benign sea conditions and may be time consuming in structurally complex reef (McShane 1994; Gorfine *et al.* 1998). In addition length – frequency distributions that are unbiased and include a large sample size, are useful in determining the health of a population relative to other exploited populations (Schiel and Breen 1991; King 1995). An exploited population has its largest and most obvious (emergent) animals removed first as they yield a better return. Given that recruitment is unaffected and that small animals are continually added to the population, eventually a decrease in mean length of the population occurs (King 1995; Foster 1997). In contrast, a population that is thought to be healthy will have a higher proportion of animals over the legal size limit (Tarr 1993; Godfrey 2003). It is important to note, however, that spatial variation in growth (especially as seen in abalone), variability in settlement, recruitment and natural mortality in time and space may lead to biased size structures (Day and Fleming 1992; Wood 1993; Shepherd *et al.* 1998; Shepherd 1998; Godfrey 2003). Erroneous conclusions about the health of the stock may be made if these variables are not taken into account (Godfrey 2003).

Man has been shown to be an important predator in structuring communities and populations of target species around the world (Castilla and Durán 1985; Keough *et al.* 1993; Siegfried 1994), and, in South Africa, those few localized investigations that have been undertaken, have demonstrated the significant ecological effects of subsistence exploitation, especially in the former homeland region of the Transkei, where indigenous coastal communities supplement their diets with marine resources (Hockey and Bosman 1986; Hockey *et al.* 1988; Lasiak 1991; Lasiak 1992; Griffiths and Branch 1997). In these studies, subsistence fishers were shown to have a dramatic effect on populations of the brown mussel (*Perna perna*) and limpets (e.g. *Scutellastra granularis* and *Cellana capensis*). It was shown that both the relative abundance and mean modal size of target organisms were significantly reduced in areas of high exploitation pressure (Hockey and Bosman 1986; Lasiak 1991; Lasiak and Field 1995) and in extreme cases overexploitation also reduced intertidal biodiversity (Dye 1992; Dye *et al.* 1997; Lasiak 1998). In KwaZulu-Natal, a long term study by the Oceanographic Research Institute of South Africa (ORI) showed that overexploitation affected the abundance of organisms such as mussels (*P.*

perna), rock lobsters (*Panulirus homarus*) and oysters (*Striostrea margaritacea*), and that stocks appeared to be diminishing at a rapid rate (Tomalin *et al.* 1994; Kruger *et al.* 1997). In contrast to these studies from the east coast, information on exploitation and standing stocks of target species between the Western Cape and Transkei are scarce.

Along the south east coast, the giant periwinkle *Turbo sarmaticus* and the abalone *Haliotis midae* are amongst the most heavily exploited target organisms (Kaehler, *unpub. data*, chapter 1). Both species are vulnerable to legal and illegal subsistence exploitation due to the accessibility of the zones in which they are found. Because no extensive commercial fishery exists for either *H. midae* and *T. sarmaticus* in this area, very few studies have been conducted (Newman 1969; McLachlan and Lombard 1981; Bruton *et al.* 1991; Wood 1993; Foster and Hodgson 2000; Godfrey 2003). Those studies undertaken on *H. midae* in the Eastern Cape have been focused primarily on the subtidal and have indicated that high levels of fishing effort appear to have caused a decline in emergent abalone populations (i.e. the size at which abalone move out from their cryptic habitat, usually between 75-100 mm) and average size (Newman 1969; Tarr 1993; Wood 1993; Godfrey 2003). Similarly *T. sarmaticus*, a preferred food item for many impoverished communities (Foster and Hodgson 2000), is heavily exploited, with large specimens becoming increasingly difficult to find except in marine reserves (Yssel 1989).

The aims of this chapter are 1) to investigate the effects of exploitation on the populations of two of the most heavily exploited infralittoral organisms along the south east coast and 2) to determine whether aerial surveys of collector densities and other indirect exploitation predictors (i.e. number of households, distance to access points) may be used to predict exploitation hot-spots.

2.2 Materials and Methods

2.2.1 Study sites

For the purpose of this study, 20 survey sites presumed to have different exploitation pressure were chosen along a 169 km stretch of coastline, extending from Cannon Rocks to Cove Rock, in the Eastern Cape (Fig. 2.1). Of the 20 sites surveyed, seven were located in the former Ciskei Homeland region; these were Old Woman's, Mpekweni, Begha, Bloukrans, Hamburg 3, Hamburg 2, Hamburg 1 and Kiwane. Hamburg is one of two coastal communities, the other in southern Transkei, that have received special exemption permits from the national recreational or subsistence ban on collecting *Haliotis midae*, as part of an experimental attempt to develop small-scale commercial fisheries in previously disadvantaged communities. These permits however, have not been granted again since being issued in 2003. Nevertheless, there may have been large impacts on the stocks not only in Hamburg, but also on the neighbouring stocks of abalone. In addition, two of the twenty sites surveyed were located in the Tyolomnqa coastal reserve; these being Christmas Rock and Cove Rock; and so Nature Conservation is quite prominent in the area. All sites were either rocky headlands or wave-cut platforms, consisting of quartzitic sandstone reefs extending perpendicularly from the shore out to sea; with a number of boulders in the gullies between the reef ridges. However, of these 20 sites, only 18 were surveyed for *H. midae*. At the other two sites substratum was over grown by the colonial reef building polychaete, *Gunnarea capensis*, and experienced a large amount of sand inundation, thus providing unsuitable habitats for *H. midae* (Wood 1993). Sites were also chosen for their similarity in biological communities, which were characterized by the brown mussel *Perna perna*, the colonial polychaete *G. capensis*, the red- bait *Pyura stolonifera*, the Cape false limpet *Siphonaria capensis*, the granular limpet *Scutellastra granularis*, the pink-lipped topshell *Oxystele sinesis*, the Starfish *Marthasterias glacialis*, the cushion star *Patiriella exigua*, the giant chiton *Dinoplax gigas*, the venus ear *Haliotis spadicea*, and the plum anemone *Actinia equina*. Communities were also characterized by the pink encrusting coralline algae *Lithothamnion*, *Corallina* spp., and the foliose algae *Plocamium corallorhiza*, *Hypnea spicifera*, *Gelidium pristoides*, *Eklonia radiate* and *Ulva* spp.

In particular sites were chosen for their abundance of the sea urchin *Parechinus angulosus*. A strong positive relationship has been shown to exist between *P. angulosus* and juvenile *H. midae*, with urchins playing a role as nursery sites for juvenile abalone (Day and Branch 2000, 2002b). The study was further divided into biological surveys and exploitation estimates.

2.2.2 Biological surveys

Surveys were conducted in March- June 2003, February- April 2004 and September 2004. Surveys conducted were done in the infralittoral (i.e. lower intertidal and shallow subtidal zones, modified from Stephenson and Stephenson 1972) at wading depth (not > 1.5 m depth below chart datum), below the lower distributional extent of *Gunnarea capensis.* Surveys occurred during Spring Low tides for both species. This is the area most vulnerable to subsistence exploitation. Two 30 m transects parallel to the coast were employed for sampling. Along each transect, 15 one square metre quadrats were sampled at random, excluding non-habitable areas such as sand patches. All the *Haliotis midae* and *Turbo sarmaticus* found within each quadrat (including those in caves, crevices and under boulders) were scored and their shell lengths measured to the nearest 0.1mm using Vernier Calipers (Fig. 2.2a; Fig. 2.2b).

For further analysis, total densities were sub-divided into sub-adults, sexually mature and legal-sized densities. The minimum legal size (MLS) for both species is the minimum size which may be collected and may not pass through a ring diameter of 63.5 mm shell width or 73.7 mm shell length for *Turbo sarmaticus* (Bruton *et al.* 1991) and 114 mm shell width or 141mm shell length for *Haliotis midae* (Wood 1993) . Sexual maturity was taken to be the size at which 50% of individuals were sexually mature, this being 50 mm and 53.7 mm shell length for *T. sarmaticus* and *H. midae* respectively (Wood and Buxton 1996b; Foster 1997). Individuals with a shell length smaller than the size at 50% sexual maturity were taken to be sub-adult. Population size distributions were then determined.

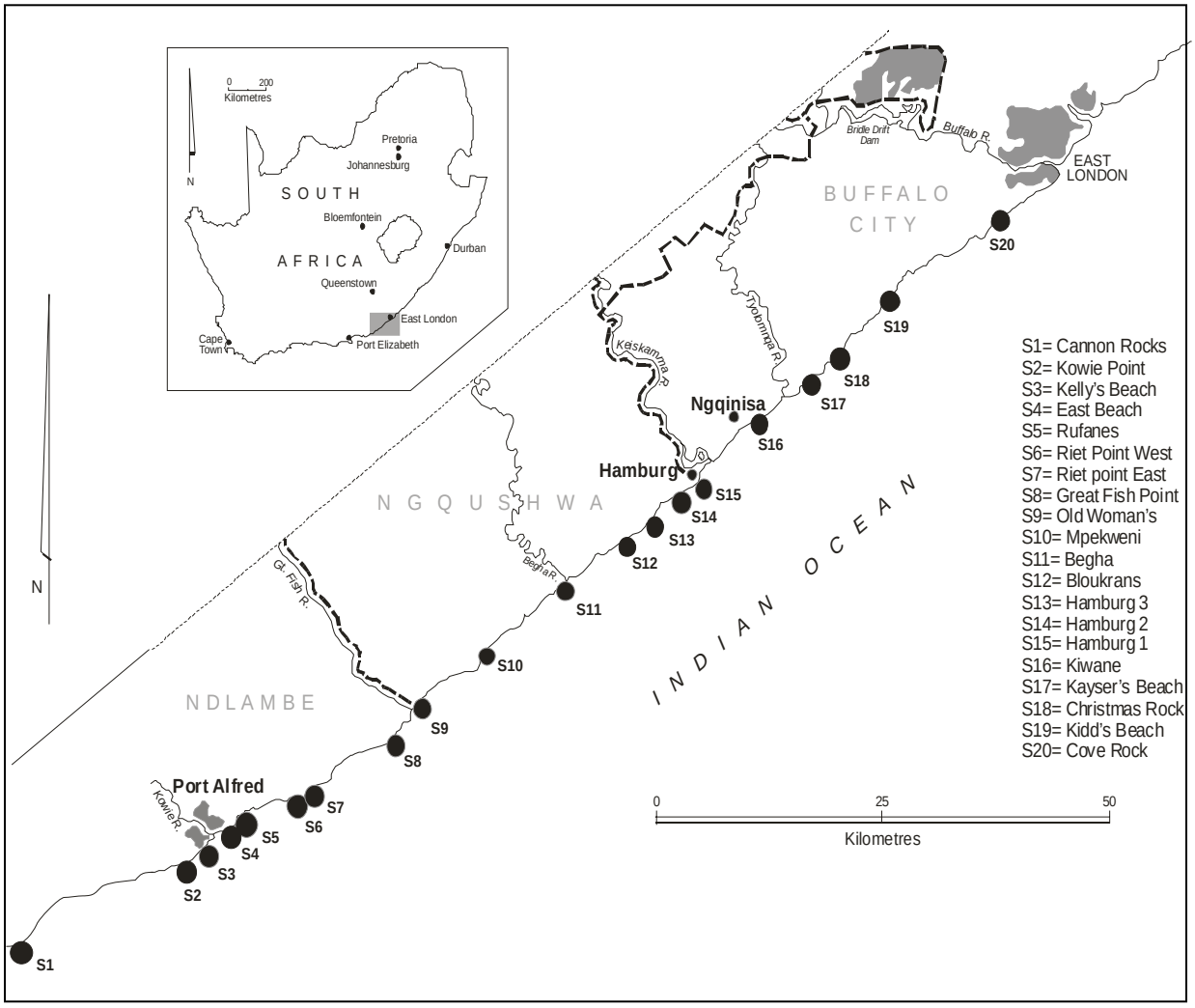


Fig. 2.1 Coastal region of the Eastern Cape surveyed, with the location of the twenty study sites.

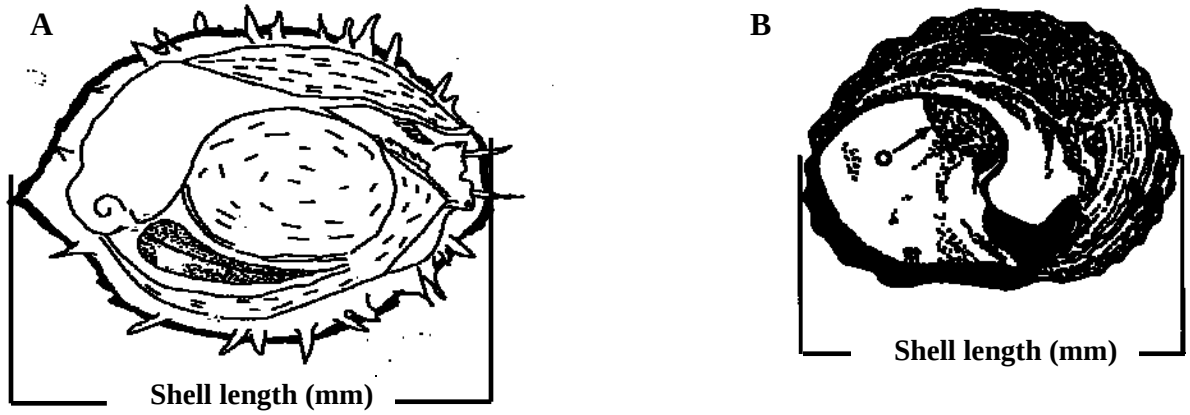


Fig. 2.2 A) Shell of *Haliotis midae* and **B)** *Turbo sarmaticus* indicating the measured dimension. O = operculum (Wood and Buxton 1996b; Foster and Hodgson 2000)

2.2.3 Exploitation estimates

Direct estimates of exploitation were obtained from seven aerial surveys conducted between Cannon Rocks (S1) and East London during 2002 - 2004. For each aerial survey the number of collectors (identified as those people on the rocks collecting or carrying bags), the number of fishermen (with rods), the number of recreational people (identified as those people on the beach swimming, walking and lying) and the number of seaweed gatherers were scored for each kilometre between Cannon Rocks and East London. From this information the number of collectors.km^{-1} was calculated for a 1.5 km linear distance of coastline on either side of each site. These distances were chosen as previous surveys in the area showed that subsistence collectors on average did not walk more than five kilometres along the shore to collect organisms (Kaehler, *pers. comm.)*. In the Eastern Cape most rocky outcrops are small (i.e. < 5 km in length) and are separated by sandy beaches. In order to obtain more indirect yet readily available predictors of exploitation pressure geo-referenced parameters of human demography (e.g. population density, unemployment density, average income etc.) were linked to the density of collectors on the shore. These data were provided by the Department of Surveys and Mapping and Population Census Data from 1996 provided by STATS S.A. and although these data are not up to date, increases are likely to have been uniform. These data were processed using ArcView 3.2; Environmental Systems Research Institute Inc. from which approximately 16 indirect estimates

were obtained. These included: the distance to the nearest access point (the distance from each site to the nearest beach entrance), the distance to the nearest beach access point (the distance from each site to the nearest beach foot path) and the number of households within a 2 km, 5 km and 7 km radius of each site. Also estimated were number of people.km^{-1}, the number of unemployed people.km^{-1} and the average annual income within a 7 km radius of each site. Of these 16 variables only six, were used due to co-linearity between variables. The variables used were the number of collectors. km $^{-1}$ within 1.5 km of coastline on either side of each site, the number of households, the number of people, the number of unemployed people.km^{-1} and the average annual income (R), all within a 7 km radius of each site, and the distance to the nearest beach access point (km).

2.2.4 Statistical analysis

ANOVA was performed to determine if density and maximum size varied significantly among sites (using Statsoft Statistica 7.0 and Statgraphics Plus 5.1). Assumptions of heterogeneity and normality for ANOVA were not met, even after square–root transformations (Underwood 1981). However, since group sizes were equal and large (n=30), ANOVA is thought to be robust against such heterogeneity (Zar 1984). ANOVA and non-parametric Kruskal-Wallis analysis were both performed on the data and both revealed similar results. Consequently only the results for the more powerful ANOVA are presented in this chapter. Indirect exploitation predictors were related to the direct predictor, density of collectors on the shore using Multiple Regression. Forward Stepwise Multiple Regressions were then performed between exploitation parameters (i.e. number of collectors. km^{-1} within 1.5 km of shore on either side of each site, number of households within a 7 km radius of each site and distance to the nearest beach access point (km)) and the densities and mean size of the largest 10% of the population of the two target species using Statgraphics. Due to non-linearity, multiple regressions were performed on log-transformed data.

2.3 Results

2.3.1 Biological surveys

Although both species sampled may not have been completely representative of the total population, (animals < 10 mm shell length are difficult to find and the sublittoral populations were not extensively surveyed), the sampling method was uniform and therefore comparable among sites (Foster 1997).

Densities of both species varied significantly among sites (*Haliotis midae,* $F = 7.50$, $P < 0.001$, $df = 17, 522$; *Turbo sarmaticus,* $F = 8.68$, $P < 0.001$, $df = 19, 580$). A Multiple Range Test further revealed that Riet River West and Cove Rock had significantly higher densities of *H. midae* than other sites. Eight homogenous groups were found, with overlapping groups existing between all sites besides Riet River West and Kiwane, which had the lowest densities (Table 2.1; Table 2.2). *T. sarmaticus* also displayed eight groupings, which tended to be homogenous with each other, with the exception of Riet River East which was significantly different from all other sites, with the highest density and the lowest densities at East Beach and Hamburg 2 (Table 2.1; Table 2.2).

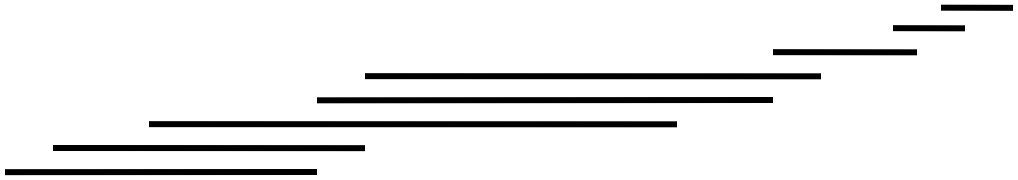
The maximum sizes of both species in each quadrat varied significantly among sites (*Haliotis midae,* $F = 10.77$, $P < 0.001$, $df = 17, 522$; *Turbo sarmaticus,* $F = 12.72$, $P < 0.001$, $df = 19, 580$). Multiple Range Tests further revealed seven homogenous groupings, with the maximum size of *H. midae* being greatest at Riet River West and Cove Rock and smallest at Hamburg 1, 2 and 3 (Table 2.1; Table 2.3). *T. sarmaticus* did not exhibit as clear a pattern, however overall Riet River East, Cove Rock, Christmas Rock, Cannon Rocks and Kidd's Beach had significantly larger maximum sizes, while Hamburg 2 and East Beach had significantly smaller individuals (Table 2.1; Table 2.3).

Table 2.1. Summary of population structures of *H. midae* and *T. sarmaticus* for this study and other studies along the Eastern Cape coastline, South Africa. [a] Foster and Hodgson (2000), [b] Wood (1993).

		Haliotis midae			*Turbo sarmaticus*		
Site name	Site	Maximum size (mm)	Mean density. m^{-2}	% Legal size	Maximum size (mm)	Mean Density $.m^{-2}$	% Legal size
Cannon Rocks	S1	130.1	0.76± 1.08	0	90.8	2.1 ± 1.97	15.9
Kowie Point	S2	119.6	0.7± 0.98	0	88.6	0.9 ± 1.3	44.4
Kelly's Beach	S3	97.4	0.67 ± 0.9	0	67.2	1.5 ± 2.4	0
East Beach	S4	-	-	-	32.7	0.03 ± 0.18	0
Rufanes	S5	93.3	0.77 ± 2.6	0	69.4	2.06 ± 2.84	0
Riet River West	S6	153.5	2.23 ± 1.8	2.9	85.9	1.13 ± 1.4	10
Riet River East	S7	115.1	1.03 ± 1.9	0	102.1	4.93 ± 4.9	12
Great Fish Point	S8	124.1	0.67 ± 1.9	0	104.4	0.9 ± 1.4	7.5
Old Woman's	S9	102.2	1.27 ± 1.6	0	79.4	2.37 ± 2.3	7
Mpekweni	S10	107.6	0.7 ± 0.9	0	87	2.2 ± 3.7	9
Begha	S11	59.3	0.67 ± 1.1	0	74.4	1.9 ± 1.9	1.75
Bloukrans	S12	-	-	-	91.4	0.3 ± 0.83	44.4
Hamburg 3	S13	63.9	0.03 ± 0.17	0	73.2	0.2 ± 0.38	0
Hamburg 2	S14	49.4	0.03 ± 0.2	0	28.3	0.07 ± 0.3	0
Hamburg 1	S15	90.5	0.3 ± 0.8	0	59.5	0.7 ± 1.4	0
Kiwane	S16	-	0	0	84.7	0.8 ± 2.02	25
Kayser's Beach	S17	85.1	0.57 ± 0.4	0	77.5	1.4 ± 1.7	7.14
Christmas Rock	S18	144.3	1.67 ± 1.77	2	84.3	2.13 ± 1.8	6.3
Kidds Beach	S19	98.4	0.67 ± 1.4	0	90.5	1.6 ± 1.9	29.2
Cove Rock	S20	125.5	1.9 ± 1.5	0	90.6	1.83 ± 1.5	11
Kelly's Beach [a]					60- 69	0.27	0
Bird Island [a]					110-120	1.5	32.2
Great Fish Point [b]		110	1.5	0			

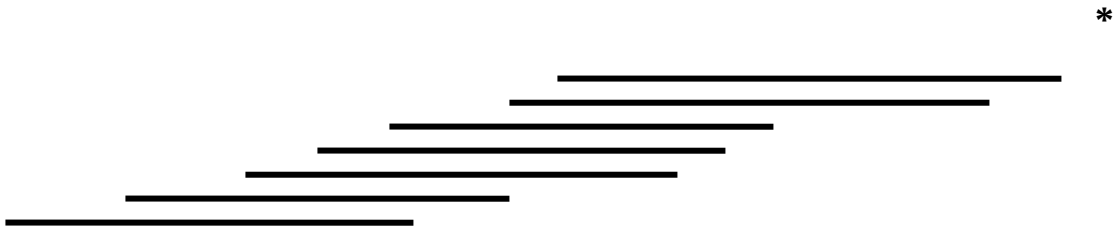
Table 2.2 Density results from a multiple range test to determine where significant differences occur along the Eastern Cape coastline, for both species. (— = homogenous groupings, * = significantly different from all other sites)

Haliotis midae



KI H3 H2 KA H1 GFP B KE KD KO CA RU MP RE OW CR C RW

Turbo sarmaticus

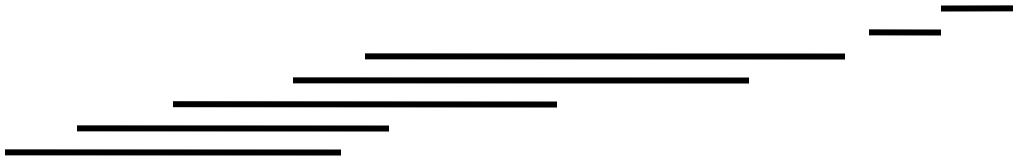


EB H2 H3 BK H1 KI GFP KO RW KA KE KD C B RU CA CR MP OW RE

CA = Cannon Rocks, KO = Kowie Rocks, KE = Kelly's Beach, EB = East Beach, RU = Rufanes, RW = Riet Point West, RE = Riet Point East, GFP = Great Fish Point, OW = Old Woman's, MP = Mpekweni, B = Begha, BK = Bloukrans, H3 = Hamburg 3, H2 = Hamburg 2, H1= Hamburg 1, KI = Kiwane, KA = Kayser's Beach, CR = Christmas Rock, KD = Kidd's Beach and C = Cove Rock

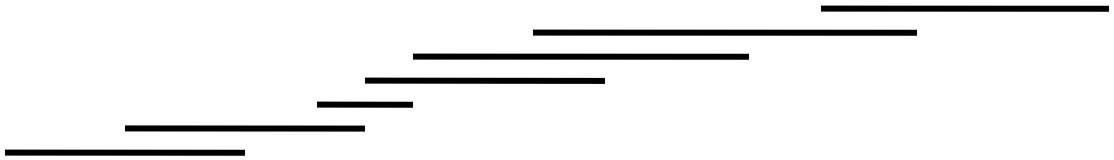
Table 2.3 Maximum size results from a multiple range test to determine where differences occur along the Eastern Cape coastline, for both species. (▬ = homogenous groupings)

Haliotis midae



KI H2 H3 KA H1 RU B KE RE KO KD MP GFP CA OW CR C RW

Turbo sarmaticus



EB H2 H3 H1 BK KI KE RU RW KO B KA MP GFP OW KD CA CR C RE

CA = Cannon Rocks, KO = Kowie Rocks, KE = Kelly's Beach, EB = East Beach, RU = Rufanes, RW = Riet Point West, RE = Riet Point East, GFP = Great Fish Point, OW = Old Woman's, MP = Mpekweni, B = Begha, BK = Bloukrans, H3 = Hamburg 3, H2 = Hamburg 2, H1= Hamburg 1, KI = Kiwane, KA = Kayser's Beach, CR = Christmas Rock, KD = Kidd's Beach and C = Cove Rock

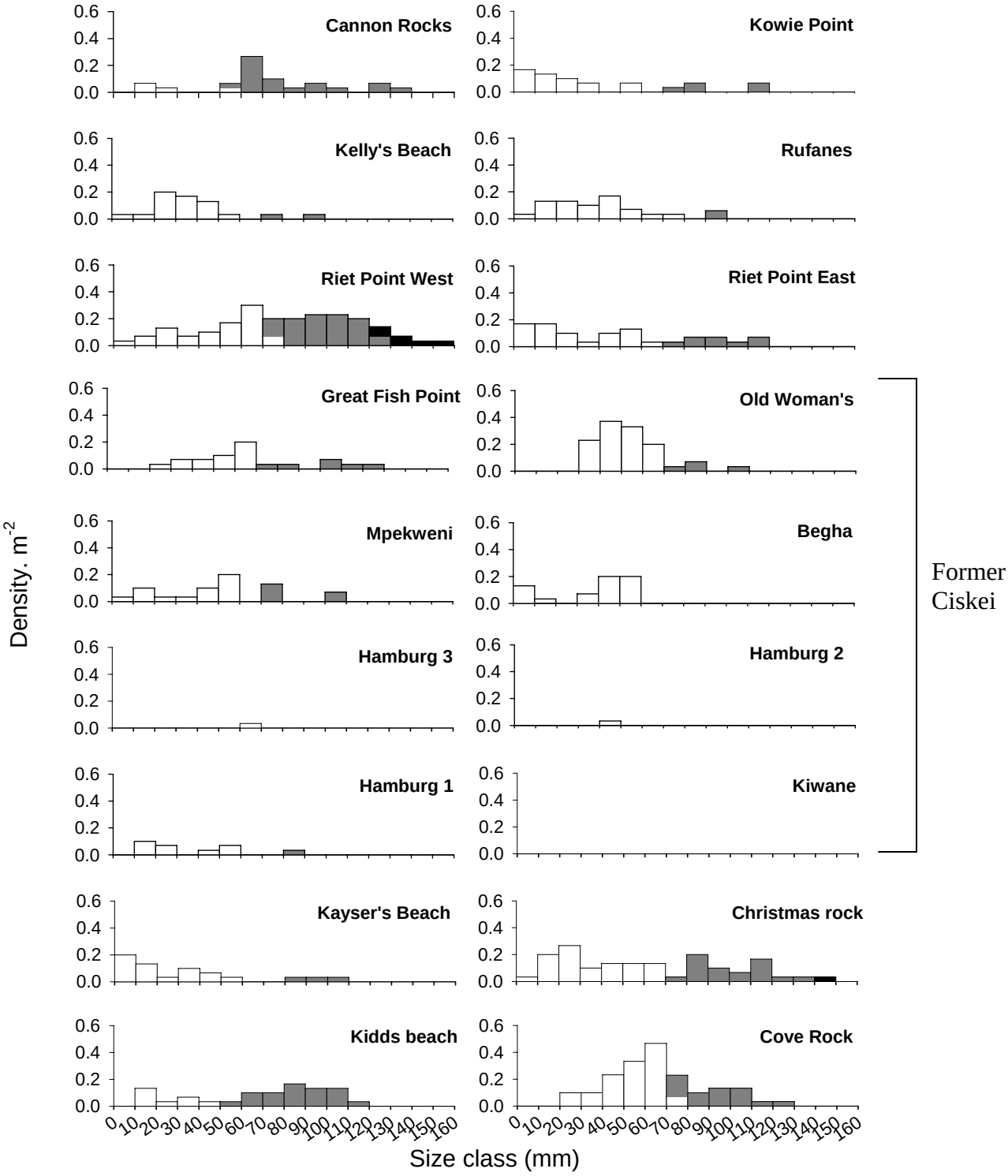


Fig. 2.3 Size frequency distributions (shell length in mm) of *H. midae* in the infralittoral region for 18 sites surveyed along the Eastern Cape coastline. (□ = <53.7 mm, sub-adult; ▒ = >53.7 mm, adult; ■ = >141 mm, legal size).

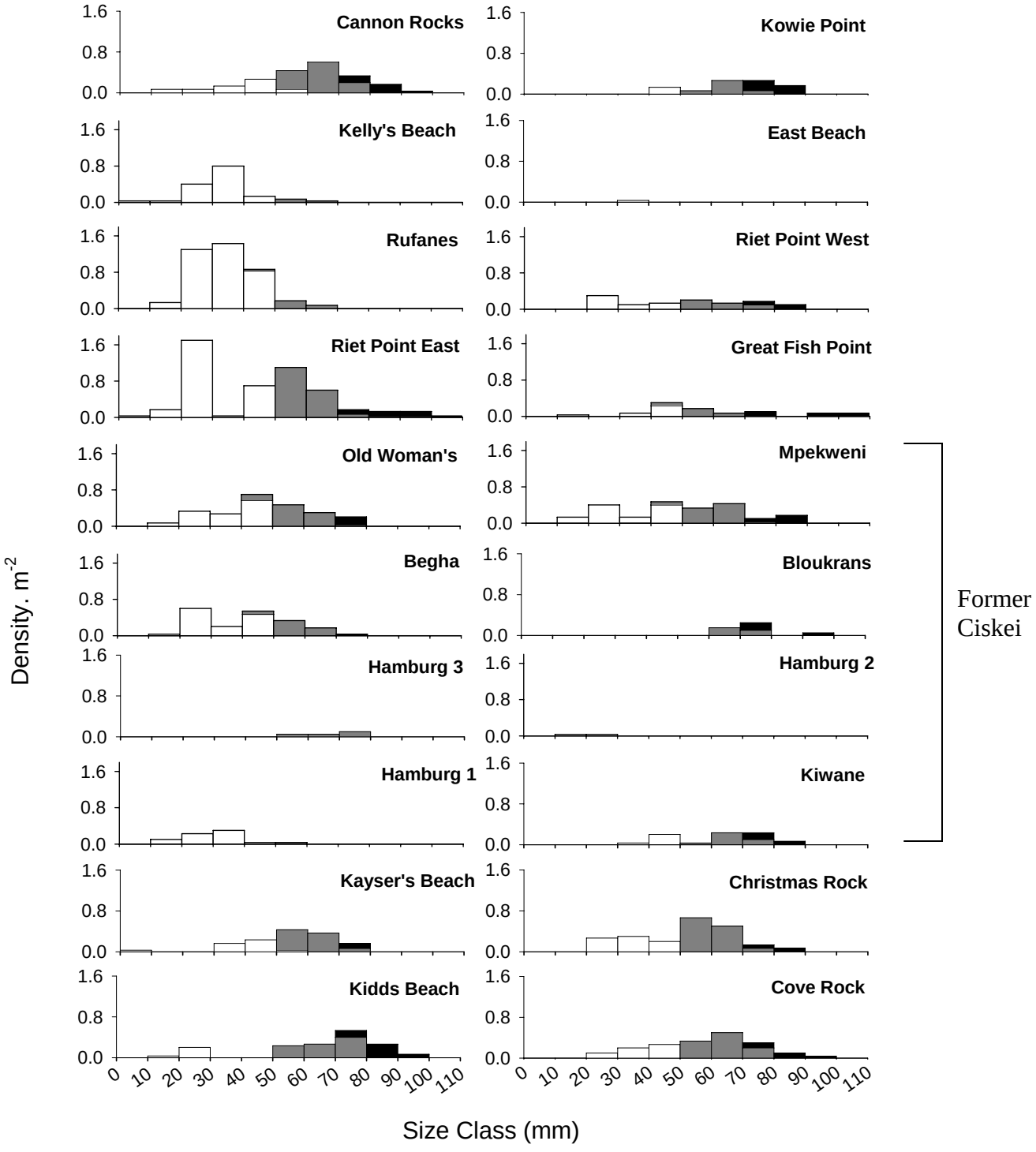


Fig. 2.4 Size frequency distributions (shell length in mm) of *T. sarmaticus* in the infralittoral region for 20 sites surveyed along the Eastern Cape coastline. (□ = <50mm, sub-adult, ▒ = >50mm, adult; ■ = >73.7 mm, legal size).

Haliotis midae at remote areas with difficult access, e.g. Riet Point West, occurred at the highest densities (2.23± 1.8 m^{-2}), and had the highest proportion of legal-sized animals (2.9%) and the largest maximum shell length (153.5 mm), which was close to the overall maximum size for the region (including subtidal) (Table 2.1; Fig. 2.3). High densities (1.67 ± 1.77 m^{-2} and 1.9 ± 1.5 m^{-2}), large maximum sizes (144.3 and 125.5 mm) and legal sized animals (2%) were also found within reserves (Christmas Rock and Cove Rock) (Table 2.1; Fig. 2.3). Populations with no legal-sized animals and maximum sizes ranging between 49.4 – 107.6 mm tended to be situated in the former Ciskei homeland and near Port Alfred (Table 2.1; Fig. 2.3). The lowest densities (0.67 ± 1.1 m^{-2}- 0.03 ± 0.17 m^{-2}) and sizes (49.4 - 63.9 mm) were at Begha and Hamburg 3 and 2, where no sexually mature animals were found, and Kiwane where no animals were observed (Table 2.1; Fig. 2.3). *Turbo sarmaticus* at Riet Point East, occurred at the highest density (4.93 ± 4.90 m^{-2}), and had a high proportion of legal-sized animals (12%) and one of the largest maximum shell lengths (102.1mm) (Table 2.1; Fig. 2.4). Cove Rock and Christmas Rock were once again found to have high densities (1.83 ± 1.5 m-2 and 2.13 ± 1.8 m-2) and large maximum sizes (90.6 mm and 84.3 mm) respectively. High proportions of legal sized *T. sarmaticus* (7 - 44 %) were found at most sites, except near the population centres of Hamburg and Port Alfred, where densities were lower and sizes smaller, with no reproductively sized animals: the smallest maximum sizes (28.3 and 32.7 mm) occurred at Hamburg 2 and East Beach respectively (Table 2.1; Fig. 2.4).

2.3.2 Exploitation estimates

The number of collectors within 1.5 km of each site ranged from 0 (Cannon Rocks) to 2.33 km^{-1} (Kiwane) (Table 2.3). The highest densities of collectors were found at areas near to large coastal settlements such as Hamburg (1.13-1.5 .km^{-1}) and the lowest densities were recorded near relatively secluded areas and reserves such as Riet River Point and Christmas Rock (0.19- 0.22. km^{-1}) (Table 2.4, Fig. 2.5A). At more secluded areas or wealthy holiday or retirement settlements, the number of households ranged between 93- 119 (Table 2.4; Fig. 2.5A). The total number of people followed a similar trend, with high numbers of people near large coastal settlements and population centres (3068- 17695) and low numbers in relatively secluded areas or near wealthy coastal settlements (247– 445.5) (Table 2.4, Fig. 2.5B). Density of unemployed

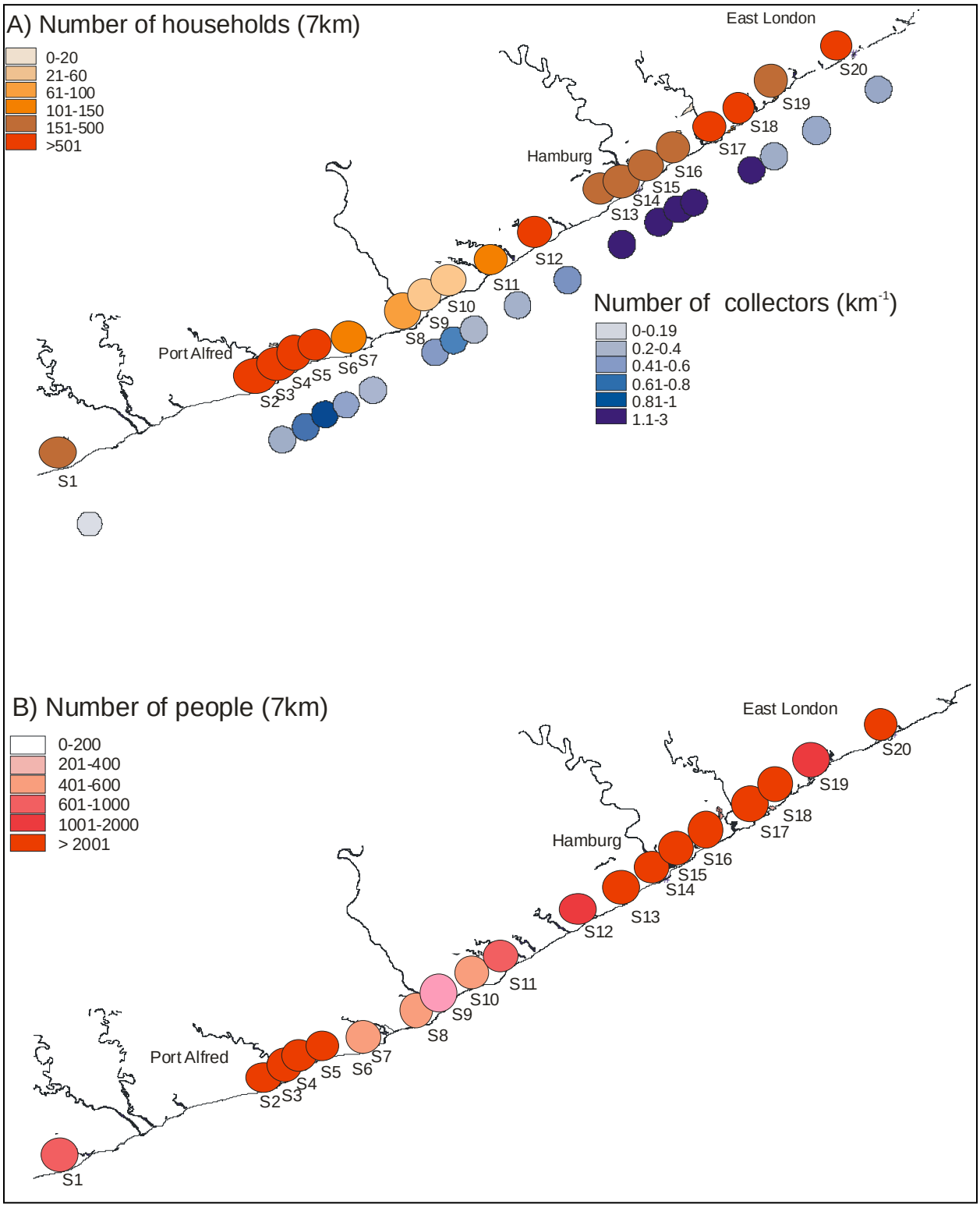
people ranged between 1- 8.km^{-1} near secluded (Great Fish Point) and wealthy coastal areas (Riet Point) to between 23-39.km^{-1} near population centres (Port Alfred) and large coastal settlements (Hamburg), whilst mean annual income varied from R3 417.72 – R 32 457.06, with lowest mean annual incomes occurring in the former Ciskei homeland region (Table 2.4; Fig. 2.5C, D). A significant relationship was seen to exist between the number of people and the density of collectors on the shore (R^2 = 0.29 P = 0.045), but no significant relationships were found for any other indirect parameter. Although we do not know the intensity of collecting at night, there was a trend of high collector densities where there were large numbers of people.

Multiple regressions were therefore performed between the population parameters of the two target species and both the indirect predictors and the direct predictor, collector density, to try to predict the state of the resource. Multiple regressions produced negative relationships between the total density of invertebrates and the direct predictor for both species (Table 2.5; Fig. 2.6A). Density of collectors was also negatively related to the mean size of the largest 10% of *Haliotis midae,* density of sexually mature animals for both species, the density of legal sized *Turbo sarmaticus* and the density of sub-adult *H. midae* (Table 2.5; Fig. 2.6C, E, H). Significant relationships did not exist for legal sized *H. midae* and sub-adult densities of *T. sarmaticus*.

Besides the direct predictor, indirect predictors also exhibited significant relationships in predicting the state of resources. The mean size of the largest 10% of the *Turbo sarmaticus* population was significantly related to the total number of people within a 7 km radius (Table 2.5, Fig. 2.6D). The total density of *Haliotis midae* was also seen to exhibit significant negative relationships with the number of unemployed people and the total number of people within a 7 km radius, and a model is predicted for these two variables and collector density (Table 2.5, Table 2.6, Fig. 2.6B). For *T. sarmaticus,* negative relationships exist between the densities of unemployed people and both the density of legal sized and the density of sexually mature animals (Table 2.5, Fig. 2.6I).

Table 2.4. Data on exploitation predictors used for Multiple Regression analysis.

		Direct predictors	*Indirect predictors*				
Site name	Site	Number of collectors (km^{-1})	Distance to access point (km)	Number of households (7 km radius)	Total number of people (7 km radius)	Number of unemployed people (km^{-1}) (7 km radius)	Mean annual income (R)
Cannon Rocks	S1	0	0.58	230	950	8	20008.1
Kowie Point	S2	0.38	0.55	2817	13404	39	23192.73
Kelly's Beach	S3	0.77	0.48	3525	17692.5	38	21147.37
East Beach	S4	0.91	0.78	3523	17695	38	21141.44
Rufanes	S5	0.47	1.03	2291	12438	31	14480.5
Riet River West	S6	0.19	1.46	119	407.5	2	20799.95
Riet River East	S7	0.22	1.15	124	431	2	26329.7
Great Fish Point	S8	0.41	3.3	93	445.5	1	14920.75
Old Woman's	S9	0.22	0.45	34	247	1.5	3417.72
Mpekweni	S10	0.36	0.79	46.3	497	14	7544.79
Begha	S11	0.22	0.86	146	950	38	12493.41
Bloukrans	S12	0.41	5.24	318	1873.5	35	6878.73
Hamburg 3	S13	1.13	0.59	336	2034	24	7072.71
Hamburg 2	S14	1.13	0.3	446	2774	23	7288.7
Hamburg 1	S15	1.5	0.71	491	3068	24.5	7284.55
Kiwane	S16	2.33	0.71	413	3030	23	5463.76
Kayser Beach	S17	1.36	0.19	622	3133	11	27343.18
Christmas Rock	S18	0.2	0.71	801	3317	11.5	24689.22
Kidds Beach	S19	0.4	0.13	431	1758	8	21142.48
Cove Rock	S20	0.36	0.39	2328	13192	34	32457.06


A) Number of households (7km)
0-20
21-60
61-100
101-150
151-500
>501
East London
S20
S19
S18
S17
Hamburg
S16
S15
S14
S13
S12
S11
S10
S9
S8
Port Alfred
S7
S6
S5
S4
S3
S2
S1
Number of collectors (km-1)
0-0.19
0.2-0.4
0.41-0.6
0.61-0.8
0.81-1
1.1-3
B) Number of people (7km)
0-200
201-400
401-600
601-1000
1001-2000
> 2001
East London
S20
S19
S18
S17
Hamburg
S16
S15
S14
S13
S12
S11
S10
S9
S8
Port Alfred
S7
S6
S5
S4
S3
S2
S1

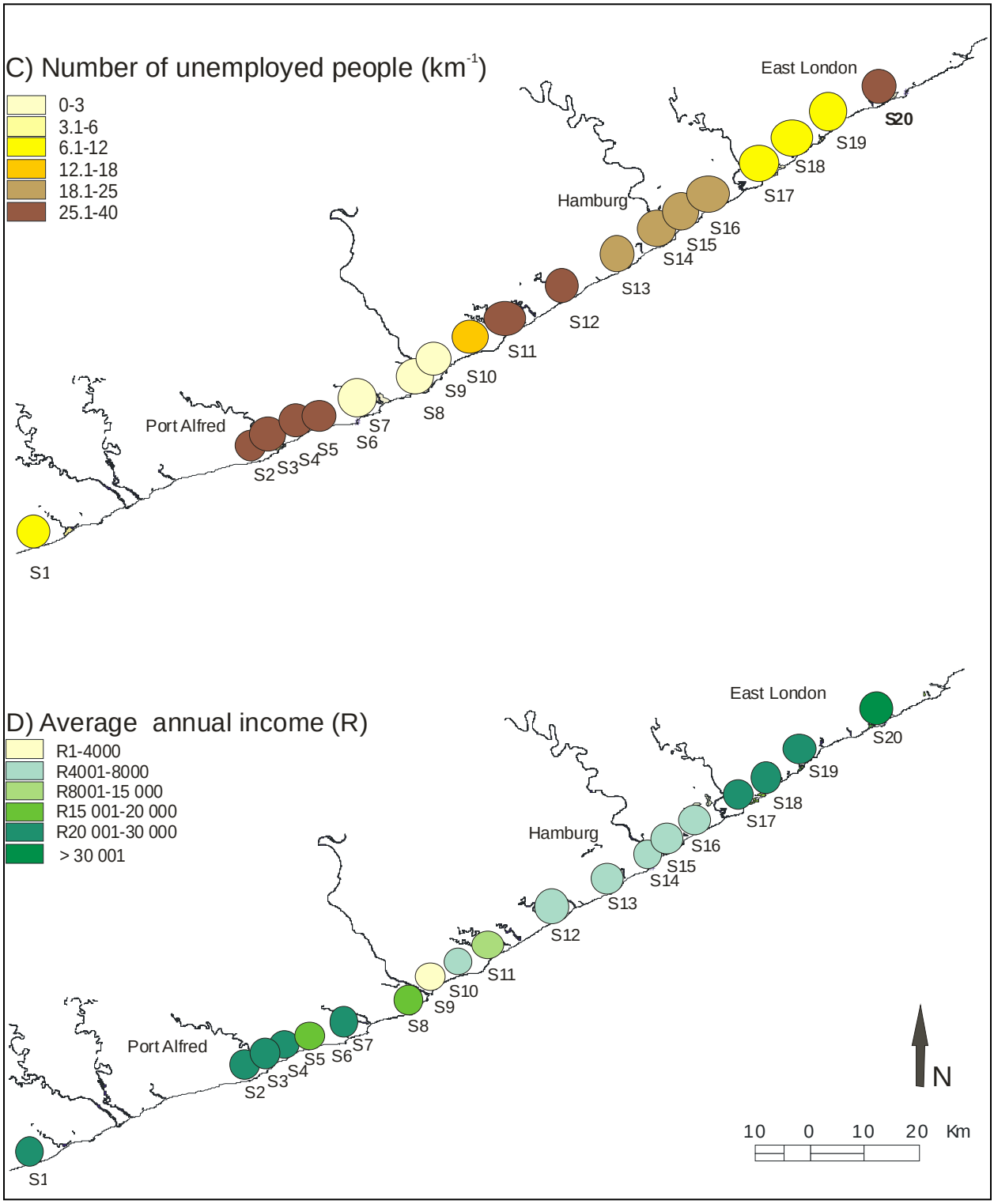


Fig. 2.5 Exploitation predictors determined for study sites along the Eastern Cape coastline: **A** = number of collectors (km^{-1}) and number of households (7 km radius); **B** = total number of people (7 km radius); **C** = number of unemployed people (km^{-1}) and **D** = average annual income (R).

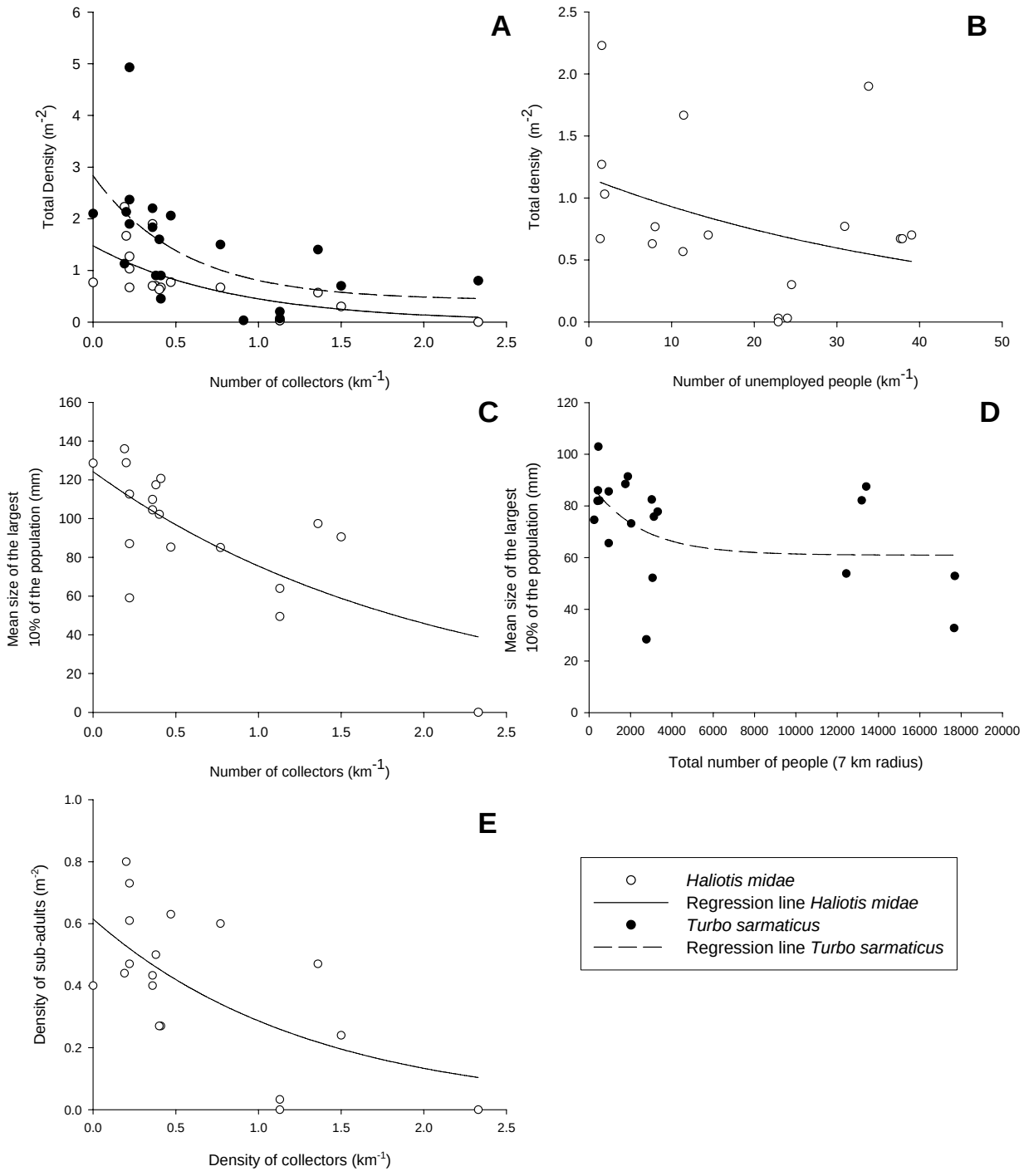
Table 2.5 Multiple regression analysis of potential exploitation indicators (i.e. number of collectors (km^{-1}), distance to access point (km), total number of people (7 km radius), density of unemployed people (km^{-1}) on population parameters (i.e. total density, density of sub-adults, density of sexually mature individuals, density of legal-sized individuals, mean size of largest 10%) of *T.sarmaticus* and *H. midae*. Only statistically significant models (at the 95% confidence level) are presented.

Haliotis midae

	Std. Err.	p-value
Total density (R^2 = 0.68; df 3)		
Model	0.09	0.001
Collector density (km^{-1})	0.17	0.001
Density of unemployed people (km^{-1})	0.09	0.048
Total people (7 km radius)	0.06	0.050
Largest 10% (R^2 = 0.45; df 1)		
Model	0.36	0.002
Collector density (km^{-1})	0.63	0.002
Sexually mature density (R^2 = 0.37; df 1)		
Model	0.1	0.007
Collector density (km^{-1})	0.18	0.007
Sub-adult density (R^2 = 0.44; df 1)		
Model	0.06	0.003
Collector density (km^{-1})	0.1	0.003

Turbo sarmaticus

	Std. Err.	p-value
Total density (R^2 = 0.33; df 1)		
Model	0.15	0.007
Collector density	0.27	0.007
Largest 10% (R^2 = 0.20;df 1)		
Model	0.13	0.046
Total people (7 km radius)	0.05	0.046
Legal sized density (R^2 = 0.33; df 3)		
Model	0.05	0.03
Collector density (km^{-1})	0.1	0.15
Density of unemployed people (km^{-1})	0.03	0.1
Sexually mature density (R^2 = 0.557; df 3)		
Model	0.1	0.006
Collector density (km^{-1})	0.2	0.05
Distance to access point (km)	0.18	0.01
Density of unemployed people (km^{-1})	0.06	0.05


A
Total Density (m-2)
Number of collectors (km-1)
B
Total density (m-2)
Number of unemployed people (km-1)
C
Mean size of the largest 10% of the population (mm)
Number of collectors (km-1)
D
Mean size of the largest 10% of the population (mm)
Total number of people (7 km radius)
E
Density of sub-adults (m-2)
Density of collectors (km-1)
Haliotis midae
Regression line Haliotis midae
Turbo sarmaticus
Regression line Turbo sarmaticus

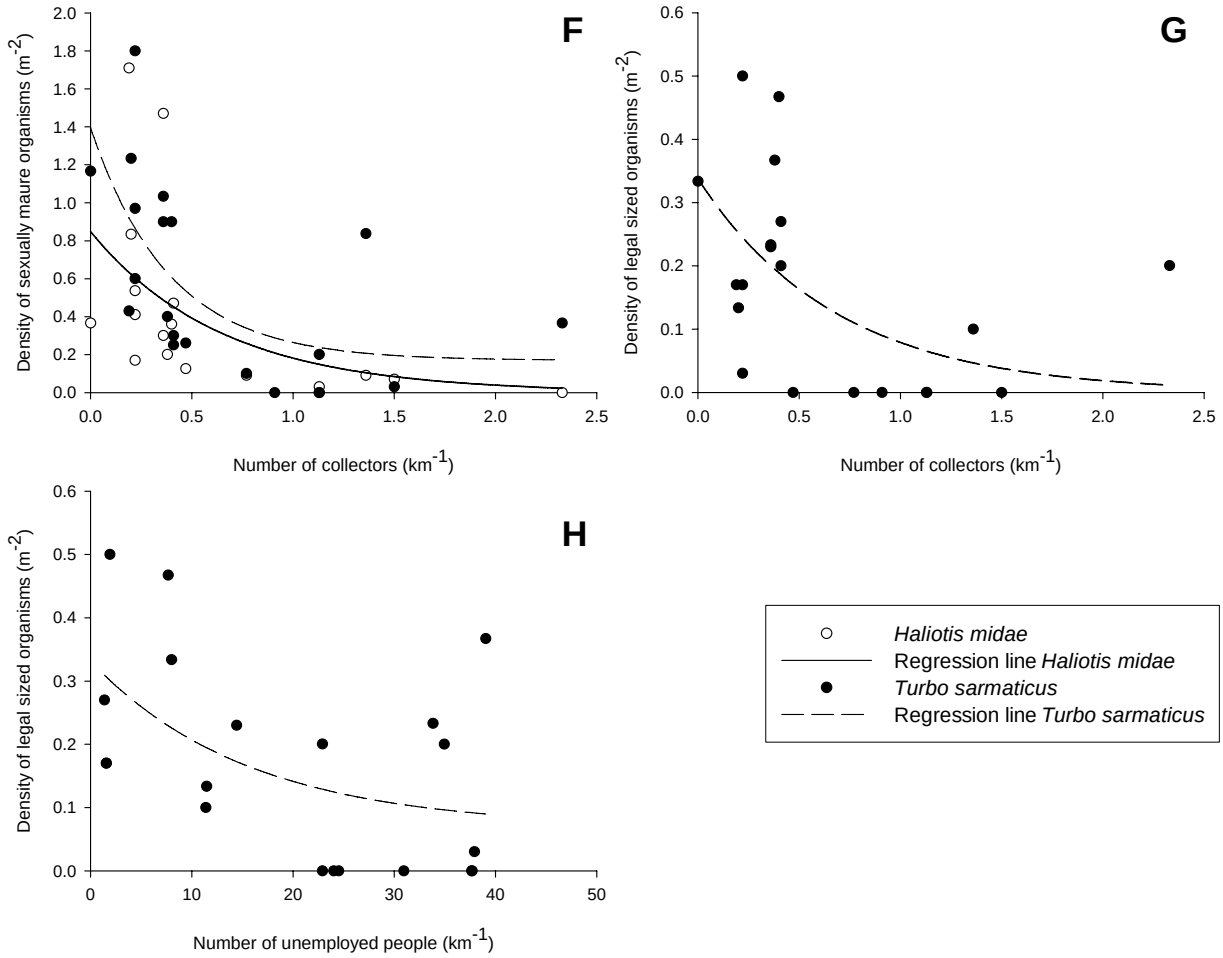


Fig. 2.6 Significant regressions ($p < 0.05$) for **A)** total density and the number of collectors; **B)** total density and number of unemployed people; **C)** mean size of the largest 10% of the population and the number of collectors; **D)** mean size of the largest 10% of the population and the total number of people; **E)** the density of sub-adults and the number of collectors; **F)** density of sexually mature individuals and the number of collectors; **G)** density of legal sized individuals and the number of collectors and **H)** the density of legal sized individuals and the number of unemployed people, for both *Turbo sarmaticus* and *Haliotis midae*.

Table 2.6 Summary of significant ($P < 0.05$) model equations for both *Haliotis midae* and *Turbo sarmaticus.*

Haliotis midae	Model
Total density	Log total density of *H. midae* = 0.136 - 0.726 x Log collector density – 0.184 x Log density of unemployed people + 0.135 x total number of people (7 km radius)
Largest 10%	Log mean size of the largest 10% of *H. midae* population = 2.32 – 2.31 x Log collector density
Sexually mature	Log *H. midae* sexually mature density = 0.233 – 0.55 x Log collector density
Sub-adult	Log sub-adult density *H. midae* = 0.212 – 0.364 x Log collector density
Turbo sarmaticus	
Total density	Log total density *T. sarmaticus* = 0.511 – 0.816 x Log collector density
Largest 10%	Log mean size of the largest 10% of *T. sarmaticus* population = 2.22 – 0.11 x Log total number of people (7 km radius)
Legal sized	Log *T.sarmaticus* legal sized density = 0.15 – 0.05) x Log density of unemployed people – 0.14 x Log collector density
Sexually mature	Log *T. sarmaticus* sexually mature density = 0.537 – 0.433 x Log distance to access point – 0.488 x Log collector density – 0.133 x Log density unemployed

The density of sexually mature *Turbo sarmaticus* was also positively correlated to the distance to the nearest access point (Table 2.5). Total density of *Haliotis midae*, density of legal sized and sexually mature *T. sarmaticus* can be expressed by the model equations in Table 2.6. Densities of sexually mature and sub-adult *H. midae* and total density of *T. sarmaticus* as well as the mean size of the largest 10% of the population for both species are also predicted by models expressed in Table 2.6.

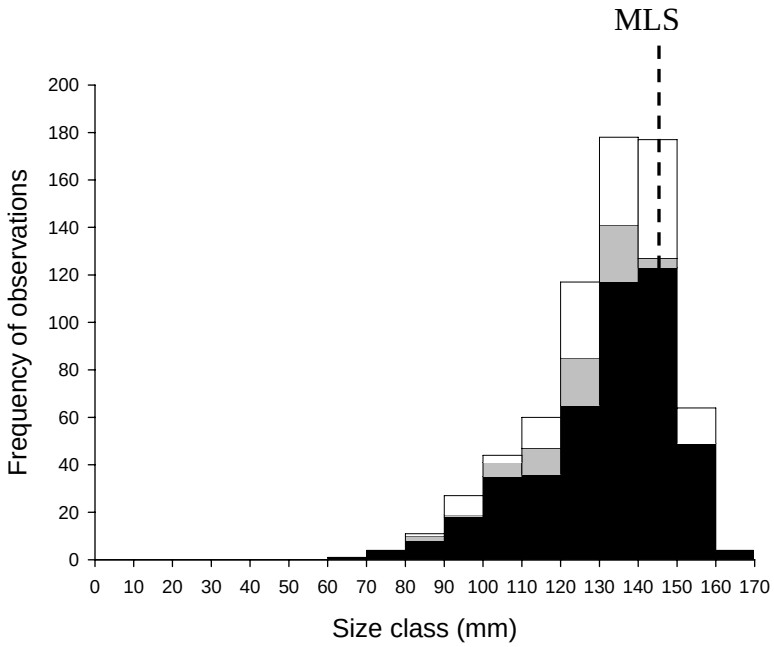


Fig. 2.7 Size range of harvested *H. midae* seen from middens of poached shells from "non-divers" at, Great Fish Point = ■, Mpekweni = ▒ and Rufanes = □

2.4 Discussion

2.4.1 Biological surveys

In this study, population parameters of both *Haliotis midae* and *Turbo sarmaticus* varied significantly among sites. Overall, densities were lowest and sizes smallest near the human population centres of Port Alfred and coastal settlements in the former Ciskei homeland region (i.e. Kelly's Beach, Rufanes, Begha and Hamburg 1, 2, 3), while higher densities and larger sizes were found at more remote locations, near wealthy coastal settlements and in coastal reserve sites (Old Woman's, Riet Point, Christmas Rock and Cove Rock). Population structures for both *T. sarmaticus* and *H. midae* were dominated by individuals in the middle size intervals, with few individuals in the smallest and largest size intervals (Fig. 2.3; Fig. 2.4), an indication of both the exploitation of the larger sexually reproductive individuals and a loss of reproductive output (Fogarty *et al.* 1991). According to Prince *et al.* (1988c), in relatively stable populations with

minimal exploitation, size structure is maintained by the effects of growth and natural mortality, with the smallest length intervals being the most abundant, the middle length classes the least abundant and the largest size intervals moderately abundant. All study sites were chosen for their similarity in physical and biological communities, and therefore it is likely that human exploitation pressure was at least partially responsible for the observed differences in population structure among sites.

Many intertidal taxa have decreased considerably in abundance and even disappeared in some locations due to over-exploitation (Hobday *et al.* 2001). In the former Transkei, for example, populations of *Perna perna* and the limpet *Cymbula oculus* have been shown to be highly susceptible to stock depletion as a result of traditional gathering (Van Erkom Schurink and Griffiths 1990; Lasiak 1991). *C. oculus* was shown to have smaller adult sizes, lower densities, smaller biomasses and lower survivorship at harvested sites in comparison to populations in Marine Protected Areas (Branch and Odendaal 2003). Marked differences in abundance, modal size and mean size of the brown mussel *P. perna,* were demonstrated between exploited and unexploited sites (Siegfried *et al.* 1985; Hockey and Bosman 1986; Lasiak and Dye 1989), while for the limpet *Helcion concolor* a reduction in maximum size could be directly related to excessive collection (Branch 1975).

Similar patterns of exploitation have been described in other parts of the world (e.g. Chile, Costa Rica and Australia), where human predation has been shown to have significant effects on densities, mean sizes, population structures and faunal and floral assemblages (Moreno *et al.* 1984; Castilla and Durán 1985; Oliva and Castilla 1986; Moreno *et al.* 1986; Ortega 1987; Durán and Castilla 1989; Godoy and Moreno 1989; Castilla and Bustamante 1989; Siegfried 1994; Keough and Quinn 2000). For example, *Siphonaria gigas* along the Pacific Coast of Costa Rica have reduced mean and maximum sizes at sites accessible to fisherman (Ortega 1987), *Fissurella crassa* and *F. limbata* (key- hole limpets) on the coast of central Chile were shown to exhibit differences in size distribution and density between harvested and non-harvested areas (Oliva and Castilla 1986) and in southeastern Australia, the removal of barriers in a marine reserve resulted in changes in sizes and abundances with *Turbo undulatus* and *Cellana tramoserica,* showing reductions of ~ 15% in mean size (Keough and Quinn 2000).

2.4.2 Exploitation estimates

In the current study, the demographic status of both target species was poorest in the vicinity of coastal settlements, with few or no sexually mature animals within 7 km of major population centres (Hamburg 1 and 2, Kiwane, Kelly's Beach, East Beach and Rufanes), suggesting that the two species were over-exploited at these sites. This is backed up by the high density of collectors, the easy access to most of these sites and the high density of unemployed people. Hamburg has also received special exemption permits in the past, which have allowed for the collection of abalone, resulting in heavy exploitation in this area. The number of people in these areas is high as they are situated near to large population centres or settlements which were seen to be positively correlated to the density of collectors (see also Hockey *et al.* 1988).

Total densities of both *Turbo sarmaticus* and *Haliotis midae* were significantly negatively related to the number of collectors on the shore, as well as the number of unemployed people and the total number of people within a 7 km radius of each site for *H. midae*. Collector density was the most important factor contributing to the total density of *H. midae* with significant but weak relationships being seen for the density of unemployed people and the total number of people. The lowest densities of abalone ranged between 0 – 0.3.m^{-2} in the vicinity of Kiwane and Hamburg where collector densities were high, while the highest densities ranged between 1.03-2.23.m^{-2} at relatively secluded areas such as Riet Point and in the coastal reserve, where collector density was low (Table 2.1; Table 2.4). For *T. sarmaticus*, total densities close to population centres (0.03 - 0.7 individuals.m^{-2}) were similar to those previously recorded from exploited sites (0.4 – 0.68 individuals.m^{-2}) (McLachlan and Lombard 1981; Foster and Hodgson 2000), while less accessible sites or coastal reserve sites exhibited typically higher densities (1.83 – 4.93 individuals.m^{-2}) than those reported from unexploited shores in previous studies (1.27- 2.85 individuals.m^{-2}) (McLachlan and Lombard 1981; Foster and Hodgson 2000). Densities were also similar to those found for *Turbo* species elsewhere (0.5 – 5 individuals.m^{-2}) (Davidson and Chadderton 1994; Ompi 1994). This suggests that while *T. sarmaticus* was over-exploited close to population centres, relatively unexploited refuge populations persist in more remote areas. Similar trends of reduced size and densities in response to human exploitation have previously been described for *T. sarmaticus* (McLachlan and Lombard 1981; Branch and

Moreno 1994; Griffiths and Branch 1997; Foster and Hodgson 2000; Pulfrich and Branch 2002).

While no comparative studies are available for infralittoral populations of *Haliotis midae*, exploitation has previously been shown to reduce subtidal densities (Tarr 1993; Griffiths and Branch 1997; Hobday *et al.* 2001), and shallow surveys conducted (< 2 m depth) in the Transkei at exploited sites by Fielding (1995), have shown similar densities (0.08 – 0.44 individuals.m^{-2}) to those determined in this study at sites with high collector densities (0 – 0.67 individuals.m^{-2}). In other regions of the world, for example, in the Sagay Marine Reserve, Phillipines, *H. asinina* was found to have densities ranging between 15.8 – 18.1 individuals.100 m^{-2} along protected reefs and densities ranging between 2.0 – 3.1 individuals.100 m^{-2} along unprotected reefs (Maliao *et al.* 2004), which is similar in magnitude to the differences found between exploited and unexploited reefs in this study.

The significant, but, weak relationship (R^2 = 0.20) between size of *Turbo sarmaticus* and the total number of people, can be explained by the presence of large animals at most sites, except near population centres and large rural coastal settlements (i.e. East Beach and Hamburg). This suggests that over-exploitation of *T. sarmaticus* only occurs at nearby areas with easy access and where there are a high number of collectors. Maximum sizes for both *H. midae* and *T. sarmaticus* were reduced at the sites that exhibited strong exploitation in the form of either collector density or high human population densities in the vicinity, which has seen in other studies where reduced maximum sizes were present in areas heavily exploited (McLachlan and Lombard 1981; Branch and Moreno 1994; Griffiths and Branch 1997; Foster and Hodgson 2000). For both *H. midae* and *T. sarmaticus*, large animals (>115 mm; > 73.7 mm respectively) were observed at secluded sites (Riet Point) and coastal reserve sites, while only small animals were present at sites near population centres and large coastal settlements (< 95 mm; < 59.5 respectively).

The two target species exhibited very different responses to exploitation pressure on individual size classes. A species collected for subsistence purposes would be affected by the number of unemployed people, the accessibility of a site, the density of collectors on the shore and human population density, as seen for *T. sarmaticus*. This is especially true for the density of collectors

on the shore, which was shown to be a significant predictor in most models for *T. sarmaticus.* Densities of sexually mature animals and legal sized animals were significantly correlated to collector density, density of unemployed people and distance to the nearest access point, which is not surprising, because *T. sarmaticus* has no commercial value and is typically harvested only by subsistence fishers within a radius of 7 km from their homes (Kaehler, *unpubl. data*). Of the 20 sites surveyed, 14 still retain a high proportion (11-44%) of legal sized animals in remote or coastal reserve areas, which is similar to that found for the marine reserve Bird Island (32%) (Foster and Hodgson 2000). Densities of sub-adults were not significantly related to parameters, which would be expected for an animal that is harvested for subsistence purposes, as larger organisms provide a better return in terms of food. Therefore harvesting tends to be size selective, as shown in the Transkei, where 50% of the animals taken are over 60 mm shell length, and therefore larger organisms will often be more affected by exploitation than juveniles (Lasiak 1991). Also, although sites of heavy exploitation may have had few sub-adult organisms in the infralittoral, inaccessible subtidal stocks and /or sites with refuge populations, would allow recruitment still to occur (see also Lasiak 1991; Hauck and Sweijd 1999).

On the other hand, a commercially valuable species would tend to be affected primarily by the density of collectors as seen by *Haliotis midae.* Other parameters such as distance to nearest access point, density of unemployed people, population density and annual income would not be important, as a commercially valuable species would be worth harvesting not only near population centres, but also in secluded areas. This was seen for abalone, where no relationship was found for legal sized animals and a very weak relationship was seen for sexually mature densities. This was primarily due to overall low densities of legal sized *H. midae* at all but two of the sites, Riet Point West (2.9%) and Christmas Rock (2%). While the scarcity of infralittoral *H. midae* may be due in part to the fact that larger abalone tend to aggregate in deeper waters (Newman 1969; Wood 1993; McShane 1996), the presence of legal-sized and/or larger numbers of reproductive organisms at the least accessible intertidal sites suggest that exploitation of *H. midae* is far more intense and widespread than exploitation of *Turbo sarmaticus*. This is seen by the middens of poached shells, where the majority of shells are under the legal size limit (Fig. 2.7). Due to the high commercial value of abalone, illegal harvesting has spread into remote and secluded locales (Herbig and Joubert 2002), where previously only local abalone were harvested.

It is now financially worthwhile to hire transport, equipment or even professional divers to exploit ever less accessible sites. While many professional poachers harvest subtidally, the removal of adults is likely to reflect the abundance of juveniles and sub-adults higher up the infralittoral. In rural areas however, most poaching occurs without SCUBA gear. Furthermore, with larger individuals becoming increasingly scarce, many smaller and illegally sized individuals are now being harvested (Fig. 2.7; Hauck and Sweijd 1999; Herbig and Joubert 2002).

A commercially valuable species may also exhibit a relationship between sub-adult density and collector density, where smaller sizes may be harvested or recruitment may be affected by reduced reproductive output by adult densities. This relationship was observed for *Haliotis midae,* with young abalone being scarce at exploited sites, especially in the vicinity of Hamburg. As previously mentioned, Hamburg has periodically been granted special exemptions permits from the national recreational ban on the collection of abalone and both infralittoral and subtidal populations of *H. midae* have been heavily exploited in this area for several years. As the harvesting of large numbers of small individuals is unlikely to be as profitable, the observed scarcity of juvenile abalone in the vicinity of Hamburg seems to suggest that the over-exploitation of sexually mature organisms, both intertidally and subtidally may have reached a point where local reproductive output is diminished and stocks may be failing to recover (see also Hobday *et al.* 2001).

Similar patterns of exploitation have been demonstrated on other shores, for example Durán *et al.* (1987) determined that on rocky shores at Las Cruces, Chile, intertidal populations of *Concholepas concholepas, Fissurella crassa* and *F. limbata* were more exploited in areas of high collector density. Keough *et al.* (1993) revealed that in Phillips Bay, Australia, there were differences in size distributions in marine invertebrates collected on a regular basis at certain sites compared to those where they were not; and Addessi (1994) showed that people concentrated in an area with a 200 m radius centred on a primary access on the southern coast of California, disturbed the rocky intertidal community more dramatically than areas farther from these points. In the Transkei, Hockey *et al.* (1988) described correlations between collecting

intensity and human population density, length of rocky shore and influences of geographical region and geology.

2.4.3 Conclusion

In the study area, both *Turbo sarmaticus* and *Haliotis midae* were locally heavily over-exploited. For *T. sarmaticus* however, 14 out of 20 study sites most likely acted as reproductive refuge sites, as they still supported large, legal-sized and sexually mature individuals. It is unlikely that remote populations of *T. sarmaticus* will be more heavily exploited in the near future, because this species is harvested only on a local scale by subsistence collectors who are concentrated in a small number of widely dispersed coastal settlements. Bruton *et al.* (1991) determined that in the Cape St. Francis region of South Africa, the yield potential of *T. sarmaticus* was sustainable at the exploitation level at the time of the study. However decreasing the MLS should not be considered, with the increase in human population density and high poverty, the sustainable use of *T. sarmaticus* may become threatened. In contrast, *H. midae* was far more negatively affected by exploitation. With the exception of Riet River West and the coastal reserve site Christmas Rock and Cove Rock, sexually mature individuals were scarce at most sites and even the abundance of sub-adults was reduced in areas of high exploitation pressure. Additional evidence also suggests that the condition of abalone populations is deteriorating. At the remote Great Fish Point, for example, infralittoral abalone densities have decreased by almost 60% since sampling was first conducted (Wood 1993), and since the current survey, a further estimated 6000 individuals were removed during a single poaching event in 2004 (Proudfoot, *unpubl. data*). With few exceptions, even the most remote locations are now being targeted for the collection of *H. midae* and the sizes of harvested individuals are steadily decreasing. Because the poaching of abalone is not restricted to the infralittoral, it is likely that even remote and subtidal refuge populations will soon be over-fished. Taking into account the reduction in reproductive output and the limited dispersal capabilities of haliotid larvae (Prince *et al.* 1987; McShane *et al.* 1988a), stocks of *H. midae* may soon reach a point where sustainability and recovery are unlikely.

On average, approximately 42% of the variability in population structure between sites could be explained by the density of collectors and indirect estimates of exploitation pressure. Although the collectors counted on the shore may not have been collecting *Turbo sarmaticus* and *Haliotis midae* specifically and most of the illegal collection of *H. midae* occurs at night (when aerial surveys could not be conducted), of the six exploitation predictors used, the direct measurement of collector density, was the most important and valuable in relation to densities and sizes of both species. Other factors may also influence the density and population structure of intertidal animals and much of the residual variation seen is likely to have been due to natural environmental variation in wave exposure, coastal hydrography and/or productivity, intraspecific zonation, algal dietary requirements and temperature (Newman 1969; Branch 1975; McQuaid and Branch 1984; Yssel 1989; Bruton *et al.* 1991; Foster and Hodgson 2000). Site specific factors may also play a role on the density and structure of intertidal animals, such as: permit systems for the area, policing intensity, conservation status and whether there are houses overlooking the beach or not.

The densities, population structures and maximum sizes of both species tended to be highest in remote locales and in coastal reserve areas and in this and other studies, it was noticed that most subsistence collection occurred in poorer rural areas where a large proportion of collectors were unemployed and the average income was low (Kaehler, *unpubl. data*). In contrast, coastal areas inhabited by wealthier holiday or retirement home owners, tended to retain healthier stocks, as local interest groups were generally able to ensure that no large-scale poaching activities occurred, as well as in marine protected areas where marine control is more prevalent. Exploitation predictors may therefore prove to be a useful tool in locating potential exploitation hotspots and more refined models may help in the future to facilitate decision making of remedial actions.

In this chapter it was found that exploitation of *Turbo sarmaticus* was not as extensive as exploitation of *H. midae*, and due to the fact that they have no commercial value, remote populations and subtidal stocks still persist. It was therefore decided to concentrate effort on *H. midae* only for further studies in this thesis.

CHAPTER 3

GROWTH OF *HALIOTIS MIDAE*

3.1 Introduction

Understanding the growth rates of commercially exploited invertebrates is fundamental to the proper management of their populations (Poore 1972; Bergen Wright 1975; Keesing and Wells 1989). Growth rates are important as they provide information for estimating sustainable yields through egg-per-recruit and yield-per-recruit models, and they determine the time lag between spawning and reproductive recruitment (Poore 1972; Day and Fleming 1992; Tarr 1993). This time-lag is important to population dynamics as it sets the period of pre-productive mortality and thus the proportion of juveniles surviving to reproductive recruitment (Day and Fleming 1992). Analysis of growth rates has also been used to set minimum legal sizes for many fisheries, which have then been applied to large geographic regions (Breen 1992; Naylor *et al.* 2006). Hence the accurate determination of growth proves to be crucial for mathematical models used for the formulation of management strategies (Poore 1972; Ricker 1975; Butterworth *et al.* 1989). This has led to the initiation of several studies on the growth of abalone species around the world (Leighton and Boolootian 1963; Forster 1967; Poore 1972; Bergen Wright 1975; Hayashi 1980; Prince *et al.* 1988a; McShane *et al.* 1988b; Tutschulte and Connell 1988; Keesing and Wells 1989; Siddeek and Johnson 1997; Catchpole *et al.* 2001).

The growth of abalone has in the past been measured in a variety of ways, the most common of these being: 1) mark-recapture, 2) cohort analysis and 3) growth band analysis. Each of these methods has its own benefits and pit-falls.

Mark-recapture is the most widely used method for the assessment of growth in abalone (Leighton and Boolootian 1963; Forster 1967; Newman 1968; Poore 1972; Bergen Wright 1975; Hayashi 1980; Shepherd and Hearn 1983; McShane *et al.* 1988b; Tutschulte and Connell 1988; Tarr 1993; Tarbath 1999). Tagging techniques are of one of two types: those that attach tags to the shell with adhesives and those that attach tags to the respiratory pores with fishing line, wire,

split pins or metal (Prince 1991). However the tagging of animals requires several assumptions: 1) that the tagging process does not affect growth, 2) that the tag itself does not affect growth, and 3) that animals tagged and recaptured are a random subset of the population. All of these assumptions have rarely been tested (Day and Fleming 1992). Sample sizes also need to be large, as recovery of abalone tends to yield low rates of returns despite the relatively sedentary nature of the species (Prince 1991).

Cohort analysis has been used to identify and isolate cohorts or size-classes and in so doing determine length-at-age (Shepherd and Hearn 1983; Day and Fleming 1992; Wood 1993; Siddeek and Johnson 1997). This is essentially the study of modal shifts in population length frequencies with time (Tarr 1995). There are now several computer programmes available that are utilized to analyze these data and provide maximum likelihood estimates of the mean lengths of the component cohorts (MacDonald and Pitcher 1979; Schnute and Fournier 1980; Siddeek and Johnson 1997). However, estimation of year classes is not usually possible unless the species has a narrow spawning season, short larval phase and rapid growth rate, so that the interpretation of cohorts is not erroneous due to the merging of cohorts that result when spawnings are close together and juvenile growth rates are highly variable (Newman 1968; Shepherd and Hearn 1983; Keesing and Wells 1989; Day and Fleming 1992; Wood 1993). Cohorts can also be confounded by the slowing of growth rates with age, which leads to modes coalescing, especially in multi-cohort stocks, such as abalone (Siddeek and Johnson 1997; Godfrey 2003), and there may be a certain degree of subjectivity in the identification of the cohorts themselves (Siddeek and Johnson 1997).

Growth band analysis is a direct study of either disturbance marks on the surface of the shell or of growth rings that are deposited during calcification, within the shell. Several species of abalone have visible marks on the surface of their shells that have been shown to be formed during periods of reduced growth, either during the spawning season or in winter (Forster 1967; Poore 1972; Shepherd and Hearn 1983). If growth marks are deposited at known intervals, growth parameters can be determined by measuring shell length at each mark (Day and Fleming 1992). The advantage of this method is that growth may be measured over a number of years without a long and costly field programme (Day and Fleming 1992). However, validation of

growth marks is required to determine whether the marks occur at regular time intervals, so that increments between marks represent a consistent time period (Day and Fleming 1992). This has been shown to be problematic as different species exhibit large variation in the formation of the marks and disturbances such as tagging may produce extra checks that are sometimes not clearly distinguishable from annual marks (Forster 1967; Shepherd and Hearn 1983; Day and Fleming 1992; McShane and Smith 1992). Hence other methods of estimating age are preferred.

Abalone shell growth can also be determined by counting growth rings laid down within the shell (Breen 1992; Turrubiates-Morales and Castro Oritz 1992). As molluscs grow, they deposit layers of nacre in the shell, which consist of alternate layers of conchiolin (dark) and aragonite (light) and can be seen as rings of different densities (Turrubiates-Morales and Castro Oritz 1992; Wood 1993). By grinding down the tip of the spire, Muñoz Lopez (1976) estimated growth through these alternate layers of conchiolin and aragonite. He found that dark conchiolin was deposited in the winter, while the light aragonite was deposited in the summer for three species of abalone (i.e. *Haliotis corrugata, H. fulgens* and *H. rufescens*) and related the number of layers to shell length for *H. corrugata*, assuming that layers were annual (Day and Fleming 1992). From a different species, *H. rubra*, it was assumed that one growth ring is laid down each year and Prince *et al.* (1988a) found strong evidence for this in south-eastern Tasmania. However McShane and Smith (1992) studied populations in Victoria and found that this assumption could not be made in other parts of Australia. Validation of the number of rings laid down each year is therefore required, as growth rings may not be annual. Further problems have since been noted with this methodology as animals with boring organisms in the spire may provide unreliable counts due to extra layers being deposited around holes (Forster 1967; Prince *et al.* 1988a; Day and Fleming 1992), and older animals can prove to be more difficult to age as there may be masking of the rings which become compressed up against the prismatic layer in larger shells (Wood 1993). Methodologies used for internal growth band analyses are also time consuming and labour intensive. The preparation of acetate peels, thin sections for slides and grinding of the spire takes time and requires large effort. However, if growth bands have been validated for the species and a method is developed that requires little labour and reduced time effort; this method could prove to be useful for large-scale applications.

The South African abalone fishery is reliant exclusively on *Haliotis midae*, however information on growth in the wild is limited to a few studies, with the majority of these studies focused on single localities (Newman 1968; Wood 1993) and only one large spatial scale growth study has been conducted (Tarr 1995). In the Eastern Cape, only three sites have been studied: Great Fish Point, Bird Island and Cape Recife (juvenile growth) (Wood 1993; Tarr 1995; Godfrey 2003). Current management strategies for *H. midae* (size limits, bag limits, fishing quotas etc.) have been set on limited data from the west coast, and may be inappropriate for the rest of South Africa. As Wood (1993) suggested, a regional approach might be more appropriate when setting management strategies. Growth rates and maximum size have been shown to vary over a range of spatial scales (Shepherd and Hearn 1983; Day and Fleming 1992), and hence more information is needed on the growth rates of abalone around the South African coastline, as management models are frequently based upon biologically inappropriate information.

This study had two aims: 1) to estimate the growth rate of *Haliotis midae* on the south coast by employing three techniques: mark – recapture, cohort analysis and growth band analysis. In conjunction, which method was most useful for estimating growth was determined and a new technique developed for visualizing growth bands was validated. 2) To determine whether there is systematic variation in growth rates along the South African coastline, from the east to the west coast that may be used to develop regional management strategies.

3.2 Materials and Methods

3.2.1 Mark-recapture study

A tagging study was undertaken at Kowie Rocks, Port Alfred from June 2004 to August 2005 (Fig. 3.1A). The site was chosen as previous surveys revealed relatively healthy *Haliotis midae* populations i.e. the site was representative of the entire size range of *H. midae* (Chapter 2). This site consists primarily of quartzitic sandstone headlands with gullies that contained boulders between the reef ridges. The area chosen for tagging was surrounded by sand and hence, thought to be a good tagging site as abalone tend not to be tolerant of sand and therefore movement

would be restricted to the area of tagging (Tarr 1993; Foster 1997). Various techniques were employed for tagging *H. midae* as problems arose with certain tagging methods.

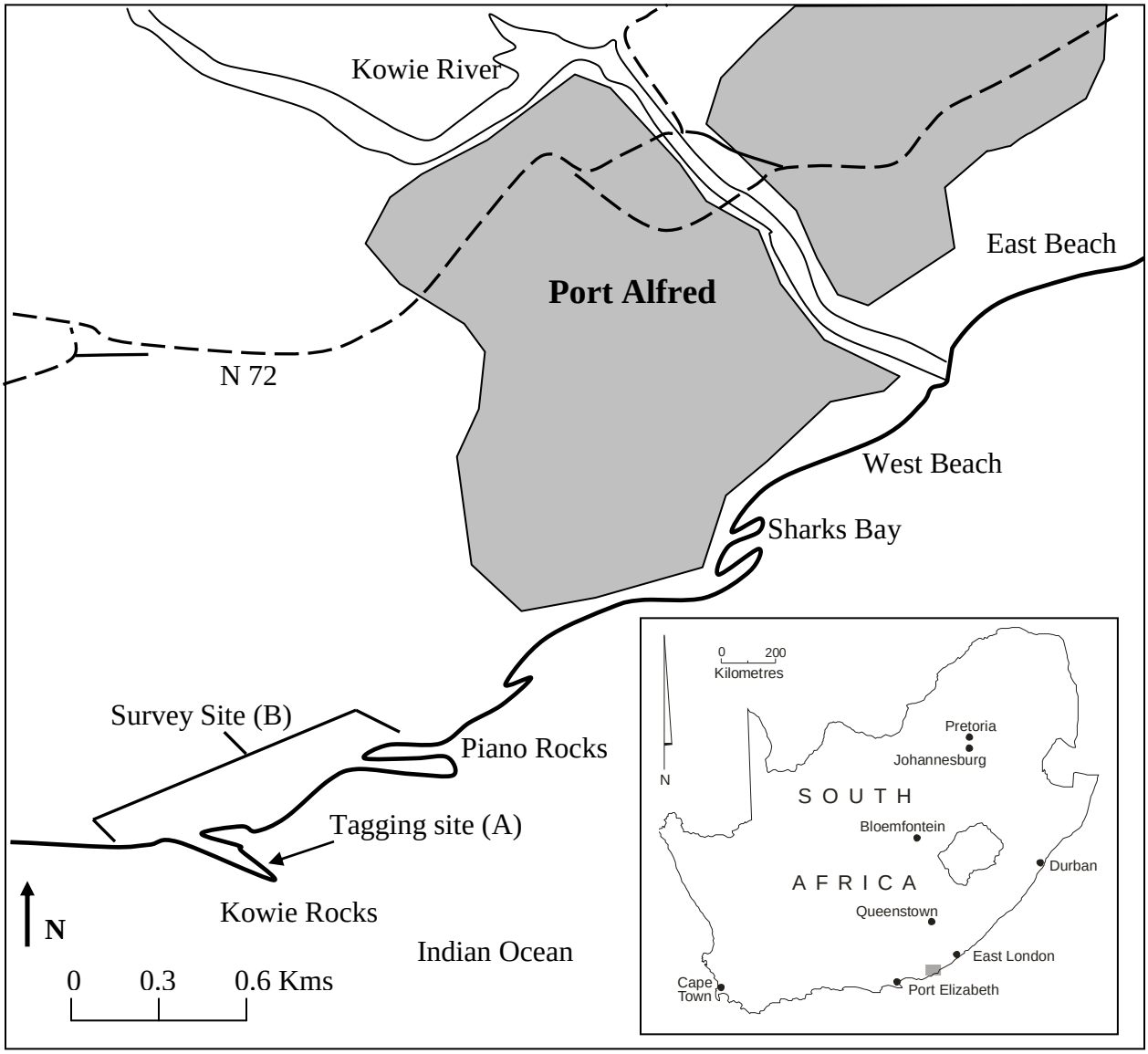


Fig. 3.1 Location of tagging site (**A**) for mark recapture study and survey site (**B**) for cohort analyses, Kowie Rocks, Port Alfred, Eastern Cape.

Tagging attempt 1 (Putty tagging in situ): In June 2004, during Spring Low tides, an attempt was made to tag abalone *in situ* using Pattex Epoxy Putty. Copper discs of 14 mm and 17 mm diameter with punched numbers and numbered bee tags were used to tag abalone. Abalone < 30 mm shell length were tagged using bee tags, 14 mm copper discs were used on abalone ranging between 31 – 100 mm shell length and 17 mm copper discs on abalone > 100 mm. Copper discs and epoxy putty were chosen due to their antifouling properties as described by Wood (1993). The study area at Kowie Rocks was searched for abalone by three snorkel divers. Once an abalone was located, a wire brush was used to clean the shell of algae and seaweeds, three helpers then prepared the epoxy putty and placed a numbered copper disc in the putty, which was then given to the snorkeller to place on the animal *in situ*. Shell lengths (mm) and tag number were then recorded. Due to the highly dynamic nature of the site, the cryptic habit of the organisms and difficulties with applying the putty under water, *in situ* marking met with only limited success (13 abalone shells were tagged). In order to increase the number of successful tags, it was therefore decided to remove abalone from the water prior to tagging.

Tagging attempt 2 (Putty tagging out of water*): Haliotis midae* were removed with blunt putty knives and specially designed hard plastic abalone removal tools obtained from Wild Coast Abalone, at Haga Haga in the Eastern Cape. Great care was taken to remove abalone rapidly and without damaging them as abalone contain no anticoagulation enzymes (Hobday *et. al.* 2001). Animals that were noticeably injured were not tagged and recorded; however, the incidence of injured animals was minimal. Four collectors searched the study area for abalone, during Spring Low tides in June 2004. Collected abalone were then scrubbed clean using a wire brush, and a copper disc was embedded in epoxy putty and placed on the top of the abalone shell (Fig. 3.2A). Once tagged, shell lengths were measured to the nearest 0.1 mm with Vernier Calipers and the tag number recorded. Abalone were kept in a shallow rock pool on mesh netting for approximately 15 minutes to allow the epoxy putty to harden. Once the epoxy putty was secure animals were placed back into the areas from where they were previously collected and held in place until they reattached themselves to the rock substratum. This method however was once again unsatisfactory as the putty tended to crack and the copper discs did not embed satisfactorily into the putty (33 animals marked). As a result, the use of a different adhesive was attempted.

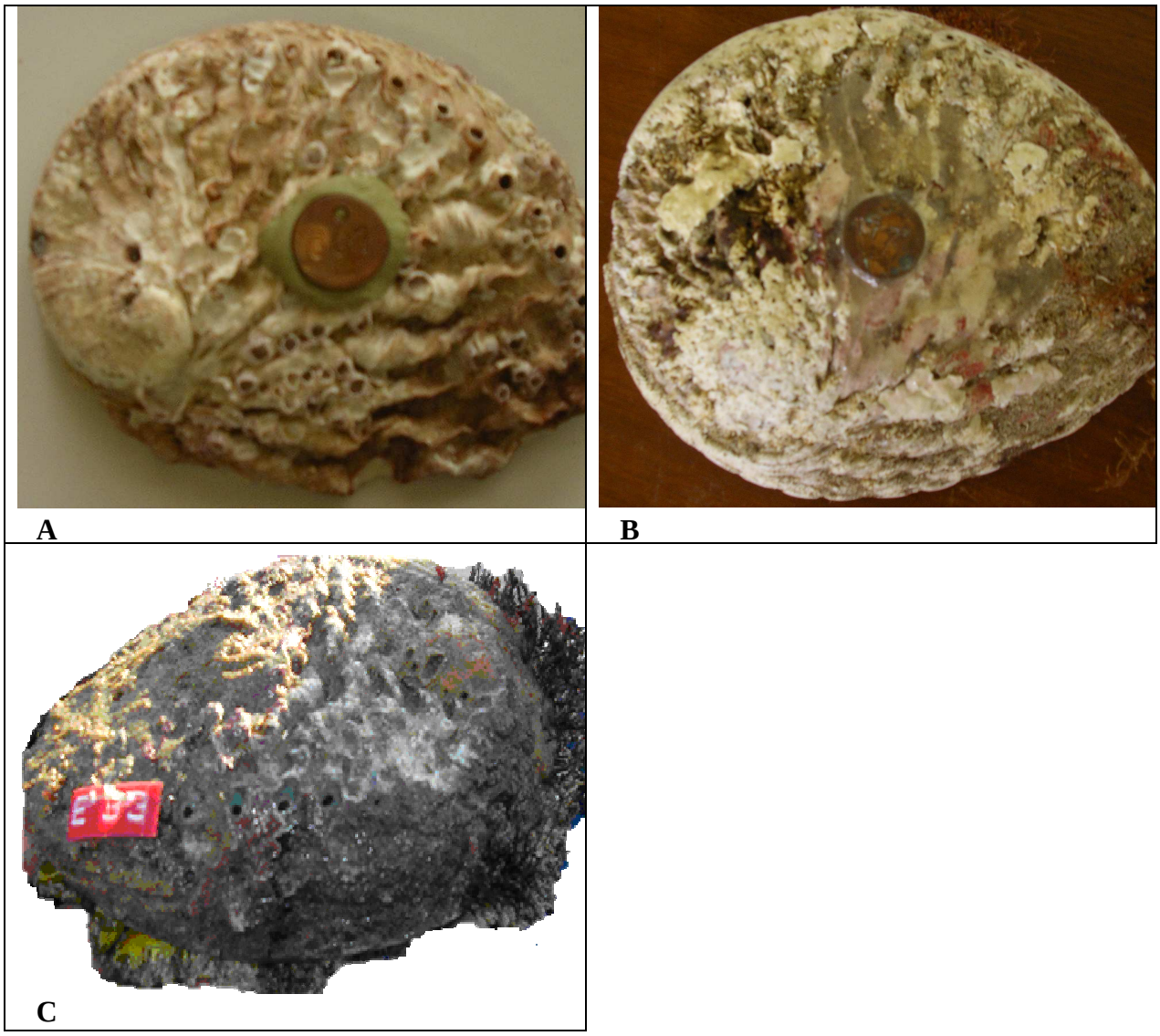


Fig. 3.2 Shell of *H. midae* illustrating the position and shape of tag **A)** embedded in epoxy putty, **B)** embedded in epoxy glue and **C)** using dymo tags attached through the respiratory pores.

Tagging attempt 3 (Epoxy glue tagging out of water): Four snorkellers collected all abalone found in the study area during Spring Low tides. Tagging occurred in July, August and October 2004 for approximately two days of the Spring Low tide cycle during each month, whenever sea conditions allowed. Removed abalone were scrubbed clean using a wire brush and numbered copper discs were then attached to the shell of the animal with Alcolin Rapid Epoxy Glue (Fig.

3.2B). Tagged shell lengths (mm) were measured and the tag number recorded. Animals were kept on a moist surface on mesh netting for approximately 20 minutes while the glue dried before being returned to the area of collection. In order to determine whether this tagging method was successful, animals were double marked. The second mark was made by filing a distinct shape into the shells of the animals (120 animals tagged).
This method proved to be more feasible than methods using putty, however, recapture rates were low and several double marked animals were found that had lost their tags. This method was eventually discarded in February 2005 due to the uncertainty of tag retention.

Tagging attempt 4 (respiratory pore dymo tags)*:* In April 2005 snorkellers collected abalone from the study area during Spring Low tides. Collected abalone were then marked using numbered plastic Dymo tags. Three helpers on shore threaded nylon fishing line through two respiratory holes on the abalone shell, preferably the 3rd and 4th respiratory pore, to prevent any interference to the physiology of the animal. A Dymo tag was then attached to the shell of the abalone using nylon fishing line (Fig. 3.2C). Shell lengths were measured and the Dymo tag number recorded. This procedure took approximately 10 minutes and once animals were tagged they were kept in rock pools until they could be released back into the habitat from which they had been collected. This method proved to be the most feasible of the three tagging techniques and was undertaken in April and May 2005 (100 animals tagged).

For all three techniques search and recovery of marked animals was undertaken by two divers monthly after tagging events during Spring Low tides in the area into which the abalone were released. Marked animals recovered were recorded and their shell lengths measured to the nearest 0.1 mm *in situ.*

Growth was assumed to follow the standard von Bertalanffy growth curve. To calculate growth from mark recapture data, the special von Bertalanffy equation, adapted by Shepherd and Hearn (1983) was fitted to the growth increment data using a non-linear least-squares algorithm. This gives the same parameter estimates as those of Fabens (1965) least squares algorithm (Shepherd and Hearn 1983) and is expressed as follows:

3.1)

$$\Delta L = \left(1 - e^{-K\Delta t}\right)\left(L_{\infty} - L_1\right)$$

Where, L_1 = the measured length at release, Δt = the period of time from marking to final recapture, K= the growth constant, L_{∞}= asymptotic length (the average maximum attainable size) and ΔL = growth over the time interval. For the standard von Bertalanffy model, estimation for t_0 (i.e. the hypothetical time at which length is zero) is required, however this is not available from length increment data and is therefore assumed to be zero (Tarr 1993).

3.2.2 Cohort analysis

This study was conducted at Kowie Rocks (Fig. 3.1B). Length-frequency distributions were sampled between September 2004 – September 2005 during spring low tides. The attempt was made to sample every three months, however owing to bad sea conditions, sampling occurred in September 2004, January 2005, April 2005 and September 2005.

The study site was sampled for two days consecutively during the Spring Low tides, in different study areas approximately 30 m apart, in order to increase sample size, while not measuring the same animals twice. On the first day the shallow subtidal zone was sampled where animals ranging between 50 mm and 150 mm shell length were found. This area was surveyed by two snorkellers for approximately three hours. On the second day the upper infratidal zone, i.e. the sublittoral fringe, was surveyed by two people, where all boulders and crevices were checked for abalone less than 50 mm. For each month of sampling new survey transects were chosen. Shell lengths of these animals were recorded to the nearest 0.1 mm using Vernier Calipers.

Cohorts were identified from length frequency distributions sampled using the software R2.0.0, and the mixture analysis method or MIX algorithm (Mixdist); a maximum likelihood principle developed by MacDonald and Pitcher (1979) to decompose a time series of length frequency

data into year classes. For each combination of modes identified, estimated parameters (means, proportions and standard deviations), standard errors of the parameters, the goodness-of-fit, chi-square statistic and the P-values were generated. The best solution of cohorts yields the best p-value or chi-square value. Data were smoothed over an average of three size classes and are presented in 3 mm shell length size classes. The resulting size-frequency cohort plots were then compared and cohorts assigned letters, in order to follow their modes.

From the resultant size–frequency cohort plots obtained in RMix, growth parameters were estimated, and assumed to follow the Schnute (1981) growth function (3.2). Software fitting, for example by Fisat and Multifan, was not used, as available packages only allow for the von Bertalanffy growth functions to be estimated. However, in the growth band section below (3.2.3) the Schnute (1981) model provided a much better fit for the data collected. The mean size determined for each cohort was related to age and then plotted to determine growth estimates and an age-length based key. Estimates of the Schnute growth function (where a ≠ 0, b ≠ 0), and L_∞ are expressed by the following equations:

3.2)

$$L(t) = \left[L_1^{\,b} + \left(L_2^{\,b} - L_1^{\,b}\right)\frac{1-e^{-a(t-\tau_1)}}{1-e^{-a(\tau_2-\tau_1)}} \right]^{1/b}$$

Where, *b* is a dimensionless parameter that relates to the ratio of the two heights or sizes of the sigmoidal curve, the bottom arc and the full S curve, the parameter *a* has units time $^{-1}$ and is also equal to the parameter *K* in the von Bertalanffy growth curve, L_1 and L_2 are the mean sizes at τ_1 and τ_2 respectively, τ_1 being the youngest age, *t*, i.e. age t can be computed from size $L(_t)$ (Schnute 1981).

3.3)

$$L_{\infty} = \left[\frac{e^{a\tau_2} L_2^{\,b} - e^{a\tau_1} L_1^{\,b}}{e^{a\tau_2} - e^{a\tau_1}} \right]^{1/b} \qquad a \neq 0,\ b \neq 0$$

3.2.3 Growth band analysis

In this study, an attempt was made to determine growth rates from internal growth bands of *Haliotis midae* from dead shells collected along the shore or in the intertidal zone. Preliminary investigations showed that alternate layers of dark (conchiolin) and white (aragonite) were visible in the nacreous layer through the shell whorl of *H. midae* (Fig. 3.3).

For each site, between 50 and 80 dead shells were collected, except for Great Fish Point where 99 shells were collected. Shells ranging from 20 - 190 mm shell length were collected from each site. Shells were washed clean and then, using a Logitech Ltd. CS10 thin section cut- off saw, the shells were cut from the edge of the shell nearest to the shell whorl and through the shell whorl, so as to include all growing layers (Fig. 3.4). Another cut was then made on the right hand side of the first cut and the section was then removed from the shell (Fig. 3.4). Sections were then viewed under low power magnification with a fluorescent microscope provided by the Rhodes University Electron microscopy Unit. A fluorescent microscope (Olympus UMWU 350-385) was used due to the ability of proteinaceous compounds to autofluoresce (Vakorina *et al.* 2005), and as conchiolin is a scleroprotein and aragonite is a fluorescent mineral, alternate layers of fluorescent conchiolin and aragonite could easily be seen (Thompson *et al.* 2000). Alternate layers of conchiolin and aragonite (dark and light) were counted three times by one reader using UV light for fluorescence. Discrepancies in the counting of layers led to the shell being rejected. Shells that were heavily infested with the boring polychaete *Polydora hoplura* were excluded as extra layers of nacre are said to be deposited around the boreholes for support and growth maybe retarded by infestations which may then lead to erroneous results (Prince *et al.* 1988a; Day and

Fleming 1992). Shells that were visibly eroded, i.e., had holes through the shell, were also excluded from analysis. This technique has not previously been used to age and estimate growth parameters of *Haliotis midae* and was compared to the more time consuming and more common thin-sectioning technique (Wood 1993).

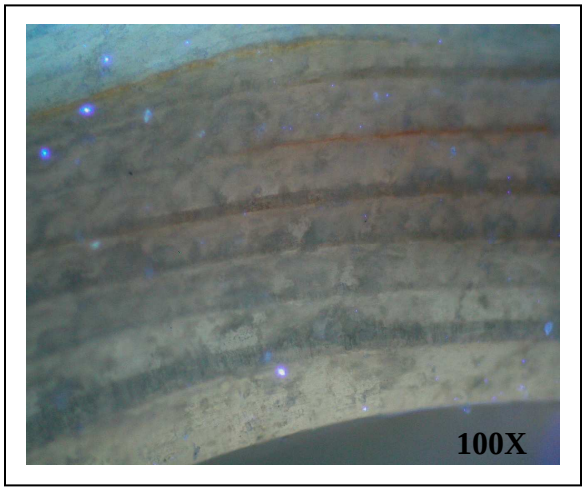


Fig. 3.3 Cross section through spire of a *H. midae* shell revealing alternate layers of dark (conchiolin) and light (aragonite) under the UV fluorescent microscope, low power magnification.

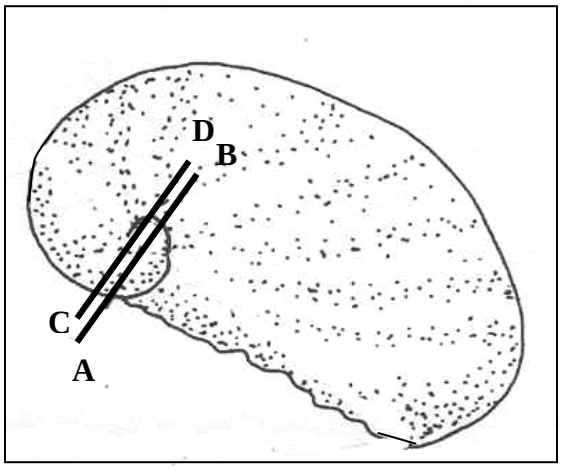


Fig. 3.4 Shell of *H. midae*, indicating the first cut through the shell whorl **(A – B)** and the second cut **(C-D)** for the section removed (modified from Erasmus *et al.* 1994).

Wood (1993) in his analysis of growth on the south coast, used the data presented by Erasmus (1992) in which preliminary growth trials at the University of Cape Town showed that two sets of rings were laid down in the nacreous layer annually, i.e. one set of rings includes one conchiolin (dark) and one aragonite (light) layer. However a study on the internal shell structure and growth lines using acetate peels revealed that three lines were deposited in the first year and one in each subsequent year of growth in *Haliotis midae* (Erasmus *et al.* 1994). In this study, in order to validate that two sets of rings are laid down annually, *H. midae* of known age provided by the Marine Growers abalone farm at Hougham Park, Port Elizabeth, were processed. Twenty-nine abalone of various sizes and known age were sectioned as above. Sizes ranged between 13.1 mm and 90.7 mm shell length and age varied between six months and four years. Sectioned abalone were viewed under the fluorescent microscope, and the number of rings was then related to the known age of the abalone. A strong correlation between the number of rings and age coincided with Erasmus's (1992) preliminary growth trials of two sets of rings being laid down annually (Fig. 3.5). This method was also compared to that used by Wood (1993), to determine if there was a difference in the number of rings seen between the two methods. Wood (1993) sectioned the immediate area around the whorl, which was removed, embedded in resin and sectioned with a diamond saw to between 0.1-1 mm, mounted on a slide and viewed under a stereo dissecting microscope. The number of rings counted was then related to the shell length of the individuals to determine mean lengths and hence growth.

Preliminary growth curves did not show a standard von Bertalanffy growth curve, but a sigmoidal growth curve. Tarbath *et al.* (2000) stated that the age-length relationship was sigmoidal when small animal sizes were included and that the von Bertalanffy was therefore not useful in fitting growth data, and rather sigmoidal growth functions, such as Schnute or Gompertz, should be fitted to growth data. The Schnute growth function (3.2) was chosen to determine growth and includes four parameters. For the purpose of this study, full growth curves were obtained by adding the known size at which abalone settle, 0.5 mm (Gavin Johnston, *pers comm.*) and taken to be age 0 from time of settlement. Hence τ_1 and L_1 are 0 years and 0.5 mm respectively for each site (3.2). L_∞ for each site was determined from the Schnute (1981) equation (3.3), for comparison with previous studies. Comparisons were then made between

growth band analysis and cohort analysis parameter estimates for Kowie Rocks, using Log Likelihood ratio tests (Punt and Leslie 1991).

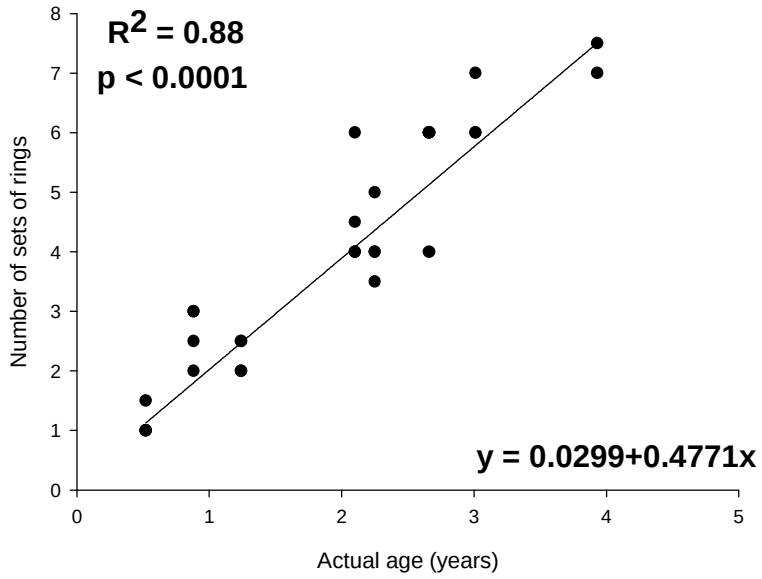


Fig 3.5 The correlation between number of rings counted and the actual age (years) of *H. midae*, suggesting that two sets of rings are deposited per year. Data are presented in non-integer numbers. For e.g. three bands is the same as one and half sets of rings.

3.2.4 Variation of growth around the coast

Haliotis midae were collected along the South African coastline at: Sandy Point (Transkei), Cove Rock, Great Fish Point, Kowie Point, Cape Recife, Cape St. Francis, Natures Valley (Eastern Cape), Gansbaai, Melkbos and Saldhana Bay (Western Cape) (Fig. 3.6). The growth band method (3.2.3) was used on animals from all sites.

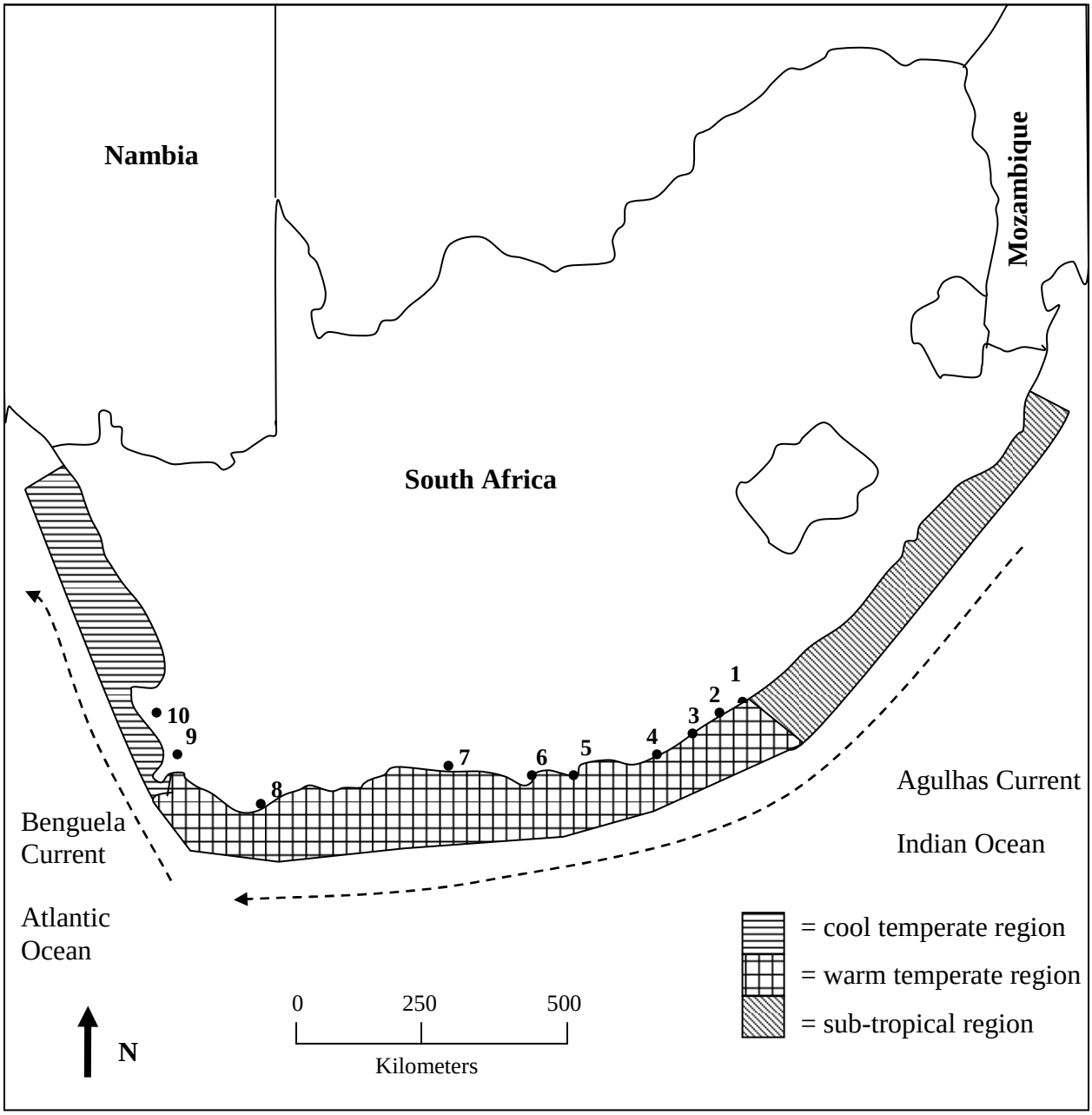


Fig 3.6 Location of the ten study sites along the South African coastline, including biogeographic coastal regions (adapted from Whitfield 1994). 1 = Sandy Point, 2 = Cove Rock, 3 = Great Fish Point, 4 = Kowie Rocks, 5 = Cape Recife, 6 = Cape St Francis, 7 = Natures Valley, 8 = Gansbaai, 9 = Melkbos and 10 = Saldhana Bay

To determine differences in the growth of *Haliotis midae* among sites, each curve was broken into sections that of sub-adult growth (0-4 years), adult growth (4-6 years), and mean maximum size attained (using raw data of sizes in years where the graph has levelled). Slopes of the sections were compared using ANCOVAs and growth rates determined. For the mean maximum size of the oldest age class attained, comparisons were made between sites. Significant differences were determined using a one-way model ANOVA. For each test a Fisher LSD post hoc test was performed to identify significantly different sites. Analyses were performed using Statsoft, Statistica v7.0.

3.3 Results

3.3.1 Mark-recapture

A total of 267 *Haliotis midae* were tagged over the study period using all three techniques. Forty-seven animals were successfully marked with the epoxy putty, 120 animals were marked using epoxy glue and 100 animals were tagged with Dymo tags. Animals tagged ranged between 11.2 mm to 170.5 mm (Fig. 3.7). A total of 32 *H. midae* were recaptured between August 2004 and August 2005, rendering a recapture rate of only 12% (Table 3.1). Of the total number recaptured, none were marked by epoxy putty, 13 were marked with the epoxy glue and 19 were marked with Dymo tags. On search and recovery trips, the Dymo tags yielded the best return of tagged abalone with an average of 50% of the individuals recaptured being recovered over two search and recovery trips. While animals tagged with epoxy on average yielded a return of 23% of individuals recaptured over seven trips with some attempts not yielding any returns. Only one abalone was recaptured more than once (Table 3.1). The low number of returns could be due to any number of reasons, from tagging mortality, tag loss, limited search intensity and movement out of the study site (Newman 1966; Wood 1993). However tagging mortality was only estimated to be 2.5% with only seven dead tagged shells being found, tag loss did not seem to be a problem as only 1.4% of the total number of double tagged individuals were found with no tag and a filed notch.

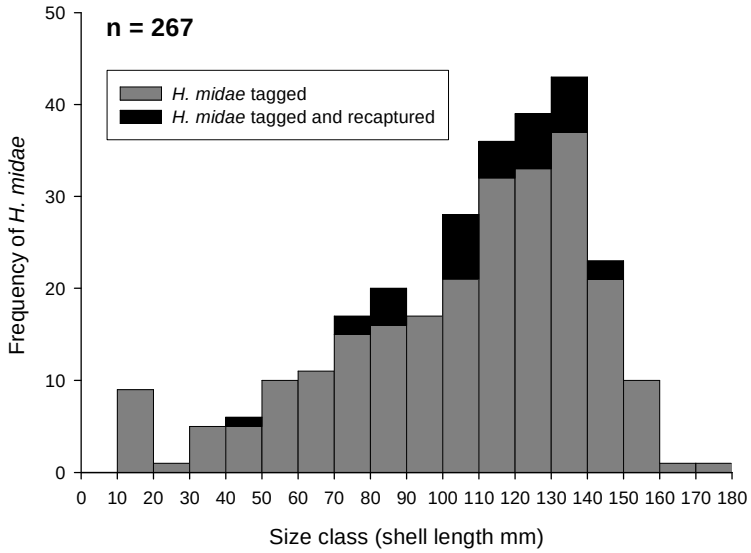


Fig. 3.7 Size distribution of *Haliotis midae* tagged at Kowie Rocks.

This however does not mean that tagging mortality was not possibly higher. A more likely reason for low recovery rates was poaching. Poaching is quite prevalent in the area (*pers. obs.*) and may be greater on marked animals, as they are more conspicuous. Also, during the study period there was a large movement of sand into the study area and this may have caused high mortality to occur, as abalone tend to be intolerant of sand (Wood 1993). The infralittoral area is also highly dynamic and on many occasions was very difficult to survey. As mark recapture provided few data (primarily from large animals) and much of the data made little biological sense (e.g. less growth after one month than after three days), it was decided not to use the data as parameters of the growth function as they would not be accurate and were biased towards a larger size class. The growth increments were also imprecise, as measurements were difficult to take in the dynamic environment in which the abalone were recaptured; hence errors in measurements probably occurred (Table 3.1). Furthermore, the removal and tagging procedure might have stressed animals to the extent that very little growth or increased growth in larger sizes occurred (Table 3.1) and the effect of tagging has been documented by McShane *et al.* (1988b). Growth was shown to have no seasonal effect either, with large variability within season and size (Fig. 3.8).

Table 3.1 Summary of recapture data for *Haliotis midae* at Kowie Rocks.

Tag number	Date tagged	Initial length (mm)	Date of recapture	Number of days released	Length at recapture (mm)	Length increment (mm)	Growth rate (mm.30 days^{-1})
258	01/07/2004	124	18/08/2004	48	124.1	0.1	0.06
273	01/07/2004	135.5	29/08/2004	60	136	0.5	0.25
45	01/07/2004	134.9	30/08/2004	61	134.9	0	0
54	23/07/2004	139.7	18/08/2004	26	142	2.3	2.65
248	23/07/2004	129.9	18/08/2004	26	134.6	4.7	5.42
209	23/07/2004	125.7	18/8/2004	26	129.3	3.6	4.15
	19/08/2004	131.4	29/08/2004	10	132.2	0.8	0.60
24			28/09/2004	40	132.2	0	
279	29/08/2004	134.4	30/08/2004	1	134.4	0	0
129	29/08/2004	80.1	28/09/2004	30	85.6	5.5	5.50
153	29/08/2004	124.8	28/09/2004	30	124.8	3.6	3.60
7	23/07/2004	121.9	15/10/2004	84	122.1	0.2	0.07
62	01/07/2004	101.9	15/10/2004	106	102.2	0.3	0.08
121	13/10/2004	146.4	10/01/2005	89	152.1	5.7	1.92
D50	23/04/2005	103.6	22/05/2005	29	103.6	0	0
A26	23/04/2005	85.2	22/05/2005	29	85.5	0.3	0.31
D31	23/04/2005	113.8	22/05/2005	29	113.9	0.1	0.10
A6	23/04/2005	103.2	22/05/2005	29	103.4	0.2	0.21
A30	23/04/2005	143.3	22/05/2005	29	143.3	0	0
A38	23/04/2005	104	22/05/2005	29	104.1	0.1	0.10
A35	23/04/2005	76.4	22/05/2005	29	76.5	0.1	0.10
D15	23/04/2005	117.9	22/05/2005	29	118.1	0.2	0.21
D79	23/04/2005	135	22/05/2005	29	135	0	0
D82	23/04/2005	103.2	22/05/2005	29	103.3	0.1	0.10
A23	23/04/2005	75.2	22/05/2005	29	75.2	0	0
D49	23/04/2005	119.3	05/08/2005	104	121	1.7	0.49
D19	23/04/2005	124.4	05/08/2005	104	124.7	0.3	0.09
A87	22/05/2005	84.7	05/08/2005	75	84.9	0.2	0.08
B98	22/05/2005	48.3	05/08/2005	75	49	0.7	0.28
E55	22/05/2005	106.2	05/08/2005	75	106.3	0.1	0.04
E62	22/05/2005	80.6	05/08/2005	75	82	1.4	0.56
R 97	22/05/2005	106	05/08/2005	75	107.4	1.4	0.56
B78	22/05/2005	112.3	05/08/2005	75	112.7	0.4	0.16

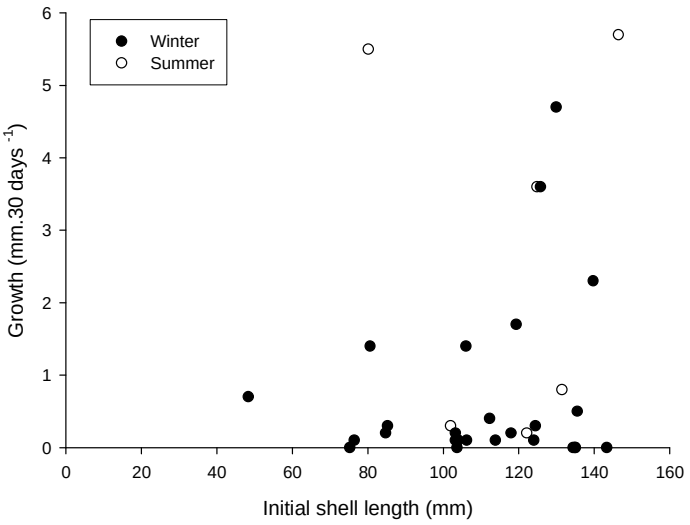


Fig. 3.8 The relationship between initial shell length (mm) and growth 30 days^{-1} for both summer and winter seasons.

3.3.2 Cohort analysis

In general eight cohorts were identified at Kowie Rocks over the period of study from September 2004 to September 2005 and were assigned letters in alphabetical order. The youngest cohort representing a recruitment period or 0+ age class (mean size of 4.52 mm shell length) in September 2004, was assigned the letter A (Fig. 3.9A). In January 2005 and April 2005 an additional ninth cohort was introduced (I) with a mean size of 168.01mm shell length, which was due to a larger sample size being surveyed (Fig. 3.9B, C). In September 2005, a new recruitment period was identified and the new cohort was assigned the letter K (mean size of 8.4 mm shell length). However, cohorts H and I were not detected, and only six cohorts could be matched to the previous months (Fig. 3.9D). This may be due to both bad sea conditions during this sampling time resulting in a small n for the larger size cohorts, or to poaching events occurring in the area. These size frequency distributions also suggest that settlement of *Haliotis midae* occurs a few months before September of each year at Kowie Rocks, with cohort A in September 2004 being identified as being approximately three months old. Growth varied for each cohort over the year, with slow growth occurring in the smallest/youngest size cohorts and the largest/oldest size cohorts and accelerated growth occurring in the middle size cohorts (Table 3.2). Growth also showed a slight seasonal component, with mean growth in cohorts decreasing slightly over

the winter period between April and September 2005 (Table 3.2).

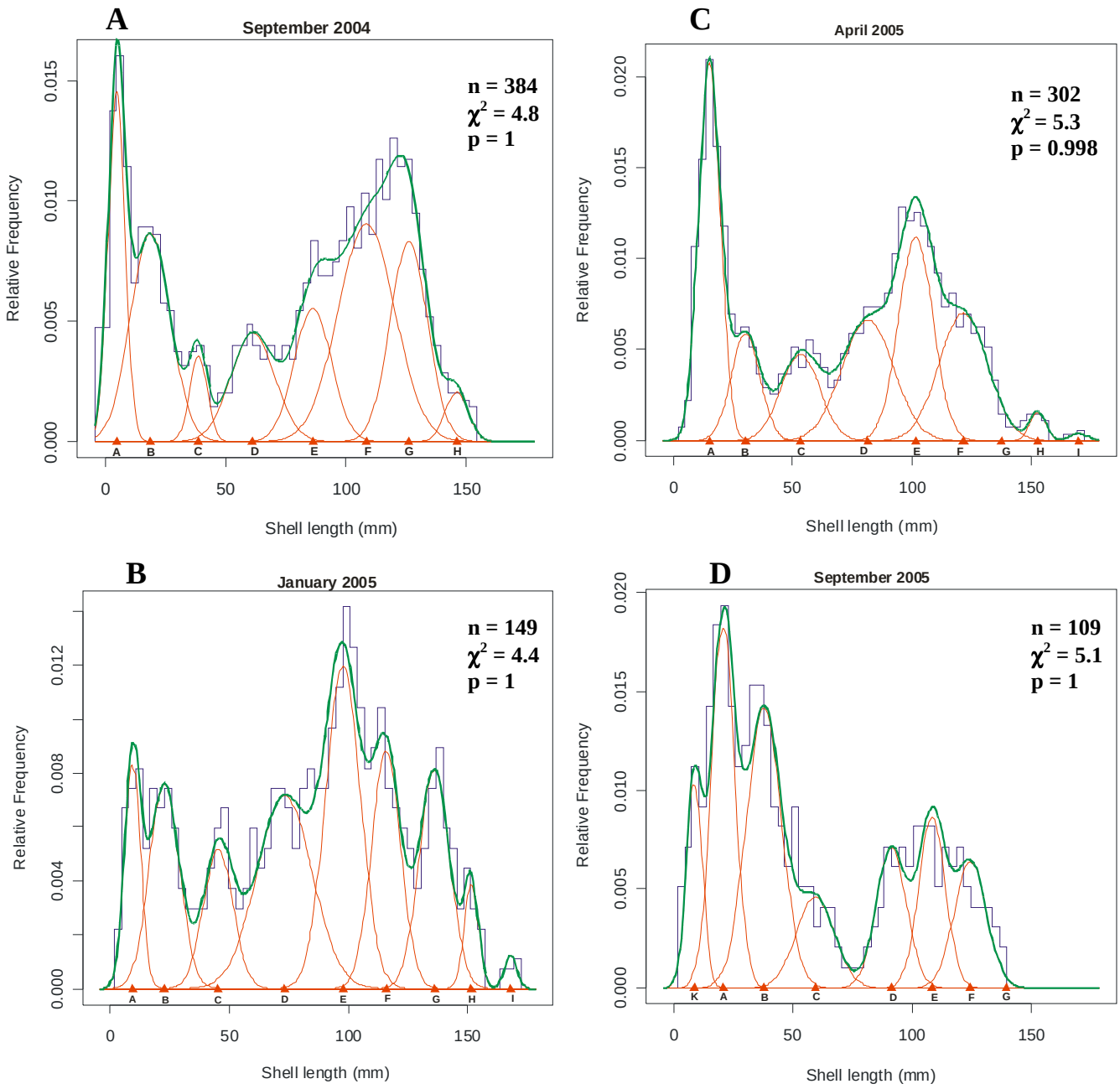


Fig. 3.9 A-D) Cohorts of *Haliotis midae* identified from size-frequency distributions from September 2004 – September 2005 at Kowie Rocks, Port Alfred, using RMix. Alphabetical letters identify specific cohorts, n = number of individuals in the sample, p = probability of goodness-of-fit of cohort curves, green line = observed curve and red line = expected curve.

Table 3.2 Summary of cohort mean size in mm (μ) and growth rate (shell length mm.month^{-1}) among sampling months.

Cohort	September 2004	January 2005		April 2005		September 2005	
	μ	μ	Growth rate (mm. month^{-1})	μ	Growth rate (mm. month^{-1})	μ	Growth rate (mm. month^{-1})
A	4.52	9.17	1.17	14.91	1.92	20.56	1.12
B	18.51	22.55	1	30.1	2.5	37.23	1.5
C	38.5	45.18	1.6	53.13	2.7	59.16	1.22
D	61.27	73.1	2.9	81.44	2.8	91.4	1.96
E	86.38	97.65	2.8	101.59	1.42	107.9	1.35
F	108.7	115.73	1.76	121.59	1.77	124.26	0.64
G	126.2	136.07	2.4	137.58	0.5	139.50	0.44
H	146.08	151.48	1.35	152.86	0.47		
I		168.02		169.86	0.6		
K						8.4	

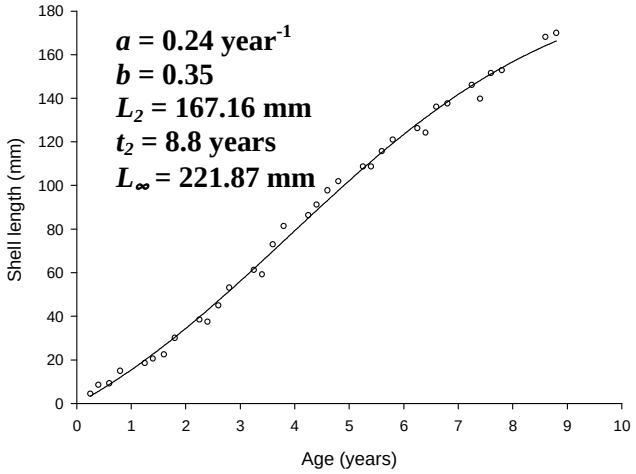


Fig. 3.10 The estimated Schnute growth curve for *Haliotis midae* at Kowie Rocks, Port Alfred, from RMix data; shell lengths taken from Table 3.2.

The parameters estimated for the Schnute growth function from these cohorts were as follows; a = 0.24 per year, b = 0.35, L_2 = 167.16 mm shell length, t_2 = 8.8 years and L_∞ = 221.87 mm shell length. From these estimated parameters the Schnute growth curve was fitted to the data (χ^2 = 287.9, $p < 0.00001$) (Fig. 3.10).

3.3.3 Growth band analysis

A comparison of the technique used in this study (the use of a fluorescent microscope on sections cut through the spire) and the technique used by Wood (1993) (mounted thin sections) revealed the same result, i.e. two sets of rings laid down annually with alternate dark and light bands (Fig. 3.11A, B). It is far easier and quicker to cut sections through the spire as described in 3.2.3 and then view through a fluorescent microscope. This is in comparison to having to embed sections in resin, and then cut using a diamond saw, mounting the section on a slide and only then being able to view it under a stereo dissecting microscope.

The growth estimates for the cohort analysis at Kowie Rocks were very similar to those obtained for the growth band analysis at the same site (Fig. 3.12). For the cohort analysis, a = 0.24, b = 0.35, L_2 = 167.16 and L_∞ = 221. 87; for the growth band analysis, a = 0.3, b = 0.49, L_2 = 153.1 and L_∞ = 193.2, the curve of the graph being very close for both methods. A log likelihood ratio test showed that overall there was no significant difference between the two growth curves (χ^2= 6.7, p = 0.1).

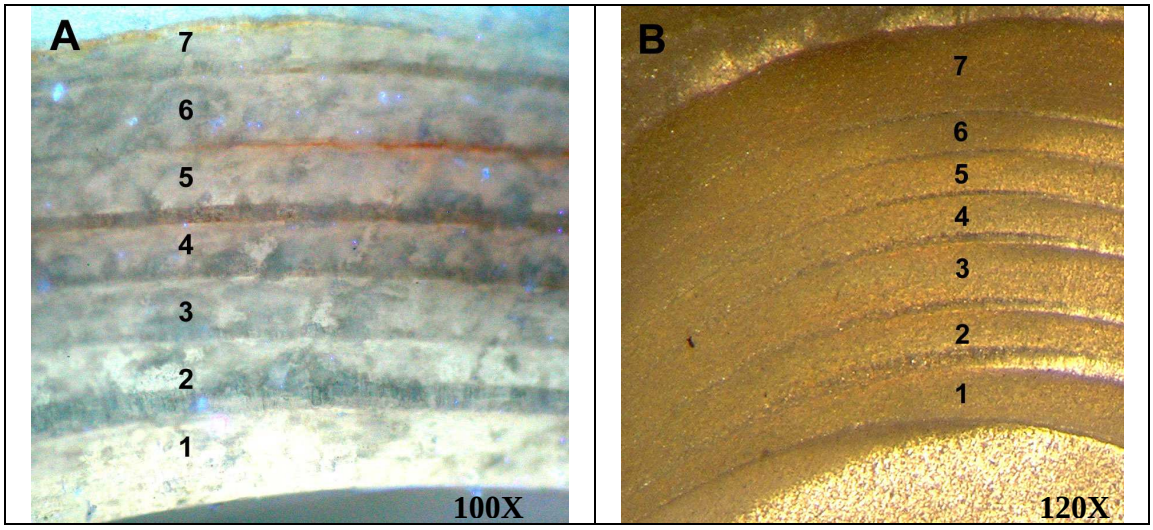


Fig. 3.11 Cross section of *H. midae* (85.6 mm shell length) viewed under a **A)** fluorescent UV microscope and **B)** under stereo dissecting microscope (Wood 1993), with seven sets of rings being visible, indicating that the animal was in its 4th year of growth, the actual age of this animal being 3.93 years old.

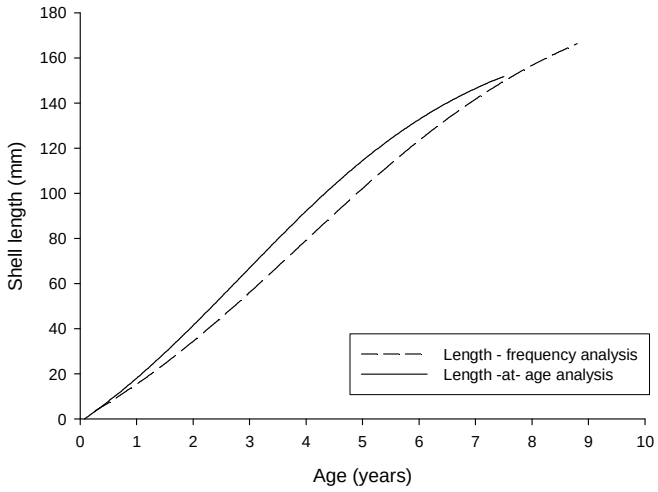


Fig. 3.12 The Schnute growth curves for both the cohort analysis and the growth banding analysis at Kowie Rocks, Port Alfred.

3.3.4 Variation of growth around the coast

For each site a comparison between the absolute error models of the von Bertalanffy growth function and the Schnute growth function showed that the models were different when testing the F distribution ($P < 0.05$). Residuals were homescedastic and random at each site, and therefore comparisons of models were valid (A. Booth, *pers. comm.*). The Schnute growth function was used, as the model with the most parameters should be chosen when models are different, this being the Schnute growth function (Schnute 1981; Cerrato 1990). For all ten sites the parameters for the Schnute growth function were determined from their growth curves (Table 3.3; Fig. 3.13). The maximum number of age classes identified was 12, with a maximum shell size of 189 mm shell length being recorded at Saldhana Bay. The growth curve parameter *a*, which has units of $time^{-1}$ for the Schnute growth curve, ranged from 0.84 at Melkbos to 0.15 at Cape St Francis and L_2 ranged between 138.92 to 198.2 mm at Cove Rock and Gansbaai respectively. L_∞ values ranged between 278 mm at Cape St. Francis to 145 mm at Melkbos.

In general growth between 0-4 years was fastest on the east and south east coasts, with growth decreasing with an increase in age (6-4 years), and maximum growth rates were attained at a younger age, resulting in a smaller overall maximum size than on the west coast (Table 3.4; Fig. 3.13). On the south west coast and west coast growth rates between 0-4 years tended to be slower, with decreasing growth with age (4-6 years) and maximum growth being attained at a much older age; maximum sizes were larger (Table 3.4; Fig. 3.13). One site, however, did not fit into this pattern, Melkbos on the west coast had the smallest L_∞ and a high *a* value, which was not similar to the results obtained for Saldhana on the west coast. Although only two sites were sampled on the west coast (Saldhana Bay and Melkbos), one of which tended to be an outlier (Melkbos, Table 3.3), for the purposes of this study, Saldhana Bay was referred to as the west coast and Gansbaai the south west coast.

Table 3.3 Estimates of Schnute growth parameters a, b, τ_2, L_2, and the von Bertalanffy parameter, L_∞. SS refers to the sum of squares and *lnL* to the log likelihood function and χ^2 was used to determine if fits were significant. For all sites the goodness of fit (χ^2) was significant for the parameters estimated ($P < 0.05$).

Site	Latitude	Longitude	n	a	b	τ_2	L_2	L_∞	SS	*lnL*	χ^2
Sandy Point	32.788°S	28.180°E	66	0.37	0.38	8	157.23	177.1	3776.24	277.8045	91.44394
Cove Rock	33.09°S	27.82°E	51	0.4	0.44	6	138.92	175.6	7720.62	339.2482	214.3313
Great Fish Point	33.52°S	27.11°E	100	0.5	0.17	8.5	153.93	163.2	12745.29	614.4751	764.7852
Kowie Rocks	33.63°S	26.86°E	51	0.3	0.49	7.5	153.1	193.2	4251.475	258.3225	52.47993
Cape Recife	34.027°S	25.700°E	52	0.43	0.17	8.5	152.26	166.1	4055.067	252.881	41.5969
Cape St. Francis	34.208°S	24.836°E	54	0.14	0.68	8.75	172.26	289.2	3220.427	235.5084	6.851871
Natures Valley	33.970°S	23.562°E	53	0.35	0.24	9.25	159.85	179.7	4630.93	268.4904	72.81579
Gansbaai	34.580°S	19.344°E	53	0.34	0.09	11	198.28	206	11780.66	413.0609	361.9567
Melkbos	33.730°S	18.441°E	53	0.81	-0.4	8	145.19	148.7	11338.88	405.7245	347.284
Saldhana Bay	33.038°S	17.933°E	51	0.2	0.6	12.5	195.25	229.3	8743.07	359.3774	254.5897

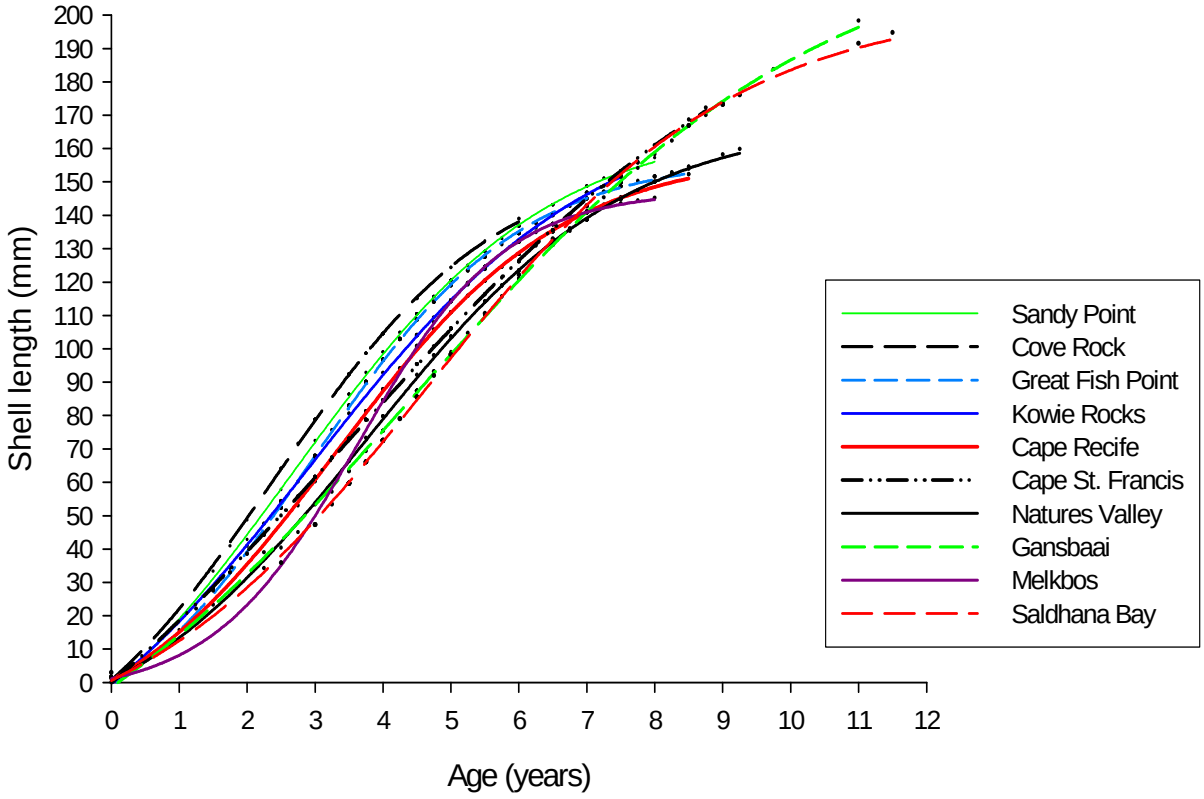


Fig. 3.13 Mean length -at -age Schnute growth curves for *H. midae* at all ten sites surveyed along the South African coastline. (Legend lists sites from East to West)

There was also high variability seen for intermediate sites, with a large degree of overlapping and very little separation (Fig. 3.13). ANOVA revealed that there were significant differences among sites for the mean size for the oldest age class attained. A further post hoc Fisher LSD test further displayed that a separation in significant differences between the east and west existed ($F = 16.93$, $P < 0.001$, $df = 7$) (Table 3.4; Table 3.5), with the largest sizes being attained on the south west and west coasts.

Table 3.4 Estimated mean maximum length and mean lengths and growth rates for *Haliotis midae* from ANCOVA and ANOVA results.

Site	Mean maximum length attained (mm)	Mean length (mm) 0 - 4 yrs	Mean growth rate (mm.year $^{-1}$) 0 – 4 yrs	Mean length (mm) 4 – 6yrs	Mean growth rate (mm.year^{-1}) 4 – 6 yrs
Sandy Point	149.92	76.46	24.75	120.63	18.55
Cove Rock	-	81.01	26.11	117.43	17.24
Great Fish Point	150.45	71.93	24.16	113.73	18.99
Kowie Rocks	143.38	65.35	23.19	117.69	19.81
Cape Recife	147.22	63.75	21.83	109.78	20.65
Cape St. Francis	-	62.97	21.08	104.77	20.9
Natures Valley	153.6	57.27	19.88	108.02	21.96
Gansbaai	180	55.97	18.8	95.5	23.9
Melkbos	144.36	58.71	22.27	113.83	20.74
Saldhana	181.72	53.67	20.95	75.02	20.09

ANCOVA's revealed significant differences in growth rates among sites for both 0-4 years ($F= 18.32$, $P < 0.0001$, $df = 9$) (Table 3.4; Table 3.6) and 4-6 year old animals ($F= 18.04$, $P< 0.0001$, $df = 10$) (Table 3.4; Table 3.7). For growth rates between 0-4 years, the east and south east coasts had faster growth rates than sites on the south west and west coasts, while animals between 4-6 years had slightly faster growth rates on the south west and west coast (Table 3.4; Fig. 3.13). However although significant differences were observed among growth rates for animals between 4-6 years, growth rates did tend to become similar during this period of growth (Table 3.4; Fig. 3.13).

Table 3.5 Fisher LSD post hoc test demonstrating significant differences between sites for mean maximum size attained in the last year of growth shown (▬ = homogenous groups). SP = Sandy Point, GFP = Great Fish Point, KO = Kowie Rocks, CR = Cape Recife, NV= Natures Valley, GB= Gansbaai, SD= Saldhana

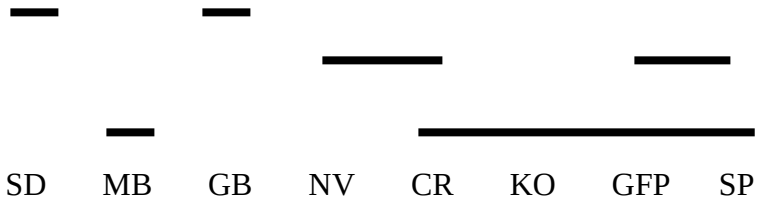


Table 3.6 Fisher LSD post hoc test demonstrating significant differences between sites for growth between 0-4 years (▬ = homogenous groups). SP = Sandy Point, CO= Cove Rock, GFP = Great Fish Point, KO = Kowie Rocks, CR = Cape Recife, CS= Cape St. Francis, NV= Natures Valley, GB= Gansbaai, SD= Saldhana

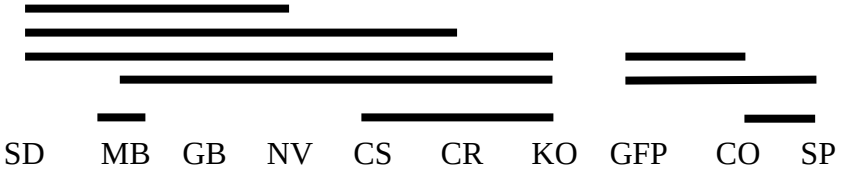
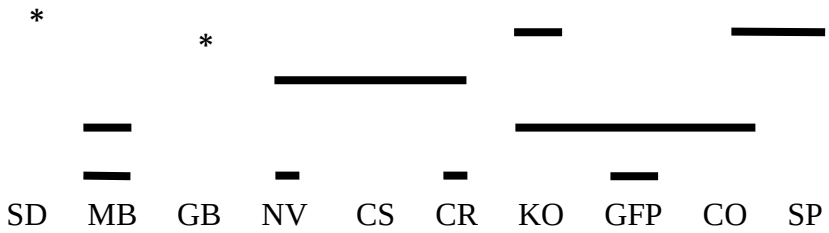


Table 3.7 Fisher LSD post hoc test indicating significant differences between sites in growth between 4-6 years (▬ = homogenous groups, * = significantly different from all other sites). SP = Sandy Point, CO= Cove Rock, GFP = Great Fish Point, KO = Kowie Rocks, CR = Cape Recife, CS= Cape St. Francis, NV= Natures Valley, GB= Gansbaai, SD= Saldhana



3.4 Discussion

3.4.1 Mark-recapture

In this study, of the three methods used to determine the growth rate of *Haliotis midae* along the south coast, mark-recapture proved to be the most unsatisfactory as recapture rates were very low (12%) and growth increments too variable (Fig. 3.8; Table 3.1). Previous studies in which this technique was successful, (Leighton and Boolootian 1963; Forster 1967; Newman 1968; Shepherd and Hearn 1983; Keesing and Wells 1989; Shepherd *et al.* 1991; Wood 1993; Tarr 1995; Naylor *et al.* 2006) generally had recapture rates and/or sample sizes that were higher than in this study. While the observed recapture rate of 12% fell well within the range of previous studies for abalone and other gastropods (1-54% recapture rate), sample sizes in these studies were much larger (> 800 animals tagged) (Leighton and Boolootian 1963; Darby 1964; Frank 1965; Forster 1967; Hayashi 1980; Perron 1983; Foster 1997; Tarbath 1999; Naylor *et al.* 2006).

In South Africa, Tarr (1995) showed variable recapture rates ranging from 4 -42% return rate, Newman (1968) had a return rate of approximately 10% and Wood (1993) a return rate of 11.93%. These return rates are similar to those obtained in this study, however except for Wood (1993) large numbers of *Haliotis midae* were tagged (> 650 animals at each site). Only 244 animals were marked by Wood (1993) at Great Fish Point in the Eastern Cape, and as in this study, no growth curve could be determined. Low marking and recapture rates plus high variability in growth in this study are most likely a result of the difficult working conditions experienced in the high energy infratidal. The dynamic environment made it difficult to remain in the same position while trying to remove, spot or measure abalone. Snorkellers were mostly "washed around" while attempting to do the above mentioned tasks. Atypical growth may have also been due to animals being stressed or there may have been a tag effect on the growth of the animal, especially in animals that were tagged with fishing nylon through their respiratory pores, as has been recorded by McShane *et al* (1988b). In this study, most of the tagged animals had exceptionally low growth rates and were therefore most likely stressed in one. Furthermore, the period between tagging and recovery was possibly not long enough for accurate increment measurements; with most recoveries occurring less than two months after release, in comparison

to successful studies where intervals between tagging and recovery are long (> three month intervals) (Newman 1968; Poore 1972; Shepherd and Hearn 1983; Tarr 1995; Aviles and Shepherd 1996; Tarbath 1999). Low recapture rates may have been due to the cryptic nature of abalone (Tarr 1993; Wood 1993), limited search intensity and a higher mortality than my tagging results suggest; abalone may have been placed into unfavourable microhabitats and the high energy infralittoral zone made reattachment difficult for the animals in rough sea conditions. Poaching events in the area may also have contributed to low recapture rates, with large numbers of shucked abalone shells being found in the study area.

3.4.2 Growth band analysis and cohort analysis

More reliable estimates of growth were obtained from the growth banding study, in which internal growth bands in the nacre of abalone shells were used to estimate growth rates along the south coast. Several authors have commented on the usefulness of counting growth bands in the nacreous layer of shells when estimating growth rates of many gastropod molluscs and bivalve species (Lutz 1976; Ekaratne and Crisp 1984; Richardson 1987; Anwar *et al.* 1990; Richardson *et al.* 1990; Arnold *et al.* 1991). The estimation of growth rates using internal growth bands for species such as; *Nucella lapillus*, *Littorina littorea*, *Patella vulgata*, *Mytilus edulis*, *Anadara granosa*, *Modiolus modiolus* and *Mercenaria mercenaria*, provides reliable estimates of growth, as long as banding is validated, and has been related to tidal rhythms, seasonal temperatures and breeding cycles (Lutz 1976; Ekaratne and Crisp 1984; Richardson 1987; Anwar *et al.* 1990; Richardson *et al.* 1990; Arnold *et al.* 1991). The use of internal growth bands provides a high resolution growth estimation method suitable for both long-term and short-term growth studies and accurate estimates can be obtained from a single sample of the entire size range of the population. However, in older specimens, close spacing of periodic increments has frequently caused lines to become indistinguishable near the shell margin (Lutz 1976; Ekaratne and Crisp 1984; Richardson *et al.* 1990). Growth bands have been noted for many abalone species, for example *Haliotis tuberculata* (Guernsey), *H. mariae* (Dhofari coast), *H. rubra* (Tasmania), *H. fulgens* and *H. corrugata* (Mexico), and *H. australis* and *H. virginea* (New Zealand) (Forster 1967; Poore 1972; Muñoz Lopez 1976; Prince *et al.* 1988a; Turrubiates-Morales and Castro Oritz 1992; Shepherd *et al.* 1995a; Tarbath 1999). However, the use of internal growth bands for

species such as *H. roei* (Western Australia) and *H. rubra*, has been shown to be unreliable due to the variation in frequency of bands between populations, the inability to count rings in most individuals, difficulty of separating bands in older animals (Keesing and Wells 1989; McShane and Smith 1992), and counting being made difficult by boring organisms that obliterate layers or by extra bands that may have been deposited around these organism (Prince *et al.* 1988a). The validation of growth bands is essential when using this method (Day and Fleming 1992) and has been successful using fluorochromes and manganese vital staining or other methods of determining growth for *H. australis, H. virginea, H. rubra, H. mariae, H. fulgens, H. tuberculata* and *H. laevigata* (Poore 1972; Muñoz Lopez 1976; Turrubiates-Morales and Castro Oritz 1992; Day *et al.* 1995; Shepherd *et al.* 1995a; Pirker and Schiel 1995; Day *et al.* 2000).

For *Haliotis midae* in South Africa, alternate dark and light growth bands are easily seen and have been used successfully to determine estimates of growth in the Eastern Cape by Wood (1993) at Great Fish Point and Mgwalana combined. Deposition of these alternate layers in the shells of abalone is thought to be related to seasonal temperatures, diet, spawning season, and photoperiod (Sakai 1960; Forster 1967; Erasmus *et al.* 1994); however Erasmus *et al.* (1994) concluded that, for *H. midae*, deposition of growth bands was not directly related to environmental variables but was more likely to be controlled by endogenous rhythms related to the growth cycle. Woods (1993) validated his growth estimates with mark-recapture data from the same sites. In this study two sets of rings were used for analysis as done by Wood (1993), as *H. midae* of known age showed a strong correlation between two sets of rings and their actual age (Fig. 3.5). This was further validated by the cohort analysis undertaken at Kowie Rocks, where very similar growth curves and parameters (a = 0.3 length-at–age, a = 0.24 length-frequency) were estimated for each method at this site (Fig. 3.12). In addition, log likelihood ratios revealed that overall there was no significant difference between the growth curves, although differences in L_1 and L_2 were found due to the sampling method. For the growth band study at Kowie Rocks, a maximum of eight generations was found, the eighth generation having a mean size of 158 mm shell length. In the cohort analysis a maximum of nine generations was observed, the ninth having a mean size of 170 mm shell length. The eighth generation however had a mean size of 157 mm shell length and therefore growth was similar between the two studies; the ninth generation being

under sampled in the growth banding study. The growth banding data did show slightly faster growth at Kowie Rocks in comparison to the cohort data. This may be due to older age groups not being easily distinguishable. There was a high degree of overlapping of cohorts in the larger size classes, and there is a degree of subjectivity when identifying older cohorts. Larger size classes were also surveyed more readily for the cohort analysis.

The new technique described in this study is similar to that described by Tarbath (1999). However, in the 1999 study, sections were viewed under a binocular microscope, whereas in this study, bands were viewed using a fluorescent microscope. This technique produced the same results as those found by Wood (1993) and is far faster and less labour intensive than other techniques that have previously been used to age shells (Muñoz Lopez 1976; Prince *et al.* 1988a; Shepherd *et al.* 1995a). Growth functions could be easily determined for an entire site within a day, after cutting and viewing sections under the fluorescent microscope, in comparison to other techniques that require far more time to prepare shells and sections for determining growth functions.

The advantage of using shell aging techniques in determining growth estimates is that it allows reliable, rapid assessment of growth from a single sample of the population which includes the entire size range (Prince *et al.* 1988a; Richardson *et al.* 1990; Foster 1997; Tarbath 1999). The difficulty with mark-recapture studies is that recaptures often do not include juveniles due to their cryptic nature, and for cohort studies there is a degree of subjectivity in the process and modes also tend to overlap as animals grow older (McShane *et al.* 1988b; Tarr 1993; Wood 1993; Siddeek and Johnson 1997), hence cohort data and mark-recapture data are often used in combination to determine growth (Poore 1972; Shepherd and Hearn 1983; Tutschulte and Connell 1988). This study has therefore shown the large potential for both length-at-age data and the new technique described for estimating *Haliotis midae* growth in South Africa.

In this study, unlike previous studies on the growth of *Haliotis midae*, growth was found to be sigmoidal rather than following a standard von Bertalanffy growth curve (Newman 1968; Tarr 1993; Wood 1993). Although Tarr (1993) stated that there was no agreement among workers as

to which mathematical model best describes the growth pattern of abalone (for example Logistic, Gompertz or von Bertalanffy models), the majority of authors have applied the von Bertalanffy growth curve to their studies, not only for abalone species but also for other gastropod species (Frank 1965; Forster 1967; Poore 1972; Hayashi 1980; Shepherd and Hearn 1983; Ekaratne and Crisp 1984; Prince *et al.* 1988a, 1988c; McShane *et al.* 1988b; Tutschulte and Connell 1988; Keesing and Wells 1989; Richardson *et al.* 1990; Arnold *et al.* 1991; Shepherd *et al.* 1991; Turrubiates-Morales and Castro Oritz 1992; McShane and Smith 1992; Shepherd *et al.* 1995a; Foster 1997; Siddeek and Johnson 1997; Tarbath 1999; Naylor *et al.* 2006). The von Bertalanffy growth model describes the growth of abalone as relatively linear in the first few years of growth, with annual growth increments decreasing in larger sexually mature organisms (Forster 1967; Shepherd and Hearn 1983; Clavier and Richard 1986; Tutschulte and Connell 1988). However, it was found that when juvenile abalone were included in the analyses for *H. rubra*, the sigmoidal Gompertz model best described growth (Nash 1992, 1995) and Tarbath *et al.* (2000) stated that the von Bertalanffy growth function was therefore not useful for fitting data when small sizes were included and sigmoidal functions such as Gompertz and Schnute should be used. In this study the sigmoidal growth was best described by the Schnute (1981) growth curve, with slow growth in the first few years, then accelerated growth, followed by decelerated growth in the larger size classes (Fig. 3.13) (Schnute 1981). Estimates of growth rates determined from the Schnute growth function were very similar to those obtained using the von Bertalanffy growth function by Wood (1993), Tarr (1993) and Newman (1969) for sites along the South African coastline (see next section).

3.4.3 Geographic variation

There were significant differences in growth rates among the sites along the South African coastline, but differences varied with the age/size of the animals. Variability in growth rates between individuals of the same species is not uncommon in molluscs (Poore 1972; Branch 1974; McLachlan and Lombard 1981; Yssel 1989; Foster 1997) and has been reported for *Haliotis midae* at other sites along the South African coastline (Tarr 1993; Wood 1993). Variation in growth rates of the same species at different localities has been even better documented for abalone species (Poore 1972; Shepherd and Hearn 1983; McShane *et al.* 1988b;

McShane and Smith 1992; Tarr 1993; Tarbath 1999; Naylor *et al.* 2006). There are many sources of intra- and inter-population variation. Intra-population variation in growth rates may be attributed to differences in wave exposure at sites, with more exposed sites having faster growth rates (McShane *et al.* 1988b); differences in tidal depths (Hayashi 1980; Keesing and Wells 1989); differences in habitat types (Arnold *et al.* 1991); seasonality and gonad maturation (Leighton and Boolootian 1963; Shepherd and Hearn 1983; Turrubiates-Morales and Castro Oritz 1992); density of conspecifics (Breen 1980) and variation between genders (Shepherd and Hearn 1983). However, although a high degree of variability has been shown within individual populations for *H. midae* (Tarr 1993; Wood 1993), this was not the scope of this study. Of more interest was the variation between populations along the South African coastline.

It was found that growth along the south east and east coasts tended to be faster within the first four years of growth, with growth rates being lower towards the southwest and west coasts (Table 3.4). Between 4-6 years there was a general decline in growth that was more dramatic for sites along the east (Sandy Point) and south east coasts (down to Kowie Rocks) than for sites on the south west and west coast. There was a general tendency of animals on the southwest and west coast coasts to attain larger mean maximum sizes and L_∞ values, than those on the east and south east coasts (Table 3.3; Table 3.4; Fig. 3.13). This suggests that animals on the south east and east coasts initially grew faster and attained their maximum sizes at a younger age. In contrast individuals on the west coast initially grew slower, but growth continued over a longer period of time, resulting in overall greater maximum sizes when compared to the east/south east coasts. The Schnute growth parameter *a* increased from west to east (along the south east coast) (Table 3.3), with two exceptions. These were Cape St Francis with an exceptionally slow growth rate (0.14 year $^{-1}$) for the south east coast (Tarr 1993) and Melkbos with an extremely high growth rate (0.81 year^{-1}) for the west coast (Newman 1968; Tarr 1993; this study). These exceptions may have been due to atypical local conditions such as an increase in sea-temperatures at Melkbos which is situated near to the Koeberg power station. However, as environmental variables were not measured, further studies are required to determine reasons for these anomalies.

Average growth rates for the first four years of growth from Cove Rock to Cape St Francis (on the south east coast) ranged from 21 – 26 mm.year^{-1} (Table 3.4). This is comparable to size estimates from previous studies at Great Fish Point and Mgwalana (25 mm.year $^{-1}$, Wood 1993), Cape Recife (24 mm.year $^{-1}$, Godfrey 2003) and Bird Island (24.25 mm.year $^{-1}$, Tarr 1993). After the first four years of growth, growth rates then decreased (Table 3.4), as has been recorded by Wood (1993) and Tarr (1993) at their sites along the south coast. Estimates of growth obtained on the south west and west coasts during the first four years ranged between 18.8 – 20.95 mm.year $^{-1}$. These were similar to estimates obtained for Stony Point (19 mm.year $^{-1}$, Newman 1968), but were slightly lower than estimates obtained for Danger Point, Betty's Bay and Robben Island (20 – 30 mm.year $^{-1}$, Tarr 1993; 1995).

Inter- population variation between populations may be the result of differing temperature regimes and differing food supply (Leighton and Boolootian 1963; Shepherd and Hearn 1983; McShane *et al.* 1988; Naylor *et al.* 2006). Newman (1968) suggested that temperature differences between regions are the primary factor causing discrepancies in growth rates. Populations in warmer waters near the Agulhas Current along the south east and east coasts achieve faster growth rates and smaller maximum sizes than those along the west and south west coasts, where the colder Benguela Current is predominant and regular upwelling events occur (Tarr 1995). Wood (1993) corroborated this in the Eastern Cape, saying that the cooler waters may inhibit growth in *Haliotis midae*, assuming that food was not a limiting factor. Differences in growth rates due to differing sea surface temperatures (SST) between sites have been shown by Naylor *et al.* (2006) for *H. iris* where growth was related to the SST. The fastest growth occurred in areas with a lower mean monthly SST and size at sexual maturity decreased with increasing temperature (Naylor *et al.* 2006). Tarr (1993) however found that growth rates on the south east coast were similar to those on the west coast and postulated that temperature may not directly affect growth rates as had previously been suggested. Tarr (1995) suggested instead that food availability was the most significant factor causing variation between sites. Nutrient concentrations on the west coast are high due to regular upwelling and drift kelp is abundant, which may result in the high growth rates obtained by Tarr (1995) in this area. Food type and availability may have caused rates of growth to be similar to those obtained on the west coast in this study, and not be higher as was expected by Tarr (1995). However, Wood (1993) stated that

even though *H. midae* predominantly graze the brown kelp *Ecklonia biruncinata* in the Western Cape and the red seaweeds *Plocamium corallorhiza* and *Hypnea spicifera* in the Eastern Cape, food was not limited in any region and doubted that the differences in dietary composition would affect growth to such great extents. Food supply has been noted to be important, and the effect on growth rates has been noted by Shepherd and Hearn (1983) for *H. laevigata* and *H. rubra* and by Leighton and Boolootian (1963) for *H. cracherodii.* McShane *et al.* (1988b) also noted for *H. rubra* that differences seen in growth among sites may have been related to food supply, as areas that were exposed would probably obtain more food than sheltered areas and hence have faster growth rates. In contrast, in this study (which is the largest to date) distinct differences between growth rates were found along the coast. This agrees with Newman (1968) who found lower rates of growth on the west coast than those obtained on the south east coast by Tarr (1995) and Wood (1993) and in this study. L_∞ values determined by Wood (1993; 176. 99 mm) and Tarr (1995; 155 mm) for *H. midae* on the south east coast were very similar to those obtained in this study (163 – 193 mm), and L_∞ values obtained by Newman (1968; 224 mm) and Tar (1995; 210.32 mm) on the south west and west coasts were also similar to those obtained in this study for sites along these coastlines (206-230 mm; Table 3.3). The lower L_∞ values recorded for Sandy Point (Transkei) to Great Fish Point may reflect the fact that these sites are close to the northern most limit of this animal's distribution. It is thought that variation between the different coasts for *H. midae* is however not due exclusively to any one of these factors, and as suggested by Shepherd and Hearn (1983), Keesing and Wells (1989) and Wood (1993), it is rather the combination of temperature regime, food availability and locality that is responsible for variation in growth between sites.

In comparison to other haliotid species, *Haliotis midae* has a relatively fast growth rate along the South African coastline (Table 3.8). The fastest growth in the first year was observed by *H. mariae*, with intermediate values of L_∞ (Table 3.8). L_∞ values and growth rates for *H. midae* were comparable to *H. corrugata* and *H. fulgens* (Table 3.8) and growth curves of *H. midae* are similar to *H. rubra* in Australia, with both showing sigmoidal growth and similar rates of growth (Nash 1992, 1995; Tarr 1993).

Table 3.8 Comparison of growth in the first year and L_∞ estimates for various haliotid species.

Species	Date	Authors	Country	Shell length (mm) (first year)	L_∞ (mm shell length)
H. australis	1972	Poore	New Zealand	24.4	87
H. corrugata	1988	Tutschulte & Connell	California	15.2 - 25	169-202
H. cracherodii	1963	Leighton & Booloottian	California	26-30	n.a.
H. fulgens	1988	Tutschulte & Connell	California	16.11- 23	179-205
	1991	Shepherd *et a/*	Baja California Mexico	35	183
	1992	Turrubiates-Morales & Ortiz		35-45	177
H. iris	1972	Poore	New Zealand	22	146
	1991	Schiel & Breen		15- 25	130-153
H. kamtschatkana	1980	Schnute & Fournier	British Columbia	26	133
H. laevigata	1983	Shepherd & Hearn	South Australia	30-50	138-148
H. mariae	1995a	Shepherd *et al.*	Sultanate of Oman	43.6 -45.4	139-149
H. midae	1968	Newman	South Africa	26	224
	1993	Wood		23	177
	1993	Tarr		25-30	156-210
	This study			18.8-26	149-289
H. roei	1989	Keesing and Wells	Western Australia	40	85.2
H. rubra	1983	Shepherd & Hearn	Australia	37-45	139-144
	1988b	McShane *et al.*		29-32	117-133
	1999	Tarbath		26-40	141.6-154.1
H. sorenseni	1988	Tutschulte & Connell	California	27	210
H. spadicea	1984	Muller	South Africa	23-28	95
H. tuberculata	1967	Forster	Guernsey	15-16	99-119
	1980	Hayashi		20	114.5
H. virginea	1972	Poore	New Zealand	19-22	62-64.4

It is important when comparing growth parameters to note however that varying techniques used may result in varying growth parameters, for example, in mark-recapture studies if tag returns are over a short interval K could be underestimated and L_∞ overestimated, and may not be representative of the population (Shepherd and Hearn 1983; Keesing and Wells 1989).

3.4.4 Conclusion

The new method described in this study for determining growth using internal growth band data, has been shown to be more reliable than mark-recapture and cohort analyses and has good potential for future growth studies on *Haliotis midae.* Growth was found to be sigmoidal and best described by the Schnute growth function, as reported for *H. rubra*. Variation in growth was seen to exist along the South African coastline, with populations on the south east and east coasts having faster rates of growth, attaining sexual maturity faster but reaching smaller maximum sizes (Fig. 3.13), in comparison to those on the south west and west coasts, where juvenile growth in particular was slower, sexual maturity attained later but larger maximum sizes recorded.

This study suggests that current national management strategies do not optimally manage abalone stocks as they do not take into account regional variability in growth and maturity. It indicates the need for large-scale spatial studies when estimating growth parameters so that generalizations are not made about growth, leading to erroneous decisions about management strategies and egg-per-recruit and yield-per-recruit models. For example most management strategies for *Haliotis midae* have been based on the study by Newman (1968) in the Western Cape. In his study it was recorded that 50 % sexual maturity was attained at approximately 100 mm shell length or at an age of 7 years and that minimum legal size (MLS) of 141 mm shell length was attained at an age of 12.33 years. In this study however it was found that if *H. midae* matures sexually at 100 mm shell length, this length is attained between 3-4 years on the south east and east coasts and approximately 2 years earlier on the south west and west coast (Fig. 3.13) than the proposed 7 years by Newman (1968). However Wood and Buxton (1996b) found that 50 % sexual maturity was attained at 53.7 mm shell length for animals on the south east coast. In this study, 53.7 mm shell length would be attained after just two years of growth and is

similar to results obtained by Wood and Buxton (1996b). Also MLS was attained between 6-7 years along the south east and east coasts which is similar to the 6.83 years recorded by Wood (1993), and between 7-8 years along the south west and west coasts which is comparable to the 7.6-9 years recorded by Tarr (1993) (Fig 3.13). The fact that populations reach MLS and sexual maturity earlier than suggested by Newman (1968) has significant implications for the above mentioned modelling approaches.

CHAPTER 4

VARIATION IN RECRUITMENT AND MORTALITY OF *HALIOTIS MIDAE* AT SITES OF VARYING EXPLOITATION PRESSURE

4.1 Introduction

Understanding recruitment and mortality rates is an important aspect in the management of commercially valuable exploited species. Models such as yield-per-recruit and egg-per-recruit analyses require knowledge on these life parameters (Sainsbury 1982b; Shepherd *et al.* 1991). The size of a natural population is generally agreed upon to be the result of recruitment and mortality patterns, with density dependant factors playing an important role (Possingham and Roughgarden 1990; Caselle 1999). Hence a link between these life parameters and the size of the population exists. The local population density may affect the demographic rates of local recruitment and mortality (especially shortly after settlement), these life parameters then in turn regulate the size of the natural population (Caselle 1999). This line of thought has resulted in the suggestion that recruitment failure is the primary reason for the collapse of abalone fisheries world-wide (Sainsbury 1982b; Sluczanowski 1984; McShane 1995; Stevenson and Melville 1999; Shepherd and Rodda 2000). In addition it has been postulated that post recruitment factors such as mortality are dependent on the recruitment density into a population (Caselle 1999). Even though recruitment and mortality are the principal mechanisms in regulating the size of natural populations, and hence the persistence of target species stocks, they are difficult to estimate, particularly for marine molluscs (Shepherd 1990; Shepherd and Partington 1995). Recruitment in abalone is especially difficult to measure, due to the cryptic nature of juveniles (i.e. living in crevices and under boulders) (Shepherd 1990).

Recruitment is defined as “the influx of new members into a population by reproduction or immigration” (Lincoln *et al.* 1993) or “the number of juveniles growing and surviving into the adult population each year” (Defreitas 2003). Abalone recruitment patterns have been linked to

larval dispersal, preferential settlement of larvae onto crustose coralline algae or under sea-urchins, post settlement processes and spawning patterns of adults (Prince *et al.* 1987; McShane *et al.* 1988a; Shepherd *et al.* 1992; McShane 1995; McShane and Naylor 1995; Sasaki and Shepherd 1995; Stevenson and Melville 1999; Gallardo and Buen 2003). A popular view is that recruitment of animals into the population is regulated by the abundance of spawners. This has resulted in the development of egg-per-recruit models, where the size dependent fecundity is examined as a function of growth and mortality (McShane *et al.* 1988a; Shepherd *et al.* 1992; McShane 1995). This model makes use of 'critical levels' of egg production as reference points below which recruitment failure is assumed to occur (McShane 1995). The term "recruitment overfishing" has therefore become very familiar to fishery scientists and its importance to stock – recruitment relationships has led to predictions being made about the abundance of exploited stocks under different harvesting regimes (Sissenwine and Shepherd 1987; McShane *et al.* 1988a; McShane 1995). Recruitment overfishing is defined as the point at which a population has been exploited to an extent where recruitment is substantially reduced or fails (McShane *et al.* 1988a).

Abalone species have been shown to vary greatly in their vulnerability to overfishing (Nash *et al.* 1995). Poor recruitment may be a result of low fertilization success due to infrequent spawning at low spawner densities (Nash *et al.* 1995). However, settlement or recruitment of animals occurs only occasionally in high numbers, even when egg production is high, as settled larvae suffer high mortality before they recruit to the adult population (McShane 1991; Nash *et al.* 1995; Naylor and McShane 2001). Linked to the view that spawner density affects recruitment is the suggestion that the settlement of free-swimming lecithotrophic larvae with a short larval lifespan (several days in haliotids) is highly localized. The dispersal of *Haliotis rubra* larvae, for example, was shown to be limited to a scale of 0-50 m (Prince *et al.* 1987; Prince *et al.* 1988b; McShane *et al.* 1988a; Shepherd *et al.* 1992). Hence recruitment was limited to the immediate vicinity of the spawner stock (Prince *et al.* 1987; Prince *et al.* 1988b; McShane *et al.* 1988a; Shepherd *et al.* 1992). Other factors may, however, also contribute to the variation or reduced recruitment seen in many abalone (McShane 1995). These include poor fertilization, variation in timing and intensity of gamete production, transport of pelagic larvae away from their benthic

habitat, surface topography, wave exposure and coastal hydrography, larval predation and high post settlement mortality (McShane 1995; McShane and Naylor 1996; Defreitas 2003).

Mortality is defined as the "death rate as a proportion of the population expressed as a percentage or as a fraction" (Lincoln *et al.* 1993). M (the natural mortality rate of a population), is one of the most important parameters of population dynamics and is used in egg-per-recruit analyses (Nash 1992; Shepherd and Breen 1992). However, mortality is still poorly understood (Nash 1992; Shepherd and Breen 1992). According to Shepherd and Breen (1992) management of abalone populations requires knowledge of mortality at all phases of the life history: larval, juvenile and adult. However, mortality of natural populations of recruits and juvenile abalone is poorly documented in comparison to the mortality or survival rates of mature abalone (Sainsbury 1982a; Shepherd *et al.* 1982; Prince *et al.* 1988c). Causes of natural mortality include: environmental disturbances (e.g. storms), disease, pollution, harmful commensals (e.g. boring polychaetes), parasites and predators (crabs, octopus and fish), the last of which tend to be the most common cause of natural abalone mortality (Shepherd and Breen 1992). It is generally accepted that, for marine molluscs, younger age classes experience higher rates of mortality than mature age classes (Creese 1981; Yssel 1989) as juveniles are more prone to predation (Prince *et al.* 1988c). This has previously been documented for abalone (Prince *et al.* 1988c; Shepherd and Breen 1992), although mortality is usually assumed to be constant once individuals have reached a certain size (Shepherd *et al.* 1982; Shepherd and Breen 1992). Furthermore, mortality of juveniles has been suggested to be density independent when settlement is light and density dependent when settlement is heavy, and limited evidence suggests that strong settlement periods result in higher abundances later (Shepherd and Breen 1992). Rates of mortality have been shown to be highly variable between species and between and within stocks of a species, yet our understanding of mortality processes, especially those affecting abalone recruits and juveniles is very limited (Shepherd and Breen 1992).

In South Africa, natural variation in recruit densities and mortality of *Haliotis midae* recruits in the wild has not been studied. Previous studies on recruit and juvenile abundances have focused primarily on the relationship between sea urchins and juvenile recruit abundances (Day and Branch 2000, 2002), while studies on the natural mortality of juvenile *H. midae* have focused on

the mortality of artificially seeded juveniles in stock enhancement experiments (De Waal and Cook 2001; Godfrey 2003; De Waal *et al.* 2003).

This study aims to investigate variability in recruit densities and juvenile mortality rates at sites of varying exploitation pressure and adult densities. In more detail, the objectives are: 1) to determine if densities of recruits and juveniles vary among sites and whether this variation could be related to the densities of reproductive adult stocks in the immediate vicinity, 2) to determine whether recruitment overfishing was occurring at the most exploited sites and 3) to determine the degree of mortality of recruits and juveniles and whether mortality rates varied among sites. In the process of this investigation the potential utility of *in situ* artificial recruit collectors for quantifying recruitment densities was also assessed.

4.2 Materials and Methods

4.2.1 Artificial collectors

As the cryptic nature of juvenile abalone often requires destructive surveys to expose the animals, and as irregular habitats make it difficult to standardize areas that are searched (Davis 1995), uniform artificial recruit collectors have been successfully used in previous studies (Keesing *et al.* 1995; Davis 1995; McShane and Naylor 1996; Defreitas 2003). In this study, an attempt was made to determine the utility of using artificial collectors to quantify recruit densities under local conditions.

Artificial collectors were constructed of two, 25 x 30 cm corrugated plastic roofing plates that were kept apart by 1.5 cm wooden spacing pegs and slotted into aluminium frames (26 x 31 cm) that themselves were attached to concrete paving slabs (38 x 38 x 5 cm). During preliminary trials, two collectors were placed in the lower intertidal at Kowie Rocks in November 2004. Collectors were easily transported and placed during low tides. After one month, a complement of encrusting coralline algae had developed, both on the concrete and the plates. The structure of the collectors however, had started to disintegrate. Consequently, the plastic plates were

replaced with corrugated asbestos plates and the aluminium frames were replaced by welded mild steel (Fig. 4.1A).

After modifications to artificial collectors 10 collectors were placed during Spring Low tide at each of Riet Point and Kelly's Beach (Port Alfred) on consecutive days during May 2005 (Fig. 4.2). Once collectors were in place they were firmly secured with boulders (Fig. 4.1B). At Riet Point all 10 collectors were placed into the intertidal zone (~ 40 cm above Chart Datum), while at Kelly's Beach five collectors were placed in the intertidal zone and five were placed into the subtidal zone (~ 2.5 m). Collectors were checked every month for four months, and coralline crusts colonized the plates while invertebrates such as urchins, winkles and alikreukel settled on them. As with the previous design, however, intertidal collectors did not stand up to high swell conditions. The metal frames of the collectors started to rust and disintegrate after varying time periods while the asbestos plates broke and were lost after two months. Subtidal collectors withstood conditions better, but were difficult to manipulate in the surge. After four months only three juvenile *Haliotis midae* (22.1-31.6 mm shell length) had been found on the collectors. Unlike previous studies in more sheltered environments (Nash *et al.* 1995; Keesing *et al.* 1995; Davis 1995; McShane and Naylor 1996; Naylor and McShane 2001; Defreitas 2003) artificial collectors could not therefore be used in local conditions and will not be discussed further. Instead, the study reverted to standard recruitment surveys (section 4.2.2).

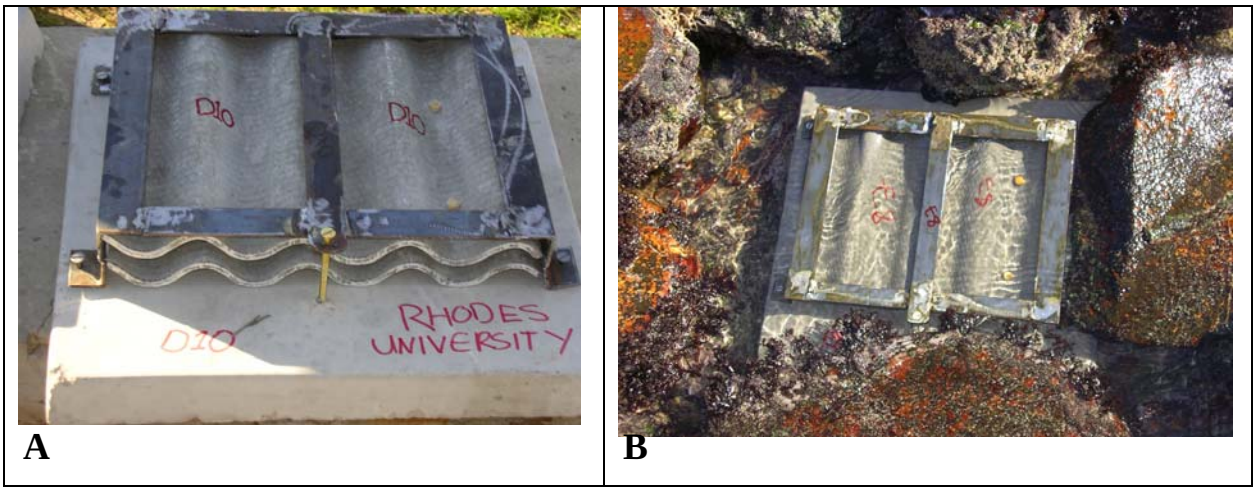


Fig. 4.1 A) Artificial collector and **B)** artificial collector secured with boulders in the intertidal zone; to determine their utility in quantifying juvenile recruit densities of *Haliotis midae.*

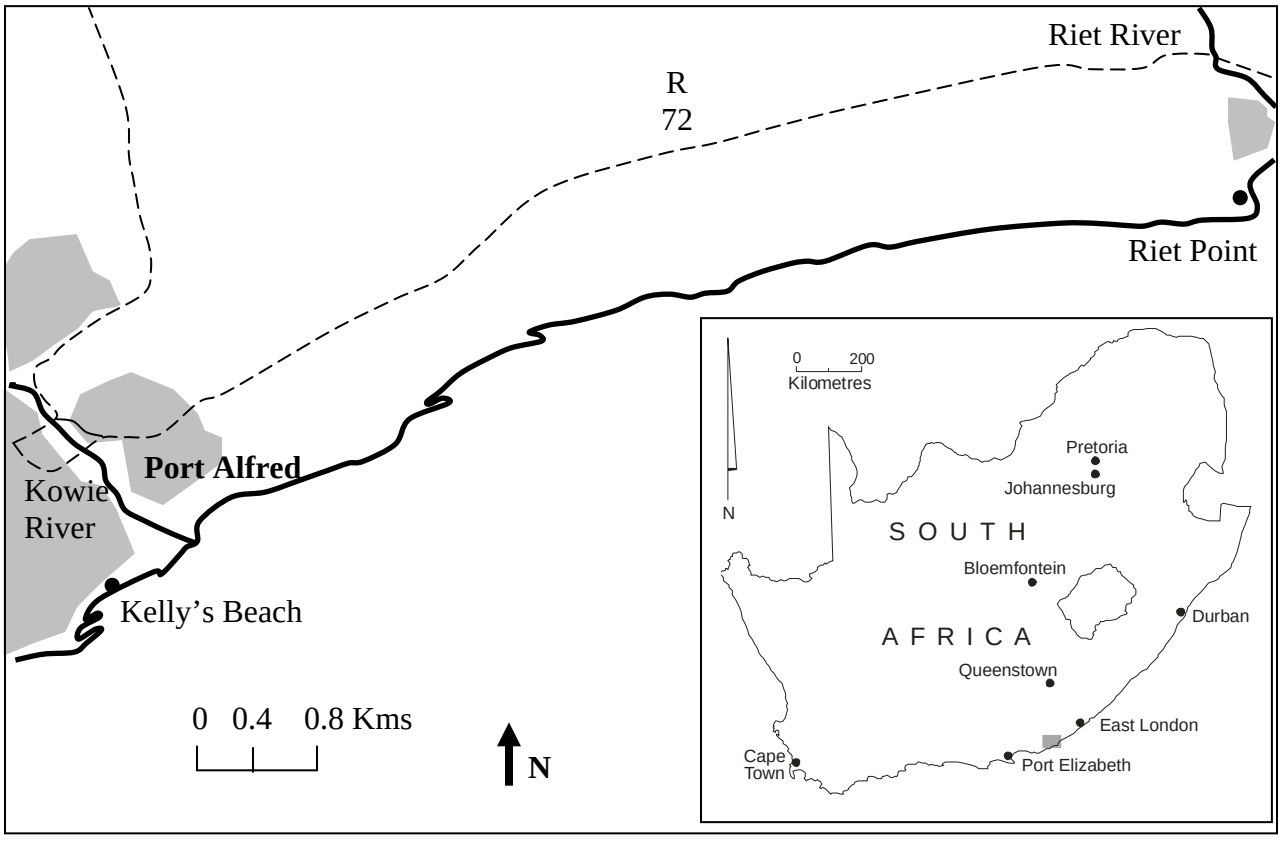


Fig. 4.2 Location of the two study sites used to test artificial collectors for *Haliotis midae* recruits.

4.2.2 Recruitment surveys

Seven sites of varying exploitation pressure (established in chapter 2), were chosen along an 86 km stretch of coastline in order to determine if variation in recruitment among sites may be the related to exploitation and remaining adult stocks. These sites were Kowie Rocks, Kelly's Beach, Riet Point, Mpekweni, Begha, Hamburg and Christmas Rock (Tyolomnqa coastal reserve) (Fig. 4.3).

In order to determine the most suitable habitat and tidal height for the surveys of recruit and juvenile abalone densities, a once-off survey of 35 quadrats of 1 m^2 was undertaken at Kleinemonde in May 2005. The type of habitat in which the abalone was found was recorded as either: under Boulder, under Overhang, in Crevice, in Seaweed and Emergent. The positions of quadrats on the shore were recorded in relation to the distribution of the tubiculous worm *Gunnarea capensis*, (i.e. above, below, in lower, middle or upper part of the *G. capensis* zone).

Quadrats were related to the distributional height of *Gunnarea capensis*, as tidal benchmarks were difficult to define at most sites and from personal observations (chapter 2) abalone tended to inhabit substratum along the distributional range of *G. capensis.*

A χ^2 test revealed that there were significant differences among habitat types ($\chi^2 = 209.02$, $p < 0.0001$, df = 5) and distribution heights related to *Gunnarea capensis* ($\chi^2 = 438.7$, $p < 0.0001$, df = 4). The data suggested that abalone recruits and juveniles were found predominantly in boulder and crevice habitats and between the upper, middle and lower limits of the vertical distribution of *G. capensis* (Fig. 4.4A, B). Accordingly, these habitats and tidal heights were used in the recruitment surveys (see below).

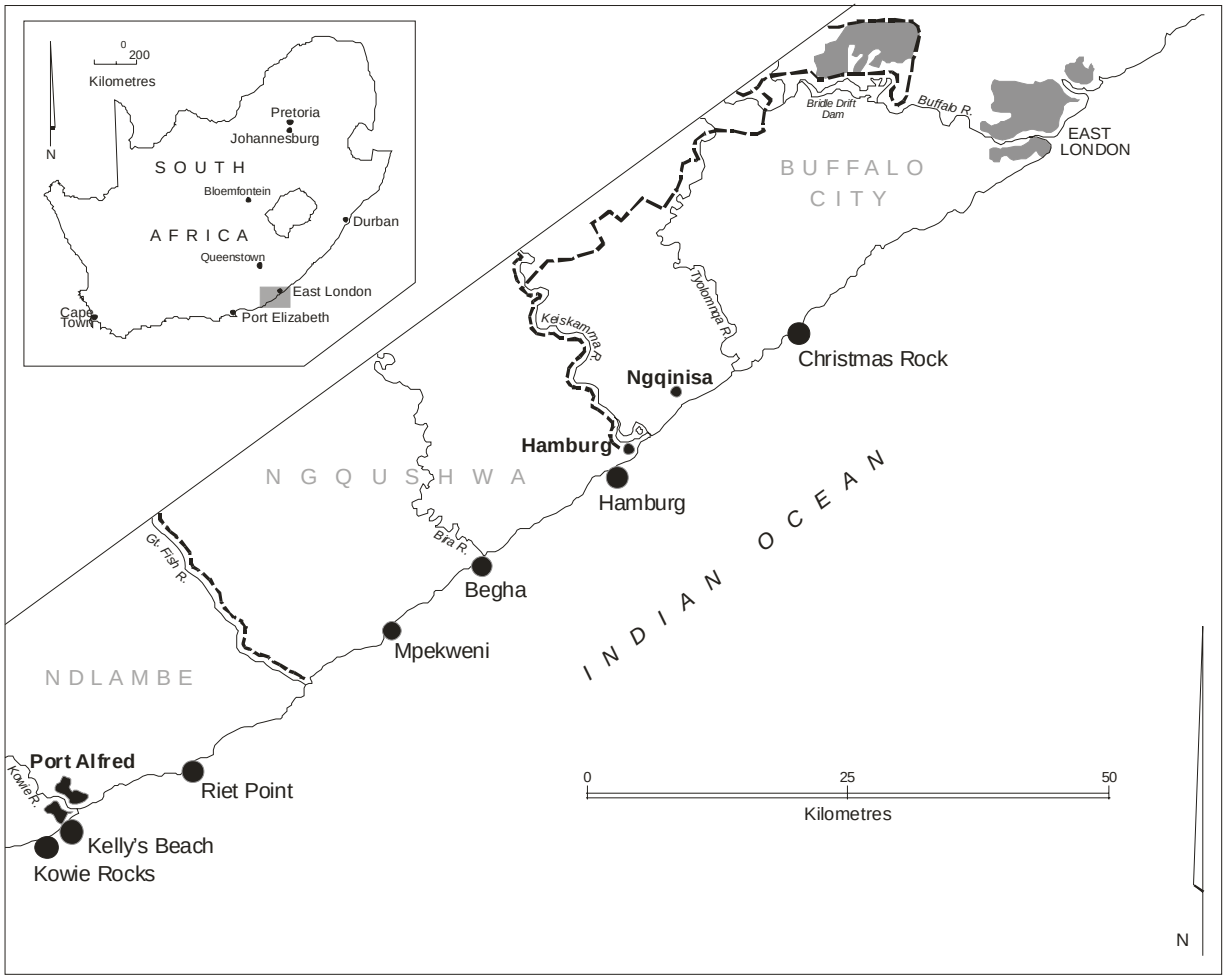


Fig. 4.3 Location of the seven study sites surveyed for juvenile recruits of *H. midae* along the Eastern Cape coastline.

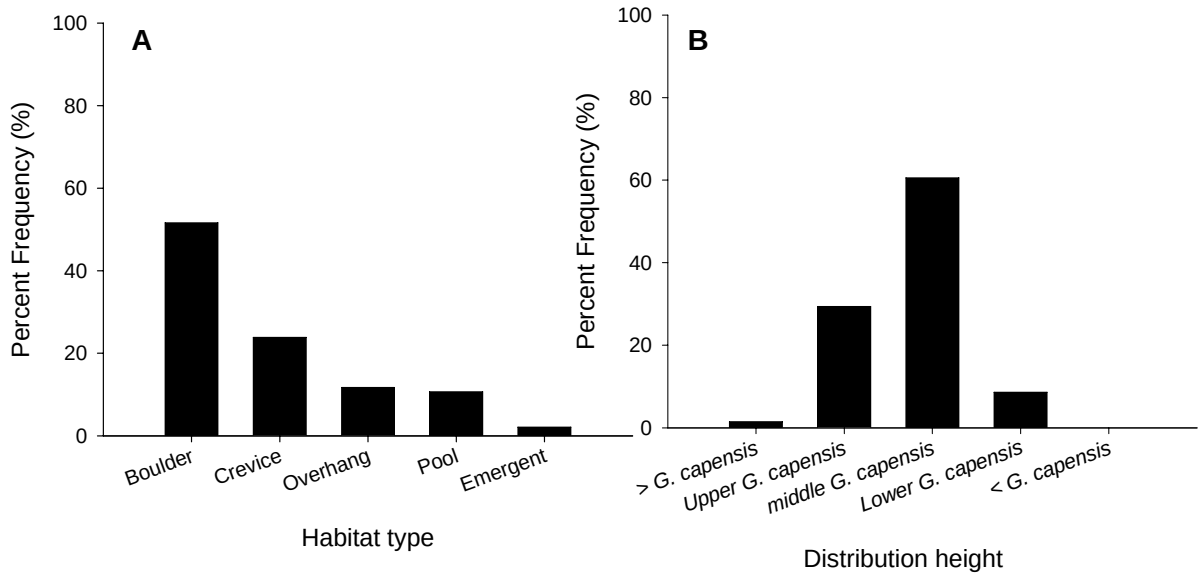


Fig. 4.4 The percentage occurrence of abalone recruits and juveniles in **A)** different habitat types and **B)** at different tidal heights (in relation to the vertical distribution of *Gunnarea capensis*) (n = 54).

Sampling occurred in May / June 2005, October / November 2005 and February / March 2006, during Spring Low Tides. Thirty quadrats of 1 m^2 were employed at random in suitable areas for abalone recruitment (i.e. excluding sand patches). Quadrats were placed into boulder, overhang and crevice habitats and into the upper, middle and lower *Gunnarea capensis* zone, as these were shown to be preferred habitat types and distribution heights (Fig. 4.4A, B). Destructive sampling was undertaken in which boulders were overturned, sea urchins removed, and crevices and overhangs cleared of organisms in order to uncover abalone recruits.

All abalone found within each quadrat were measured to the nearest 0.1 mm shell length with Vernier Calipers. Densities of abalone could then be determined and compared among sites and months. Day and Branch (2002) defined recruits as individuals < 3 mm (when they are associated with encrusting corallines pink or off-white in colour), and juveniles as individuals of 3-35 mm shell length. For the purposes of this study, it was decided after preliminary studies to sub-divide densities into recruits (0.1-12 mm shell length) and juveniles (12.1-35 mm) for analyses. The size class for recruits was taken to be <12 mm shell length as this was the typical size up to which first cohorts still increased in size (i.e. settlement was still occurring). Measuring larval recruitment has proved to be difficult in the past and therefore measuring

juvenile recruitment (i.e. a combination of recruit and juvenile densities) has been suggested to provide an effective measure of population replacement potential (Davis 1995; Defreitas 2003).

4.2.3 Mortality Rates

Mortalities of juveniles and recruits were determined by following the densities of animals in individual cohorts over time at each site. The software R2.0.0 and the mixture analysis (Mixdist) package were used, where possible, to identify cohorts. However, cohorts could not always be resolved using these packages, as recruit densities were low at several sites (Begha, Hamburg and Mpekweni). Hence visual identifications of cohorts were made at these sites using size frequency distributions with different size class ranges. Individual cohorts were ignored where not suitably defined. Using age-length keys described in chapter 3 from the analysis of growth, the mean size of cohorts identified were assigned an estimated mean age in months. Using the methods described by Prince *et al.* (1988c), instantaneous rates of mortality (M) and crude estimates of M were then obtained. Cohorts increasing in mean size as a result of settlement were omitted from analysis. Mortality was taken to be the natural mortality (M) and not total fishing mortality (Z), as below two years (< 50 mm), mortality is assumed not to be due to fishing effort. Estimates of crude instantaneous mortality rates were then used to determine the percentage mortality for each cohort at its estimated age. For each site, percentage mortalities were then regressed against the average age of each cohort and a linear equation derived. From the equation, percentage survival curves and density survival curves were determined for the first two years of *H. midae* at each site. Density mortality curves were determined by relating the maximum density estimated for the recruitment period to the percentage mortality estimated for each month over 24 months.

4.2.4 Statistical analysis

Two-way model II ANOVAs were performed on densities of *H. midae* recruits and juveniles; to test if there were significant differences among sites and month. Assumptions of heterogeneity and normality for ANOVA were not met, even after square–root transformations (Underwood 1981), but since the group sizes were equal and large (n=30), the ANOVAs (performed on raw

data) were thought to be robust against such heterogeneity (Zar 1984). A Fisher LSD was used to perform post hoc tests and was chosen due to the small sample sizes obtained at some sites (M. Villet, *pers. comm.*). Simple logarithmic regressions were used to test for significant relationships between recruit / juvenile densities and adult (or sexually mature, > 53.7 mm shell length) densities. Infralittoral adult densities were taken from Chapter 2, and used as an index of the health of the infralittoral adult population (2003-2004). Exploited sites were defined as those sites that had low densities and reduced mean maximum sizes in comparison to relatively unexploited sites. However, Riet Point (taken to be a relatively unexploited site) was found to be an outlier during regression analyses. Since the initial infralittoral surveys, exploitation has been found to have increased dramatically in this area (S. Raemakers, *pers .comm.*) and during a snorkel survey at Riet Point in October 2005, it was found that adult stocks had been drastically reduced, with no sexually mature animals being observed (*pers. obs*). Hence it was decided to remove Riet Point from most analyses as adult densities could no longer be assumed to be an index of the previously relatively unexploited site. All tests were performed using Statsoft, Statistica v7.0.

4.3 Results

4.3.1 Recruitment Surveys

The two–way ANOVA revealed that there were significant differences in recruit densities among sites ($F = 5.1$, $p = 0.00004$, $df = 6$) and among months ($F = 16.72$, $p < 0.001$, $df = 2$) (Table 4.1; Fig. 4.5), with recruit densities being higher at certain sites and in certain months. A significant interaction of site and month was also observed for recruit densities ($F = 2.7$, $P = 0.002$, df 12). A post hoc Fisher LSD test further showed that there were five homogenous groupings (Table 4.2). When Riet Point was removed, relatively unexploited sites (i.e. Kowie Rocks, Christmas Rock) had significantly higher recruit densities than more exploited sites (e.g. Kelly's Beach, Hamburg) (Table 4.1; Table 4.2). In addition, a Fisher LSD test revealed that for the factor month, May / June 2005 was significantly different from October / November 2005 and February / March 2006 (Table 4.3), with May / June having significantly lower densities of recruits (Table 4.1).

Table 4.1 Summary of population parameters for recruits and juveniles of *H. midae.*

Site	Month	Mean recruitment (<12 mm) density (m^{-2})	Mean juvenile (12.1-35 mm) density (m^{-2})	Minimum size (mm)	Maximum size (mm)
Kowie Rocks	June 2005	0.17 ± 0.46	0.7 ± 1	2.4	41.3
	October 2005	1.33 ± 1.7	0.4 ± 0.7	2.1	29.9
	March 2006	0.67 ± 0.72	0.8 ± 1	3.5	47.8
Kelly's Beach	May 2005	0.17 ± 0.4	0.5 ± 0.8	6.2	50.1
	October 2005	0.37 ± 0.6	0.5 ± 0.7	1.1	39.3
	March 2005	0.1 ± 0.3	0.3 ± 0.5	4.2	47
Riet Point	June 2005	0.1 ± 0.3	1.3 ± 1.7	10.1	43.6
	November 2005	0.63 ± 1	0.6 ± 0.9	1.2	40.2
	February 2006	0.5 ± 0.63	0.54 ± 0.7	3.1	66.7
Mpekweni	June 2005	0.33 ± 0.8	0.77 ± 1.1	5.1	72.6
	October 2005	0.5 ± 1.2	0.6 ± 0.9	2.1	38.4
	February 2006	0.65 ± 1	0.53 ± 0.8	1.5	48.4
Begha	June 2005	0.2 ± 0.4	0.33 ± 0.7	5.4	30.7
	October 2005	1.1 ± 1.7	0.1 ± 0.3	1.1	32.1
	March 2006	0.5 ± 0.9	0.8 ± 1.1	4.1	49.2
Hamburg	June 2005	0	0.23 ± 0.4	13.6	66.2
	October 2005	0.6 ± 0.8	0.23 ± 0.77	2.1	72.1
	March 2006	0.27 ± 0.74	0.2 ± 0.6	6.4	53.3
Christmas Rock	June 2005	0.6 ± 1.23	0.65 ± 1.1	4.7	59.9
	October 2005	0.6 ± 1	0.7 ± 1.1	1.3	110.5
	March 2006	1.21 ± 2	0.68 ± 1.1	2.6	53.3

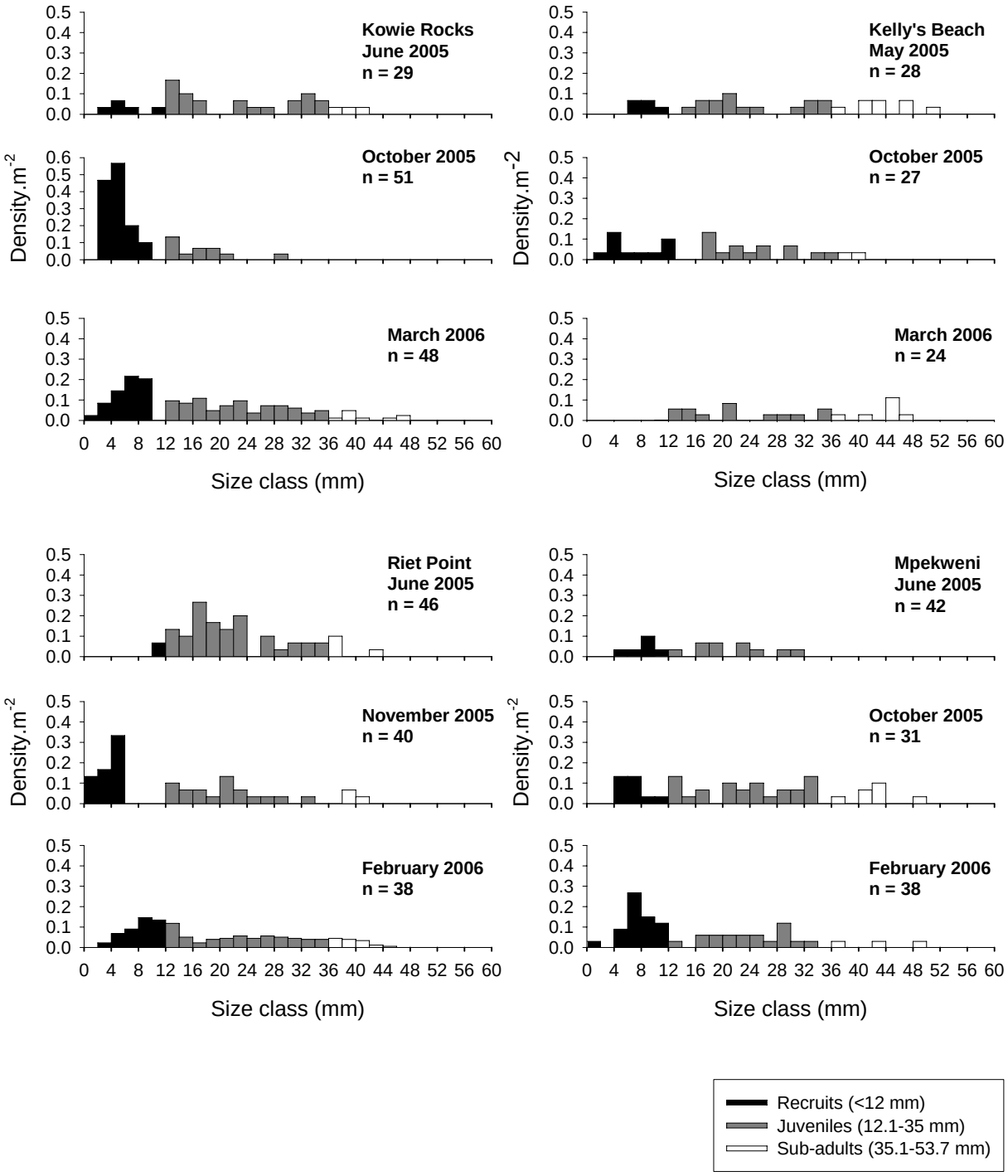


Fig. 4.5 Size frequency distributions of *H. midae*, showing juvenile recruits (< 35 mm shell length) and individuals > 35 mm in the area of study at sites surveyed along the Eastern Cape coastline.

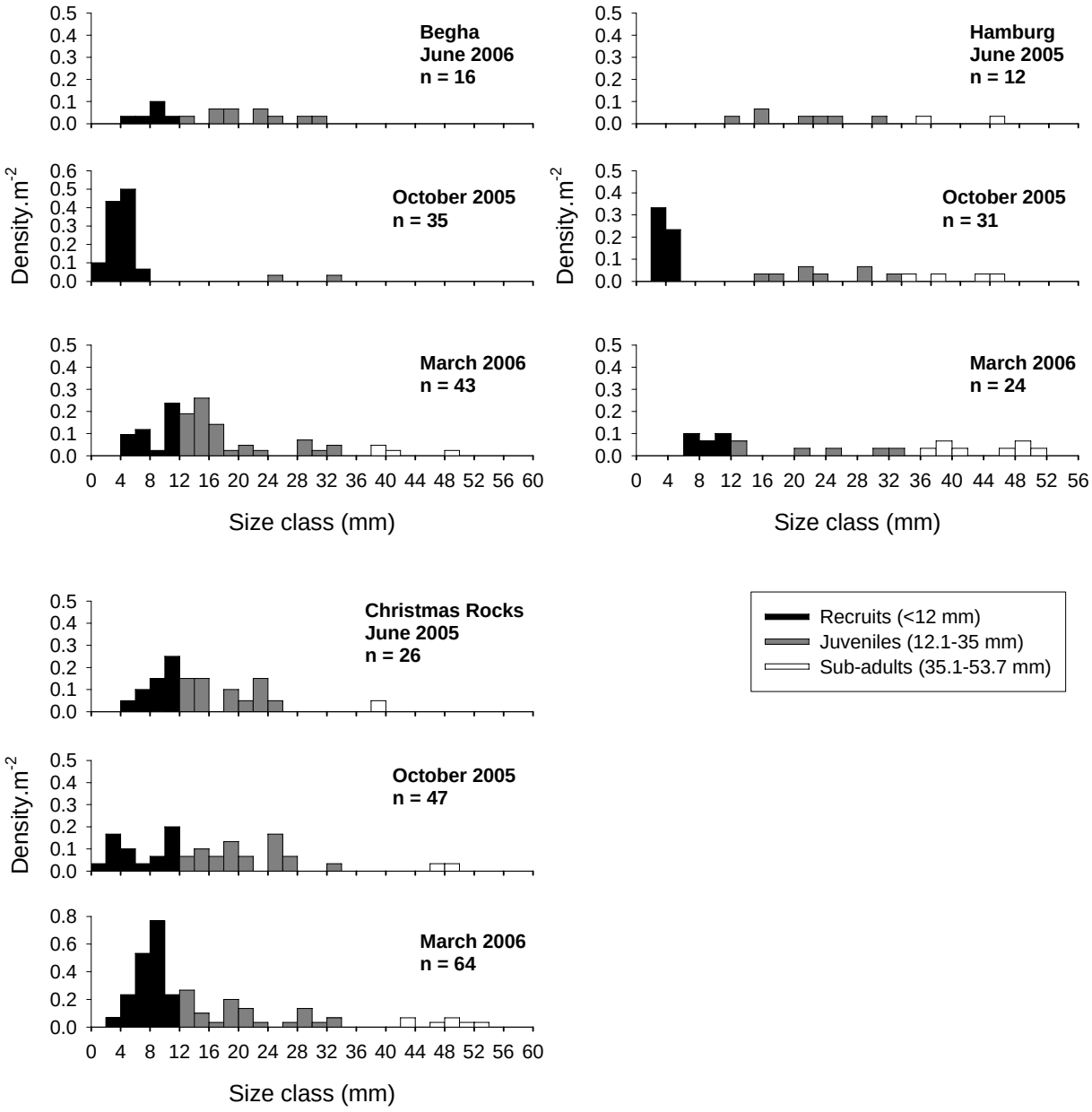


Fig. 4.5 contd. Size frequency distributions of *H. midae*, showing juvenile recruits (< 35 mm shell length) and individuals > 35 mm in the area of study at sites surveyed along the Eastern Cape coastline.

Recruit densities increased for most sites in October / November 2005, with Christmas Rock and Mpekweni increasing in February / March 2006 only (Table 4.1; Fig. 4.5). October 2005 seemed to be the peak recruitment period for *Haliotis midae*. The significant interaction between site and month was the result of significantly increased recruit densities in October / November 2005 for Kowie Rocks and Begha but in February / March 2006 for Christmas Rock (Table 4.1; Fig. 4.5).

For juvenile densities of *Haliotis midae* significant differences were found between sites ($F = 4.67$, $p = 0.0001$, $df = 6$). Densities of juveniles remained relatively constant, however, and there were no significant differences between months ($F = 2.79$, $p = 0.06$, $df = 2$; Table 4.1; Fig. 4.5) and no significant interaction between month and site ($F = 1.1$, $p = 0.31$, $df = 12$). The post hoc Fisher LSD test further revealed three homogenous groupings (Table 4.4). Exploited sites (Begha, Kelly's Beach and Hamburg) formed a distinctive group, with low juvenile densities, and relatively unexploited sites (Christmas Rock, Riet Point and Kowie Rocks) were similar to each other and had the highest juvenile densities (Table 4.1; Table 4.4; Fig. 4.5). There was some overlap between homogenous groups (Table 4.4.), resulting in only the most exploited (Hamburg) and most unexploited (Christmas Rock) sites being significantly different from each-other.

When all sites were considered, regression analyses revealed that there were no significant relationships between recruit densities and infralittoral adult populations for May / June 2005 ($R = 0.2$, $p = 0.67$), October/ November 2005 ($R = 0.2$, $p = 0.64$) and February / March 2006 ($R = 0.36$, $p = 0.43$). However, when Riet Point was removed from the analysis, significant relationships between recruit densities and adult densities were found for May / June 2005 and February / March 2006 (Fig. 4.6A, C). No significant relationship was found during October / November 2005 (Fig. 4.6B), when recruitment peaked at all sites except Mpekweni and Christmas Rock. When a regression was done on adult densities vs. recruit densities during peak recruitment periods (Table 4.1; Fig. 4.7) no significant relationship was found (even with the removal of Riet Point). Thus, during periods of peak recruitment, even some of the over-exploited shores received a high number of recruits. A significant relationship was found between juvenile densities and adult densities only during May / June 2005 (Fig. 4.6D).

Table 4.2 Post hoc Fisher LSD test showing significant differences in recruitment densities between sites along the Eastern Cape coastline. (━ = homogenous groupings, __= exploited sites) KO = Kowie Point, KB = Kelly's Beach, RP = Riet Point, MP = Mpekweni, B = Begha and H = Hamburg

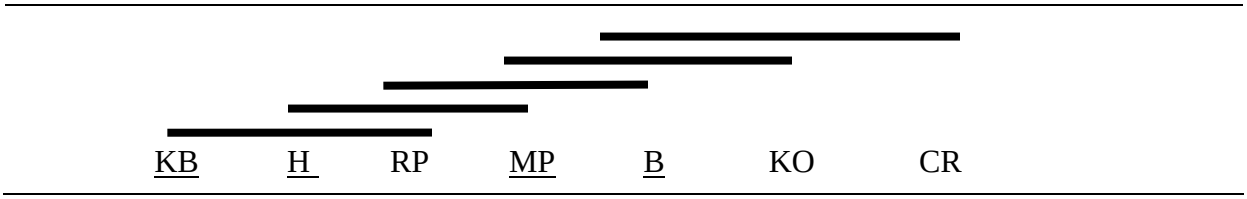


Table 4.3 Post hoc Fisher LSD test showing the significant differences between months of sampling for recruitment densities (━ = homogenous groupings, *= significantly different from all other groups)

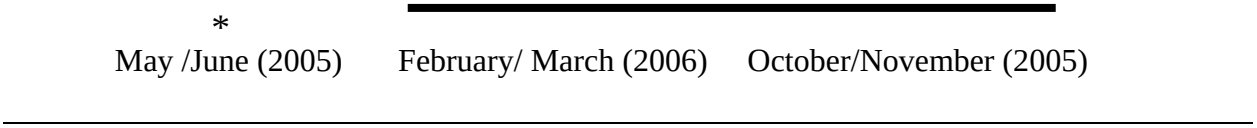


Table 4.4 Post hoc Fisher LSD showing the significant differences in juvenile densities between sites along the Eastern Cape coastline (━ = homogenous groupings, __= exploited sites) KO = Kowie Point, KB = Kelly's Beach, RP = Riet Point, MP = Mpekweni, B = Begha and H = Hamburg

For October / November 2005 and February / March 2006 the relationships were non-significant ($R = 0.61$, $p = 0.145$; $R = 0.14$, $p = 0.76$ respectively). It was also found that Riet Point was once again an outlier, with juvenile densities for these periods being half those found during May / June 2005. The other sites tended to have juvenile densities which remained relatively constant over the study period (Table 4.1). Therefore it is probable that a large mortality event had occurred at Riet Point (see also above), with reductions not only in adult numbers but in juvenile numbers too. Even after removing Riet Point from the regression, October / November 2005 and February / March 2006 relationships remained non-significant ($R = 0.73$, $p = 0.09$; $R = 0.33$, $p = 0.5$ respectively). Juvenile densities did however tend to be low at sites with low adult densities and higher at sites with high adult densities (Fig. 4.6D-F). Although adult densities at Kowie Rocks were lower than at relatively unexploited sites, it was still taken to be relatively unexploited, as there are still large subtidal stocks at this site (Proudfoot 2004, *unpubl. data*).

Although there was only one significant regression between juvenile densities and adult densities (Fig. 4.6D), the ANOVA results (Table 4.4) and densities determined for each site (Table 4.1) tended to show a more distinct relationship between juvenile densities and exploitation status of the site. It was therefore attempted to relate this variation in juvenile densities to differences among sites in rates of mortality of *Haliotis midae* during the first two years of its life cycle.

4.3.3. Mortality rates

Instantaneous mortality rates obtained by regressing log densities against age, and then plotted against average age (in months) revealed no significant trends with age ($R^2 = 0.18$, $R = 0.43$, $p = 0.6$; Fig. 4.8). Hence, mortality rates for *Haliotis midae* tended to be relatively constant during the first 24 months (Fig. 4.8). Mortality rates ranged between 0.02 and 0.55 individuals.m^{-2}.month $^{-1}$ and were highly variable within and between sites (Fig. 4.8). From the crude estimates of instantaneous mortalities, the hypothetical percentage survival curve showed variable but high rates of recruit and juvenile mortality within the first two years of life, with 10-30% of the population surviving after 24 months (Fig. 4.9A). Percentage survival curves were, however, very similar, with the exception of Mpekweni which showed a higher rate of mortality (lower survivorship) (Fig. 4.9A).

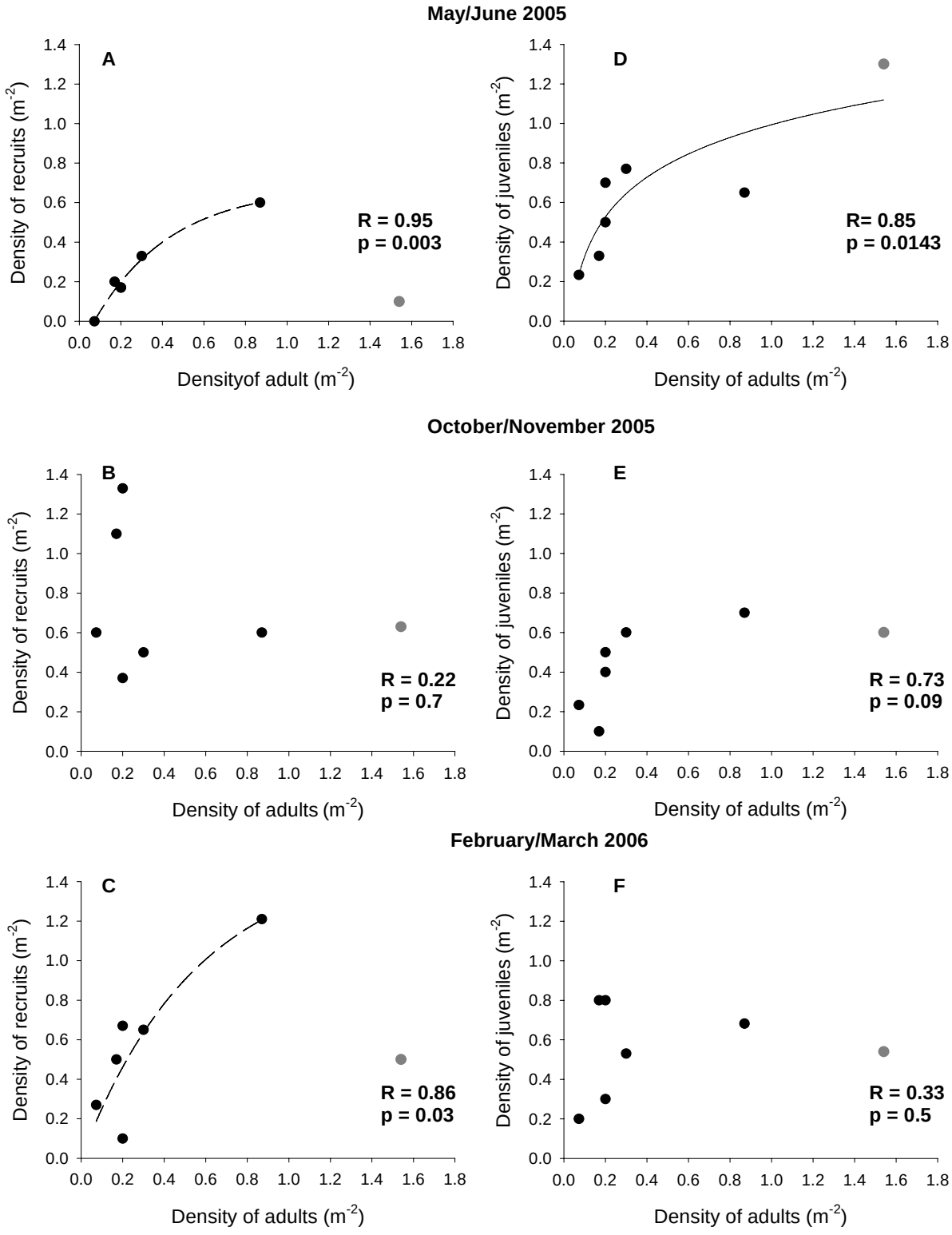


Fig. 4.6 Regressions between infralittoral adult densities and recruitment densities **(A-C)** and juvenile densities **(D-F)** for each month of sampling for all sites. (= Riet Point, omitted from regression analysis, see text)

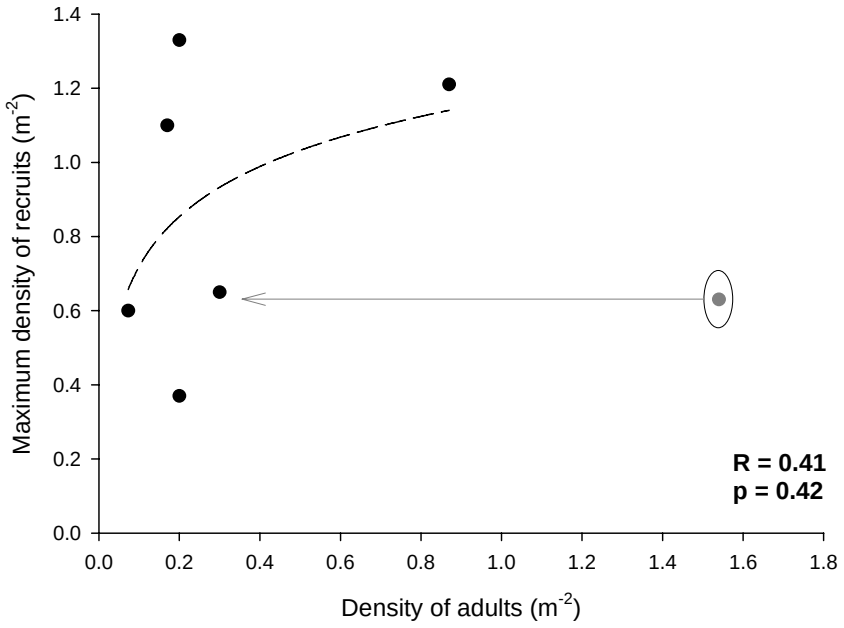


Fig. 4.7 Regression between infralittoral adult densities and maximum recruit densities for each site (● = Riet Point, omitted from calculation).

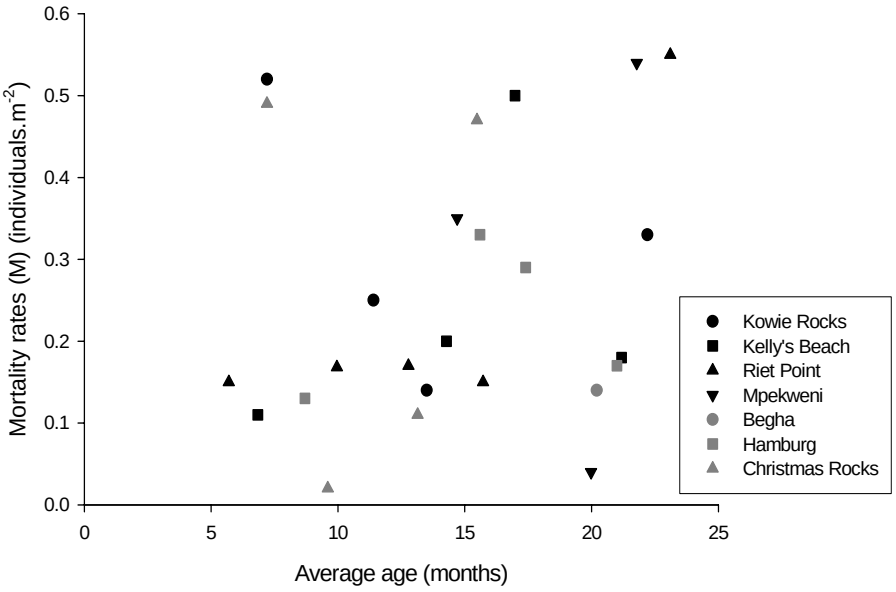


Fig. 4.8 Instantaneous mortality rates for *Haliotis midae* for all recognizable cohorts plotted against mean age (months) of each cohort for each site ($R = 0.43$, $R^2 = 0.18$, $p = 0.6$).

This may be due to the fact that the survivorship curve for Mpekweni was determined on a very small sample size and that cohorts were not easily distinguishable, which may have affected the result. Kelly's Beach (an exploited site) tended to have the highest percentage survival (± 30%) and Mpekweni (another exploited site) the lowest percentage survival (± 10%) after two years (Fig. 4.9A). No pattern could be discerned among sites of varying exploitation, with both exploited and unexploited sites showing similar survival curves (Fig. 4.9A).

When taking original recruit densities into account (Fig. 4.9B), the survivorship curves did exhibit a trend of less exploited sites showing a higher number of juvenile recruits surviving after 24 months when compared to the more exploited sites (again with the exception of Riet River which no longer conformed with other unexploited sites). Begha had to be excluded from these analyses due to difficulty in identifying cohorts and therefore curves could not be determined. The density survival curves once again show high rates of mortality within the first two years and that survival rates tend to be similar between sites of varying exploitation pressure (Fig. 4.9B). Overall, variation in initial recruit densities was therefore more important in determining the densities of persisting juveniles that variation in mortality rates (which was low between sites).

4.4 Discussion

4.4.1 Recruit and juvenile surveys

Caputi (1993) hypothesized that recruit densities should be related to adult spawner stock. In this study, for *Haliotis midae*, such a relationship was found for two out of the three sampling periods. No relationship between adult and recruit densities was, however, exhibited during October / November 2005 (when peak recruitment occurred at most sites) or when relating peak recruit densities at all sites to adult densities (Fig. 4.6B; Fig. 4.7). The outcome of this study was, therefore, not conclusive. Similarly, in the literature, positive spawner-recruit relationships have been shown to exist for populations of *H. rubra* and *H. laevigata* (Prince *et al.* 1987; Prince *et al.* 1988b; McShane *et al.* 1988a; Shepherd and Partington 1995; Shepherd and Rodda 2000).

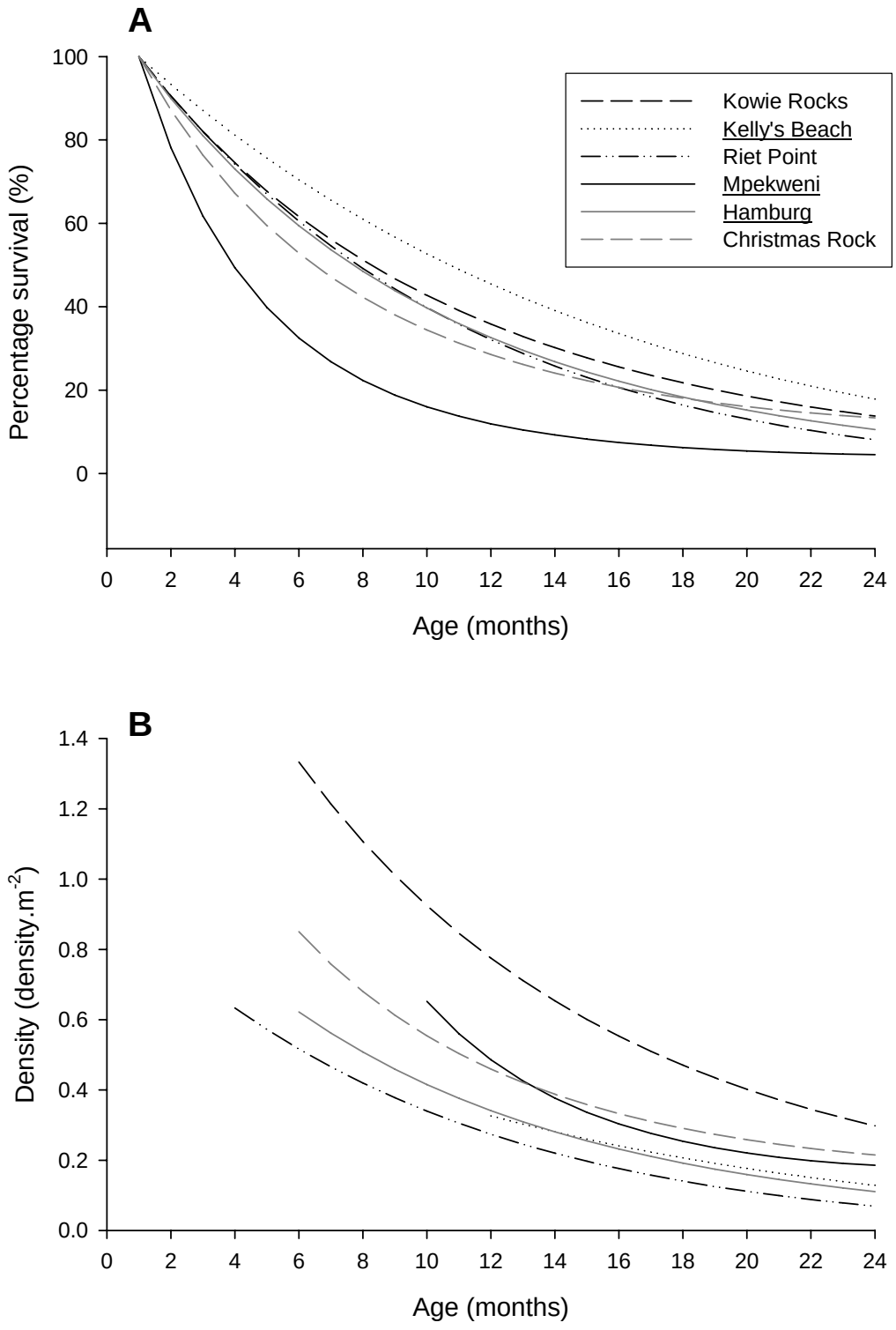


Fig. 4.9 Survivorship curves shown for **A)** Percentage survival over time (months) and **B)** Change in densities over time (months) for each site. (__ = Exploited sites)

Shepherd and Partington (1995) and Shepherd and Rodda (2000) stated that at adult densities between 0.15 and 0.2 m^{-2}, populations are highly vulnerable to recruitment failure. Conversely McShane (1995) noted in his review that there was a lack of empirical evidence to suggest such a relationship, with Shepherd (1990), Shepherd *et al.* (1992) and Tegner *et al.* (1992) concluding in their studies on *H. laevigata, H. fulgens* and *H. rufescens* respectively, that no relationship tended to exist between spawner stock and recruits. The literature therefore is divided and there seems to be little agreement as to whether or not spawner-recruit relationships actually exist for Haliotids. Such relationships are therefore possibly species or population specific.

Godfrey (2003) came to the conclusion in his study at Cape Recife in the Eastern Cape, that for *Haliotis midae,* juvenile densities did not reflect the stock abundance in the immediate area. In this study spawner-recruit relationships tended to be strongest during periods of low recruitment and weakest during periods of peak recruitment. Even though recruit densities were related to infralittoral adult densities from different years, infralittoral adult densities did serve, for the most part, as a good index of the health of the population. Exploited sites tended to have recruit densities lower than those found at unexploited sites (Table 4.1). During periods of low recruitment (May / June 2005 and February / March 2006), density dependent spawner-recruit relationships seemed to be strongest, resulting in low recruit densities being observed at sites with low adult densities. When recruitment is low, the density of settlers tends to reflect the density of spawners in the immediate area more predominantly and settlement tends to be more localized. In addition, it has been suggested that larvae will settle more readily in areas that have many mucous trails of their conspecifics (Gallardo and Buen 2003) and therefore settlement will be more intense at sites with high adult densities and less intense at sites with few adults. During periods of high recruitment (October / November 2005), in this study, the spawner-recruit relationship was weak. This suggests that during times of peak recruitment (presumably linked to times of high reproductive output), the abundance of larvae in the water may facilitate a larger scale dispersal and result in higher settlement rates and recruitment on many / most shores. In contrast, during periods of low reproductive output, dispersal may be more local, with most larvae that do not settle in the immediate vicinity not surviving. A similar recruitment pattern was shown for barnacles, where larval-recruit density dependence was exhibited during periods of low recruitment, but little density dependence was exhibited during periods of peak

recruitment (Connell 1985). A more in depth study, with higher replication and a larger number of sites is required to determine conclusively whether such a relationship exists.

Variation in recruitment between particular sites is possibly the result of differential settlement, post-settlement mortality, larval dispersal, habitat, wave exposure and coastal topography (Keough and Downes 1982; Shepherd *et al.* 1992; McShane and Naylor 1996; Naylor and McShane 2001). It has been suggested that larval dispersal for *Haliotis* species is relatively localized to the parent reef, and hence the assumption of a spawner-recruit relationship. Limited larval dispersal patterns have been inferred by Prince *et al.* (1987, 1988b) and McShane *et al.* (1988a) for *H. rubra*, where the larval dispersal was estimated to be limited to a few 100 meters (Prince *et al.* 1987, 1988b) or retained locally by near-bed currents and local hydrography (McShane *et al.* 1988a). Shepherd *et al.* (1992) and Sasaki and Shepherd (1995) ascertained that for *H. laevigata* and *H. discus hannai* respectively, larval dispersal could occur at much greater distances than previously shown, depending on currents and winds in the vicinity.

In the current study, variation in recruitment between sites and the lack of a spawner-recruit relationship during periods of maximum recruitment are thought to be due mostly to the ability of *Haliotis midae* larvae to disperse to sites outside of their immediate vicinity. *H. midae* have been shown to have a larval period of between 5 and 7 days, depending on the water temperature (Genade *et al.* 1988). Along the east and south coasts of South Africa, the Agulhas Current dominates offshore circulation with various north-flowing counter-currents existing further inshore. East of Cape Padrone, the Agulhas Current follows the edge of the continental shelf, which is narrow (30 km) and steep in this region (Lutjeharms 1998) and flows at approximately 2 m. s^{-1} at its core with a volume flux of approximately 65 million cubic meters per second (Lutjeharms and van Ballegooyen 1988; Lutjeharms 1998). In addition to the Agulhas Current, there is an upwelling cell that has its centre off Port Alfred and this cold water inshore of the warm Agulhas Current may extend up to a maximum of 300 km upstream, with a large amount of mixing occurring (Lutjeharms *et al.* 2000; Lutjeharms 2005). There are also occasional strong counter currents to the Agulhas Current, for example cyclonic eddies that move north-eastwards, while water movement close to the coast is wind driven, the upper layer of the water column following the wind direction (Lutjeharms 1998). The high degree of water movement and

mixing in this area south and north along the coast, and the larvae having a pelagic larval phase of between 5-7 days may allow for greater dispersal capabilities than previously anticipated. Sites extended along approximately an 80 km stretch of coastline, with distances between sites not being more than 20 km apart, so that dispersal between sites is highly likely during periods of high larval abundance. It is therefore suggested, that variability in recruit densities among sites may be a result of more than the infralittoral spawner–recruit relationship alone. Although recruitment overfishing or failure has been implicated in the decline or potential collapse of many abalone fisheries as a result of overfishing (McShane 1995; McShane and Naylor 1995; Shepherd *et al.* 1995b), in this study it was concluded that recruitment overfishing was not yet occurring along the south east coast. Recruitment still occurred at heavily exploited sites (adult densities < 0.2 individuals.m^{-2}) even during periods of low recruitment and during periods of high recruitment recruit densities were high at most sites. However, continued exploitation of *H. midae* at high intensities of harvesting, may result in recruitment overfishing occurring at heavily exploited sites.

The decline from recruit densities to juvenile densities is the result of various post-recruitment processes. These post-recruitment processes may affect juvenile densities to a degree where relatively unexploited sites retain higher densities of juveniles than found for exploited sites. Possible post-recruitment or post-settlement processes include; density dependant mortality, recruitment mortality due to the high degree of wave action in the preferred shallow habitat of juveniles causing dislodgment, or increased sedimentation that may cause mortality due to smothering of recruits, predation by crabs, fish, octopus, "bulldozing" or pedal smothering of recruits by larger grazers (Keough and Downes 1982; Prince *et al.* 1987; McShane 1991; Shepherd *et al.* 1992; Nash *et al.* 1995; McShane 1995; Shepherd and Partington 1995; Naylor and McShane 2001). All these post-recruitment processes essentially result in high post-recruitment mortality. None of the processes themselves were investigated in this study and can therefore not be commented on. However an attempt was made to explain differences in juvenile densities between sites based on between-site variation in post-recruitment mortality.

4.4.2 Mortality rates

Instantaneous mortality rates were highly variable among cohorts within each site and could not be related to age (Fig. 4.8). Instantaneous mortality rates were also highly variable between sites but did not vary significantly over the first 24 months of growth (Fig. 4.8). Due to the overall constant mortality rate and the nature of the mortality curves during the first two years, a type III survivorship schedule was deduced for *Haliotis midae* recruits, where mortality rate is constant on logarithmic data (Southwood 1966). This is similar to that proposed for *H. rubra* (Prince *et al.* 1988c), however for *H. laevigata* a type II survivorship curve was found to be applicable (Shepherd *et al.* 1982), indicating that a constant number of individuals die per unit time on arithmetic data (Southwood 1966). The current and previous studies of abalone mortality (Shepherd *et al.* 1982; Prince *et al.* 1988c) are, however, difficult to compare, as different time frames were used (i.e. the first 24 months vs. the entire life of the species investigated).

Differences in mortality between sites tended to be slight, with percentage survival curves being mostly constant between sites, with the exception of Mpekweni (Fig.4.9A). Mpekweni showed a much faster rate of mortality than the other sites. At this point the possibility cannot be excluded that the lower survivorship estimates for Mpekweni were an artefact due to low recruit densities and resulting difficulties with cohort identification. When taking into account initial recruit densities, survivorship curves did reveal a pattern. Overall, relatively unexploited sites such as Kowie Rocks and Christmas Rock exhibited higher densities of juveniles surviving than the most exploited sites (Hamburg and Kelly's Beach). This suggests that juvenile densities (i.e. the density of individuals that have survived past the age where percentage mortality curves stabilize) are determined primarily by initial recruit densities and not by differential mortality rates.

The percentage of surviving *Haliotis midae* after 24 months, although variable, was between 10-30% which is extremely low (Fig. 4.9A) and similar to other studies. Natural mortality rates for Haliotids have been well documented for mature populations, but poorly documented for recruits and juveniles. Mortality rates have been shown to be variable between species and populations (Shepherd 1990; Shepherd and Breen 1992; Tarbath 1999). Rates of mortality for Haliotids > 2

years of age have been shown to be as low as 0.07 year $^{-1}$ for *H. fulgens* (Olsen 1971, cited in Sainsbury 1982a) and as high as 0.7 year $^{-1}$ for *H corrugata* (Tutschulte 1976, cited in Shepherd and Breen 1992). Juvenile survival however has been documented to be as low as 12% for natural populations of *H. rufescens* (Tegner and Butler 1985), and mortality rates documented for individuals > 6 months and < 2 years range between 0.26 year^{-1} for *H. tuberculata* (Clavier and Richard 1986) and 1.1 year^{-1} for *H. scalaris* (Shepherd and Godoy 1989). Mortality rates are thought to decline with age, with high survival rates observed in adult populations and low survival rates in juveniles (Prince *et al.* 1988c). Mortality of natural *H. midae* populations has not been previously estimated for recruits and juveniles, and this study provides mortality estimates that range between 0.24-3.6 year^{-1} which at the lowest extreme are comparable to other abalone species during this time period (Shepherd and Breen 1992). However at the highest extreme, mortality rates observed in this study were found to be three times that found for other abalone species (Shepherd and Breen 1992). This high mortality rate may be the result of extremely harsh conditions along this highly dynamic coastline or high predation densities at sites.

It is suggested here that, variation in juvenile densities was not the result of differential mortality among sites but mostly the result of initial recruit densities and overall high rates of mortality at all sites (i.e. relatively unexploited sites tended to have higher juvenile densities due to higher initial recruit densities in comparison to heavily exploited sites; but similar mortality rates).

4.4.3 Conclusion

Artificial collectors were unsuccessful in determining recruit and juvenile densities for *Haliotis midae* along this coastline; however, with improvements in design, they may be useful in measuring the dynamics of recruits, juveniles and possibly settlement. Although chapter 2 showed a relationship between sub-adult density and collector density, implying that reduced sub-adult densities in areas of high exploitation could be related to limited reproductive output from exploited adults, this pattern was not constant in the current study. Significant relationships between recruit densities and infralittoral adult densities were found only for May / June 2005

and February / March 2006 but not during times of peak recruitment. This suggests that spawner-recruit relationships occur only during periods when larval abundance and settlement is reduced. In contrast, during periods of high larval abundance, dispersal might be sufficient to supply settlers / recruits to even the most exploited shores (i.e. shores with low adult densities). Therefore it was concluded that recruitment overfishing was not yet occurring along the south east coast, however continued intense harvesting of *H.midae* at heavily exploited sites may result in recruitment failure occurring at these sites. The investigation into post-recruitment mortality suggested that mortality rates on the south east coast are high when compared to other studies but relatively constant over time and between sites. Variation in juvenile densities between sites, therefore, tended to be a product of initial recruit densities rather than differences in survivorship.

In terms of management, this study suggests that even depleted shores have a chance of recovering during years / periods of high spawning / larval abundance, as long as refuge sites still exist. The latter should be of main concern for management planners. On the other hand mortality curves suggest that reseeding with small animals is not feasible and that animals used for seeding should be approximately two years in age, when mortality tends to be reduced. Although larger seed are more expensive than smaller seed, higher survival rates have been shown for larger seed and is more feasible in the long-term for stock enhancement (De Waal and Cook 2001; Godfrey 2003).

CHAPTER 5

GENERAL DISCUSSION

Maintaining maximum sustainable yields of any exploited species requires that management preserves stocks at a level that acts as a buffer against poor recruitment years and retains a minimum spawning stock (King 1995; Foster 1997). Yet an increase in human population densities in coastal areas and the high economic value of certain species, place considerable pressure on many exploited species and increase the chance of over-exploitation (Foster 1997). As in the study undertaken by Foster (1997), comparisons of the population structures of two frequently collected species (*Haliotis midae* and *Turbo sarmaticus*) were made by comparing sites of varying exploitation pressure. The assumption was that sites exploited by "man" would exhibit reduced mean maximum sizes and densities (King 1995; Foster and Hodgson 2000; Godfrey 2003; Branch and Odendaal 2003).

In this study, exploitation patterns for *Turbo sarmaticus* revealed that the species was only exploited at a local scale, with reduced densities, few legal sized animals and reduced mean sizes being found near to large population centres (Kelly's Beach and East Beach Port Alfred) or in the former Ciskei region, where large rural coastal settlements exist (e.g. Hamburg). In addition exploitation patterns were closely related to the average density of collectors on the shore, with highest collector densities being found near population centres and rural settlements in the former Ciskei region. These localized exploitation patterns are comparable to those seen for other species such as *Cellana tramoserica, Austrocochlea constricta, Turbo undulatus, Cymbula oculus, Fissurella crassa* and *Siphonaria gigas* (Oliva and Castilla 1986; Ortega 1987; Keough *et al.* 1993; Keough and Quinn 2000; Branch and Odendaal 2003), that are harvested primarily by subsistence fishers and have little commercial value. Exploitation models described in this study are also similar to those by Hockey *et al.* (1988) and Addessi (1994) for species harvested by subsistence fishers and include the exploitation predictors, human population densities and distances to sites. In this study, refuge populations of *T. sarmaticus* still existed, as subsistence fishers do not travel far to exploit this organism and even at exploited sites subtidal stocks should

still persist as they don't dive and the distribution of *T. sarmaticus* goes down to approximately 8 m in depth. Consequently, infralittoral populations should be able to recover from exploitation, as has also been suggested by Lasiak (1991). The present regulations of five *T. sarmaticus* per person per day and the MLS of 73.7 mm shell length therefore seem to be sufficient in protecting alikreukel stocks at a regional scale. Exploitation hotspots such as areas near to population centres or large settlements should be the focus of management facilitators, as in these localities collection may soon become unsustainable (Foster 1997).

In contrast to *Turbo sarmaticus*, *Haliotis midae*, although also exploited heavily at a local scale, tended to be exploited over much larger areas, with even the most secluded or remote infralittoral populations being targeted; it is also known to be heavily exploited subtidally (Godfrey 2003). Of the 16 sites surveyed, only two sites retained legal sized animals. Although significant models were presented in this study for *H. midae* to facilitate management (largely relationships between the density of collectors and the density of organisms), the high economic value of abalone has been the cause of exploitation being far more wide spread and for all but the smallest size classes to be subject to heavy exploitation by the illegal sector. The latter exploitation models of widespread and intense harvesting on all sizes classes agrees with exploitation models found for other high value organisms such as other *Haliotis* spp., *Concholepas concholepas*, *Fissurella crassa*, *F. limbata*, *Buccinum undatum*, *Strombus* spp. and *Turbo truncatus* (Castilla and Durán 1985; Branch and Moreno 1994; Daniels and Florens 1998; Leiva and Castilla 2002).

The significant relationship seen to exist between the density of sub-adult abalone and the density of collectors on the shore suggests that exploitation levels of sexually mature organisms have reached a point at which reproductive output may be very limited and recruitment reduced. Similar patterns have been described for other Haliotids such as *H. rubra* and *H. laevigata* (Prince *et al.* 1988b; McShane *et al.* 1988a; Shepherd and Partington 1995; Shepherd and Rodda 2000). In the current study, there was further evidence (Chapter 4) that during two out of the three study periods, recruit densities were directly and significantly related to the local densities of reproductive adults. This pattern was not, however, consistent over time and was significant only during periods of low recruitment. Other indirect density dependent factors such as larval abundance and variability in dispersal distances may therefore also have affected recruit

densities. It was suggested that dispersal of larvae of *H. midae* along the highly dynamic environment of the south east coast is not as limited as previously suggested for Haliotids (see above references), and may account for the weak spawner-recruit relationship observed during peak recruitment periods. Variation in recruit densities was concluded to be a combination of the dispersal capability of larvae and density dependence (depending on the intensity of recruitment). This agrees with the suggestion by McShane (1995) that there is a lack of evidence to suggest that densities of recruits are exclusively the result of stock-recruit relationships for Haliotids. In addition, it was concluded that at present recruitment overfishing was not occurring at heavily exploited sites, due to the dispersal capability of *H. midae* larvae along the south east coast. However, continued exploitation at these exploited sites may lead to recruitment overfishing in the future.

Variations in juvenile densities were the result of initial recruit densities and high post-recruitment mortality, with higher recruit densities leading to higher juvenile densities. No evidence for differential mortality among shores was found, suggesting that recruitment is the main determining factor for differences in juvenile densities among sites.

The dramatic expansion of exploitation and high intensity of exploitation on all size classes suggests that, of the two species, *H. midae* is by far the more in danger of overexploitation. Decimation of patchily distributed stocks along the south coast is of great concern as remaining refuge populations or subtidal stocks are currently being diminished (S. Raemaekers, *pers comm.*) to such an extent that infralittoral populations will be unable to recover. Even the subtidal populations of abalone at our previously most pristine sites (e.g. Great Fish Point, Riet Point, Kowie Point) are currently being depleted by poachers using SCUBA equipment (S. Raemaekers *pers comm.*). As previously mentioned by Wood (1993), *H. midae* is highly susceptible to over-exploitation along the south east and east coasts due to: 1) its preference for shallow water, extending to approximately 5 m in depth; 2) emergent legal sized animals occupying exposed positions on rock surfaces; 3) the lack of coagulating agents in their blood; 4) the dynamic environment of the rocky intertidal surf zone, which contributes to unpredictable recruitment; 5) and the patchy distribution of reefs along the south coast, which restricts movement resulting in small isolated populations that are highly susceptible to fishing intensity.

In this study, systematic geographic variation in growth of *Haliotis midae* was observed among sites along the South African coastline, as also suggested by Newman (1969) and corroborated by Wood (1993). Populations on the east and south east coasts had faster growth rates, smaller maximum sizes and the size at sexual maturity was attained sooner than for populations on the south west and west coasts (Chapter 3). Also, as found by Tarr (1993), growth was faster than proposed by Newman (1968). This study strongly highlights the need for management initiatives to be at a regional level and not a national level (e.g. blanket restrictions) and for management strategies to be based on several studies and not solely on one investigation (McQuaid and Payne 1998). Restrictions based on a small number of investigations, as is largely the case for *H. midae*, may lead to both erroneous models being developed and wrong conclusions being drawn about the species (Naylor *et al.* 2006). For example, in this study a MLS of 114 mm shell width or 141 mm shell length was attained between 6–7 years on the south east and east coasts and between 7-8 years on the south west and west coasts, in comparison to the proposed 12.33 years by Newman (1968). Sexual maturity was attained after two years on the south east and east coasts and after 4 years on the south west and west coast and not 7 years as proposed by Newman (1968). These differences have important implications on the management of *H. midae* along the South African coastline.

Management suggestions

The management of *Haliotis midae* is largely based upon a few studies undertaken in the Western Cape (Newman 1967, 1968). At present, harvesting of *H. midae* at MLS is restricted to the commercial sector, with a closed season during their peak reproductive activity (Wood 1993). No commercial fishery exists along the south east coast and the experimental small-scale fishery in Hamburg has been terminated (Wood 1993; Godfrey 2003). This study however illustrates, that even though no large-scale commercial fishery exists along the south coast and a national ban has been imposed on recreational and subsistence collection, the high financial value of abalone has resulted in stocks being intensely exploited in the infralittoral zone (chapter 2) and the subtidal zone (Godfrey 2003). If the main objective of management is the sustainability of the species, management along the south east coast needs to be addressed, as the collapse of abalone stocks is impending in this area.

From the information obtained on *H. midae*, it is possible to suggest new potential management proposals. Marine reserves or marine protected areas have been noted as a viable management option in the past, with direct input into the closed area and larval dispersal to surrounding areas (Tarr 1992; Dugan and Davis 1993; Wallace 1998; Allison *et al.* 1998; Rogers-Bennett *et al.* 2002). The selection of appropriate areas for marine protected sites is important in facilitating the restoration of a species such as abalone (Rogers-Bennett *et al.* 2002). Exploitation models obtained in this study have identified certain areas along the coast that have the potential to be turned into ideal closed areas or marine protected areas (e.g. Fish River Point, Riet Point) which will allow adjacent or nearby populations to benefit from the spawner stock or larval drift. These sites tend to be areas in which relatively healthy populations of *H. midae* have been found and which still retain sufficient spawner densities to allow the replenishment of populations. Nonetheless, any plans of protecting these areas would have to be implemented soon, as organized poaching syndicates are currently in the process of decimating abalone stocks even at these most inaccessible sites. At the rate of current poaching levels, it is unlikely that viable abalone populations will survive a few years down the line.

Sites identified here as making good potential protected areas are not heavily populated and poverty levels in these areas are lower than in the former Ciskei region and near to large population centres. This could possibly curb illegal subsistence collection which has been noted for other sites. Model reserve sites should also take the suitability of the substratum into account. For example reserve sites should have the preferred substrate of boulders and crevices (Fig. 4.4.A) for recruitment and areas should not be inundated with sand, as abalone has been shown to be intolerant of sand (Wood 1993). Although migration of *H. midae* has been shown to be restricted (Tarr 1993), especially along the south east coast due to the patchiness of the reef (Wood 1993), exploited populations will likely benefit more from larval dispersal from protected sites. As suggested in chapter 4, larval dispersal (during high recruitment periods) along the south east coast may not be as limited as suggested for other Haliotids (Prince *et al.* 1987) due to the highly dynamic nature of the environment along the south east coast. Marine protected areas would therefore allow for depleted shores being replenished. Selecting marine protected areas along the south east coast is highly beneficial, as abalone tend to have faster growth rates, attain sexual maturity sooner in this region and have greater larval dispersal capabilities than predicted,

which will allow for marine reserves to be productive to *H. midae* populations sooner than reserves selected on the south west and west coasts.

Stock enhancement by seeding juveniles has also been mentioned as a possible management option and has been addressed globally (Tegner and Butler 1985; Zhao *et al.* 1991; Schiel 1992; McCormick *et al.* 1994; Preece *et al.* 1997; Sweijd *et al.* 1998; Kitada 1999; Godfrey 2003). Stock enhancement has been shown to be economically expensive because survival rates of seeded animals are low, with factors such as size at release, planting method, habitat type, food availability and predation influencing survival rates (Tegner and Butler 1985; Zhao *et al.* 1991; McCormick *et al.* 1994; Rogers-Bennett and Pearse 1998; De Waal and Cook 2001; Godfrey 2003; De Waal *et al.* 2003). Nevertheless, in South Africa reseeding has been suggested by Sweijd *et al.* (1998) as offering good prospects for stock enhancement. Along the south east coast, experimental seeding of juveniles into areas pinpointed as heavily exploited (former Ciskei region) may be worth attempting in order to enhance stocks. This is likely to be feasible, however, only with the active support of local communities. Current national management strategies provide very little incentive for local communities to harvest sustainably. Property or resource rights may have to be discussed.

As post-recruitment mortality was shown to be extremely high, enhancing heavily exploited stocks should therefore be undertaken with juveniles of optimum survival size, this being determined as 27 mm shell length (De Waal and Cook 2001) or from this study as between 18 and 24 months in age or 35-45 mm shell length (chapter 4, 5). At the juvenile stage post-recruitment mortality curves level and theoretically more animals should survive to enhance the adult population. To obtain relatively high juvenile densities requires high initial recruit densities due to the high rates of mortality and therefore if animals are seeded at the juvenile stage, it may be more economically feasible as fewer animals will have to be seeded. In addition, to increase survival of released animals into exploited populations, this study has shown that the optimum substrata to release into would be the preferred boulder and crevice habitat types (preferably where there are lots of sea urchins) and at the upper or middle distributional range of *Gunnarea capensis* (Fig. 4.4.A, B).

Another possible management option for heavily exploited sites (i.e. the former Ciskei region) along the south east coast is to assign limited or private ownership of resources using an area-based management strategy such as a territorial user right fishery (TURF) (Hilborn 1992; Prince *et al.* 1998; Godfrey 2003). Sedentary target species, such as abalone with inshore fisheries, lend themselves to this type of practice (Caddy 1999). This sense of ownership will create an incentive among rights holders to manage abalone stocks in a sustainable manner for maximum economic return and will encourage right holders to protect their resources (possibly curbing the intensity of illegal exploitation in the area) (Godfrey 2003). This management option could be further enhanced at exploited sites in combination with the use of stock enhancement (Godfrey 2003). Wood (1993) suggested that if the MLS is implemented at the size attained one year after 100% sexual maturity is attained (as based on Western Cape growth parameters), then a new reduced MLS of 119 mm shell length or 93 mm shell width should be imposed along the south coast. Due to the smaller maximum sizes attained along the south east coast this suggested legal size would be more appropriate for stocks along the south east coast and would be attained between 4-5 years (Fig. 3.13). The faster growth rates, a reduced MLS and sexual maturity being attained sooner would result in the establishment of TURFs / stock enhancement being an incentive to right holders, as the economic return will be faster and stocks will become productive sooner. This would be attractive to right holders. It is also suggested from this study, especially on growth, that management strategies should be implemented by regions, with different management strategies being applied to the south east and east coasts and to the south west and west coasts.

In addition to the information obtained on *H. midae* and the new management suggestions, a new technique for ageing abalone shells and determining growth using growth bands was validated in this study by cohort analysis and ageing shells of known age. Although growth banding analysis is controversial (Day and Fleming 1992; McShane and Smith 1992), it has been used successfully to determine growth for *H. midae* in the Eastern Cape by Wood (1993). The new technique described in chapter 3, which is similar to that described by Tarbath (1999), was however far less time consuming and labour intensive than previous methods described for ageing shells (Muñoz Lopez 1976; Wood 1993; Erasmus *et al.* 1994). This new technique takes approximately two hours to measure and mark the shells of between 50-70 animals, an hour to

cut sections from these shells and approximately an hour and a half to then age the shells under a fluorescent microscope. It therefore takes approximately four and a half hours to determine the growth for one site and within a day the growth of two sites of between 50-65 shells can easily be determined. This is far less time consuming and labour intensive than for example the method described by Wood (1993), which requires that shells not only be cut, but then embedded in resin, sectioned, mounted on a slide, polished and only then aged under a stereo microscope. This technique of ageing shells, for example for one site, would require approximately a week if not more to obtain results. Acetate peels described by Erasmus *et al.* (1994) would require approximately the same amount of time, and the grinding down of the shell spire to expose growth bands as described by Muñoz Lopez (1976), although faster than sections and acetate peels, would possibly involve more time and labour than the technique described in this study. Also, unlike mark recapture studies which are time consuming, labour intensive and have low recapture rates (McShane *et al.* 1988b; Tarr 1993; Wood 1993) or cohort analysis which tends to be subjective (Siddeek and Johnson 1997), this technique allows reliable, rapid assessment of growth over the entire size range of a population using dead shells. Therefore the use of this technique would potentially be beneficial in determining growth rates rapidly at sites along the South African coastline.

Conclusion

Readily observed effects of exploitation are direct changes in the population density and size structures of the exploited species themselves (Griffiths and Branch 1997), and have been observed in this study. Both *H. midae* and *T. sarmaticus* were heavily exploited on a local scale, though exploitation on *H. midae* was far more widespread and intense. However the indirect effects of exploitation are less well understood. Removal of exploitable species may have profound effects on community structure and may change biological interactions within a community (Durán and Castilla 1989; Dye 1992; Griffiths and Branch 1997). *H. midae* and *T. sarmaticus* are considered to be important macro algal grazers and over–exploitation of the species will not only result in the depletion or demise of stocks and thus lowering of yields and loss of an important protein source (*T. sarmaticus*) to impoverished communities, but exploitation will also reduce the role both species play within the ecosystem (Griffiths and Branch 1997; Foster 1997). *T. sarmaticus*, at present tends to be regionally sustainable due to

adjacent refuge and subtidal populations that still persist, although more information on recruitment patterns and the indirect effects of exploitation may be of interest. The present management strategies for maintaining sustainable yields of *H. midae* along the south coast are not viable, with abalone stocks rapidly declining due to intense exploitation by the illegal sector. Implementation of more closed protected areas at relatively unexploited sites and area-based management fisheries together with stock enhancement measures in heavily exploited areas may prove to be feasible alternatives to present management strategies along the south east coast. Faster growth rates, reduced maximum sizes and therefore possibly reduced MLS, and sexual maturity being attained sooner should result in a faster economic return to the efforts of right holders, and therefore establishment of TURFs should be an attractive prospect. In addition a new technique for ageing and determining growth rates was described, which may prove to beneficial for rapid assessment of growth rates not only in South Africa but possibly *Haliotis* spp. elsewhere.

In the future an investigation of the extent to which *H. midae* larvae are able to disperse may be worthwhile, possibly using genetic techniques. Long term monitoring of recruitment and spawner stocks and investigations into the indirect effects of exploitation should be undertaken along the south east coast. Management strategies and models will need to be revised as a result of the differences in *H. midae* dynamics observed between regions and studies. More information will also be required on the feasibility of stock enhancement along the south east coast and increasing seed survival. In addition, an experimental TURF fishery may be worth implementing at a heavily exploited site (for e.g. Kiwane) along the south east coast in order to determine whether such management schemes will be successful.

CHAPTER 6

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