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FACTORS INFLUENCING THE RANCHING OF THE ABALONE SPECIES
HALIOTIS MIDAE ALONG THE NAMAQUALAND COAST OF
SOUTH AFRICA

BY

S.W.P. DE WAAL

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UNIVERSITY OF CAPE TOWN

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DECLARATION

This thesis documents original research carried out in the Zoology Department of the University of Cape Town, between 1998 and 2002. It has not been submitted in whole or in part for a degree at any other university. Data presented here are original, and any other sources of data are fully acknowledged. All uncited interpretations are my own, and any assistance that I have received other than the normal guidance of my supervisor, Professor Pete Cook, is also acknowledged.

Signed by candidate

S.W.P. de Waal

ABSTRACT

The Namaqualand coast of South Africa has been targeted as a potential ranching area for the abalone *Haliotis midae*. A series of experiments and models were designed to: assess to what extent the area's habitat may support seeded juveniles, identify the characteristics of successful seeding sites, determine optimal seeding strategies, and investigate population dynamics and economics that may most influence commercial ventures. Most of the experiments took place on the north-west Namaqualand coast; others were carried out along the south-west coast near the Gouritz River.

In preliminary experiments, 16 sites in Namaqualand were seeded with abalone ranging 8–18 mm in size. Recovery rates were low (0–13 %) and the cause of failure was attributed to the adverse effects of the ocean currents and wave action. New sites with limited wave action were selected in McDougall's Bay where the effect of using magnesium sulphate as an anaesthetic was first tested. There was no significant difference between the recovery of anaesthetized and non-anaesthetized seeded abalone or in their shelter-seeking behaviour – provided at least 1–2 h were allowed to elapse between anaesthetization and release. However, initial post-seeding mortality was high (>50%) for both anaesthetized and non-anaesthetized animals. Also, the presence of boulders that provide shelter seemed more important for the survival of juvenile abalone than the presence of sea urchins, contrary to the results of previous studies.

Experiments in McDougall's Bay (a sheltered locality) and in Gouriqua (a wav-exposed site) showed that recovery was greater at the more sheltered locality, and seeding size appeared to influence recovery rate, with 26-mm animals having double the recovery rate (56%) compared to 14-mm abalone (24%). Urchin-exclusion experiments at McDougall's Bay indicated that urchins played an insignificant role in the survival of seeded abalone. However, abalone still actively sought urchins as refuge. Boulders <30 cm in diameter played a significant role in providing shelter for seeded abalone. Seeding with 45-mm animals yielded the highest recovery rates (>80% over 60 days).

Dispersal from the points of release was limited (<3m over periods of up to 60 days), but greater at the exposed Gouriqua sites, which may have contributed to lower recovery rates. A spreadsheet-model simulation showed that initial seeding-induced mortality played a larger role than long-term age-specific differential mortality in determining total mortality (Z). The model showed that increasing seeding size decreased Z, but in economic terms seeding juveniles of at least ~ 25 mm yields the best returns.

Based on published figures for the potential yield from abalone ranching on the Namaqualand coast, the model was also used to test assumptions about the relationship between kelp-bed surface area and abalone production. Risk was investigated using Z as an indication of potential risk. The relationship between suitable seeding habitat and total kelp-bed habitat was shown to powerfully influence the economic viability of seeding.

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CHAPTER 1.

GENERAL INTRODUCTION

Background

The abalone *H. midae* is a valuable commercial species that occurs in South Africa along the coast from St. Helena Bay, Western Cape Province, to the Transkei region, Eastern Cape Province (Tarr 2000, Sampson et al. 2001, Figure 1.1, 1.2). Although the species occurs both east and west of Cape Agulhus a Total Allowable Catch (TAC) has been implemented for commercial catches only along the south-west coast (Figures 1.1, 1.2). Within this area, *H. midae* occurs most abundantly in subtidal kelp beds (Barkai & Griffiths 1986, Tarr 1995, Sweijd et al. 1998, Sampson et al. 2001) wherein *Ecklonia maxima* and *Laminaria pallida* are the predominant algal species. Beyond the range of *H. midae*, similar kelp beds are found from St. Helena Bay northward up to the Orange River. There are, however, fossil records of an abalone species, *Haliotis saldanhae* (Sweijd et al. 1998), that occurred in this area until approximately two million years ago.

The abalone resource in South Africa is widely perceived as under threat of over-exploitation as a result of increased illegal fishing (Dichmont et al. 2000, Tarr 2000). Poaching has become a serious problem, both with respect to the impact this has on present stock levels and with respect to potential broodstock available for natural recruitment and for abalone farms. This, and the ever increasing demand for the species commercially, has resulted in an increased number of land-based abalone farms over the last few years. Because abalone farming requires extensive capital

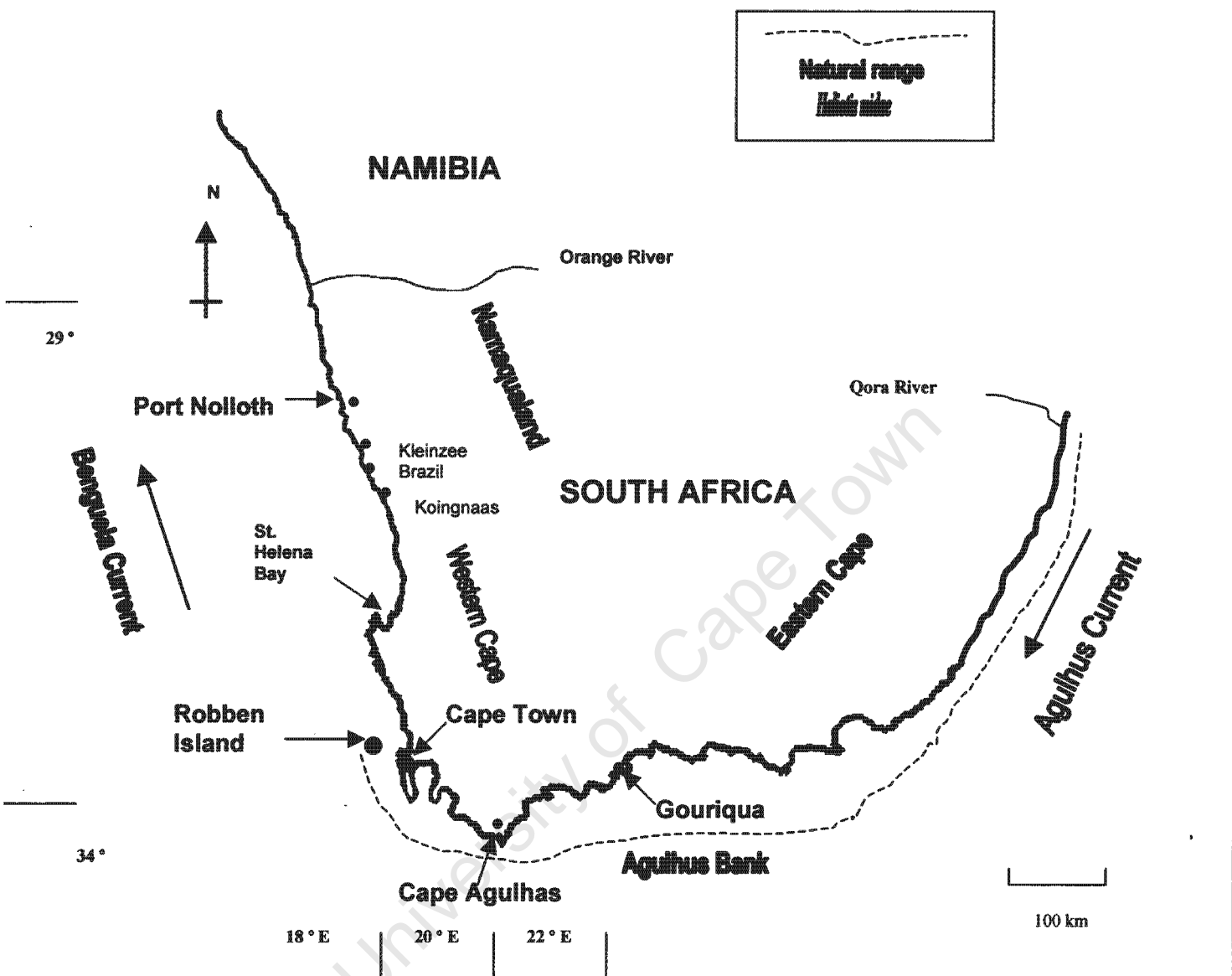


Figure 1.1 Map of southern Africa showing the primary experimental areas, Port Nolloth and Gouriqua. The ranching experiment was carried out along 60-kms of the Namaqualand coast between Kleinzee and Koingnaas.

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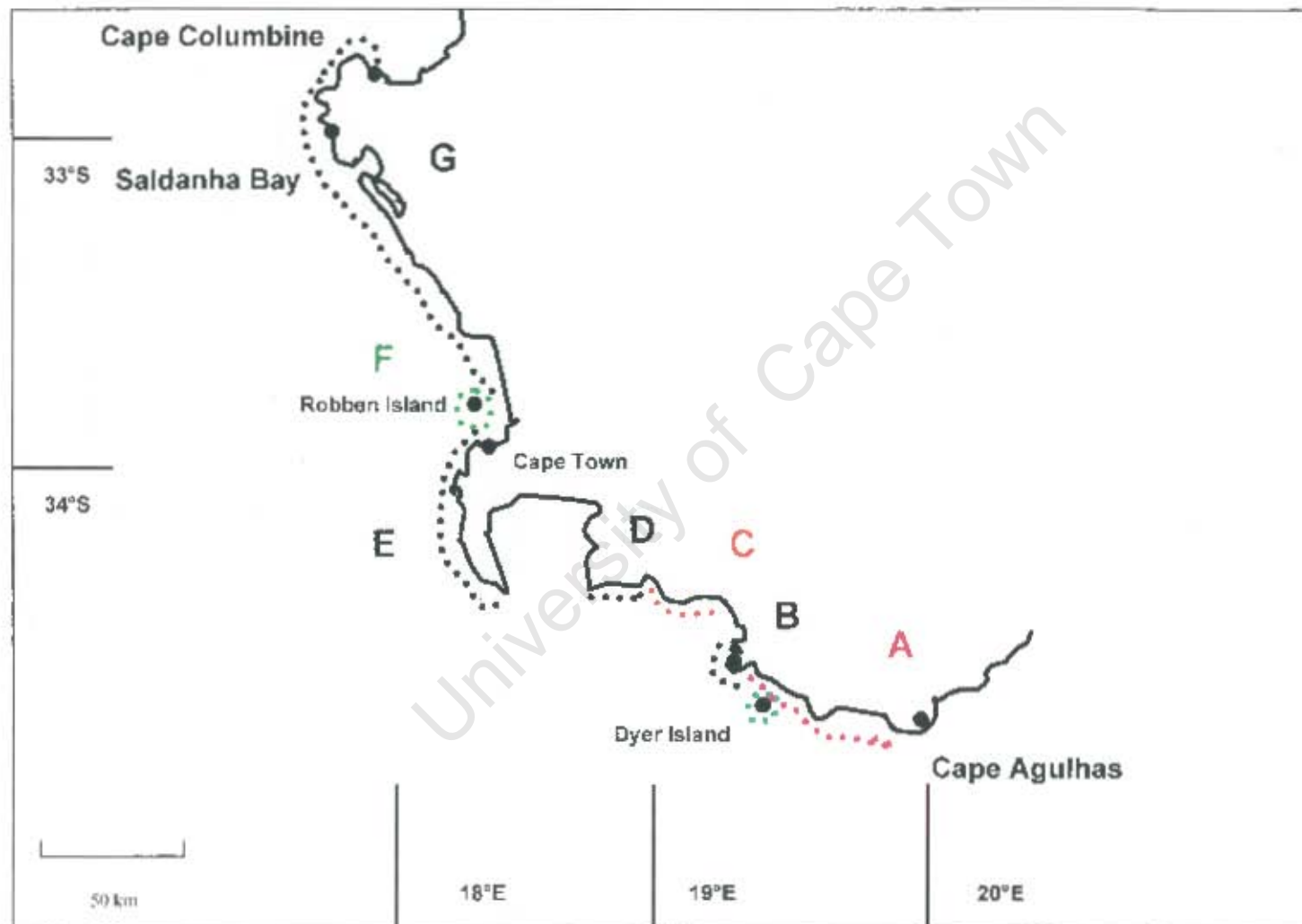


Figure 1.2 Map of the commercial total allowable catch (TAC) zones for abalone west of Cape Agulhas.

investment and involves high overheads with respect to labor and the cost of feeding grow-out abalone, an attractive alternative may be ranching. Abalone ranching involves the release of hatchery-produced juveniles into the ocean, with the aim of harvesting them at a later date (Momma 1972, Saito 1979, Kojima 1981, Saito 1984, Tegner & Butler 1985, Inoue 1987, Ebert & Ebert 1988, Emmet & Jamieson 1988, Tegner & Butler 1989, Tegner 1992, Schiel 1992, 1993, McCormick et al. 1994, Kojima 1995, Day 1998, Rogers-Bennet & Pearce 1998, Sweijid et al. 1998, Shepherd et al. 2000, Tegner 2000, Scott et al. in prep.). In exercises carried out over the last 10 years, a number of adult *H. midae* have survived transplantation from the Cape Town area to Port Nolloth on the Namaqualand coast, which lies beyond their natural range (Figure 1.1, Q. Snethlage, pers. comm.). Sweijid et al.(1998) undertook experiments to determine the extent to which artificially reared juvenile *H. midae* may survive and grow if released along this stretch of coast. The results of their work showed survival rates and growth rates that were promising enough to warrant a large-scale seeding experiment, coupled an experiment in a commercial environment undertaken by Port Nolloth Sea Farms (Sweijid et al.1998). Meanwhile, in the Northern Cape Province Fishing and Mariculture Sector Plan, abalone ranching has been specifically identified as one option that could potentially provide an economic boost to Namaqualand (Britz et al. 2000).

While the experiment in Port Nolloth was underway, interest from a commercial fishing company, Irving & Johnson, resulted in support for additional experiments to be carried out along the south coast, at the Gouriqua nature reserve, west of the Gouritz River mouth (34°22'S, 21°15'E). This stretch of coastline lies east of the commercial fishing areas TAC, and west of the Eastern Cape, which supports natural

stocks of *H. midae* not yet commercially fished. Presently, the Gouriqua area has very low numbers of abalone, and surveys done there in 1986 recorded no abalone were present at all (Baird et al. 1986).

The Namaqualand coastal fauna lies in the Benguela Current ecosystem, a nutrient-enriched upwelling system that has produced a seaweed flora quite distinct from that east of Cape Agulhus (Figure 1.1, Bolton & Levitt 1987, Branch et al. 1987). Variations in inshore temperatures in this region are relatively small; a ten-year mean shows a difference of between 2–4°C between the coldest and warmest months. This is in contrast to the south coast where a temperature variation up to 7°C has been recorded, and temperatures are higher on average. The abundant kelp species *Ecklonia maxima* and *Laminaria pallida* are both regarded as the major source of nutrition for west and south-west coast *H. midae* (Barkai & Griffiths 1986, Tarr 2000), to the extent that potential abalone yield has been projected based on the distribution and abundance of kelp beds (Sampson et al. 2001).

Ecologically, the Gouriqua coastal area differs substantially from the commercially fished areas and the Namaqualand coast. Gouriqua lies to the east of Cape Agulhas, in the zone known as the Agulhus Bank, an area intermediate between the warmer Agulhas current and the cooler Benguela current. Water temperatures are slightly higher here than in areas where abalone are commercially fished (Shannon 1989). Along the coast near Gouriqua the predominant vegetation consists of smaller algae, while algal biomass and cover are lower than on the west coast. The most common species are *Ralfsia* sp., *Lithoamnion* sp., *Sargassum elegans*, *Amphiroa rigida*,

Arthrocardia palmata, *Gelidium pristoides* and *Ulva* sp. (Baird et al. 1986, Wood & Buxton 1996).

The natural distribution of abalone along the South African coast, together with the distribution of abalone farms, has resulted in farm broodstock originating from all the major abalone-producing areas along the west and south-west coast. As a result, there has been a mix of genetic material in the juvenile spat generated on these farms. To address this, the Department of Marine and Coastal Management (MCM) has decided that, for the purpose of seeding experiments along the South African coast, the east coast should be differentiated from the west coast, the demarcation between the two areas being Cape Agulhas. Experimentally raised animals may only be released in the respective broad areas from which the broodstock originates, either east or west of Cape Agulhas.

Ecology and biology of abalone, and the implications on seeding

For any re-introduced species to successfully experience natural recruitment, it must be able to fulfill its entire lifecycle. All the biological and physical factors influencing its life cycle must occur within specific limits. Obviously, the more complex the lifecycle of the species, the more problematic its introduction or restoration. *H. midae* spawns naturally once or twice a year, depending on the area in which it occurs (Genade et al. 1988, McShane 1992, Wood & Buxton 1996). Spawning depends on a number of biological and physico-chemical factors. Biological factors of importance are the physiological status of the animal, its gonadal condition and its general status in terms of stress and condition. More complex, however, are the environmental cues

that initiate spawning and the conditions that must be in place for successful external fertilization and larval settlement. However, it is quite possible for adults to survive in an area for some time without spawning taking place. Alternatively, spawning may take place but fertilized larvae may not necessarily settle successfully. Adult survival, therefore, does not necessarily indicate that all the life-cycle stages will be successful. *H. midae* is a broadcast spawner, with external fertilization of gametes and very specific larval settlement requirements (Figure 1.3). Its complex lifecycle, involves a number of other species, both plant and animal (Wood & Buxton 1996, Day 1998, Day & Branch 2000 a, b). Abalone larvae are estimated to survive in the pelagic phase for 3–10 days, with the length of this stage determining the extent of dispersal of the larvae. Although abalone larvae can potentially disperse widely, the complex topography of abalone-inhabited reef and the association between abalone and macroalgal species, tend to localize larval drift, keeping the larvae in the vicinity of the adult broodstock (McShane 1992). Settlement occurs almost exclusively on species of crustose coralline algae. Coralline algae provide both concavities for the larvae to settle into and nutrition in the form of the cuticle and epithelial layer of the algae (McShane 1992, Slattery 1992, Wood & Buxton 1996, Day 1998, Kawamura 1998, Daume et al. 1999, Day & Branch 2000a). Although temperature and local hydrodynamics largely determine the extent to which recruitment is successful, the complexity of these factors and the small size of the juvenile abalone make it very difficult to quantify other different factors involved in this stage of the abalone lifecycle. Recruits of *H. midae* that grow to the juvenile stage have been found predominantly under sea urchins, remaining in very close association with the urchins until they are 3–4 years old (Tarr et al. 1996, Day & Branch 2000b, in press). The association between urchins and abalone is well documented for various abalone

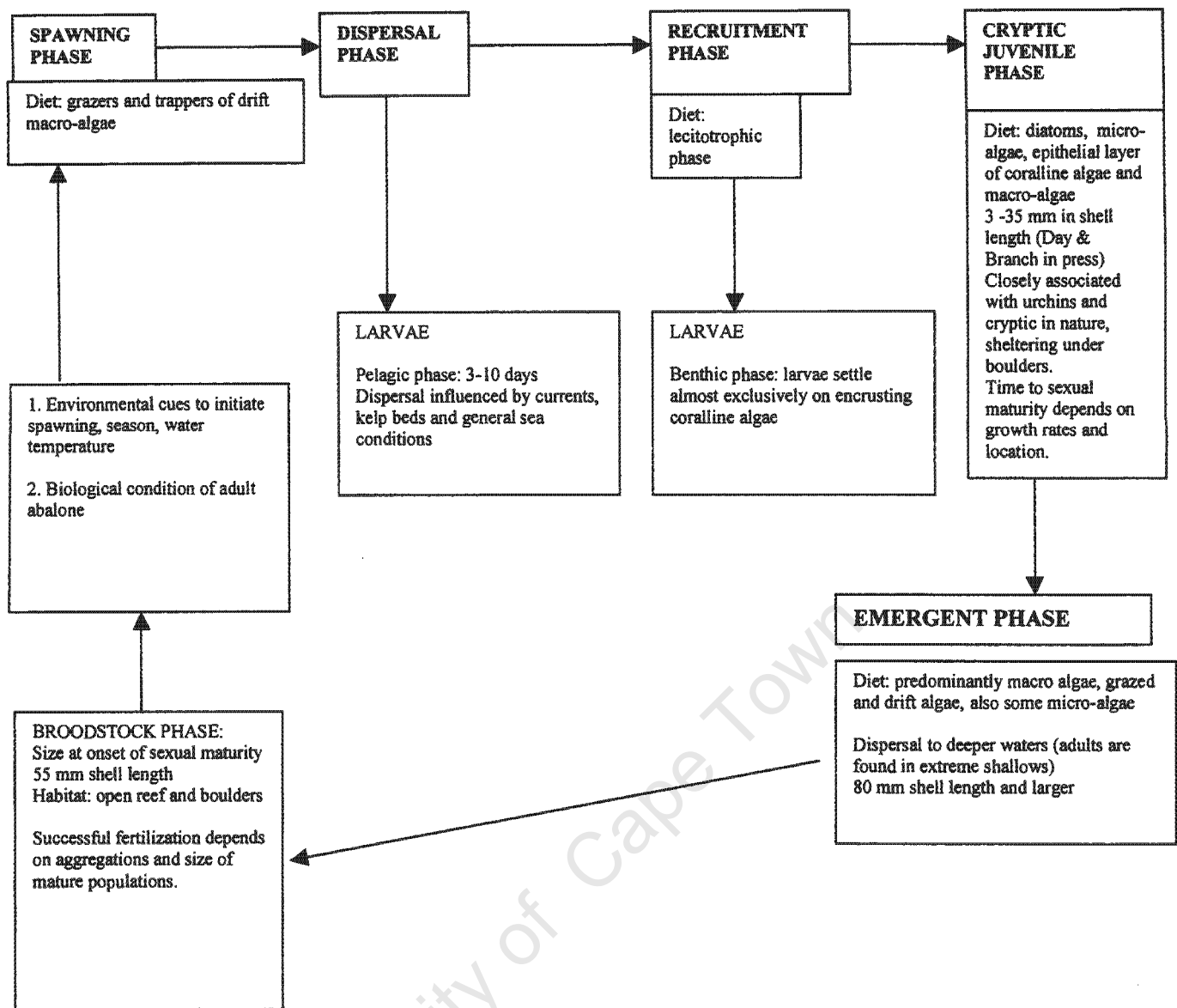


Figure 1.3 Schematic representation of the lifecycle *Haliotis midae*. For ranching to be viable, survival of sufficient numbers of abalone from the seeding stage (cryptic juvenile phase) to the size of harvesting, is vital.

species worldwide. However, there are many instances where the opposite has been found. In southern New South Wales, for instance, densities of abalone and sea urchins were found to be segregated on several spatial scales (Andrew & Underwood 1992). Since many factors influence the association between urchins and abalone species, it is important to compare these associations in context. Data gathered showing a close relationship between *H. midae* and the urchin *Parechinus angulosus* refer to areas in which there are specific urchin densities and particular types of habitats available to juvenile abalone. Introducing hatchery-raised animals into the wild involves processes of behaviour, genetic selection, and natural selection in terms of individuals selected for release and the effects of the mechanical process of release (Kojima 1981, Schiel 1993, Shepherd et al. 2000, Tegner 2000). Stocking densities, natural movement and exposure to predation are all affected by the mode of release; as a result, mortality is caused by both natural and artificial factors.

As mentioned above, degree of complexity of an animal's life cycle determines, to a large degree, the extent to which the restoration or introduction of the species will be successful. In the case of a species with a lifecycle as complex as that of *H. midae*, one must inquire which stage of its lifecycle produces the most viable product for seeding? To answer this question, the probability of survival at each stage of its lifecycle must be quantified. The abalone farming industry in South Africa has developed to the point that all life-cycle stages of *H. midae* are available for experimental purposes. Thus, various options for abalone seeding can be investigated. Larval seeding is problematic in terms of determining short-term success, and in terms of confining larvae to experimental areas (Shepherd et al. 2000, Tegner 2000). The transplanting of juveniles, however, allows the monitoring of all life-cycle stages

from juvenile through to adulthood, an observations can be carried out with minimal equipment. In this study, I have concentrated on the post-larval stage. Apart from a number of tagged adults (approximately 60) that were translocated from Robben Island to Kleinsee, the study investigated the effects of seeding juvenile abalone ranging in approximate length from 8 mm to 45 mm, i.e. the cryptic juvenile phase (R. Tarr, MCM, pers. comm). These animals differ in diet and behaviour from adult animals. *H. midae* becomes emergent at approximately 110-mm length (R. Tarr, MCM, pers. comm), moving onto exposed sites on reefs or boulders. Adult *H. midae* are grazers as well as drift trappers of a range of seaweed species, with the choice of species depending on the area and the abundance and diversity of seaweeds present (Barkai & Griffiths 1986, Wood & Buxton 1996). Juveniles, on the other hand, have been shown to be grazers; algal species that make up the drift component in the adult's diet are not found in the gut contents of juveniles (Wood & Buxton 1996). The epithelial layer of the encrusting corallines on which the recruits are found, together with benthic diatoms, are a source of nutrition for recruits and small juveniles. Large juveniles have been shown to prefer *Laminaria pallida* to *Ecklonia maxima* (Stepito & Cook 1996, Day 1998). Adult abalone occupy a different habitat to that of juveniles. There are few data available at present concerning the behaviour of juveniles in the cryptic phase, although it would be useful to know to what extent that habitat suitable for juveniles is suitable for adults (Tegner & Butler 1989).

Development and structure of this thesis

Although experimental seeding of artificially reared abalone has been ongoing in many countries for a number of years, Japan is the only country to date where this is

has been attempted on a commercial basis (Saito 1979, Kojima 1981, Saito 1984, Inoue 1987, Suda 1987, Hayashi & Yamakawa 1988, Kojima 1995, Masuda & Tsukamoto 1998). In the United States, Australia, New Zealand and South Africa, seeding experiments have produced varying degrees of success (Emmet & Jamieson 1988, Tegner & Butler 1989, Schiel 1992, Rogers-Bennet & Pearse 1998, Sweijd et al. 1998, Shepherd et al. 2000, Tegner 2000). What is clear from the work done so far, including the work done by the Japanese, is that recovery rates are site-specific and depend on a number of basic factors (Schiel 1992, McCormick et al. 1994, Shepherd et al. 2000, Tegner 2000). Such factors include: physical site and substratum in the release area, size of the juveniles at seeding, presence of vital symbionts, and sea conditions at time of release.

Physical habitat, particularly the abundance of boulders, cracks and crevices, has proved to be very important in selecting abalone seeding sites. Mortality due to predation, which has serious implications for juvenile abalone, can be countered to some extent by placing the juveniles in an environment that provides adequate cover and protection (Tegner & Butler 1989, Schiel 1992, Schiel 1993, Rogers-Bennet & Pearse 1998, Shepherd et al. 2000). Smaller abalone have been shown to be selective of habitats with certain sized boulders, and the extent to which boulder habitat availability influences survival cannot be overemphasized (Tegner & Butler 1989, McCormick et al. 1994). The movement of sand and silt, or any loose or unstable substratum, will also severely affect seeded and natural juveniles (Schiel 1992, 1993).

Most of the Japanese data indicate a clear trend for increasing percentage survival of seeded juvenile abalone by increasing seed size. Although this has not been the case

with all species, it has become a fairly accepted concept (Tegner & Butler 1989, McCormick et al. 1994, Kojima 1995, Masuda & Tsukamoto 1998, Shepherd et al. 2000, Tegner 2000). Obviously there is a point at which the cost of keeping an animal in land-based tanks becomes too high to risk losing it in a seeding operation. These financial trade-offs must be investigated and will be specific to each production situation and to each seeding site (Schiel 1992).

With regard to the biological attributes of a seeding site, the presence of sea urchins has been shown to play a symbiotic role in the survival of juvenile abalone, both of natural populations (Kojima 1995, Tarr et al. 1996, Day 1998, Mayfield 1998, Day & Branch 2000a, b, in press) and of seeded populations (Kojima 1981, Rogers-Bennet & Pearse 1998, Sweijd et al. 1998, Scott et al. in prep.). *H. midae* juveniles have a close association with the urchin *Parechinus angulosus*, to the extent that numbers of juvenile abalone have been seen to mimic urchin population numbers in areas where urchin abundance has been experimentally reduced or has undergone a severe natural decline (Tarr et al. 1996, Day 1998, Mayfield 1998, Day & Branch 2000a, b, in press).

The research was developed to investigate these factors experimentally, and to use the results to investigate the economic implications associated with seeding and ranching projects. The success of a ranching or seeding operation is based on the general hypothesis that the area selected can support at least those stages of the life cycle necessary to achieve a viable yield (Hypothesis 1, Figure 1.4). If the habitat cannot support the natural reproductive, dispersal and recruitment stages of the species, repetitive seeding of juveniles could replace these phases. To test whether or not a

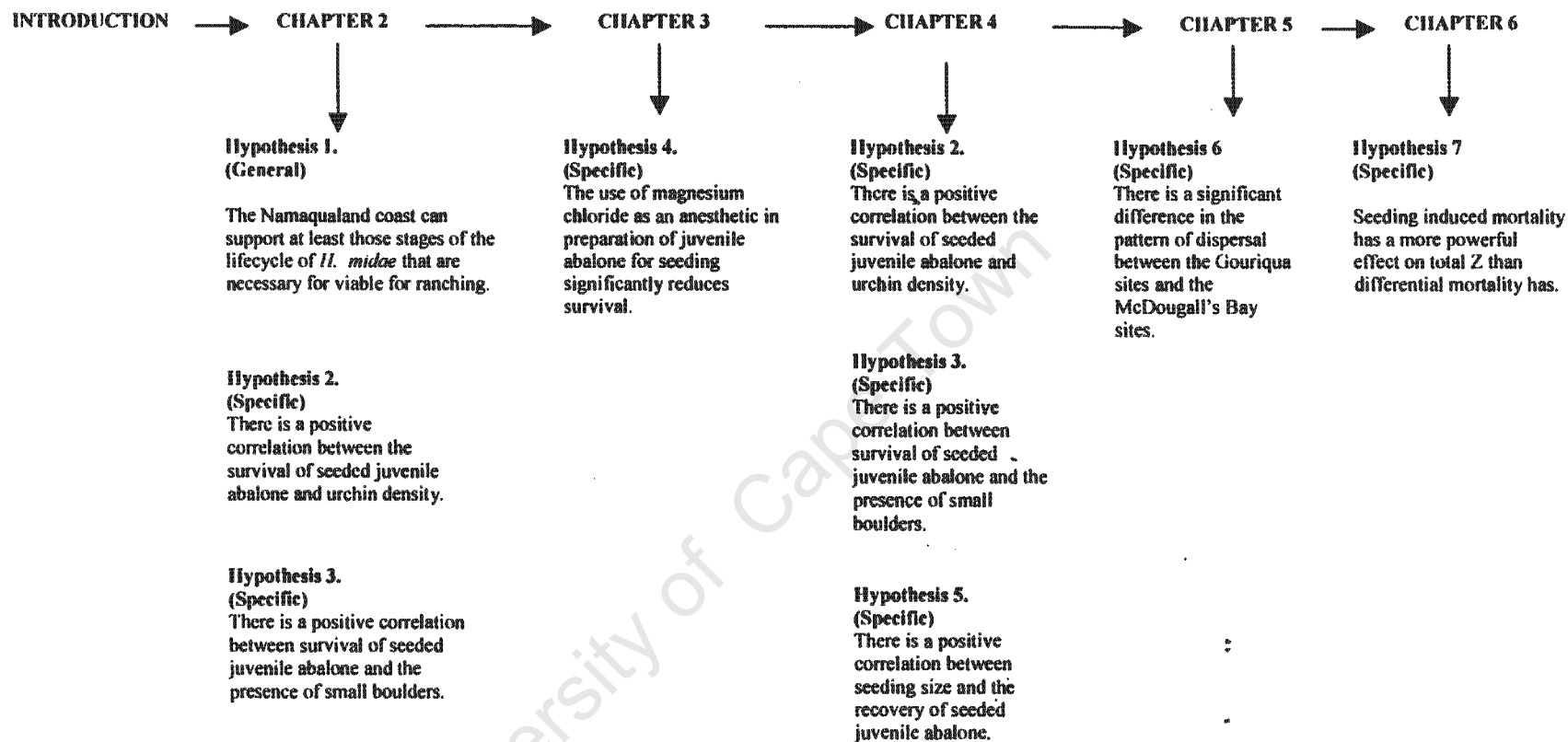


Figure 1.4 Flow chart showing the development of hypotheses based on seeding experiments in chapters 2, 3, 4, 5, and 6.

particular habitat can support all the life-cycle stages of *H. midae*, ideally it would be necessary to seed animals at the cryptic juvenile phase and to leave them in the ocean long enough to achieve sexual maturation, spawning, fertilization, settlement of larvae and growth to the juvenile phase. This was beyond the scope of this work, and perhaps unnecessary in terms of determining whether or not a given area could support viable ranching. However, based on criteria identified in the contemporary literature, it was possible to test more specific hypotheses over the short-term. Figure 1.4 outlines these hypotheses and the sequence in which they are addressed in the thesis. The hypotheses relate to both the physical and biological attributes of selected seeding sites that influence juvenile survival, and to the selection and treatment of seeding material. The interpretation of the experimental results, and the use of the data to make economic predictions, can ultimately play a principal role in determining the potential economic viability of ranching operations in South Africa.

To test the general hypothesis that the Namaqualand coast can support those stages of *H. midae* necessary for viable ranching, requires a demonstration that *H. midae* can survive in the area from the seeded juvenile stage through to a size large enough for harvesting. However, to understand the factors contributing to survival, a series of specific hypotheses needed to be formulated and tested. The first was that there is a positive correlation between the presence of the urchin *Parechinus angulosus* and juvenile abalone survival (Hypothesis 2). The second was that, in habitat where no urchins are present, the presence of an alternative under-boulder habitat would correlate positively with juvenile abalone survival (Hypothesis 3). The results from initial experiments were ambiguous and analysis did not allow ranking of site attributes that optimised survival. A major reason for this was the effect that wave

action and strong currents have on seeding attempts. However, it seemed possible that the failure of the earlier experiments was due either to the use of an anaesthetic or the use of juveniles of sub-optimal size. This led to a series of specific hypotheses to be tested at McDougall's Bay, Port Nolloth (Figure 1.1). McDougall's Bay was selected because it is sheltered from extreme wave action, although strong currents and swell could still reach the experimental sites (which were selected to achieve a degree of consistency with respect to the variation in sea conditions that influenced the experimental sites). The more specific hypotheses related to the use of anaesthetics in handling abalone before seeding (Hypothesis 4), and the size of abalone at seeding (Hypothesis 5). Once the influences of the anaesthetic and of juvenile size were tested and assessed, a range of experiments was performed in Port Nolloth and at Gouriqua to better test the hypotheses relating to urchins (Hypothesis 2) and to the physical complexity of seeding sites (Hypothesis 3).

The experiments performed in this study were undertaken with one fundamental concept kept in mind: The scale of any commercial ranching operation would be too large to allow the manipulation of seeding sites with respect to predators, nutrition and other environmental factors during actual commercial operations. Thus, the experiments were designed to generate techniques or knowledge that would allow an evaluation of potential of seeding areas to be used with as little management effort as possible. Therefore, the experiments took place under relatively natural conditions, and abalone survival was determined under these conditions. Criteria that would optimize seeding success were also identified in the natural environment. There are advantages and disadvantages to this approach. The main advantage is that the experiments are done under conditions that realistically will be encountered in

ranching operations. The principle disadvantage is that field experiments do not allow manipulation or control of natural environmental conditions. Furthermore, there is the risk that factors other than those being investigated could influence the results.

Recovery rates from the Namaqualand coast and Gouriqua area were used to identify attributes of optimal seeding sites. The object of the experiments was not to make a comparison between the two areas, but rather to use both areas to test the same hypotheses. Each experimental site was analysed to investigate which criteria were important in optimising abalone survival within the context of the ecological factors that prevailed in that area. Each seeding action has its own characteristics with respect to a range of environmental conditions.

One of the problems associated with generating recovery data is that juvenile abalone are cryptic in behaviour and, as a result, are difficult to find. Recovery rates cannot be equated with survival unless it is certain that the animals that were recovered were the only survivors. If dispersal differs between sites and is inversely related to detection, one cannot be certain what percentage of the survivors are reflected in the recovery figure. The Namaqualand experiments generally resulted in very little evidence of dispersal, whereas the Gouriqua experiments showed evidence that dispersal was taking place. A specific hypothesis (Hypothesis 6, Figure 1.4) was tested to determine whether or not there was a significant difference in dispersal between juvenile abalone released in the Gouriqua experiment and those from the McDougall's Bay experiments. The interpretation of recovery data and survival rates can be done with more certainty if dispersal patterns are known and understood. In comparing the dispersal patterns between the two areas, water depth and wave action were the most

obvious differences. These factors exist as major influences in dispersal, as a result, they may also influence the density of older abalone.

The first part of the thesis (Chapters 2–5) focuses on an experimental examination of the factors influencing the success of seeding. The second part of the thesis (Chapters 6–7) develops models that explore the economic consequences of various conditions.

A range of economic simulations was investigated using a simple, deterministic spreadsheet model. The model predicted population decline over time using a combination of experimental recovery data and a range of hypothetical differential survival rates per age class. The investigations focussed on seeding size, and were not conducted to determine exact figures with respect to production costs and profit, but rather to present trends resulting from utilizing juvenile abalone within specific economic parameters. The same model was used to calculate hypothetical seeding densities necessary to produce a specified yield. This approach was based on the following principals:

- 1) Under a specific set of environmental parameters, a total mortality rate (Z) will determine the rate at which a population declines over time.
- 2) Seeding size (shell length of the juvenile abalone) can determine initial population numbers. By seeding juveniles large enough to have a high initial survivorship, the highly variable recruitment phase is replaced by a more consistent or reliable supply of juveniles.

Tarr (1995) investigated growth rates for *H. midae* from a range of locations. Growth rates, combined with total mortality rates, determine the rate at which seeded

populations will decline in number over time, and the rate at which biomass will change as population numbers change. Growth rates for seeded populations are not available at present, but the growth rates from natural populations (Tarr 1995) were used in the model for cost-benefit analyses. Because differential survival data do not presently exist for seeded populations of *H. midae*, the mortality rates produced by the model could not be verified. However, economic cost-benefit analyses could be done to investigate which values of Z would allow viable ranching within a specific set of economic parameters. The concept of economic viability must be separated from the ecological parameters that drive population decline in a seeded population. In an economic environment, where selling prices are relatively high and where the exchange rate favours the export of abalone from South Africa, benefits may be so great that potential investors will be willing to risk an investment even in areas where the total mortality rates are relatively high. In such a case, the decision would be purely economic and would not reflect the ecological parameters that drive population decline over time. Likewise, adverse economic factors, such as a decline in selling price, would mean that, under the same set of ecological parameters, a venture would be no longer economically viable.

Two potential applications of the development of seeding technology are stock enhancement, in areas where abalone stocks have been drastically reduced, and the introduction of abalone into areas in which they do not occur, but where habitat seems to be suitable for ranching. Although the technology necessary for either of these two potential scenarios to occur may essentially be the same, there is a difference in the way that application of the technology would have to be evaluated. The enhancement of a natural stock, for the purpose of avoiding extinction of a species, involves

esoteric values that are beyond those of short-term commercial interests (Schiel 1992, Cacha 1994, Craik 1994, Munasinghe 1994, Post 1994, Tisdell 1994, De Alessi 1995, Stephenson & Lane 1995, Caddy 1999). The potential success of any technology depends, to a large extent, on the expectations of the people applying it. These expectations entail a fundamental difference in the philosophical approach of conservationists versus commercial farmers. As a result of fundamental differences in approach, the use of a technology may be successful for one group, while for the other it could be completely undesirable.

The creation of new abalone populations may give researchers the opportunity to investigate the extinction process in reverse. The concept of minimum viable populations of *H. midae* is becoming an important consideration as populations of the species are being impacted by illegal fishing. For example, there are populations of *H. midae* along the Eastern Cape coastline that are currently very heavily poached. These populations are in areas where little stock assessment has been done (Wood & Buxton 1996, Brian Godfrey, Rhodes University, pers. comm.). It is possible that some local populations will be exploited to below viable levels without any record of this happening, or without any record of population decline. If the establishment of populations of the species in new areas leads to successful natural recruitment, this will allow investigation into the dynamics of population growth and metapopulation theory as it applies to this species (Shepherd & Brown 1993). Such ecological data are extremely valuable with respect to the conservation of species in general and, in particular, with respect to marine invertebrates, as there are very few data available regarding minimum viable populations of abalone (Shepherd & Brown 1993).

Limitations and constraints of the research.

In the experiments on seeding size, presence of urchins and the use of anaesthetic, replicates were done for each treatment. When assessing the characteristics that influence site suitability (i.e. density of urchins and availability of shelter), each site was treated as an independent treatment (without replication) because all sites were different. No artificial manipulations were undertaken to fix either of these factors. Consequently, the data were collected and analysed with this mind.

The survival of juvenile abalone over time is influenced by a range of factors, including abundance of predators, availability of food, abundance and quality of habitat providing protection, occurrence of adverse sea conditions and prevalence of disease (Lafferty & Kuris 1993, Ebert 1999, Tegner 2000, Friedman et al. 2001). Some of these factors were outside of the scope of the present study. In particular, the following have not been investigated in this work:

- Physico-chemical ocean conditions during seeding experiments (although some aspects were addressed and recorded in some experiments).
- The condition of the seed before release.
- Seeding densities.
- The abundance and type of predators present.
- Harmful algal blooms.
- Disease.
- Food supplies.

Over the period that experiments were done at Port Nolloth, data loggers used to measure water temperature at Port Nolloth Sea Farms were taken out of commission; at the same time, the Marine and Coastal Management data logger in Port Nolloth Harbour broke down. As a result, temperatures were only recorded for the second half of 1998. At Gouriqua, however, temperatures were measured over the full experimental period. There were no local data loggers for swell height in either of the experimental areas. Swell height was estimated on days when sampling was done, but those were usually days when sea conditions made diving safe.

The condition of juveniles or adults before release plays an important role in survival (Tegner & Butler 1989, Schiel 1992, Inoue 1997, Shepherd et al. 2000, Tegner 2000). The consequences of handling and transport stress, and even the quality of juveniles, are not always easily detected when abalone are monitored in a tank in a land-based situation. When animals are released into the ocean, pre-existing conditions can cause high short-term mortalities, induced by the seeding operation and not by the attributes of the site itself. Whereas the selection of the site, in terms of its physical and biological attributes, is important in terms of the availability of cover and natural habitat for the released abalone, this can do little to ensure the survival of poor seeding material (Kojima 1981, Emmet & Jamieson 1988, Schiel 1992, McCormick et al. 1994, Shepherd et al. 2000).

Many seeding experiments done in the past involved the release of juvenile abalone from modules or cages (Kojima 1981, McCormick et al. 1994, Rogers-Bennet & Pearce 1998, Sweijd et al. 1998). Because varying numbers of different sized juveniles were released, the concept of seeding densities was not directly addressed.

Table 2.2 Habitat attributes believed to affect abalone survival of each site in the initial experiments between Kleinsee and Koingnaas. The recovery rate from each site is included.

Site	Recovery (%)	Percentage of area consisting of boulder with diameter				% cover crustose corraline algae	Urchin density (m ⁻²)
		> 50 cm	< 50 cm > 30 cm	< 30 cm	% area exposed		
1	0	60	5	5	30	17.15	49.7
2	6	20	10	10	60	17.50	24.6
3	0	10	10	70	10	17.50	0
4	3.3	50	10	10	30	21.52	64
5	0.4	40	30	5	25	17.50	0
6	1.7	20	20	50	10	12.50	2.12
7	12.55	55	10	25	10	47.50	20.6
8	4.2	80	15	0	5	6.82	38.4
9	0	65	25	5	5	32.50	4.8
10	6.6	50	10	10	30	21.52	64

Table 1.1 List of species that may predate on abalone that are found in the two experimental areas. Densities and seasonal effects were not measured or compared between the two areas.

Species	Namaqualand Coast	Gouriqua Coast
Lobster <i>Jasus lalandi</i>	X	X
Star fish <i>Marthasterias glacialis</i>	X	X
Whelks <i>Thais capensis</i> , <i>T. castanea</i> , <i>Burnapena</i> spp.	X	X
Common dogwhelk <i>Nucella dubia</i>	X	
Dog whelk <i>N. cingulata</i>	X	
Cape stumpnose <i>Rhabdosargus capensis</i>		X
Red roman <i>Chrysoblephus laticeps</i>		X
Octopus <i>Octopus</i> sp.	X	
Stingray <i>Myliobatus aquila</i>	X	X
Stingray <i>Dasyatidae</i>	X	X
Bareheaded goby <i>Caffrogobius nudiceps</i>	X	
Hottentot fish <i>Pachymetopon blochii</i>	X	
Giant clingfish <i>Chorisochismus dentex</i>	X	X
Parrot fish <i>Oplegnathus connayi</i>	X	
Klipfish <i>Clinidae</i>	X	X
Two tone fingerfin <i>Chirodactylus brachydactylus</i>	X	
Blacktail <i>Diplodus sargus capensis</i>	X	X
Janbruin <i>Gymnocrotaphus curvidens</i>	X	X
White steenbras <i>Lithognathus lithognathus</i>	X	X
Dogsharks <i>Poroderma</i> spp., <i>Haploblepharus</i> spp.	X	X
Zebra <i>Diplodus sargus capensis</i>		X
Mussel crackers <i>Cymatoceps nasutus</i> , <i>Sparodon durbanensis</i>		X

rationale behind utilizing experimental areas as different as those at Namaqualand and Gouriqua was not to compare the ecological systems of the two areas, but to analyze the accumulated data within the context of each area separately. In doing so an attempt was made to determine the characteristics of each area that were important for optimizing survival of seeded abalone.

Coastal upwelling ecosystems are often identified as regions that are susceptible to seasonal blooms of harmful or toxic phytoplankton. In South Africa, blooms occur mainly along the west coast, and to a lesser degree on the south coast, particularly during late summer and autumn. The most frequently encountered causative species include *Ceratium furca*, *C. lineatum*, *Prorocentrum micans*, *Alexandrium catanella*, *Dinophysis acuminata* and *D. fortii* (Pitcher & Calder 2000, Probyn et al. 2000). The southern Benguela area, between 32°S and St. Helena Bay, is particularly susceptible to red tide formation. In Langebaan and Saldanha, just south of St. Helena Bay, brown tide, *Aureococcus anophagefferens*, has caused growth arrest in farmed oysters and mussels; in the same area, *Alexandrium catenella* and *Dinophysis acuminata* have resulted in severe toxicity of mussels (Probyn et al. 2000). North of St. Helena Bay, at Elands Bay, massive blooms of the dinoflagellate *C. furca* have caused anoxic events and hydrogen sulphide poisoning that resulted in massive walk-outs or die-offs of species such as rock lobster and mullet (Mathews & Pitcher 1996). In the Hermanus area the toxic dinoflagellate *Gymnodinium mikimotoi* has resulted in mass abalone mortalities (Pitcher 1998). In the area between Kleinsee and Koningnaas, which has been allocated to Port Nolloth Sea Farms as an experimental ranching area, there are specific sites with an abundance of washed-out mussel shells, but whether these are the result of toxic blooms is uncertain. This has not been a deterrent to the ranching

experiment, but seeded abalone from the area have not yet been analysed for signs of toxicity; it is possible that harmful algal blooms may eventually impact on abalone ranching projects along this coast. Consideration of the potential effects of harmful algal blooms was, unfortunately, beyond the scope of this thesis.

Potential disease problems were also not considered in the thesis. Abalone species have shown radical population declines as a result of disease, good examples being the rapid spread of Withering Syndrome in the abalone *Haliotis cracherodii*, and mass mortalities in California of the same species due to sybellid-worm infections (Lafferty & Kuris 1993, Friedman et al. 2001). Potential disease problems were not, however, considered in the thesis.

Thesis structure

Following this general introduction, other chapters of this thesis are as follows:

CHAPTER 2: Preliminary seeding experiments- This chapter describes the experimental procedure, the rationale behind the development of the experimental process, and the initial selection of experimental areas and sites in Namaqualand. An attempt was made to test the general hypothesis that the Namaqualand coast can support populations of seeded *H. midae*. In addition, two specific hypothesis were tested: that a positive correlation exists between the presence of urchins and the recovery of seeded juvenile abalone, and that the availability of under-boulder habitat positively correlates with both abalone recovery rate and survival. Seeding sites were selected based on criteria derived from contemporary literature. It is important to note

that although seeding size proved significant, the preliminary experiments yielded no other significant results that could be used to relate the attributes of seeding sites to survival of seeded juvenile abalone, because the overall recovery of seeded abalone proved so low that no analyses or comparisons could be undertaken. However, on the basis of the negative preliminary results subsequent experimental design and protocols were developed.

CHAPTER 3: Use of magnesium sulphate as an anaesthetic for seeded abalone-

In commercial operations magnesium sulphate is often used as an anaesthetic when handling and transporting juvenile animals. The use of magnesium sulphate was tested to determine whether or not it had any adverse effects on animals being introduced into the sea. In the experiments done by Sweijd et al. (1998) at Port Nolloth, no anaesthetics were used and seeded juveniles were successfully established. In the preliminary seeding exercises described in Chapter 2, anaesthetics were used. The specific hypothesis tested in Chapter 3 is that the use of magnesium sulphate accounts for the differences in the recovery rates in the work presented by Sweijd et al. (1998) and that described in Chapter 2. This chapter describes the experimental procedure followed both for the sea trials and for trials using containers on land, together with the results and observations gathered from a series of short-term experiments at McDougall's Bay, Port Nolloth.

CHAPTER 4: Physical and biological attributes of successful seeding sites-

Following the results of the experiments concerning the use of anaesthetics, a series of hypotheses needed to be tested:

- The sea urchin *Parechinus angulosus* plays a direct role in the survival of seeded juvenile abalone.
- The degree of complexity and the size of the boulders at seeding sites directly impact on the survival of seeded juveniles.
- An increase in the seeding size of juvenile abalone directly influences survival rate.

Experiments were carried out in McDougall's Bay and at Gouriqua, and dispersal patterns around release modules were investigated in both areas. Other experiments were done at McDougall's Bay using 45-mm animals to investigate the dispersal and habitat selection of larger abalone as compared to smaller animals.

CHAPTER 5: Investigating dispersal- If juvenile abalone disperse rapidly from a release site, it may be difficult to detect them and, as a result, the recovery rate will be low. If dispersal has not been previously assessed, this could lead to the incorrect conclusion that survivorship is low. Differences in recovery rates were recorded between Port Nolloth and Gouriqua. To test the possibility that these differences could have resulted from differences in dispersal, one specific hypothesis was tested in Chapter 5:

- There is a significant difference in dispersal patterns between the animals released in the Port Nolloth area and those released in the Gouriqua area.

This was important to gain an understanding of the effect that dispersal can have on distinguishing potential survival rates from recovery rates.

CHAPTER 6: Quantifying the dynamics and economics of seeded abalone populations-

6A. Quantifying population dynamics of seeded abalone

This chapter describes a simple spreadsheet model used to investigate the specific hypothesis (Hypothesis 7, Figure 8.1) that the effect of short-term seeding-induced mortality plays a stronger role in determining the total mortality rate (Z) than post-seeding, age-differential, mortality and survival. The effect of seeding size was modelled, together with data depicting a range of differential survival regimes in order to investigate different scenarios of population decline over time.

6B. Quantifying the economics of seeded abalone

The model described above was then used to construct two cost-benefit analyses associated with the potential use of different-sized seed juveniles. It was shown that, whereas ecological parameters will determine the size of a population and the rate at which that population declines over time, economic viability is similarly variable and depends on specific economic parameters that are applicable under specific conditions. Ecological parameters determine population dynamics, which in turn have economic consequences. Seeding viability therefore depends on both ecological parameters and economic parameters being favourable.

CHAPTER 7: Determining potential yield of seeding sites- This chapter describes the use of the model derived in Chapter 6 to investigate assumptions that are used in published predictions about abalone yield along the Namaqualand coast. These predictions are based on the total surface area of kelp beds in the commercial abalone

fishery areas (TACs) in combination with the commercial yield from these areas. In this chapter I attempt to quantify the process of seeding through to the end product, using seeding habitat, seeding densities, adult habitat, adult pre-harvest densities and the rate of population decline over time.

CHAPTER 8: General conclusions- This chapter synthesizes conclusions about the selection of areas for abalone reseeded and ranching projects, based on the hypotheses that were tested and the results of economic modelling. Chapter 8 also discusses potential management strategies for South Africa's abalone resource that relate to the principal of long-term ownership of a resource and a vested interest in sustainable natural resources.

CHAPTER 2.

PRELIMINARY SEEDING EXPERIMENTS

2.1 INTRODUCTION

This portion of the study tests the general hypothesis that the Namaqualand coast, which does not presently support natural abalone populations, could support *H. midae* populations – or at least those phases of the lifecycle necessary for ranching (see Figure 1.4). Two more specific hypotheses were also tested: that there is a significantly positive correlation between the recovery of seeded juveniles and the abundance of sea urchins, and that there is a positive correlation between the survival of seeded juvenile abalone and the presence of under-boulder habitat. After seeding, an attempt was made to quantify these relationships.

Previous experiments done by Sweijd et al. (1998) showed extreme variation in recovery rates between seeding sites located in the same general area (100m x 100m), and exposed to apparently similar sea conditions. This variation could have been an effect of predation at the different sites and/or differences in environmental factors such as temperature and sea conditions. Differences between sites were noted in the distribution and abundance of physical shelter (related to boulder size and abundance), and the associated biological attributes such as urchin distribution and abundance. Extreme variation in habitat over a small scale (Branch et al. 1987) in rocky intertidal and shallow subtidal areas is a key part of these systems. This was expected to manifest itself in the variations in recovery rates at the different sites, but the extent to which this would take place was, however, not known.

The experiments described in this chapter were undertaken in the area between Kleinzee and Koingnaas (Figures 2.1, 2.2, 2.3), and were designed to examine the environmental requirements of juvenile abalone, on a scale that could realistically be applied to future management decisions about the suitability of such sites for ranching.

Three areas that were thought to be diverse enough to reflect the range of conditions along the Namaqualand coast were selected for seeding experiments. The most northerly was Kleinzee, 70 km south of Port Nolloth. The farm Brazil, 30 km south of Kleinzee, was the second area, and the third was Koingnaas, a further 30 kilometers south of Brazil. In each area, five experimental sites were chosen, except at Kleinzee where a sixth site was included because of convenience and the availability of extra seed animals. The initial seeding sites were chosen for what was thought to be easy and safe access, and included habitats deemed to be both suitable and unsuitable for juvenile abalone. The suitability of a seeding site was based on criteria derived from contemporary literature, and included the presence of kelp (*Ecklonia maxima*), drift kelp, species of crustose coralline algae, sea urchins (*Parechinus angulosus*), and boulders ranging in size from <30 to >50 cm in diameter (Schiel 1993, Davis 1995, Tarr et al. 1996, Sweijd et al. 1998, Shepherd et al. 2000, Tegner 2000, Scott et al. in prep.). The most important of these criteria were the presence of urchins and the presence of under-boulder habitat. The attributes measured at each site were urchin density, percentage cover of coralline algae, and boulder size and abundance. The decision to use size and abundance of boulders as a measure of rugosity was made because juvenile abalone are found predominantly under boulders. Measurements of

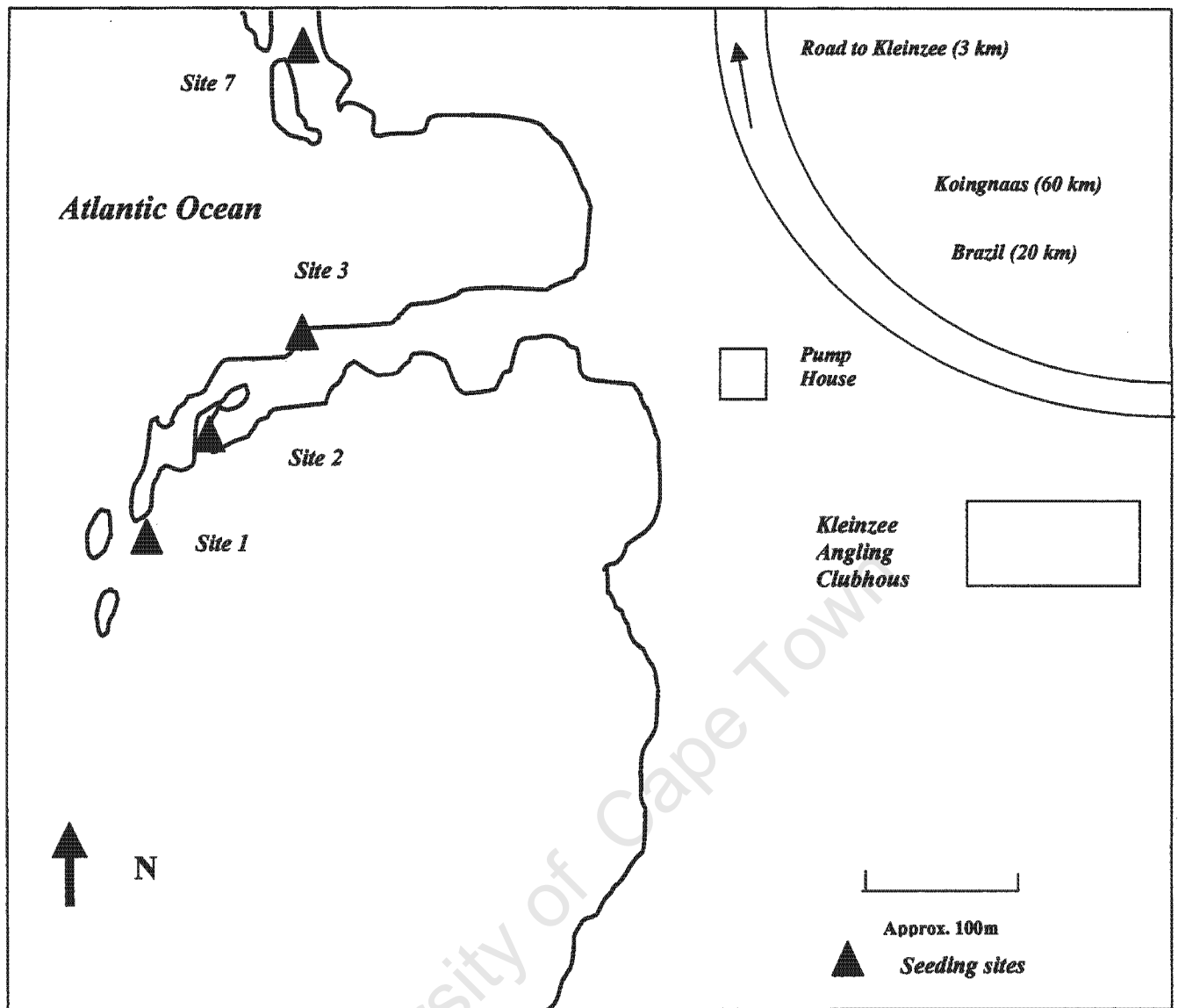


Figure 2.1 Schematic map of the Kleinzee experimental area showing the position of the seeding sites. One release module was placed at each site.

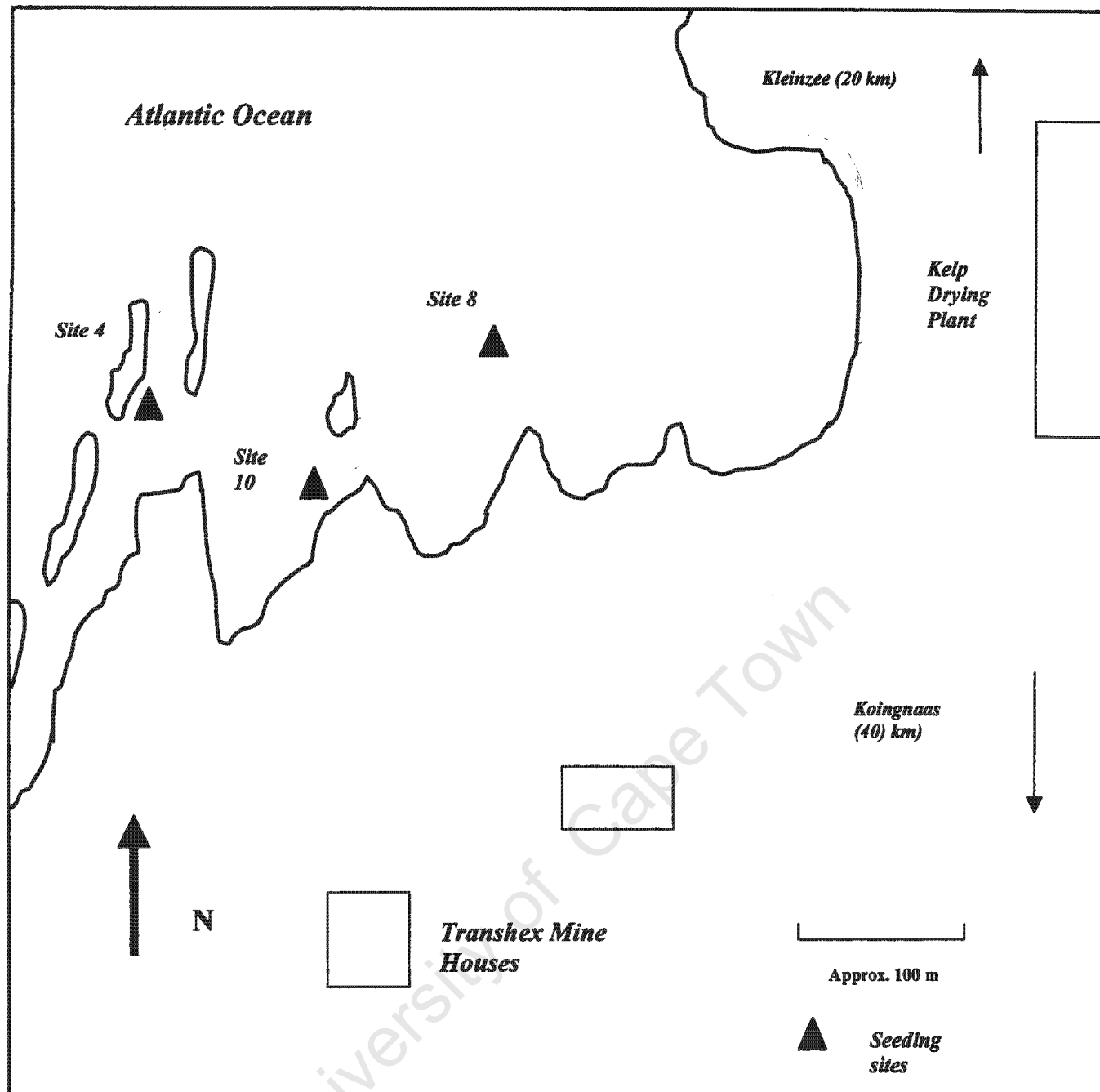


Figure 2.2 Schematic map of the Brazil seeding sites. One release module was placed at each site.

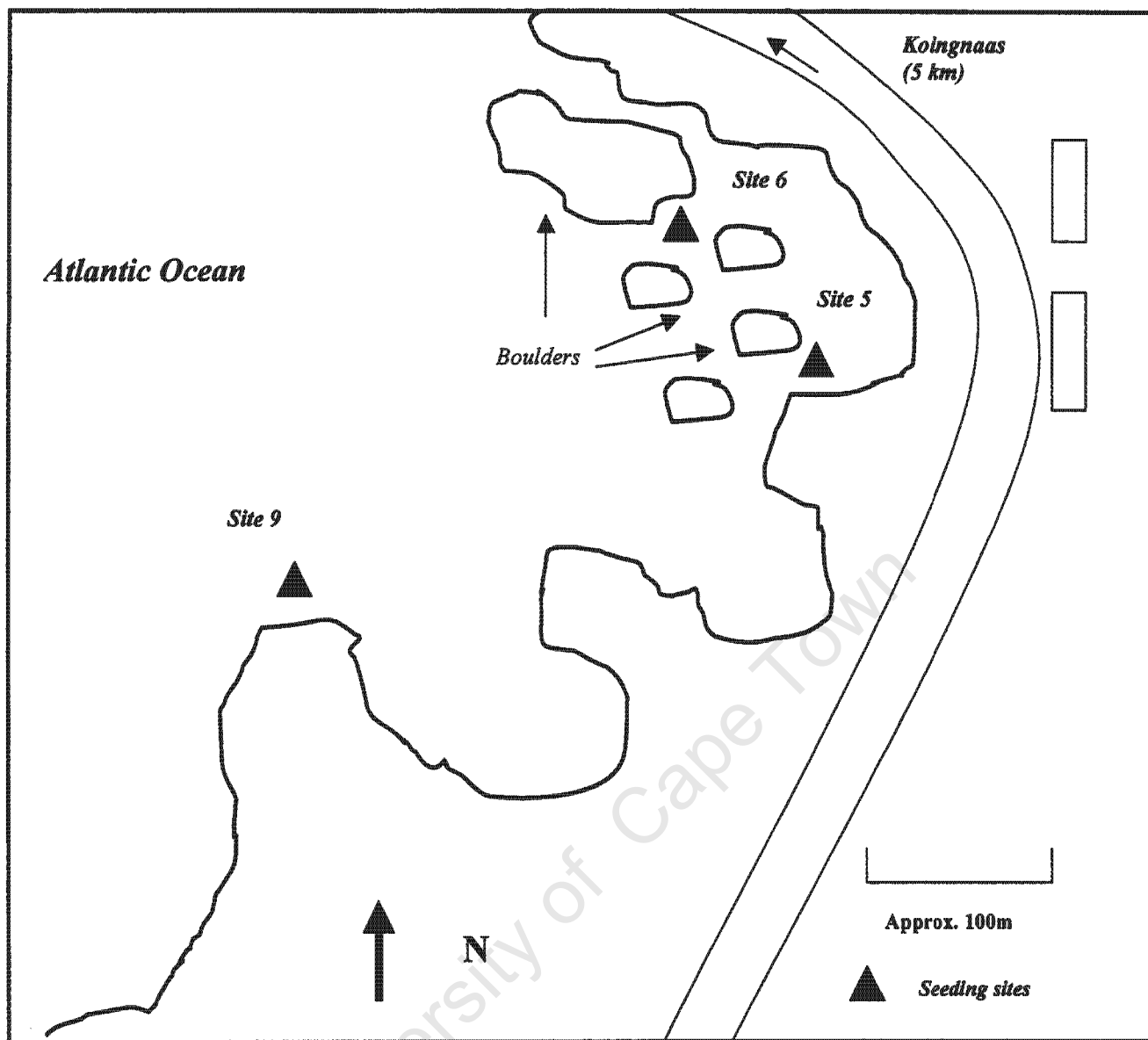


Figure 2.3 Schematic map of the Koiingnaas seeding sites. One release module was placed at each site.

habitat rugosity made by comparing the minimum distance between two points, with the actual distance measured on the sea floor between the same two points would not provide a measure of under boulder habitat or give any indication of juvenile habitat (Figure 2.4). Rather, that type of measurement would be adequate to determine adult abalone habitat. Since juvenile recovery after seeding was of primary concern, it was decided to obtain direct estimates of boulder size and abundance as an index of the availability of juvenile shelter.

The initial idea was that, by having multiple seeding experiments along a 60-km stretch of coast, running concurrently at all the sites, the effects of large-scale environmental factors could be assumed to affect all sites equally and, thus, influence recovery rates similarly. However, it was not possible to coordinate the seeding dates to that extent (Table 2.1). The analysis of seeding-site attributes and recovery rates attempted to correlate each site attribute with the recovery rate from that site (Table 2.2). While not ignoring the effect of predation, these attributes were also considered to be those that would have the most direct effect on recovery of juvenile abalone. While the effects of predation could have been investigated, the exclusion of predators on a scale relevant to ranching would not be feasible. At each site one release module was used. Each site was regarded as an unreplicated treatment and microhabitat variation between release modules meant that every site was different. This series of experiments was the first attempt in South Africa to release a large number of *H. midae* juveniles (1000 per seeding module) at a range of sites over such a large area. While certain expectations were present with respect to the suitability of the seeding sites, there was no a priori proof that the criteria selected to identify suitable seeding sites would prove consistently reliable. By choosing a wide range of

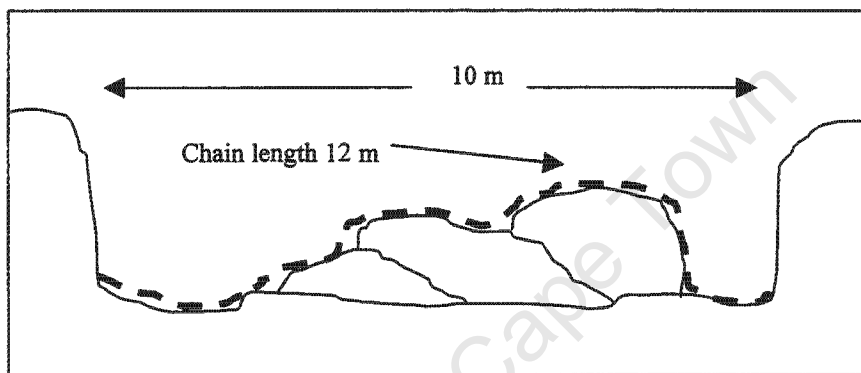
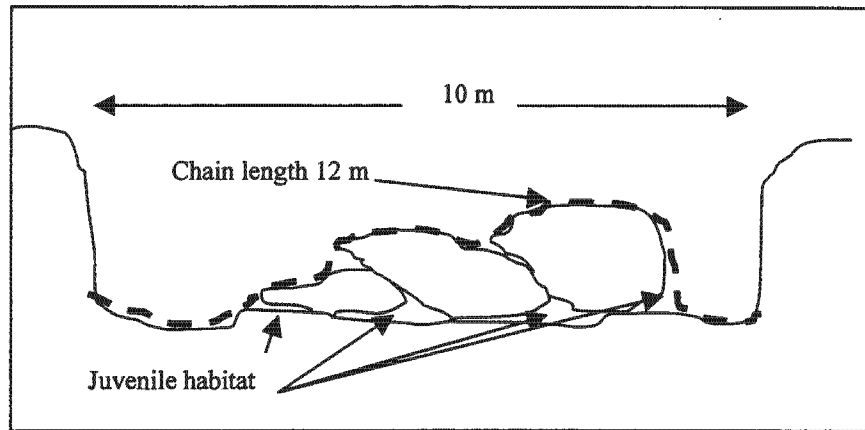


Figure 2.4 The measure of rugosity given for the hypothetical habitat in both diagrams above is the same $12/10 = 1.2$. In the top diagram there is under boulder space which is ideal juvenile habitat, and in the bottom diagram there is none. This shows that this type of measurement would be of little use with respect to juvenile abalone if there are spaces open under boulders or if boulders are lying on top of each other.

Table 2.1 Physical and seasonal conditions and dates at the time of seeding and at the time of recovery for each site in the initial set of experiments between Kleinsee and Koingnaas (See Figure 1.1 for locality). Swell height refers to mean wave height at time of seeding.

Site	Seeding date	Season	Swell height on site (m)	Depth (m)	Recovery date	Season	Recovery (%)	Sampling period (months)
1	7 Aug 98	Winter	< 1.5 m	3-4	7 Feb 99	Summer	0	6
2	7 Aug 98	Winter	< 1.5 m	1-2	7 Feb 99	Summer	6	6
3	7 Aug 98	Winter	< 1.5 m	1-2	7 Feb 99	Summer	0	6
4	29 Nov 98	Summer	< 1.5 m	1-2	13 Jul 99	Winter	3.3	7.5
5	29 Nov 98	Summer	< 1.5 m	1-2	20 Mar 99	Summer	0.4	3.5
6	29 Nov 98	Summer	< 1.5 m	1-2	20 Mar 99	Summer	1.7	3.5
7	31 Oct 98	Summer	< 1.5 m	< 1	18 May 99	Summer	12.55	6.5
8	10 Nov 98	Summer	< 1.5 m	3-4	18 Oct 99	Spring	4.2	10.5
9	29 Nov 98	Summer	< 1.5 m	3-4	20 Mar 99	Summer	0	3.5
10	19 Mar 99	Summer	< 1.5 m	1-2	13 Jul 99	Winter	6.6	4

Table 2.2 Habitat attributes believed to affect abalone survival of each site in the initial experiments between Kleinzee and Koingnaas. The recovery rate from each site is included.

Site	Recovery (%)	Percentage of area consisting of boulder with diameter				% cover crustose corraline algae	Urchin density (m ⁻²)
		> 50 cm	< 50 cm > 30 cm	< 30 cm	% area exposed		
1	0	60	5	5	30	17.15	12.43
2	6	20	10	10	60	17.50	6.15
3	0	10	10	70	10	17.50	0
4	3.3	50	10	10	30	21.52	16
5	0.4	40	30	5	25	17.50	0
6	1.7	20	20	50	10	12.50	0.53
7	12.55	55	10	25	10	47.50	5.15
8	4.2	80	15	0	5	6.82	9.6
9	0	65	25	5	5	32.50	1.2
10	6.6	50	10	10	30	21.52	16

sites it was hoped that detrimental factors could also be identified. The approach was broad and correlative; the experiments were viewed as preliminary and likely to generate results that would guide later experiments. Although lacking statistical rigor, the results of these preliminary experiments are presented to indicate the basis upon which subsequent, more detailed experiments were based.

2.2 METHODS

Juvenile abalone in the initial experiments were released from modules similar to those used by Sweijd et al. (1998) and McCormick et al. (1994) (Plate 1). These consisted of concentric lengths of PVC piping of decreasing diameter, cut in half longitudinally, placed inside each other, and mounted on a flat plastic base. The base was then mounted on either a concrete block or on a steel plate, which acted as a weight to keep the release module stable on the ocean floor, allowing the animals to leave and return to a stable structure. The abalone ranged in size from 8 mm to 20 mm. In each release module 1000 abalone, of a similar average size, were placed after first being anaesthetized in a solution of 10% magnesium sulphate for approximately 15 min (White 1995). The release modules were then sealed at both ends with perforated plastic covers that allowed a through-flow of water, and placed in well-aerated holding tanks. After approximately 30 min, the release modules were placed on damp sponges in plastic bags, sealed and placed in Styrofoam boxes containing wrapped freezer blocks. The containers were closed and transported to the seeding sites. The trip normally took approximately one hour. On arrival at the seeding sites, the release modules were immediately taken out of the containers and



Plate 1. Release modules used for seeding juvenile abalone in place. Top left photograph courtesy B. Godfrey, bottom left photograph courtesy N. Sweijd.

placed in rock pools or in shallow water (fresh seawater). The release modules were then moved underwater to the seeding sites.

In total, 16 release modules were placed in the water, all in less than 5-m depth. Of these only 10 were sampled; seeding modules that had been moved by either people or sea currents or had been washed over by shale, had to be disregarded (Table 2.1). In 2 of the 10 sites (Sites 5 and 6) all the recovered abalone were found inside the module, and these data were not included in further analyses. It was planned that the experimental design would be adjusted according to the results, as they became available over a period of 18 months. The basic seeding experiment was designed so that sampling from specific sites in the three different areas would take place every six months, over a period of 18 months. Once a specific site had been sampled, it would not be sampled again. In practice, actual sampling times were dependant on ocean conditions and the condition of the seeding sites themselves. The harvesting or sampling strategy was destructive (Sweijd et al. 1998). In other words, each site was completely overturned, all urchins were lifted and all loose boulders were lifted in the vicinity of the seeding module. All cracks and crevices were explored. The sampling was done in a consistent manner, beginning at the release module and moving away in increasing concentric circles. This was done until no more abalone were detected. For each juvenile abalone detected, the habitat occupied and the distance from its seeding module were recorded. Habitat occupation included whether juvenile abalone had utilized urchins as shelter, where on the actual substratum this had occurred, and whether boulders or cracks and crevices were utilized. A concerted effort was made to find as many of the animals as possible. Destructive sampling yields an estimate of minimum survival per site over the time period between seeding and sampling

because it cannot account for undetected animals. Because growth is thought to be affected by seasonal temperature fluctuations and the associated ecological and physiological changes (Tarr 1995), it was assumed that sampling over a period of 12 months or more would accommodate seasonal effects, whereas the six-month sampling period would possibly reveal seasonal growth.

Unpredictable sea conditions on the Namaqualand coast meant it could not be assumed that release modules could be accessed and opened the day after they were deployed. After some initial observations, it was decided that opening the release modules approximately 15 min after placing them into position should not cause any immediate mortalities of the seed. Sweijd et al. (1998) opened their release modules after 24 hours, and expressed some concern about whelks preying on stressed juvenile abalone. In the current experiments, however, laboratory and underwater observations showed that if juveniles were not handled and were not exuding mucus, whelks did not target them.

The release modules were kept under observation for approximately 15 min before they were opened. Other than one or two animals, which were sitting on the plastic covers, no animals exited from the release module and no predators were attracted to the release module during this time. Throughout the initial seeding exercises, release modules were observed after they were opened and at no time did mortalities or predation occur immediately after opening. Release modules observed on a daily basis in the McDougall's Bay experiments, and in rock-pool observations, showed that by far the greatest majority of animals did not begin to leave the release modules until

well into the night of the first day and, in many cases, not until the second or third day.

The size range of seeded juveniles was 8–20 mm, but average sizes were kept constant at all sites. All sites were close to shore and easily accessible. Exposure to open swell and currents varied from site to site. Whereas some sites initially appeared to be sheltered from incoming wave action, it was later found that even at those sites, currents were just as strong as those sites thought to be exposed.

To quantify the physical attributes of the seeding sites, the percentage cover in a 3-m radius around each release module was estimated according to the following categories:

- Boulders with a diameter >50 cm
- Boulders with a diameter 30–50 cm
- Boulders with a diameter <30 cm
- Exposed area that provides no protection or shelter to juvenile abalone, e.g. sand or open flat reef
- Percentage cover coralline algae
- Urchin density (direct count).

To ensure consistency throughout all the experiments, the estimates were made by one person. The sites were completely independent from each other and there was no relationship between any of the sites, other than the subjective choice made by the researcher in selecting sites. Because the data sets were very small (10 treatments with

no replicates) non-parametric analyses were employed using Statistica Version 5.5 (Keller & Warwack 2000). Spearman Rank Order Correlation analyses were done to test for associations between the recovery data and boulder abundance, urchin density and percentage cover of coralline algae for those sites that could be sampled successfully.

2.3 RESULTS

The first Kleinzee site was sampled six months after seeding (Table 2.1). Due to the low initial recovery figure at the first sample site and the limited amount of data being generated, it was decided to sample additional sites from each experimental area as soon as ocean conditions allowed it. Thus, all the sites were harvested 3.5 to 10.5 months after seeding, rather than leaving some for a full year as originally planned.

Table 2.1 shows the percentage recovery, the seeding dates and the harvest dates from the different seeding sites. The highest percentage recovered was from a Kleinzee site, Site 7, which was seeded in summer and harvested at the end of summer, six months later. This site was the shallowest of all the sites (<1 m); the abalone were an average of 18 mm in length and they exhibited a monthly growth increment approximately equal to the average of all the experimental abalone recovered (0.95 mm, SD ± 0.5). This average growth rate should be seen merely as an indication that at least some of the abalone did grow. Sites 2 and 10 had the next highest recoveries. Site 2 at Kleinzee was seeded in winter and harvested in summer, the seeded abalone were relatively small, 12 mm, and they exhibited a relatively high average growth increment. Site 10 was also seeded in winter, in shallow water and the abalone were

approximately 20 mm in length. The average growth rate was in the accepted range for the species as it occurs naturally on the west coast (Sweijd et al. 1998). The average growth rate for 8–18 mm juvenile abalone in the settlement tanks at Port Nolloth Sea Farms is approximately 1.5 mm per month, calculated as an average over a year. The water temperature in these tanks is approximately 2°C warmer than ambient sea temperatures. The average ambient sea temperatures recorded over a period of six months, from February to August at both Brazil and Kleinzee, were 12.1°C (SD $\pm$ 1.20). Over a four-month period the average ambient temperature measured at the Port Nolloth Sea Farms inlet was 11.6°C (SD $\pm$ 1.96).

Seeding was carried out on days when the swell height was relatively low and sea conditions were favourable, both in winter and summer. However, if sites in which the time between seeding and sampling is similar are compared (Sites 1, 2, 3, 4, 7 and 10), there are indications that those sites seeded in summer yielded the higher percentage recovery (Sites 4, 7 and 10). When considering the depth at which these six sites were seeded, the highest values for percentage recovery were found for Sites 2, 7 and 10. Within the context of similar sampling periods, there are indications that depth of seeding influences recovery rates of seeded abalone (Table 2.1).

Table 2.2 shows the results of habitat estimates. Boulder size and abundance and extent of exposed area are shown for each site together with the percentage abalone recovered. The results indicate that the relationship between recovery of seeded abalone and habitat description is not simple. The sites that showed both the highest and lowest degree of recovery were also sites wherein the highest percentage cover of exposed habitat was found, 5–10% (Sites 7, 3 and 9). At the same time, Sites 1, 4, 5

and 10 had the same degree of exposure (30%), and the percentage recovered ranged from 0 to 6.6%. These results showed that a finer analysis was needed to investigate the relationship between under-boulder habitat and the amount of refuge it supplies to juvenile abalone.

In most cases, abalone recovered outside the release modules were found under urchins (Table 2.3). Sites 2, 4 and 8 (from Kleinsee and Brazil) all the recovered abalone were found under urchins. Apart from the percentage abalone recovered from Site 4, at which the juveniles were an average length of 8.1 mm in length, the majority of the abalone seeded at the other sites ranged between 12 and 20 mm in length. The abalone seeded at Site 7 yielded the highest percentage recovery and were 17.3 mm in length when seeded; other sites at which the juveniles were in this size class did not all yield such high results.

Table 2.4 shows the results of Spearman Rank Order Correlation analyses. There were no significant associations (at $p \leq 0.05$) between percentage recovery and urchin density, coralline algal abundance, the amount of exposed area or the measure of boulders of various sizes. However, although sample size was small ($n = 8$), and the number recovered at each site was low, a significant positive correlation was shown between seeding size and recovery rate ($p = 0.05$). The effect of time between seeding and sampling has not been incorporated into these correlations-a notable limitation that developed as a result of the conditions surrounding the initial experiments.

Table 2.3 Initial seeding results from the experiments done between Kleinzee and Koingnaas. Recovery rate is the % of abalone found at each site. One module was placed at each site, and each module contained 1000 abalone.

Site	n	Ave. size at Seeding (mm)	Ave. growth per month (mm)	Recovery rate (%)	% recovered that remained in seeding module	% recovered outside module that utilized urchins for cover
1	1	12.83	-	0	0	0
2	1	12.83	1.14	6	0	100
3	1	11.46	-	0	0	0
4	1	8.1	0.17	3.3	0	100
5	1	18.44	1.03	0.4	100	0
6	1	18.44	1.69	1.7	100	0
7	1	17.3	0.93	12.6	0	24
8	1	17.3	1.21	4	0	100
9	1	9.0	-	0	0	0
10	1	20.7	0.49	6.6	0	15

Table 2.4 Spearman Rank Order Correlations showing the relationships between site attributes and recovery rates, site attributes and percentage cover of corraline algae, and site attributes and urchin density from the initial seeding sites between Kleinsee and Koningnaas. An asterisk indicates significance at $p \leq 0.05$.

Site attributes	(a) Recovery rates			(c) Urchin density		
	n	R	p-value	n	R	p-value
% boulders with diameter > 50 cm	8	-0.08590	0.84	8	-0.96386	0.82
% boulders with diameter 30 – 50 cm	8	-0.02795	0.95	8	0.192087	0.65
% boulders with diameter < 30 cm	8	0.251577	0.55	8	0.444580	0.27
% area exposed	8	0.240526	0.57	8	-0.093213	0.83
% cover crustose corraline algae	8	0.294528	0.48	8	-0.168675	0.69
Average no. of urchins per quadrat	8	0.282256	0.50			
Depth at seeding	8	-0.65479	0.08			
Average size of abalone at seeding (mm)	8	0.703757	0.05*			
(b) % cover corraline algae						
	n	R	p-value			
% boulders with diameter > 50 cm	8	0.108434	0.80			
% boulders with diameter 30 – 50 cm	8	-0.35673	0.39			
% boulders with diameter < 30 cm	8	-0.32108	0.44			
% area exposed	8	0.509563	0.20			
Average no. of urchins per quadrat	8	-0.16867	0.69			

A number of sampled sites yielded no recovery data because they had been severely altered by sand or mussel shale movement. In some cases, the release modules had moved, as currents and sea conditions affected the modules more than anticipated. Due to the low recovery rates, very few dispersal data were collected. However, the majority of animals found were within 3 – 4 m from the release module. Site 2 was the only site from which any reliable dispersal data could be collected; the animals had all left the module and the furthest one had moved 6 m from the module.

2.4 DISCUSSION

The recovery rates obtained from the preliminary experiments were low, such that no significant conclusions could be drawn with respect to the site attributes that effected the survival of seeded juvenile abalone. This contrasted with the work done by Sweijd et al. (1998) that produced consistently high recovery rates (25.6–39.2% over a six-month period) and suggested that significant correlations should exist between certain site attributes and abalone recovery rates. A possible reason for the contrast was site selection, especially the degree of exposure to strong currents and wave action. The sites selected in the present study for the initial experiments between Kleinzee and Koningnaas were relatively more exposed than those selected by Sweijd et al. in Port Nolloth (1998). Other factors that affected the recovery data during my initial experiments were not factored into the comparison between this study and data from Sweijd et al. (1998). These were the size of the juveniles used in the seeding experiments, the different time periods that elapsed between seeding and sampling and the depth at which modules were placed.

In the present experiments, however, none of the physical or biological attributes associated with the eight seeding sites correlated with the recovery of seeded abalone. The significant correlation between seeding size and recovery rate ($p = 0.05$) was the only result that did reflect positively on contemporary research (Schiel 1993, Shepherd et al. 2000, Tegner 2000), and suggested that within the context of the sites that had been selected, seeding size did play a role in the survival of seeded juvenile *H. midae*. According to Tarr et al. (1996), Day (1998) and Day and Branch (2000a, b, in press), wild juvenile *H. midae* are found almost exclusively under urchins, so one would expect a significant correlation between survival of seeded juveniles and urchin densities. The abalone that had left the release modules did almost exclusively utilize urchins for refuge, but the correlation between survival and the density of urchins at each site was insignificant. The densities of urchins found in the three experimental areas (0–12 m⁻²) were much lower than that recorded in most of the areas in which natural stocks of *H. midae* occur, where most experimental work relating to abalone and urchins has been done in South Africa (28–55 m⁻²; Tarr et al. 1996, Day & Branch in press). The variation in seed size could also have played a role in urchin selection or utilization. At the five sites at which recoveries were recorded, the two with the largest seed size (average 20.7 mm and 17.3 mm) yielded the lowest percentage utilization of urchins, suggesting size may influence the reliance of juvenile abalone on urchins. One site in the Kleinzee area yielded a 12% recovery rate, but only 24% of the abalone were found under urchins; the rest were recovered under boulders. These boulders were exposed at spring low tide, more so than at any of the other sites. Urchins may not provide abalone protection against desiccation, so depth also seemed to play a part in the abalone-urchin relationship. In preliminary observations, juvenile abalone released in rock pools were seen to move into shade

within 20 min after release. Similar observations were made by Day (1998). While urchins did provide some of the abalone with shade, drift kelp, boulders, cracks and crevices could also provide this. Once in shade, the juvenile abalone seemed to stay in one place for a number of hours, no matter how insignificant the shade was in terms of providing protection against predators. Although not significant, the correlation between the percentage of area exposed and recovery rates was greater than that regarding the percentage cover of boulders. This made no intuitive sense in terms of shelter, since boulders provide obvious shelter whereas exposed areas provide none.

No significant correlations could be found between urchin density and the other site attributes, nor between percentage cover of coralline algae and other site attributes. This may have been a consequence of the small available data set. The sites from which recovery rates were the highest (Sites 2, 7, 8 and 10) had a relatively low percentage of cover of smaller boulders compared to Sites 3 and 6. At those sites recovery was 0 and 1.7% respectively. The possible interactions between recovery rate and attributes of a seeding site are not clear from these experiments. It is quite possible that both urchins and juvenile abalone have similar habitat requirements, but this cannot be discerned from the results.

The quality of seed, their individual behaviour once they leave the seeding module, their individual response to predators and their utilization of available shelter all determine the survival of seeded abalone (Shepherd et al. 2000). None of those factors were addressed in these experiments. It is difficult to surmise why it is possible to find a small number of abalone sitting under one boulder next to a seeding module, while right next to the module there is another boulder of similar size and shape with no

abalone. Recovery rates do not explain behaviour, and while certain boulders can provide shelter it is beyond the scope of this thesis to determine why some boulders are selected over others. What can be determined from this type of experiment is the type of habitat that can be potentially utilized by the juveniles, and what type of habitat cannot.

The design or context of the preliminary experiments was not scientifically adequate; factors that could not be standardized between experimental sites detracted from the credibility in interpreting the available data. Even so, the relationship between juvenile abalone and urchins was not as simple as previously assumed and remained to be clarified. The fact that some animals were recovered in the release module was interpreted as an indication of an unsuitable seeding site. For example, there is a complex relationship between boulder size and the arrangement of the boulders that influences the extent to which boulders may offer a three-dimensional area of protection.

One obvious problem was determining whether a low recovery rate indicates low survival, or whether it may indicate high dispersal rates that diminish chance of detection (Momma 1972, Rogers-Bennet & Pearce 1998). The recovery data were, however, too few to afford any statement concerning dispersal patterns or their effect on abalone recovery and survival.

While no significant conclusions concerning the physical and biological attributes of seeding sites were drawn from these preliminary experiments, the high recovery rates reported by Sweijd et al. (1998), made it clear that it was necessary to investigate

discrepancies in our experimental approach, with the goal of standardizing the set of experiments in future work.

The following basic differences were identified between the two sets of experiments: (1) the time taken to open the release modules and (2) the use of magnesium sulphate to anesthetize the animals prior to placing them into the release modules. The relationship between the survival and recovery of seeded abalone and other factors, such as sea urchin abundance, size of abalone at seeding and physical attributes of the site, were not clear from either of the two sets of experiments. In all the experimental releases done in my initial experiments, and in those done subsequently, the release modules were observed for some time prior to and after opening. At no time did the opening of the modules appear to cause attraction of predators, and in no instance did abalone actually leave the modules until at least the first night or even later. However, since no anaesthetic was used in the experiments done by Sweijd et al. (1998), while anaesthetic was employed in the current experiments; it appeared necessary to test the effects of the anaesthetic, as well as to test the effects of the other factors. However, this would require an environment with standardized conditions, to the extent that variable and adverse sea conditions would not mask the conclusions. The general hypothesis that the Namaqualand coast can support populations of seeded *H. midae*, and the two specific hypotheses concerning the relationship between urchins and juvenile abalone, and between boulder habitat and juvenile abalone (Figure 1.4), could not be tested from the experiments described in this chapter, because recovery was low and the data inconsistent.

Thus, the initial set of experiments and observations led to the conclusion that too many factors were influencing abalone survival, and data from these experiments were not reliable. Although valid observations were made about the behaviour of juveniles after release, the number of factors playing a role in their survival needed to be reduced experimentally. For more accurate conclusions to be drawn the experiments had to be repeated in an environment in which conditions could be standardized and in where ocean conditions allowed more constant access to the sites. It also seemed necessary to limit the amount of damage by wave and current action. While these factors are ever-present in the ocean and cannot be excluded on any large scale, for experimental purposes their restriction would allow a better assessment of the behaviour of seeded abalone.

CHAPTER 3.
USE OF MAGNESIUM SULPHATE AS ANAESTHETIC FOR
SEEDED ABALONE

3.1 INTRODUCTION

During initial experiments (Chapter 2), magnesium sulphate was used as an anaesthetic to facilitate handling and transport of juvenile abalone; similar experiments done by Sweijd et al. (1998), employed no anaesthetic. In this chapter, the hypothesis that the use of the anaesthetic affected recovery rates of juvenile seeded abalone will be tested (Hypothesis 4, Figure 1.4). Magnesium sulphate is commonly used on most, if not all, of the abalone farms in South Africa as an anaesthetic (White 1995). It has been shown to have no effect on growth of treated abalone, and has no significant effect on the rate of mortality if used at prescribed concentrations. For abalone 5–15 mm in length concentrations of magnesium sulphate ranging from 2–10 g.100ml⁻¹ have been associated with recovery and survival rates of 100%. For abalone 20–50 mm in length concentrations of magnesium sulphate ranging from 6–18 g.100ml⁻¹ may yield 100% recovery and survival rates (White 1995). Abalone from Port Nolloth Sea Farms have in the past been treated with this anaesthetic to facilitate packing of release modules with juvenile abalone. Whereas extensive research has been done on the effects that anaesthetics have on animals that are raised in grow-out facilities on abalone farms, no data were available for the effects that these chemicals may have on animals released into the ocean (White 1995).

An experiment was designed to test both the effects of using a 10% solution of magnesium sulphate as an anaesthetic on abalone in the 10–15 mm size class, and to investigate short-term behaviour and mortality in the ocean. This was carried out in McDougall's Bay at Port Nolloth (Figure 3.1). In further investigation, an experiment was done using containers on land to test for significant difference in the time taken by control animals and anaesthetized ones to seek shade. Juvenile abalone, being light sensitive, are invariably found in the shelter of boulders, crevices or underneath urchins. As mentioned in Chapter 2, seeded juveniles released into rock pools invariably sought out shade within 20 min, comparable to data found in the literature (Momma 1972). The intention was not to compare the associations between site attributes and survival: rather, the objective was to determine the role that the anaesthetic plays in seeding operations, and whether or not to use anaesthetic.

3.2 METHODS

Due to small data sets, non-parametric statistical analyses were employed for this portion of the study (Keller & Warwack 2000, Statistica Version 5.5).

3.2.1 Ocean experiments

Eight experimental sites at McDougall's Bay were selected. Selection was based primarily on the availability of boulder habitat, and secondly, on the presence of urchins (2.06 m^{-2} , $\text{SD} \pm 0.42 \text{ m}^{-2}$). The densities of urchins in the bay were generally lower than densities recorded by Day and Branch (in press). At each site, two release modules were placed in the water at stations that were, from visual observations,

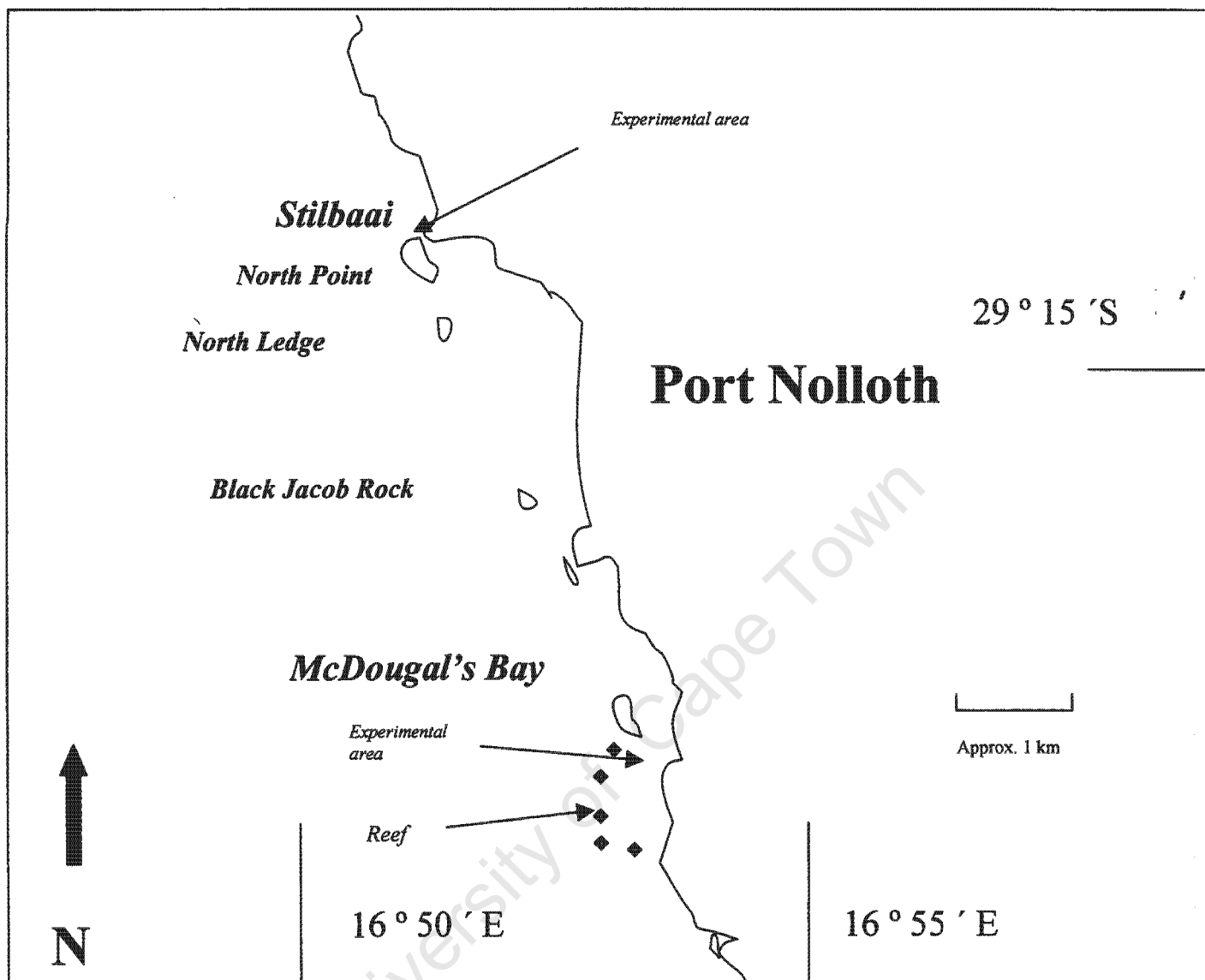


Figure 3.1 Map of Port Nolloth, showing the Stilbaai and McDougall's Bay experimental areas.

considered to be similar in habitat and depth. Seeding was done on days that swell height was under 1.5 m (Table 3.1). The two release modules were placed 10–12 m from each other so that animals from either would not be able to reach the other release module over the time periods used for the experiments. However, the impact of environmental factors (including predation) were expected to similarly affect the two modules at each site. The average depth ranged from <1–3 m. The design of the release modules was the same as in the previous seeding experiments (see Chapter 2). The animals were 10–15 mm in length, and each module contained 400 animals. Handling of the juvenile abalone followed the procedure described in Chapter 2, except that one release module of the pair in each site contained animals that had been anaesthetized for a period of 10–15 min in a 10% solution of magnesium sulphate, and the other contained abalone that had undergone the same packing and transport process without being exposed to anaesthetic. Once loaded with seed abalone the release modules were kept in holding tanks with strongly aerated and circulating seawater for 30 min. They were then placed in cooled Styrofoam boxes and transported to the seeding sites. The release modules were placed in the water on arrival and moved quickly underwater to the selected sites. The process took approximately 1.5 h before the release modules were eventually installed at the sites. Once installed, the modules were opened and observed to see if any animals left the container, either by being washed out by the current or due to their own movements. The sites were closely monitored for two days after seeding to see if any of the animals had left the modules. The modules were left for periods of 3, 5 or 8 days before destructive sampling took place. The numbers of animals that remained in the release modules, the numbers found outside and the total numbers recovered were recorded. The type of refuge used by the abalone (under boulder, in crevices or

Table 3.1 Seeding dates and sea conditions at time of seeding for the anaesthetic experiments at McDougall's Bay.

Site 1	Date in	Swell height at seeding (m)	Harvest date
1	8 June 1999	< 1.5	16 June 1999
2	8 June 1999	< 1.5	16 June 1999
3	8 June 1999	< 1.5	16 June 1999
4	19 June 1999	< 1.5	22 June 1999
5	19 June 1999	< 1.5	22 June 1999
6	19 June 1999	< 1.5	22 June 1999
7	30 June 1999	< 1.5	5 July 1999
8	30 June 1999	< 1.5	5 July 1999

beneath an urchin) was also recorded. Forty 50 x 50 cm quadrats were randomly thrown in the area directly surrounding the release modules and the number of urchins in each quadrat was counted. A Mann-Whitney U Test (Statistica Version 5.5) was conducted on each data set to determine whether 10% magnesium sulphate had any significant effect on the behaviour and recovery of the released juvenile abalone. After these analyses were complete, the effect of sampling time (3, 5 or 8 days after release) was tested by using a Kruskal-Wallis Anova analysis (Statistica Version 5.5, Keller & Warwack 2000). In these analyses the data sets for different sites with the same sampling period were pooled. This was done after no significant differences were found between anaesthetized and non-anaesthetized abalone in any of the analyses. Both the effect of magnesium sulphate as an anaesthetic and the effect of sampling period were thus addressed by these experiments. The distance moved from the seeding module by each abalone was also recorded. The data were grouped and expressed as the number found within 1 m versus the number found further than 1 m from the module. A χ^2 analysis was done on these data (Everitt 1977).

3.2.2 Container experiments

To investigate the effects that magnesium sulphate may have on the ability of juvenile abalone to seek shade, an experiment was done in which both anaesthetized and non-anaesthetized abalone were placed in containers full of seawater that were positioned in the sun. Eighty abalone, ranging in size 3–8 mm were placed in a 4% solution of magnesium sulphate for 20 min. Groups of twenty were then placed in each of four 20-l containers full of seawater. Two separate containers were each stocked with twenty animals that had not been anaesthetized, acting as experimental

controls. All six containers were placed outside in the direct sunlight. The bottom of each container contained a 15-cm long section of 10-cm diameter pipe that had been cut in half lengthwise. All the containers were monitored every 5 minutes for a period of 30 minutes. By the end of this period, either all the animals had moved into the shade or a definite pattern had emerged. The time taken for each of the experimental animals to seek shade was recorded in each of the containers. These data were pooled into two groups, <15 minutes and >15 minutes. To test for significant differences between the behaviour of the control and experimental animals, the frequency of animals that had moved into the shade within the first 15-minute period was calculated, this was repeated for the second time period beginning after 15 minutes and ending after 30 minutes. Using the frequency data for each of the time periods, 2x2 contingency tables were constructed between each control and each experimental data set individually on which χ^2 analyses were done (Everitt 1977, Statistica Version 5.5).

The experiment was repeated with animals having an average size of 28 mm, using the same concentration of magnesium sulphate. In this case only 10 animals were placed in each container, three containers contained anaesthetized animals and two were controls. This experiment was undertaken twice, but in the second case, the abalone were removed from the anaesthetic, placed in circulating seawater containers with shelter and shade, and left for a period of 2 h to acclimate. After a period of 2 h the animals were taken out of the anaesthetic solution and abalone that had been anaesthetized and control abalone were placed in separate containers. Observations were then made every 5 minutes to monitor the movement of abalone into the shade, as before.

3.3 RESULTS

3.3.1 Ocean experiment

All the animals were found within 4 m of the release module, 83% being within 2 m of the point of release (Table 3.2). The Chi^2 statistic comparing the distance moved by the anaesthetized and control abalone, between seeding and sampling, showed that there was a significant relationship between the use of the anaesthetic and the distance moved, $p = 0.05$ (Table 3.2).

The percentage recovered within the release modules, the percentage found outside the module and total recovered is shown in Table 3.3. Approximately 27% of the non-anaesthetized abalone that had left the release module were recovered, compared to 18% of anaesthetized abalone. Although not significantly different, these results suggested that the behaviour of anaesthetized and non-anaesthetized abalone differed once they had left the release module. Mann-Whitney U Tests showed that there was no significant difference in either total recovery ($p = 0.40$), percentage recovered inside ($p = 0.56$) or percentage recovered outside the modules ($p = 0.64$), (Table 3.3, Figure 3.2) between anaesthetized and non-anaesthetized abalone. Although the control abalone showed higher variability in the degree to which they came out of the seeding modules, the experimental abalone showed a slightly greater degree of variability with regard to total recovery. When the data were pooled for treated and control abalone from the different experiments, a Kruskal-Wallis Anova (Statistica Version 5.5, Figure 3.3) shows the significant effect that the period between seeding

Table 3.2 Number of juvenile abalone recovered outside the release modules and the distance moved by the abalone from the modules. A Chi² analysis showed that there was a significant difference in the movement of the treated and untreated abalone ($p = 0.05$).

Site		Distance from module	
		≤1 m	> 1 m
1	Anaesthetized	59	
	Non-anaesthetized		224
2	Anaesthetized	108	
	Non-anaesthetized		67
3	Anaesthetized		95
	Non-anaesthetized	253	
4	Anaesthetized		46
	Non-anaesthetized		29
5	Anaesthetized	39	
	Non-anaesthetized	35	
6	Anaesthetized		35
	Non-anaesthetized	73	
7	Anaesthetized		68
	Non-anaesthetized		93
8	Anaesthetized		123
	Non-anaesthetized		103

Table 3.3 Percentages of abalone that a) remained in the release modules, b) were recovered outside the release modules, and c) total recovered. A Mann-Whitney U Test showed no significant difference between the two data sets when comparing the effects of the anaesthetic in a: $p = 0.56$, in b: $p = 0.64$, and in c: $p = 0.40$. Two release modules were placed at each site, one containing 400 anaesthetized abalone and one containing the 400 control abalone that had not been anaesthetized; $n = 1$ module per treatment at each site.

Site	Sampling period (days)	a) % recovered in module		b) % recovered outside module		c) total % recovered	
		Anaesthetized	Not anaesthetized	Anaesthetized	Not anaesthetized	Anaesthetized	Not anaesthetized
1	8	36.75	4.5	14.75	56	51.5	60.5
2	8	0	7	27	16.75	27	23.75
3	8	0	0	23.75	63.25	23.75	63.25
4	3	61.75	30.5	11.5	7.25	73.25	37.75
5	3	42.25	39	9.75	8.75	52	47.75
6	3	34.25	54.25	8.75	18.25	43	72.5
7	5	15.25	6	17	23.13	32.25	29.13
8	5	13.5	13.5	30.75	25.75	43.25	39.25
Average		25.47	19.34	17.91	27.39	43.25	46.74
SD		21.87	19.60	8.32	20.96	16.08	17.33

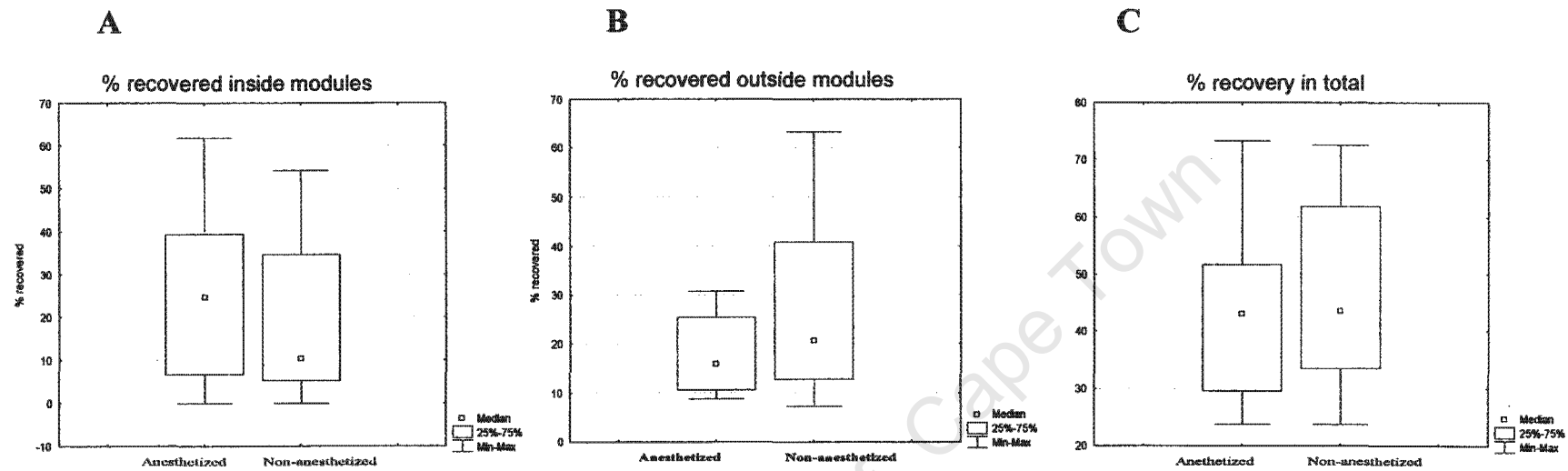


Figure 3.2 Mann-Whitney U Test showing that treatment with anesthetic had no significant effect on the number of abalone found: A) inside ($p = 0.56$), and B) outside ($p = 0.64$) the seeding modules, or on C) total recovery ($p = 0.4$).

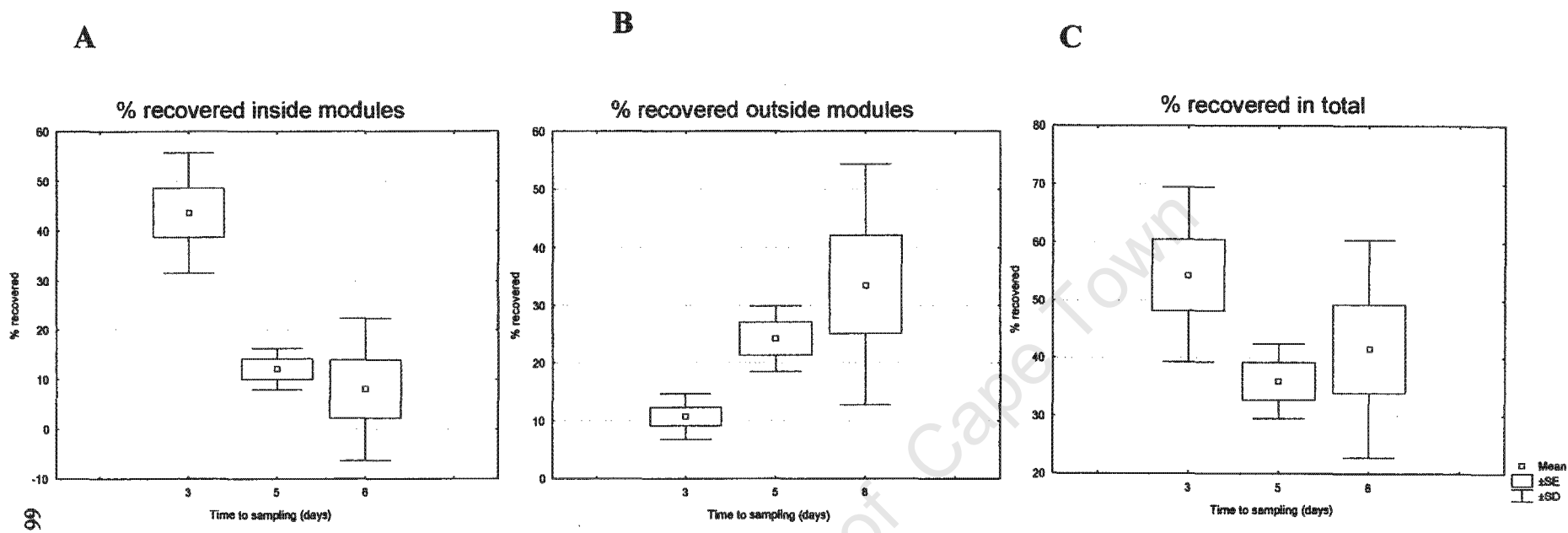


Figure 3.3 Results of Kruskal-Wallis Anova showing that time to sampling had a significant effect on A) the number of abalone that remained in the seeding module ($p = 0.007$) and B) the number found outside the module ($p = 0.014$), but not on C) total number recovered ($p = 0.43$).

and sampling had on the numbers of abalone found outside versus inside the release modules. The effect was insignificant on total recovery ($p = 0.43$), but significant on both the number found inside the modules ($p = 0.007$) and the number found outside ($p = 0.014$).

The average density of urchins per 0.25 m² quadrat was 3.73 (SD ± 2.57). The percentage of abalone that utilized urchins as refuge, was generally low (Table 3.4), with a maximum of 23% for non-anaesthetized abalone, sampled after 3 days, and 17% for anaesthetized abalone, sampled after 8 days. At the other points of release, urchin utilization ranged between 2 and 10% for anaesthetized abalone and between 0 and 21% for non-anaesthetized abalone. A Mann-Whitney U Test showed that there was no significant difference between the proportions of anaesthetized and non-anaesthetized abalone recovered outside the seeding modules that were also utilizing urchins for refuge ($p = 0.59$, Table 3.4, Figure 3.4, Statistica Version 5.5). The degree of variability with respect to the proportion of control abalone utilizing urchins for refuge was greater than that of the experimental animals. A Kruskal-Wallis Anova (Figure 3.4) showed that the time elapsed before sampling had no significant effect on the extent that treated and untreated abalone which had left the seeding modules utilized urchins ($p = 0.22$).

Table 3.4 The percentage of abalone that had left the release module and utilized urchins for refuge (all the abalone that did not utilize urchins utilized boulders for shelter). A Mann-Whitney U Test showed no significant difference in urchin utilization as a result of the use of the anesthetic ($p = 0.49$). A Kruskal-Wallis Anova done on the pooled data, and using the sampling period as the difference between treatments, showed no significant effect on urchin utilization ($p = 0.22$). All the abalone that did not utilize urchins for refuge utilized under-boulder habitat for shelter (approximately 94% of treated abalone and approximately 93% for control abalone).

Site	% of abalone utilizing urchins for refuge	
	Anaesthetized	Non-anaesthetized
1	17	0
2	3	7
3	2	3
4	2	21
5	10	23
6	6	4
7	7	1
8	5	0
Average	6	7
SD	5	9

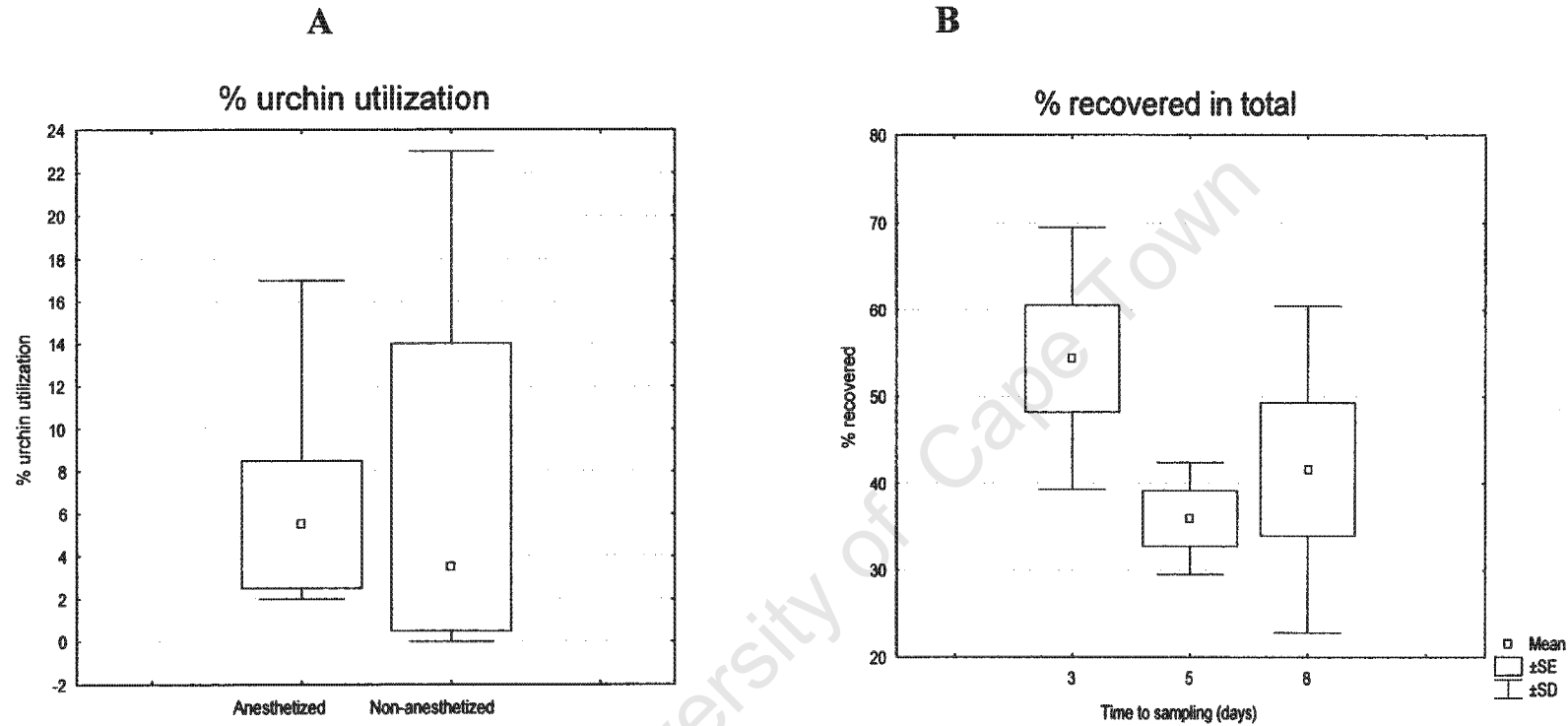


Figure 3.4 A) A Mann-Whitney U Test shows the non-significant effect that treatment with anaesthetic had on urchin utilization by abalone that had left the seeding modules ($p = 0.59$). B) A Kruskal-Wallis test shows that time to sampling also had no significant effect on urchin utilization (data pooled for treated and control animals) ($p = 0.22$).

3.3.2 Container experiments

The abalone in the containers were free to move in and out of the shade freely. As a result, some of the abalone that had been counted as being in the shade in the first 15-min period may have moved back into the sun during the second 15-min period. This means that it is possible that the total number counted in the shade in the second period, could be smaller than the total number counted in the shade (in the same container) in the first period. For 3–8 mm animals there was a distinct difference in the patterns of behaviour over the first 15 min between anaesthetized and non-anaesthetized animals (Table 3.5). All of the Chi^2 tests showed a significant difference between control and experimental abalone: the majority of the control abalone had moved into the shade while the experimental abalone remained out of the shade. However, in the second 15-minute period, only 50% of the Chi^2 tests showed that there was a significant difference between the experimental and control abalone with respect to the number that had moved into the shade. The 28-mm animals showed the same patterns with respect to movement into shade as the smaller animals in the first 15-minute period, with the majority of the control abalone in this size group having moved into the shade. The Chi^2 tests showed 66.7% with a significant difference between control and experimental abalone with respect to the number of abalone that had moved into the shade, the majority of the experimental abalone having remained out of the shade. In the second 15-minute period, all the control abalone and the majority of the experimental abalone had moved into the shade. After two hours differences recorded between control and experimental groups became less obvious, and the majority of the animals followed the same patterns of behaviour with respect to movement in and out of shade (Table 3.5).

Table 3.5 Data and results from 2X2 contingency tables using frequencies of abalone that had moved into the shade in the time intervals of < 15 minutes and >15 minutes in the container experiments. The condition of the abalone specifies whether the abalone were observed immediately (0 h) after being removed from the anaesthetic to the experimental containers (E), or after 2 hours (2 h) of acclimation in seawater. Controls (C) contained abalone that had not been anaesthetized, ($\chi^2 = 3.84$ (df = 1)). * signifies significance at $\alpha = 0.05$ % * indicates the percentage of the tests that showed a significant difference between the control and treated containers.

Condition of abalone	Time period (min)		C 1	C 2	E 1	E 2	E 3	E 4	% *
3 – 8 mm (0 h)	≤ 15	No in shade	19	19	0	0	0	0	
		No out	1	1	20	20	20	20	
		χ^2 between C1 & experimental abalone			36.2*0	36.2*0	36.2*	36.2*	100
		P					0	0	
		χ^2 between C2 & experimental abalone			36.2*	36.2*0	36.2*	36.2*	100
		P			0		0	0	
	> 15	No in shade	20	19	18	20	14	14	
		No out	0	1	2	0	6	6	
		χ^2 between C1 & experimental abalone			2.11	-	7.06*	7.06*	50
		P			0.15		0.008	0.008	
		χ^2 between C2 & experimental abalone			0.36	1.03	4.33*	4.33*	50
		P			0.55	0.31	0.04	0.04	
28 mm (0 h)	≤ 15	No in shade	10	6	0	2	1		
		No out	0	4	10	8	9		
		χ^2 between C1 & experimental abalone			20*	13.3*	16.4*		100
		P			0	0.003	0.0001		
		χ^2 between C2 & experimental abalone			8.57*	3.33	5.49		33.33
		P			0.003	0.07	0.02		
	> 15	No in shade	10	10	10	10	8		
		No out	0	0	0	0	2		
		χ^2 between C1 & experimental abalone			-	-	2.22		0
		P					0.14		
		χ^2 between C2 & experimental abalone			-	-	2.22		0
		P					0.14		
28 mm (2 h)	≤ 15	No in shade	7	5	5	2	7		
		No out	3	5	5	7	3		
		χ^2 between C1 & experimental abalone			0.83	5.05*	-		33.33
		P			0.36	0.02			
		χ^2 between C2 & experimental abalone			-	1.98	0.83		0
		P				0.16	0.36		
	> 15	No in shade	10	5	7	9	10		
		No out	0	5	3	1	0		
		χ^2 between C1 & experimental abalone			3.53	1.05	-		0
		P			0.06	0.3			
		χ^2 between C2 & experimental abalone			0.83	3.81	6.67*		33.33
		P			0.36	0.05	0.01		

3.4 DISCUSSION

Magnesium sulphate is a muscle relaxant, for abalone 10–15 mm in length, the concentration of 10 g 100 ml⁻¹ results in a mean rate of anesthesia of 0.3 ±0.3 min and a mean recovery rate of 2.9 ±2.0 min, and for abalone 20–50 mm in length, the concentration of 10 g 100 ml⁻¹ results in a mean rate of anesthesia of 8.0 ±5.3 min and a mean recovery rate of 21.8 ±8.2 min (White 1995). The period between removing the animals from the anaesthetic and their release into the sea, approximately 1.5 h, is obviously long enough for the anaesthetized animals to recover to the extent that there should be no significant behavioural difference when compared to non-anaesthetized animals. Otherwise, interpreting the results, there are a number of factors that must be taken into account.

As seen in the preliminary experiments (Chapter 2), there are occasions that juvenile abalone will not leave a release module. The conclusion made was that this may be a result of bad site selection since modules remaining in the water for up to six months still contained abalone. In the current experiments the majority of the abalone left the modules by the 8th day (Tables 3.1, 3.3). At Site 1 however, 36.75% of anaesthetized abalone were still in the module. This value may reflect bad site selection, yet Table 3.3 shows that at Site 1 56% of the control abalone had left the module by the 8th day. While the positions in the sites were selected as visually resembling each other in substratum and depth, other determining features may not have been obvious at the time of selection. Bad site selection may have played a bigger role in many of the initial seeding sites (especially at Kleinzee and Koingnaas) since the process of site selection seemed to improve as the experiments progressed. The use of cement bases

for the release modules proved to be a problem, since many of the modules were moved by strong currents. Cement bases were replaced by steel plates in the McDougall's Bay experiments. It is possible that the module with the anaesthetized abalone had been placed in an unsuitable position. Time elapsed to sampling did have a significant effect on the number of abalone found inside and outside the module (Figure 3.3), with an increase in the number found outside the module as the sampling period increased from 3 to 5 days and then to 8 days. However, time did not have a significant effect on total recovery. Assuming that there is suitable habitat available, the abalone will likely progressively move out into natural habitat. A further possible interpretation of this is that seeding-induced mortality takes place soon after the module is placed and opened, perhaps within the first 2 to 3 days. While some abalone remain in the module for extended periods, they will not necessarily "disappear" when they leave the module, which may be why total mortality did not significantly change over time (Table 3.3, Figure 3.3). The initial cause of seeding-induced mortality is not certain, but there are a number of factors that could be involved. These include stress from handling, predation and behavioural responses favouring survival that are not yet developed in juvenile abalone (Olla & Davis 1998, Shepherd et al. 2001).

The variability in response shown by the control abalone (Figures 3.2, 3.4) with respect to urchin utilization and the number found outside the modules, is not reflected in the distance moved by the animals. The proportion of recovered control abalone that were found within one meter of the module was significantly higher than that of the anaesthetized abalone (Table 3.2). The relationships between exposure and movement, and exposure and predation both play a role in determining recovery rates

(Shepherd 1990). Even though, relative to anaesthetized individuals, significantly fewer control abalone were recovered more than one meter from the module, there was no significant difference in total recovery between anaesthetized and control abalone. A degree of movement of juveniles within an area and also in and out of the module as a result of the degree of shelter provided by the microhabitat can be expected, so site selection will most certainly influence dispersal and have implications for potential predation. The fact that the total recovery rates of anaesthetized and control abalone were not significantly different, both with respect to the mean and the standard deviation, indicates that the anaesthetic had no significant effect, used as prescribed. However the variability in behaviour of the control abalone compared to that of the anaesthetized abalone does not mean that the effects of the anaesthetic are insignificant with respect to all aspects of the behaviour or the physiology of the abalone. Although these experiments were not designed to determine exactly what processes the anaesthetic affects, the container experiments did show that effects occurred with respect to behaviour, and this could influence vulnerability to predation. The container experiments also showed that while the abalone were still recovering from the anaesthetic, they were relatively slow to move into shade. After 15 minutes had elapsed, however, no significant differences existed between the frequencies of anaesthetized versus non-anaesthetized abalone entering shade. Moreover, by the time the abalone that were used in the ocean experiments had been placed in the selected sites, they appeared to have recovered completely. If the effect of the anaesthetic were still manifesting itself in anaesthetized abalone, this should be reflected in total recovery.

A possible general test for recovery from the use of anaesthetic for abalone is to see whether they have righted themselves once they have been removed from the anaesthetic (White 1995). However, the present research interest, was for potential behaviour change after removal from the anaesthetics. With respect to the container experiments, the time taken by the abalone to seek shade (and indirectly, shelter from both predators and adverse currents and water movement) was influenced both by the time the abalone had to recover from the anaesthetic and by the size of the animals. Both small (3–8 mm) and larger (28 mm) abalone initially moved into shade more slowly if they had been anaesthetized. This was true, however, only for the first 15 minutes after the animals had been released from anaesthetic. If they were observed longer than this, or held in water free of anaesthetic for 2 h prior to experimentation, no difference existed between anaesthetized and control abalone. These results and observations suggest that there may be other physiological effects that magnesium sulphate may have on abalone that are inconsequential to animals in farm tanks, but detrimental to animals released into the wild. Although this was not reflected in the total recovery rates recorded in the ocean experiments, such effects may manifest themselves if recovery times are not adequate.

Based on the ocean experiment the hypothesis regarding the use of anaesthetic as being the greater cause for low survival rates, was rejected. What was evident, however, from the Kruskal-Wallis Anova (Statistica Version 5.5) was that the period between seeding and sampling played a significant role in both the number of abalone found outside the module and those that remained in the module. The longer the abalone were in the water, the more likely they were to have left the module (Figure 3.3, Table 3.3). However, this same trend was not reflected in total recovery rates.

This particular result must be considered in the context of habitat, and also to what extent the abalone that left the modules had access to good habitat. However, the experiments discussed in this chapter did make apparent a number of factors that needed to be investigated and that were not clear from the preliminary experiments outlined in the previous chapter:

- A high percentage of losses occurred within the first few days after release. Determining survival after several months would not show the proportional impact of short-term, seeding-induced mortality on total mortality (Z), as compared to the proportional effect of long-term mortality.

- Dispersal was very limited. Even after eight days the abalone were still concentrated in the vicinity of the release modules. This observation makes the question of dispersal (as opposed to survival) more quantifiable. If abalone are dispersing, one should be able to record the extent of dispersal. If animals normally remain close to the seeding modules, then not finding any would probably mean that they have not survived. Dispersal may also be affected by the availability of habitat, food and inherent behavioural traits exhibited by individual animals.

- The presence of boulders seemed to be more important than the presence of urchins for juvenile *H. midae* seeded in McDougall's Bay (Table 3.4); most animals were found either inside the release module or underneath small boulders. This must be seen in the context of urchin density being lower in McDougall's Bay than along the south-western Cape (Day & Branch in press). Urchin density is one of the constraints within which the experiments were carried out. If the presence of boulder habitat can

provide the protection and habitat that is required by juvenile abalone, then urchin densities may become less important for the success of seeded juveniles. This must not be confused with the process of natural recruitment, a topic not addressed in this thesis. In terms of habitat selection, a contrast seemed to exist between natural populations of juvenile abalone in the south-western Cape (where urchins play a central role) and seeded populations in Namaqualand (where urchins appear less important). It was necessary to test whether this may be a result of the seeded animals being reared in captivity, or whether the relationship between urchins and juvenile abalone is not as clear-cut as previously suspected. The resolution of this issue has important implications for the selection of seeding sites because areas with very high urchin populations have been identified until now as good seeding sites for ranching operations.

As a result of the present work, the use of magnesium sulphate as anaesthetic can be regarded as safe, in prescribed concentrations (White 1995), so long as a sufficient period is allowed between anesthetizing the animals and releasing them. Hypothesis 4 is thus rejected (Figure 1.4). The results and interpretation of these data have been regarded within the context that each individual site is different, and that recovery rates, dispersal and behaviour are influenced by this variation.

The following chapter addresses three specific topics: the role of urchins in the survival (or recovery) of seeded juvenile abalone; the influence of rock topography; and the effect of abalone size on the success of seeding.

CHAPTER 4.

PHYSICAL AND BIOLOGICAL ATTRIBUTES OF SUCCESSFUL SEEDING SITES

4.1 INTRODUCTION

Results from the initial experiments recorded in Chapter 2 were sufficiently diverse and inconclusive to warrant a more controlled, standardized series of experiments wherein the impact of sea conditions could be restricted, and the number of variables influencing experimental results could be limited. McDougall's Bay in Port Nolloth, 70 km south of the Orange River at 16°52'E, 29°17'S, lends itself to this type of experiment (see Figures 1.1, 4.1 for locality). The bay is approximately two km long, with the outside reef running diagonally away from the beach to a distance of approximately 200 m. Maximum depth is approximately 5 m. The bay itself is exposed to very strong currents, and much of the vegetation and animal life that exists in the inter-tidal and sub-tidal areas outside the bay also occurs in the bay (Tables 1.1, 4.1). The fundamental difference between the bay and the outside ocean is that there is very little direct wave and surf action inside the bay. The substratum is fairly consistent; experiments could be done in habitat and terrain that looks visibly similar, and occurs at similar depths. Thus, the bay presented a fairly standardized environment as opposed to the open ocean of the coast. During the course of the experiments initiated at McDougall's Bay, the opportunity arose to conduct similar experiments at Gouriqua (west of the Gouritz River mouth, 34°22'S, 21°15'E, on the south-western coast of South Africa) (Figure 4.2). A number of experiments were repeated in Stilbaai (Port Nolloth), which is where the experiments by Sweijd et al.

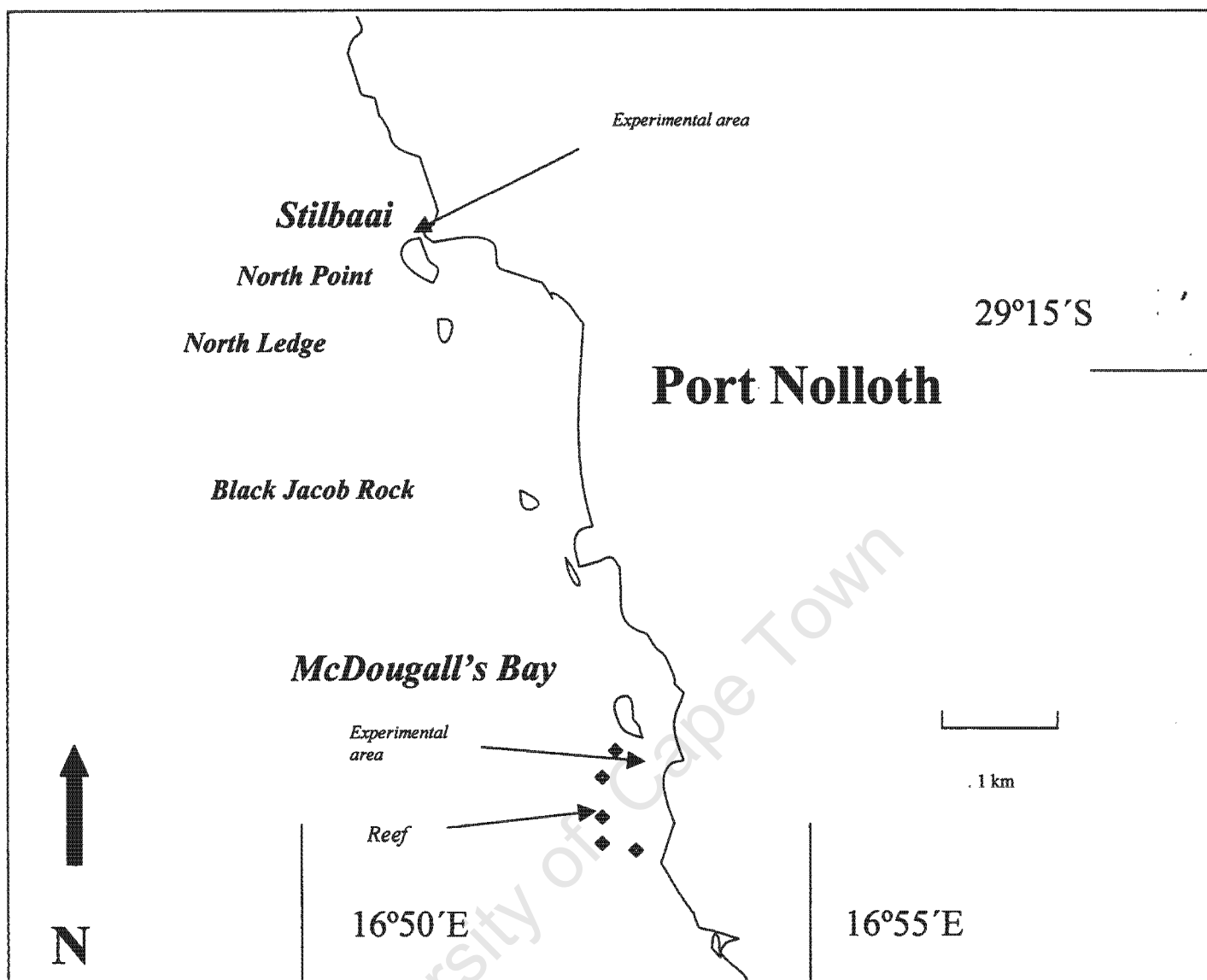


Figure 4.1 Map of Port Nolloth, showing the experimental areas at Stilbaai and McDougall's Bay.

Table 4.1 Habitat attributes and recovery rates of 26-mm and 14-mm abalone seeded at sites McDougall's Bay. Each seeding module contained 100 abalone of each size at the time installation, and one module was installed per site. An asterisk indicates sites at which urchins were excluded.

Site	Recovery of abalone (%)		Percentage of area consisting of boulder with diameter				% cover crustose coralline algae	% cover cove: urchin
14 and 16-mm abalone, urchins not manipulated								
	14-mm	26-mm	>50 cm	30-50 cm	<30 cm	% area exposed		
1	26	62	10	35	45	10	48.75	4.17
2	29	55	40	40	15	5	42.50	3.13
3	33	68	5	60	30	5	40	2.84
4	5	54	30	55	10	5	35	1.33
5	19	50	60	35	5	0	22	1.99
6	23	59	50	30	10	10	18.5	0.66
7	36	66	50	30	15	5	25.5	1.14
8	24	33	50	15	15	20	19.5	1.04
14-mm abalone, urchin exclusion experiment								
9	5.7		30	45	15	10	40	1.07
10	5.7		35	45	10	10	28.73	0*
11	15.7		25	55	10	10	46.25	1.41
12	3.3		35	45	5	15	31.25	0*
13	28.67		50	20	25	5	35	0*
14	25.33		70	10	15	5	46.25	0.71
15	28.33		75	5	5	15	41.37	0*
16	38		70	10	15	5	41.37	1.36

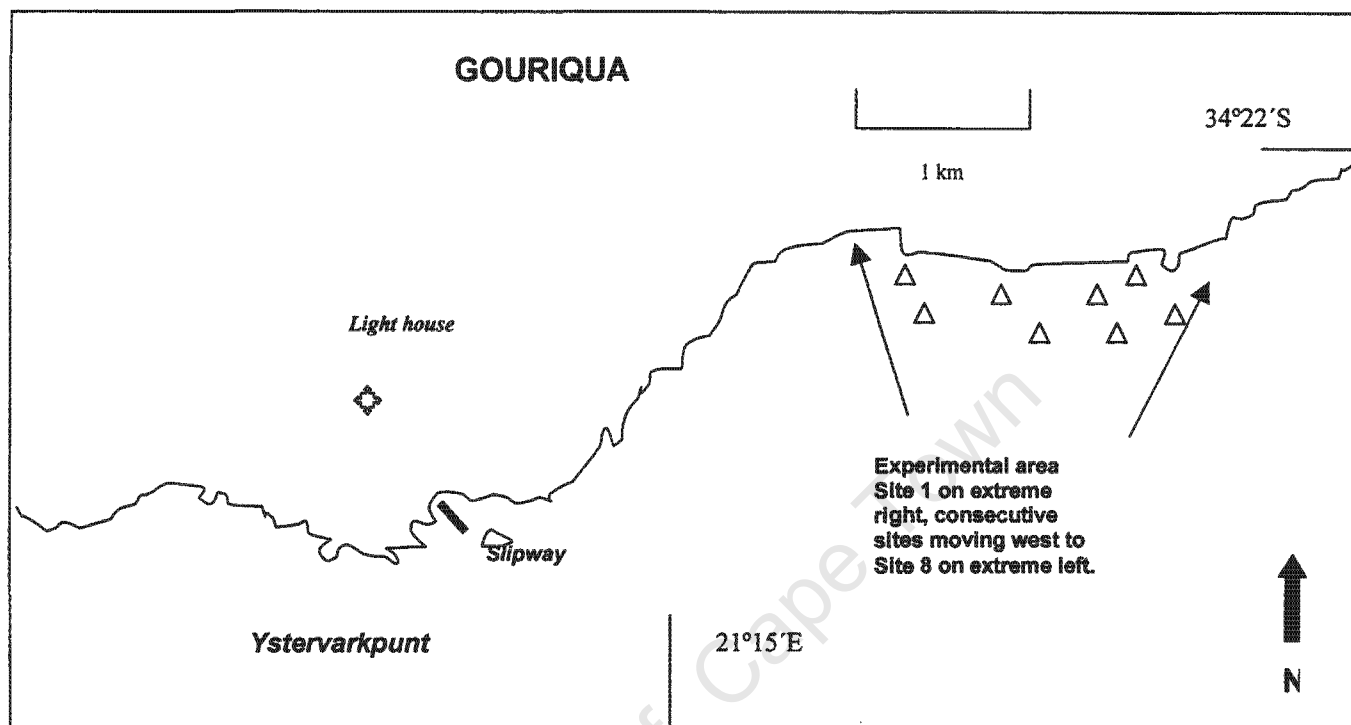


Figure 4.2 Map of the Gouriqua experimental area.

(1998) were conducted. This opportunity was taken to test the effect of the attributes that characterized this experimental area with respect to the recovery and survival of seeded juvenile abalone. Specific hypotheses (Figure 1.4), tested in a range of experiments described below, concerned the association between urchin densities and the recovery of seeded juveniles (Hypothesis 2), the association between the abundance and size of boulders and the recovery of juvenile abalone (Hypothesis 3), and the association between increased size of seeded abalone and survival (Hypothesis 5). These experiments did not investigate the process of natural recruitment or the relationship between urchins and naturally recruited abalone. Rather they were done within the context described in the introduction, i.e., to identify those criteria that exist naturally on the Namaqualand coast that may maximize the potential survival of seeded juveniles.

As a result of the experiments done in Chapters 2 and 3, much was learnt about the selection of sites, if only in a qualitative manner. As a result, all the sites referred to in this chapter, including the Gouriqua sites and the Stilbaai sites (Figures 4.1, 4.2) were selected as “suitable” sites. The analyses and conclusions are made within this context. This is important to note because any discussion concerning a comparison of results from the literature (e.g. Day 1998, Day & Branch 2000a, b, in press) is based on findings that state natural recruitment takes place, but in habitat not necessarily considered suitable for seeding juvenile *H. midae*. For example, the experimental areas described by Day and Branch (in press) comprise only approximately 25% “suitable” habitat, meaning habitat that consists of cracks and crevices and under-boulder habitat. By the same standards, the experimental sites at McDougall’s Bay comprise approximately 50% suitable habitat and at the Gouriqua area also 50%

(Tables 4.1, 4.2). The definition of “suitable habitat” used here is habitat comprising boulders <50 cm in diameter, excluding area classified as exposed or boulders >50 cm in diameter. The definition excludes area under boulders >50 cm in diameter because the surface of large boulders is effectively as exposed as open reef and will not provide shelter for juvenile abalone, it was also impossible to move boulders this size to investigate under-boulder habitat.

Vast differences exist between the Namaqualand coast and the Gouriqua coast, both with respect to general ecology in terms of algal species diversity and abundance (see Introduction, and Baird et al. 1986, Wood & Buxton 1996), physical appearance, exposure to wave action and depth at the experimental sites. The experiments were not designed to compare survival rates between sites, but to determine which attributes of each seeding site correlated significantly with recovery rates. Notably, there appeared an abundance of predators in both areas (see Table 1.1), with some common to both areas and some area-specific. There were also seasonal variations with respect to predator densities and patterns of movement. It was not, however, an objective of the present study to quantify the effects of predation or to investigate the species in the different areas. Total mortality, as measured in each seeding experiment, is a measure of all factors (known or unknown) that may play a role in mortality, whether induced by seeding or the result of natural processes. Experimental areas would not be compared with respect to survival rates; but results from the different areas would be analyzed within the ecological context peculiar to each specific area. At McDougall’s Bay it was possible to place the release modules in shallow water without the impact of direct surf action. This was not the case at Gouriqua. At Gouriqua the release modules were placed in what was deemed suitable

Table 4.2 Habitat attributes and recovery rate for abalone seeded at each site in the Gouriqua experiments. Each site had one seeding module, stocked with 100 14-mm and 100 25-mm abalone.

Site	Recovery of abalone (%)		Percentage of area consisting of boulder with diameter				No. of cucumbers per m ²	% cover urchins
	25-mm	14-mm	>50 cm	30-50 cm	<30 cm	% area exposed		
1	5	5	50	20	20	10	2.1	1.6
2	11.6	7	60	15	15	10	4.6	1.3
3	7	0	40	25	25	10	3.9	1.2
4	8	8	10	35	35	20	3.5	0.7
5	7	0	30	15	30	25	2.8	1.8
6	11	13	30	40	20	10	1.1	0.9
7	3	0	0	35	50	15	4.5	4.4
8	10.8	6	60	30	5	5	5.4	0.6

habitat, with respect to boulder size and abundance, but in water that was less than 1 m in depth. These release modules were placed at spring-low tide, and as the tide came in they lay directly in the surf zone. With respect to that alone, recovery rates recorded at Namaqualand and Gouriqua should not be compared but analysed independently. The experiments at Stilbaai, Port Nolloth were undertaken because it was in this bay that the experiments done by Sweijd et al. (1998) were done. While the Stilbaai sites were not as sheltered as the McDougall's Bay sites, they did contain "suitable" habitat, therefore it was possible to use the exact sites that had been used in the Sweijd et al. (1998) study, which yielded a 40% recovery rate when seeded with abalone of approximately 18 mm in length (Sweijd et al. 1998).

The experiments done at McDougall's Bay, Stilbaai and Gouriqua are described separately in the methods section. The different hypotheses, however, are examined in sequence in the results section, using different experiments from different areas to test particular hypotheses.

4.1.1 Sea urchins have a direct and positive effect on the recovery and survival rate of seeded juvenile abalone (Hypothesis 2).

One of the most fundamental aspects of the successful natural recruitment of *H. midae* is the association between the juveniles of the species and the urchin, *Parechinus angulosus*. This association is considered to be so strong that the presence of the urchin is considered a driving factor in the population dynamics of this abalone (Tarr 1995, Tarr et al. 1996, Day 1998, Day & Branch 2000a, in press). Associations between urchin species and abalone species have been reported in other parts of the

world, and are not restricted to the South African species (Kojima 1981, Andrew & Underwood 1992, Rogers-Bennet & Pearse 1998, Tegner 2000), but some of these are negative associations whereas others are positive. Indications are that naturally occurring juvenile *H. midae*, up to an average size of 35 mm, are found almost exclusively under urchins in the south-western Cape (Tarr et al. 1996, Day 1998, Day & Branch 2000b, in press). While there are indications that the long-term survival rate of juvenile abalone is linked to the utilization of urchins as refuge, the relationship between artificially seeded *H. midae* and urchins has never been investigated or quantified.

4.1.2 The complexity of the physical habitat and size of boulders on the substratum which offer juveniles short-term protection and shelter will result in a positive relationship between under-boulder habitat and the recovery of seeded juvenile abalone (Hypothesis 3).

Within the context of a relatively controlled physical environment in terms of the effects of direct wave action, it might be possible to quantify desirable attributes for seeding sites as compared to undesirable site attributes (Schiel 1992, 1993). The low average values for urchin density that were recorded in the initial experimental areas and at McDougall's Bay (Table 2.2, Chapter 3), and the fact that boulders did provide shelter to many of the abalone that were recovered, implied that seeding may be feasible in areas where urchins did not provide the same degree of protection that they did in the south-west Cape (Day & Branch 2000a, in press). This meant that it was necessary to investigate the correlation between the boulder habitat and abalone

recovery in greater detail. An underlying assumption and motivation behind testing this specific hypothesis was that suitable boulder habitat would, on its own, provide enough shelter to juvenile abalone so that it would be unnecessary to look for areas with high densities of urchins when selecting seeding sites.

4.1.3 An increase in size of seeded abalone results in a direct increase in short-term recovery rate (Hypothesis 5).

Previous research has shown that the bigger the seeded animals, the higher the recovery and survival rates (Schiel 1992, Schiel 1993, Kojima 1995, Masuda & Tsukamoto 1998, Shepherd et al. 2000, Tegner 2000). Sweijd et al. (1998) also hinted at this, but site attributes and environmental conditions at the time of release were not taken into account.

The experiments conducted on the Namaqualand coast and at Gouriqua used abalone that ranged in size from 8–26 mm in length. One of the questions that would inevitably result from these experiments would be: Is the habitat selected by the juveniles the same, or at least suitable, for adults (Shepherd et al. 2000)? In surveys conducted at Gouriqua, adults were found in the same area as naturally occurring juveniles. This is a common occurrence along the entire coastline where natural stocks of *H. midae* occur, although adults tend to occur in deeper water than do juveniles (Tarr et al. 1996). On the Namaqualand coast there are no naturally occurring adults and thus no comparisons could be made between juvenile and adult habitat selection. In an attempt to make a comparison with animals that were at least relatively larger than the smaller seeded juveniles, an experiment was performed at

McDougall's Bay with animals that averaged 45 mm in length. The experiments were conducted at sites similar to those involving smaller animals. The 45-mm animals can be regarded as being intermediate between juveniles and adults. Although they may still seek shelter underneath boulders, and will not often be found exposed, they are on the verge of moving into the open.

4.1.4 Gouriqua

Permission was given by Marine and Coastal Management, Department of Environmental Affairs and Tourism, for seeding experiments to be done along a stretch of coast 20 km south of the Gouritz River, some 300 km east of Cape Town, 34°22'S, 21°15'E. This area lies to the east of the line at Cape Agulhus demarcating the border between abalone that are defined as east-coast animals and those that are defined as west-coast animals (Figures 1.1, 4.2). There are also very low numbers of existing stocks of *H. midae* in this area. The experiments carried out here provided the opportunity to test the results generated in Port Nolloth against trials in other areas, and whether any of the findings about seeded juveniles were applicable to natural juveniles. Ocean temperatures near the Gouritz River are warmer than along the Namaqualand coast and, as reported by Baird et al. (1986), macroalgal biomass is small in comparison to that of west-coast kelp beds, and species composition is more diverse and different to that of the colder west-coast regions. Maximum plant height in the sub-tidal zone at Gouriqua is in the region of 20-cm compared with *Ecklonia maxima* beds in the Port Nolloth area, which can be up to 5 m long. On the west coast *E. maxima* makes up the vast majority of the algal biomass. Inter-tidal species at Gouriqua consist mainly of encrusting corallines and *Ralfsia* spp., *Ulva* spp.,

Sargassum spp. and *Gelidium* spp. Some of the same encrusting corallines occur along both stretches of coast, but total biomass of both the inter-tidal and sub-tidal part of the system is much larger on the west coast. *H. midae* recruitment is successful in both general types of algal habitat (Barkai & Griffiths 1986). The purpose of these experiments was, however, was not to investigate the effects of the habitat on natural recruitment, but to attempt to test the differences between habitats at the two regions with respect to their suitability for the seeding of artificially raised juveniles.

4.1.5 Stilbaai (Port Nolloth)

To allow comparisons with the results of the experimental work reported by Sweijd et al. (1998), the same study area was chosen. Four release modules were used (see Figure 4.1); one was positioned in the same place from which the previous investigators had reported the highest recovery rate (Table 4.3, Site 1). This was done to quantify the attributes of that specific site.

4.2 METHODS

Non-parametric statistical analyses were applied to all the data sets presented in this chapter, because of their relatively small size (Statistica Version 5.5, Keller & Warwack 2000).

Table 4.3 Habitat attributes and recovery rates of 15-mm and 23-mm abalone used in the Stilbaai experiments. Each site had one seeding module stocked with 100 15-mm and 100 23-mm abalone. The experiment ran for 123 days.

Site	Recovery of abalone (%)	Percentage of area consisting of boulder with diameter				% area exposed	% cover crustose coralline algae	% cover urchins
		>50 cm	30–50 cm	<30 cm				
	23-mm	15-mm						
1	58	15	40	10	10	20	48.50	0.3
2	51	29	35	20	25	20	47.00	0.13
3	22.5	12	30	10	10	50	56.5	0.34
4	26.5	10	60	10	10	20	32.50	0.35

4.2.1 Design, deployment and sampling of seeding modules

The seeding procedure was the same as that described in Chapter 2, except that, no anaesthetic was used on any of the abalone. The release modules (see Plate 1) were constructed as described by Sweijd et al. (1989), and consisted of lengths of PVC piping of decreasing diameter, cut in half and placed inside each other. A 1.5-cm gap was left between concentric pipe sections, and the pipes were then mounted on a flat plastic base. This base was attached to a steel plate, which acted as a weight to keep the module stable on the ocean floor, allowing the animals to leave and return to stable refuge (Schiel 1993). The juvenile abalone were gently brushed into the semi-cylindrical tubes making up the module. The release modules were then sealed at both ends with perforated plastic covers that allowed a through-flow of water, and placed in well aerated sea-water holding tanks. After approximately 30 min, the release modules were placed in plastic bags, sealed and placed in Styrofoam containers with sponge-wrapped freezer blocks. The containers were closed and transported to the seeding sites. The trip normally took approximately 20 min. On arrival at the seeding sites, the release modules were immediately taken out of the containers and placed in rock pools or in shallow water. The release modules were then moved underwater to the seeding sites.

Destructive sampling was performed in concentric circles around the release modules until no more abalone were found. During destructive sampling, all boulders were turned over, all the urchins were removed and all crevices and cracks were inspected.

The effect of diver efficiency and sighting probabilities on the recovery results were considered. Shepherd (1998) provides sighting probabilities of 0.36 for 8–19 mm abalone and 0.45 for 20–29 mm abalone. Adjusting the recovery rates using these sighting probabilities had no effect on the direction or significance of the difference between recoveries of these two size classes over a 30-day sampling period (Mann-Whitney U Test, $p = 0.02$, for unadjusted data, $= 0.02$ for adjusted data), and a 60-day sampling period (Mann-Whitney U Test, $p = 0.04$, for unadjusted data, $= 0.04$ for adjusted data). The sighting probabilities cited by Shepherd (1998) for the two size classes used in the present study are too close to each other to have a significant effect on the outcome of this experiment. As a result of this, and because of the low numbers of abalone seeded and the small areas involved in the searches, the use of these sighting probabilities were disregarded. When abundance estimates are done on a larger scale (Hart & Gorfine 1997, Hart et al. 1997), there is no doubt that diver efficiency is of cardinal importance. It was felt that on the scale of these experiments the results were sufficiently consistent to be accepted without adjustment.

4.2.2 Urchin exclusion experiment (McDougall's Bay)

To test the short-term effects of the presence of sea urchins on juvenile abalone the following experiment was carried out. Eight experimental sites at McDougall's Bay were selected in kelp beds typical to the west coast where there was an abundance of loose boulders, with biota including crustose coralline algae and sea urchins (Sites 9 to 16, Table 4.2). The sites were chosen as resembling each other as closely as possible, both in terms of physical appearance and in depth (2–4 m). Details of the date of installation and sampling and the conditions of the site are summarized in Table 4.4. In a 3-m radius around each module, an estimate was made of the relative percentage cover of different-sized boulders and the amount of exposed area between boulders. Percentage cover by encrusting coralline algae was estimated. At four of these sites (Sites 10, 12, 13 and 15), all the sea urchins within a radius of 3 m from the module were removed. At the other four sites, all those urchins collected from the first four sites were placed directly around the release modules. Each module contained 300 abalone with an average size of 12.2 mm. The release modules were monitored every few days to make sure that those from which the urchins had been removed remained clear of urchins. The sites were sampled in two groups, Sites 13, 14, 15 and 16 after 17 days, and Sites 9, 10, 11 and 12 after 23 days, with each group comprising two sites with urchins and two sites without urchins (Table 4.4). Sites 9, 10, 11 and 12 were seeded on a day when the swell was increasing and the current was relatively strong. During sampling, the number of urchins in a 3-m radius around the release modules was counted and the percentage utilization of urchins and boulders by juvenile abalone was calculated for each site, together with the abalone recovery rate. A Mann-Whitney U Test (Statistica Version 5.5) was performed on the recovery data

Table 4.4 Environmental conditions at the time of seeding and at the time of recovery for each site in the McDougall's Bay experiments. The urchin treatments indicate those sites in which urchins were removed (- urchins) or increased in number (+ urchins).

Site	Seeding date	Season	Swell height on site at seeding (m)	Depth (m)	Recovery date	Urchin treatment	Duration (days)	Season
14-mm and 26-mm abalone								
1	27 July 99	Winter	< 1.5	2-3	30 Aug 99		32	Winter
2	27 July 99	Winter	< 1.5	2-3	30 Aug 99		33	Winter
3	27 July 99	Winter	< 1.5	2-3	30 Aug 99		33	Winter
4	27 July 99	Winter	< 1.5	2-3	30 Aug 99		33	Winter
5	6 Sep 99	Spring	< 1.5	1-2	1 Nov 99		51	Summer
6	6 Sep 99	Spring	< 1.5	1-2	2 Nov 99		52	Summer
7	6 Sep 99	Spring	< 1.5	1-2	2 Nov 99		52	Summer
8	6 Sep 99	Spring	< 1.5	1-2	17 Nov 99		67	Summer
14-mm abalone (urchin-exclusion experiment)								
9	31 July 99	Winter	> 2	2-3	23 Aug 99	+ urchins	23	Winter
10	31 July 99	Winter	> 2	2-3	23 Aug 99	- urchins	23	Winter
11	31 July 99	Winter	> 2	2-3	23 Aug 99	+ urchins	23	Winter
12	31 July 99	Winter	> 2	2-3	23 Aug 99	- urchins	23	Winter
13	27 Aug 99	Winter	< 1.5	2-3	13 Sep 99	- urchins	17	Spring
14	27 Aug 99	Winter	< 1.5	2-3	13 Sep 99	+ urchins	17	Spring
15	27 Aug 99	Winter	< 1.5	2-3	13 Sep 99	- urchins	17	Spring
16	27 Aug 99	Winter	< 1.5	2-3	13 Sep 99	+ urchins	17	Spring

to test for significant differences in recovery rates of abalone at sites from which urchins were removed as compared to those with “enhanced” urchin densities.

4.2.3 Habitat selectivity

Indices of selectivity have been previously used to investigate the relationship between substrate availability and the proportional abundance of abalone on type of substrate (Day 1998, Day & Branch 2000b, in press). In this study, such indices were used to investigate the relationship between the availability of either urchins or boulders, and the proportional abundance of abalone utilizing urchins or boulders as refuge, to determine whether or not abalone actively sought or avoided either of these sources of shelter. In $\log_{10}$ form, the index W yields a range of values from $-\infty$ (negative selection) to $+\infty$ (positive selection), with 0 values indicating completely random selection. The average diameter measured for the urchins in the experiment was 54.9 mm (SD ± 8.7); this was used to convert densities of urchins to percentage cover of the substratum.

$$W = p_1 q_2 / p_2 q_1$$

p_1 = % of abalone that utilized urchins as refuge

p_2 = % of area covered by urchins

$$q_1 = (100 - p_1)$$

$$q_2 = (100 - p_2)$$

Further sets of experiments, also in the McDougall's Bay area, were conducted in which seeding size (26-mm and 14-mm) was investigated (see below for details). The

same selectivity indices were used on the data generated by those experiments. But the data from each size class were grouped and the analyses were done on each group to determine whether or not there was a difference in the strength of selection for urchins by the different size classes of seeded abalone.

4.2.4 The effect of abalone size at seeding

To accommodate the variability between sites, while at the same time investigating the effect of seeding size, both the large and small animals were placed together in the same modules. This meant that all the abalone at each site were exposed to the same environmental conditions and site characteristics on release. A similar procedure to that used in the urchin exclusion experiment was followed (Section 4.2.2), except that no urchins were removed from any area. Along with percentage cover by encrusting coralline algae (estimated per square meter for the experimental area), urchin densities were measured around each site. Eight experimental sites were selected to resemble each other as closely as possible, 200 animals were placed in each module: 100 larger ones (average size 26.6 mm) and 100 smaller ones (average size 13.8 mm) (Sites 1 to 8, Table 4.1). The release modules were sampled in two groups of four, the first group after 30 days, and the second group after 60 days. A Mann-Whitney U Test was performed on the data to determine significant differences in recovery rates between the different sized seed.

4.2.5 Quantifying the physical attributes of the seeding sites

Physical attributes of each site were quantified by estimating the percentage cover of the following categories in a 3-m radius around each release module:

- a) Boulders with a diameter >50 cm.
- b) Boulders with a diameter 30–50 cm.
- c) Boulders with a diameter <30 cm.
- d) Exposed area, i.e. flat rocky or sandy area providing little or no protection for juvenile abalone in terms of cracks or crevices.

One problem with the method of estimation is that boulders are obviously not completely round and while the estimate is made on a two-dimensional basis, the site is three-dimensional. The same person performed all estimates, contributing consistency to the series of experiments. Spearman Rank Order Correlation analyses were done between recovery rates and seeding size, and recovery rates and the physical and biological site attributes described in Table 4.1. To investigate the association between the biological attributes and the physical attributes of each seeding site, correlation analyses were also done in turn between urchin density and the percentage cover of different-sized boulders, and percentage cover of coralline algae and boulder attributes. As stated in the general introduction, due to differences in the biological and physical attributes between sites, each seeding site was regarded as a treatment, and there were no replicates per treatment. All the sites in the McDougall's Bay experiments were selected to represent suitable habitat.

4.2.6 Seeding 45-mm animals

Eight sites were selected in McDougall's Bay, and 25 abalone (of average size 45.73 mm SD ± 2.84) were released by hand at each site. The abalone were removed from seawater nursery tanks, placed into moist nylon mesh bags with pieces of kelp, and the bags were transported in cool containers to the experimental site. The journey took approximately 30 min, and the animals were in the sea within 45 min of removing them from the nursery tanks. At each site the animals were placed directly next to boulders, in a small area, less than one meter in diameter. The site attributes were quantified as in the previous chapters (see Section 4.2.5). The first four sites were destructively sampled after 30 days and the last four after 60 days. The distance from the release point to the point where each animal was found was measured, and the type of habitat noted. A Spearman Rank Order Correlation analysis was used to test the relationship between site attributes and recovery rates for the eight sites. A Mann-Whitney U Test was used to test the significance of the difference in recovery rates between the sites sampled after 30 days and those sampled after 60 days.

4.2.7 Gouriqua

The experiments that were done at Port Nolloth were repeated at Gouriqua. Figure 4.2 shows the position of the experimental area, landmarks surrounding the installation and sampling sites. Other details are outlined below.

Seeding size – Eight release modules were placed at the bottom of the shore in the sub-tidal zone with 100 small animals (average size 13.9 mm), and 100 bigger

animals (average size 26.6 mm) in each module. The modules were placed among rocks that were exposed only at spring low tide. Four sites were sampled after 30 days (Sites 1, 4, 6 and 7) and four after 60 days (Sites 2, 3, 5 and 8, Table 4.5). Site attributes were quantified with respect to boulder size, percentage boulder cover, exposed area, urchin density and density of sea cucumbers (*Cucumaria* sp.). Sea cucumber densities were recorded because of the high densities found relative to urchin densities. Spearman Rank Correlation analyses were performed to test the relationship between the listed biological and physical attributes and abalone recovery, and between both urchin density and the physical attributes of each site. A Mann-Whitney U Test was done to test the effect of seeding size on recovery over a sampling period of both 30 days and 60 days. A Mann-Whitney U Test was also done to test whether the duration of the period between release and sampling (30 or 60 days) had a significant effect on recovery rates for either of the two size classes.

Urchin and sea cucumber utilization by juvenile abalone – Large numbers of Holothuroidea and Echinoidea were found in the inter-tidal and sub-tidal areas of the Gouritz region, relative to their numbers on the Namaqualand coast. Because of this, the numbers of both urchins (*Parechinus angulosus*) and sea cucumbers (*Cucumaria* sp.) found under each boulder accommodating abalone were recorded. These data were tested for correlation with recovery rates using Spearman Rank Order Correlation analyses. The correlation analyses were initially done for both size classes grouped and then for the two different size classes separately.

Table 4.5 Environmental conditions at the time of seeding and at the time of recovery for each site in the Gouriqua experiments (see Figure 1.3 for locality). Over the period shown the average sea temperature was 14°C, with a minimum of 11.6°C and a maximum of 16.6°C, and swell height was <1.5 m.

Site	Seeding date	Season	Depth (m)	Recovery date	Duration (days)	Season
1	31-Mar-00	Summer	<1	6-Jun-00	68	Winter
2	31-Mar-00	Summer	<1	3-May-00	34	Autumn
3	1-Apr-00	Summer	<1	3-May-00	33	Autumn
4	1-Apr-00	Summer	<1	1-Jun-00	61	Winter
5	4-Apr-00	Summer	<1	3-May-00	29	Autumn
6	4-Apr-00	Summer	<1	2-Jun-00	59	Winter
7	4-Apr-00	Summer	<1	2-Jun-00	59	Winter
8	4-Apr-00	Summer	<1	4-May-00	30	Autumn

4.2.8 Stilbaai experiments (Port Nolloth)

In these experiments the same procedure was followed as in the McDougall's Bay experiments. Four release modules were placed in the vicinity of the experiments done by Sweijd et al. (1998). One was specifically placed at the same site from which they recorded highest recovery of abalone (Site 1, Table 4.3). Table 4.6 summarizes the dates of installation and sampling and the physical circumstances of the sites.

Each of four release modules contained 100 animals of average size 15.5 mm (SD ± 2.14) and 100 animals of average size 23.1 mm (SD ± 1.93). The sites were sampled after 123 days (Table 4.6). A Mann-Whitney U Test was performed to test the effect of seeding size on juvenile abalone recovery rates. The site attributes were estimated and recorded as for previous sites. A Spearman Rank Order Correlation analysis was performed to determine the importance of each attribute with respect to recovery rates, and with respect to urchin density and percentage cover coralline algae. The size classes were first analysed separately, after no significant relationships were found between any of the site attributes and recovery, the data from the different size-classes were pooled, and the analyses repeated.

4.2.9 Determining abalone habitat preferences using selectivity indices

The selectivity indices described above (Section 4.2.3) and used in the analysis of the urchin exclusion experiments were used to investigate the relationship between juvenile abalone and the different size class of boulders. The percentage of abalone recovered beneath the different-sized boulders and the respective abundance of each

Table 4.6 Environmental conditions at the time of seeding and at the time of recovery for each site in the Stilbaai experiments. The period between seeding and sampling was 123 days.

Site	Seeding date	Season	Swell height on site (m)	Depth (m)	Recovery date	Season
1	24 Sep 99	Spring	< 1.5	2-3	25 Jan 2000	Summer
2	24 Sep 99	Spring	< 1.5	1-2	25 Jan 2000	Summer
3	24 Sep 99	Spring	< 1.5	1-2	25 Jan 2000	Summer
4	24 Sep 99	Spring	< 1.5	1-2	25 Jan 2000	Summer

size class of boulders were used in the calculation of the selectivity index $\text{Log } W$ (Day & Branch 2000b, in press).

4.3 RESULTS

4.3.1 Recovery relative to seeding-site attributes

The results of Spearman Rank Correlation analyses testing the relationship between the recovery rates of juvenile abalone in McDougall's Bay and various site attributes are shown in Table 4.7a, b and c. In Table 4.7a the data from the two different size classes are pooled. A significant positive association existed between recovery rates and the percentage cover of boulders <30 cm. The table also shows two negative but non-significant associations, between recovery and habitat made up of boulders 30-50 cm, and between recovery and the amount of exposed habitat. There was a significant negative association between the density of urchins and exposed habitat. There were no significant associations between percentage cover of coralline algae and any other site attributes (Table 4.7a). In Table 4.7b and c the same analyses are shown for the two size classes. Table 4.7b shows that the association between recovery rates and boulders <30 cm was positive and significant for 14-mm abalone, while the negative association between recovery rates and boulders 30–50 cm remained not significant. For both size classes, the association between exposed habitat and recovery rates remained negative but insignificant. The larger abalone also showed a non-significant association with boulders >50 cm in diameter (Tables 4.7b, c).

Table 4.7a The relationship between site attributes and abalone recovery rate, site attributes and percentage cover by urchins, and site attributes and percentage cover by coralline algae in McDougall's Bay, using Spearman Rank Order Correlations. In these analyses both size classes of abalone (14 mm and 26 mm) were grouped. An asterisk indicates significance at $p \leq 0.05$.

		Recovery rates	
Categories of site attributes	n	R	p-level
% boulders with >50 cm diameter	24	0.003089	0.99
% boulders 30–50 cm diameter	24	-0.109507	0.61
% boulders with <30 cm diameter	24	0.407414	0.05 *
% exposed area	24	-0.322266	0.13
Ratio of boulders over exposed area	24	0.344539	0.1
% cover coralline algae	24	0.42995	0.84
Urchin density	24	0.402841	0.05*
Abalone size	24	0.700911	0.0001 *
% of abalone utilizing urchins	24	0.095773	0.66
		% cover urchins	
	n	R	p-level
% boulders with >50 cm diameter	16	-0.3009	0.23
% boulders 30–50 cm diameter	16	0.358008	0.15
% boulders with <30 cm diameter	16	0.315177	0.20
% exposed area	16	-0.52311	0.03*
		% cover coralline algae	
	n	R	p-level
% boulders with >50 cm diameter	16	-0.24647	0.32
% boulders 30–50 cm diameter	16	0.062796	0.80
% boulders with <30 cm diameter	16	0.458957	0.06
% exposed area	16	0.178254	0.48

Table 4.7b, c The relationship between site attributes and abalone recovery rate at McDougall's Bay, using Spearman Rank Order Correlations. The analyses in (b) are for the 14-mm abalone, and in (c) for 26-mm abalone. An asterisk indicates significance at $p \leq 0.05$.

b) 14-mm abalone		Recovery rates	
Categories of site attributes	n	R	p-level
% boulders with > 50 cm diameter	16	0.37492	0.15
% boulders 30 - 50 cm diameter	16	-0.47373	0.06
% boulders with < 30 cm diameter	16	0.585126	0.02*
% exposed area	16	-0.38758	0.14
% cover coralline algae	16	0.278229	0.30
Urchin density	16	0.404344	0.12

c) 26-mm abalone		Recovery rates	
	n	R	p-level
% boulders with > 50 cm diameter	8	-0.56114	0.15
% boulders 30 - 50 cm diameter	8	0.337374	0.41
% boulders with < 30 cm diameter	8	0.589234	0.12
% exposed area	8	-0.08939	0.83
% cover coralline algae	8	0.428571	0.29
Urchin density	8	0.407193	0.32

When both size classes of abalone were grouped, the results from the Gouriqua experiment showed non-significant negative associations between recovery rates and both habitat consisting of boulders <30 cm and exposed habitat. Interestingly, urchins had a positive association with boulders <30 cm, although the association was not significant (Table 4.8a). The strongest positive association was between recovery rate and boulders 30–50 cm. The negative correlation between recovery and both small boulders and exposed area was evident for both the 14-mm and the 26-mm abalone (Tables 4.8b, c). However, both associations were stronger for the larger abalone as compared to the smaller abalone.

The correlation analyses using the Stilbaai experimental data for the two size classes of abalone grouped, showed positive associations between recovery rates and boulders 30–50 cm. Negative associations were shown between recovery rates and both exposed habitat and boulders >50 cm; however, both these associations were non-significant (Table 4.9). The association between urchin density and the same site attributes were shown to be the opposite. In this case there were significant negative associations between urchin density and boulders <30 and 30–50 cm (Table 4.9). The associations between site attributes and percentage cover of coralline algae were all negative except for the association between coralline algae and exposed area; the association between boulders >50 cm and coralline algae was significant. At Stilbaai, the site that produced the highest recovery rate was the same at which Sweijd et al. (1998) reported the highest recovery rate (Site 1, Table 4.3). While 40% of the area around the release module there consisted of boulders >50 cm diameter, with 20% exposed and only 30% consisting of smaller boulders, the boulders were layered in a three dimensional rock pile. This terrain provided very good shelter and protection for

Table 4.8a The relationships between site attributes and abalone recovery rate, and between site attributes and percentage of cover urchins at Gouriqua, using Spearman Rank Order Correlations. In these analyses both size classes of abalone (15 mm and 23 mm) are combined. An asterisk indicates significance at $p \leq 0.05$.

Categories of site attributes	n	Recovery rate	
		R	<i>p</i> -level
% boulders with diameter > 50 cm	16	0.208156	0.44
% boulders with diameter 30 - 50 cm	16	0.277542	0.30
% boulders with diameter < 30 cm	16	-0.422793	0.10
% exposed area	16	-0.201431	0.45
Urchin density	16	-0.602087	0.01*
Cucumber density	16	-0.09538	0.73
Abalone size	16	0.355133	0.18
	n	% cover urchins	
		R	<i>p</i> -level
% boulders with diameter > 50 cm	8	-0.33737	0.20
% boulders with diameter 30 - 50 cm	8	-0.38557	0.14
% boulders with diameter < 30 cm	8	0.491027	0.05*
% exposed area	8	0.395877	0.13
Cucumber density	8	-0.16667	0.78

Table 4.8b, c The relationship between site attributes and abalone recovery rate at Gouriqua, using Spearman Rank Order Correlations. In these analyses recovery data from (b) the smaller abalone (15-mm) and (c) larger abalone 26-mm) have been separated. An asterisk indicates significance at $p \leq 0.05$.

b) 15-mm abalone		Recovery rate	
Categories of site attributes	n	R	p-level
% boulders with diameter >50 cm	8	0.135813	0.75
% boulders with diameter 30–50 cm	8	0.432132	0.28
% boulders with diameter <30 cm	8	-0.3927	0.34
% exposed area	8	-0.13086	0.76
Cucumber density	8	-0.19518	0.64
Urchin density	8	-0.65873	0.08

c) 26-mm abalone		Recovery rate	
	N	R	p-level
% boulders with diameter >50 cm	8	0.490918	0.22
% boulders with diameter 30–50 cm	8	0.006061	0.99
% boulders with diameter <30 cm	8	-0.6506	0.08
% exposed area	8	-0.38541	0.35
Cucumber density	8	0.167668	0.69
Urchin density	8	-0.63474	0.09

Table 4.9 The relationship between site attributes and recovery rates, site attributes and percentage cover of urchins and site attributes and percentage cover of coralline algae for the Stilbaai experiments, using Spearman Rank Order Correlations. An asterisk indicates significance at $p \leq 0.05$.

Recovery rate			
Categories of site attributes	n	R	p-level
% boulders with diameter >50 cm	8	-0.048795	0.91
% boulders with diameter 30–50 cm	8	0.503953	0.20
% boulders with diameter <30 cm	8	0.503953	0.20
% exposed area	8	-0.37700	0.36
Seed size	8	0.654654	0.08
% cover coralline algae	8	-0.04900	0.91
Urchin density	8	-0.6600	0.07
% cover urchins			
	n	R	p-level
% boulders with diameter >50 cm	4	0.11	0.6
% boulders with diameter 30–50 cm	4	-0.82	0.01*
% boulders with diameter <30 cm	4	-0.82	0.01*
% exposed area	4	0.54	0.16
% cover coralline algae	4	0.11	0.81
% cover corraline algae			
	n	R	p-level
% boulders with diameter >50 cm	4	-0.8	0.02*
% boulders with diameter 30–50 cm	4	-0.2582	0.54
% boulders with diameter <30 cm	4	-0.2582	0.54
% exposed area	4	0.8	0.02*

the juvenile abalone, even though the area was exposed to both direct wave action and strong currents. In hindsight, it appears that the site selected fairly randomly by Sweijd et al. (1998) contained the attributes most highly suited to juvenile abalone survival.

Spearman Rank Correlation analyses of the data from the experiments with the 45-mm abalone in McDougall's Bay showed a positive (but non-significant) association between recovery rates and habitat consisting of boulders 30–50 cm. Negative associations were shown between recovery rates and all other site attributes, but all these associations were non-significant (Table 4.10).

Selectivity analyses done on the data from the different experiments at McDougall's Bay and Gouriqua, showed that the different size-classes of abalone had different selectivity strengths for different habitats (Table 4.11). Abalone at Gouriqua showed the strongest selection preference for habitat consisting of boulders <30 cm. The smaller abalone used in McDougall's Bay also show a preference for the smaller boulders. The larger 26-mm abalone in McDougall's Bay showed a preference for boulders 30–50 cm, while 45-mm abalone showed a preference for boulders with a diameter >50 cm (Table 4.11). The data set used in the experiment with 45-mm abalone is, however, very small.

The correlation analyses shown in Table 4.7a show that when the abalone size-class data from the McDougall's Bay experiments were grouped, there was a significant positive relationship between urchin density and abalone recovery. This correlation did not emerge as being significant when the analyses was done on the two size

Table 4.10 Spearman Rank Order Correlation analyses showing relationships between recovery rate of abalone and the percentage area that consisted of boulders of various sizes, exposed area or coralline algae. The data are for twenty five 45-mm abalone seeded at each of eight sites in McDougall's Bay.

Categories of site attributes	n	R	<i>p</i> -value
% boulders with diameter >50 cm	8	-0.128	0.76
% boulders with diameter 30–50 cm	8	0.348	0.40
% boulders with diameter <30 cm	8	-0.475	0.23
% exposed area	8	-0.075	0.86
% cover coralline algae	8	-0.297	0.48

Table 4.11 Results of selectivity indices calculated for the different size-classes of abalone for boulders of different sizes from both McDougall's Bay and Gouriqua experimental areas. Bold figures highlight the largest values recorded for each size group.

		Average Log W values (SD)		
Size class		Boulders with diameters of		
		>50 cm	30–50 cm	<30 cm
McDougall's Bay	14-mm	-0.35	0.34 (0.44)	0.38 (0.7)
	26-mm	-0.31 (0.86)	0.36 (0.4)	0.18 (0.45)
	45-mm	0.24 0.46	0.04 0.40	0.22 0.45
Gouriqua	14-mm	-0.27 (0.86)	-0.32 (0.43)	0.49 (0.46)
	26-mm	-0.29 (0.94)	-0.24 (0.45)	0.40 (0.58)

classes separately (Tables 4.7b, c). The same correlation analyses done on the data from Gouriqua, when the size classes were grouped, showed a highly significant negative correlation between the density of urchins and abalone recovery (Table 4.8a). This negative correlation was also reflected in each size class of abalone separately, but the relationship was not significant at a 95% confidence level (Tables 4.8b, c). Among the seeded juveniles were found a small number of wild *H. midae* juveniles, but these never occurred under urchins. (It was possible to distinguish between natural and seeded abalone because of the color difference resulting from the artificial diet of the seeded juveniles, making them bright blue, with the natural ones being dark brown.)

4.3.2 Urchin exclusion experiment

Table 4.4 shows the recovery rates for the different sites in the urchin-exclusion experiment done at McDougall's Bay. A Mann-Whitney U Test done on the recovery data (Figure 4.3) shows that there is no significant difference in recovery rates between sites with urchins and sites without urchins.

Table 4.12 shows the results of a selectivity analysis done using data from the McDougall's Bay sites, wherein urchins were not removed. The analysis shows a large positive *Log W* value for urchins and a smaller negative *Log W* value for boulder habitat. Table 4.13 shows the results when the same analysis is done on the data from the sites at McDougall's Bay, when seeding size was tested. Again there was a positive selection for urchins exhibited by both the 14-mm and the 26-mm size-classes of seeded abalone; there is little difference, however, in the strength of

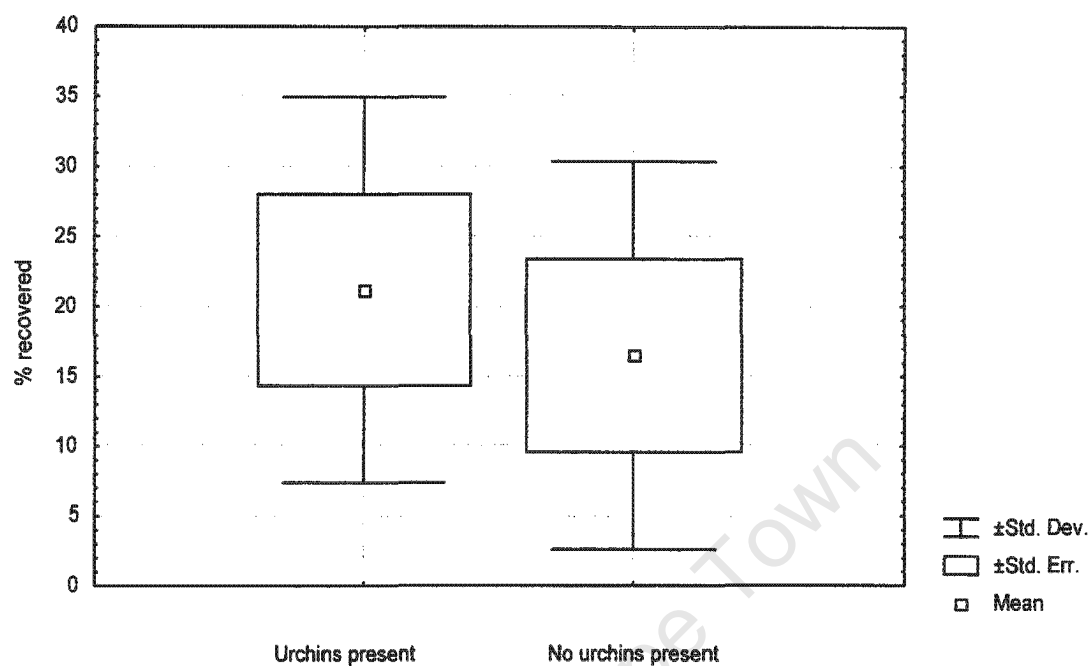


Figure 4.3 Abalone recovery rate for sites with and without urchins at the McDougall's Bay experimental area. A Mann-Whitney U Test showed no significant difference between the two treatments ($p = 0.67$).

Table 4.12 Urchin densities and juvenile abalone recovery rates from the urchin inclusion/exclusion experiment at McDougall's Bay. The total number of urchins was counted in a 3-m radius around each trap. Sites 9, 10, 11 and 12 were sampled after 17 days and Sites 13, 14, 15 and 16 after 23 days. A positive value of $\text{Log}_{10} W$ indicates active selection by the abalone, and a negative value indicates active avoidance by the abalone. The greater the value, the stronger the selection. The values of $\text{Log}_{10} W$ are not defined in cases where the urchin density was zero.

Site	% total recovery rate	Urchin density per m ²	% of total area under urchins	% of abalone utilizing urchins as refuge	$\text{Log}_{10} W$ for urchins as refuge	% of area under boulders	% of abalone utilizing boulders as refuge	$\text{Log}_{10} W$ For boulders as refuge
9	5.67	5.93	1.07	35.29	1.7	88.39	64.71	-0.62
10	5.67	0						
11	15.67	5.93	1.40	27.66	1.43	87.88	72.34	-0.44
12	3.3	0						
13	28.67	0						
14	25.33	4.52	0.70	39.47	1.97	93.93	60.53	-1.00
15	28.33	0						
16	38	5.72	1.35	29.82	1.49	92.96	70.18	-0.75
Ave.					1.65			-0.70
SD					0.24			0.24

Table 4.13 Results from the McDougall's Bay sites in which seeding-size experiments were done, showing the strength of selection for urchins by the two size classes of abalone juveniles. No urchins were utilized at Site 3, thus $\log_{10} W$ could not be calculated.

Site	% area covered by urchins	% abalone utilizing urchins	% abalone not utilizing urchins	% area not covered by urchins	W	$\log_{10} W$
14-mm abalone						
1	0.19	3.85	96.15	99.81	21.01	1.32
2	0.14	41.38	58.62	99.86	503.50	2.70
4	0.13	6.06	93.94	99.87	49.56	1.70
5	0.09	26.00	74.00	99.91	390.04	2.59
6	0.03	13.00	87.00	99.97	497.93	2.70
7	0.05	8.30	91.70	99.95	180.93	2.26
8	0.05	1.00	99.00	99.95	20.19	1.31
					Ave	1.82
					SD	0.99
26-mm abalone						
1	0.19	3.85	96.15	99.81	21.01	1.32
2	0.14	17.31	82.69	99.86	149.29	2.17
4	0.13	7.35	92.65	99.87	60.97	1.79
5	0.09	10.00	90.00	99.91	123.35	2.09
6	0.03	6.70	93.30	99.97	239.30	2.38
7	0.05	60.10	39.90	99.95	3011.03	3.48
8	0.05	2.00	98.00	99.95	40.80	1.61
					Ave	1.86
					SD	1.06

selection between the two size classes. The *Log W* value from the urchin exclusion experiment was larger than values generated for the rest of the sites.

On the Namaqualand coast 39% of all abalone utilizing urchins did so on a vertical surface, and 45% did so positioned upside down under a boulder. Only 5% of utilized urchins were observed on the horizontal bottom of the sea floor (Table 4.14).

4.3.3 Sea conditions at time of seeding

Although the urchin exclusion experiments yielded no significant differences in recovery rates between treatments, Figure 4.4 shows a significant difference in the recovery rates between the two groups seeded on different days. This is probably a reflection of the sea conditions at the time of seeding and not a reflection of time elapsed to sampling. The longer (23-day) period resulted in greater recovery rates. This is the batch of sites that was seeded in calm water; whereas the batch sampled after 13 days was seeded in rough water.

4.3.4 The effect of abalone size at seeding

Eight release modules used to test the effects of abalone seeding-size were installed in McDougall's Bay. There was a significant positive relationship between an increase in seeding size and the recovery of seeded abalone (Figure 4.5). The experiment was divided into two batches of four sites each, one batch sampled after 30 days and the second after 60 days (Table 4.4). Mann-Whitney U Tests done on the recovery data for the two size classes of abalone over both sampling periods showed that, regardless

Table 4.14 Specific positioning of urchins selected by abalone as refuge, all Namaqualand sites combined.

Horizontal on bottom (%)	Vertical on bottom of reef (%)	Vertical, upper crack or ledge (%)	Vertical, upper depression (%)	Under boulder, off bottom (%)
4.62	38.67	0.03	3.38	45.44

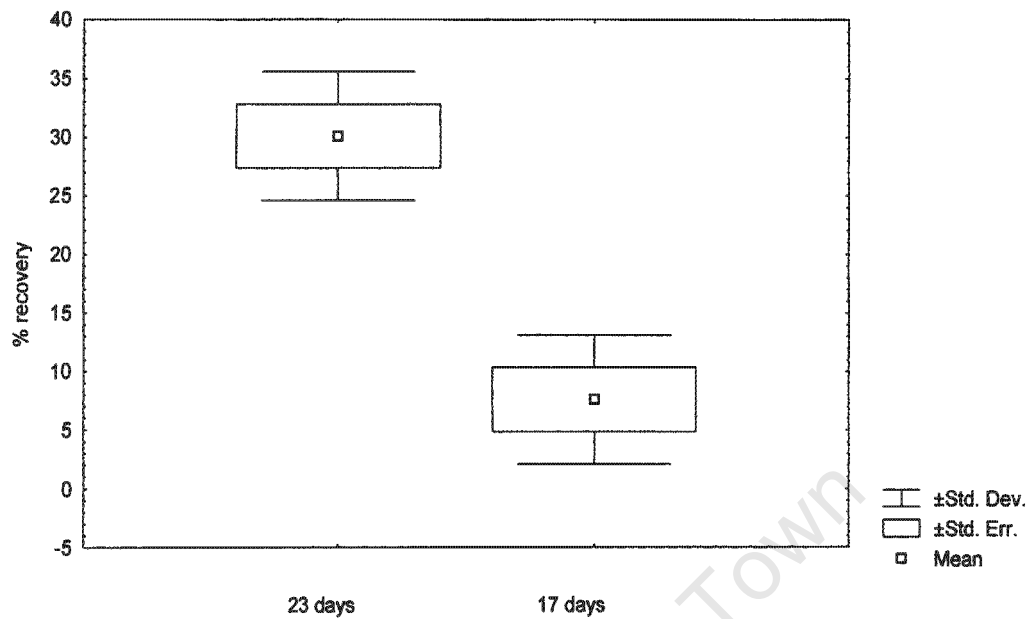


Figure 4.4 Results from the urchin-exclusion experiment at McDougall's Bay showing a significant difference in recovery rates between the two sets of sites sampled after 17 days and after 23 days (Mann-Whitney U Test, $p=0.02$). This is a reflection of sea conditions at the time of seeding. Recovery rates from the sites sampled after 23 days, seeded in calm water, were significantly greater than those sampled after 17 days, seeded in rough water.

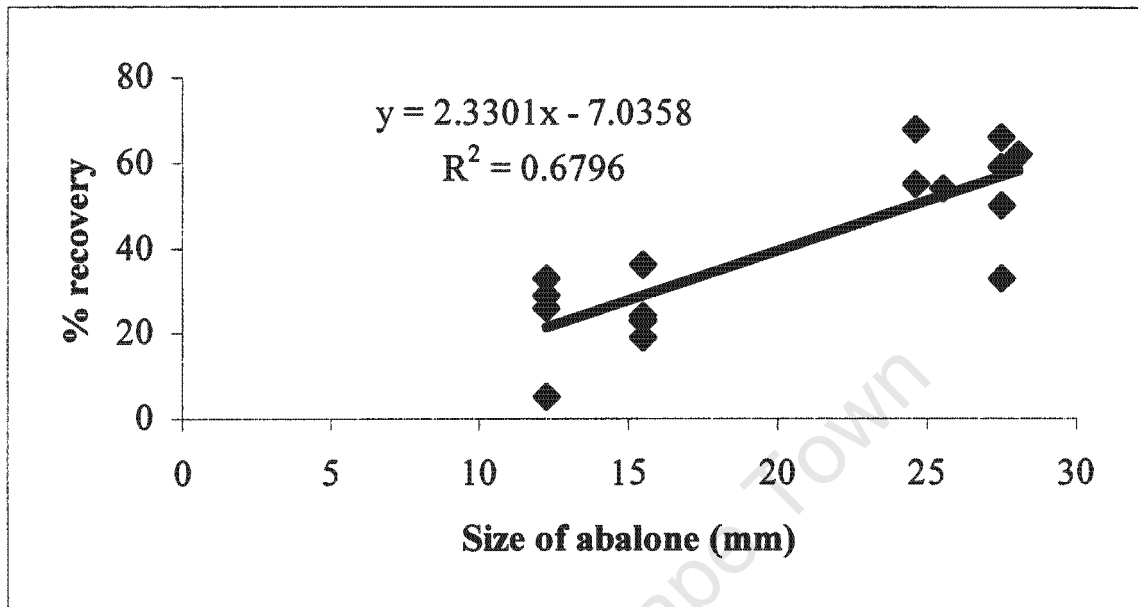


Figure 4.5 Seeding size and juvenile recovery for the McDougall's Bay experiments (See also Figure 4.6). One seeding module was placed at each site containing 100 abalone of each general size (≈ 26 mm and ≈ 14 mm).

of sampling period, there was a significant difference in recovery rate between the two sizes (14-mm and 26-mm) (Figure 4.6, $p = 0.02$ for the 30-day period, and $p = 0.04$ for the 60-day period). The same analysis conducted on the two different size classes to test the effect of the period to sampling on recovery, showed that time had no significant effect on recovery for either the 26-mm abalone ($p = 0.39$) or the 14-mm abalone ($p = 0.77$).

The same procedure was followed for the Gouriqua experiments (Table 4.2). In this case a Mann-Whitney U Test (Figure 4.7) showed a significant difference in recovery rates between size-groups when the sites were sampled after 30 days ($p = 0.04$), but after 60 days the effect of seeding size was insignificant ($p = 1.0$). A Mann-Whitney U Test, conducted to test the difference in recovery rates for each size class over the two time periods, showed that sampling period had an insignificant effect on both the 26-mm ($p = 0.39$) and the 14-mm abalone ($p = 0.39$).

The Stilbaai experiments were likewise analysed. In this case, four sites were sampled after 123 days (Table 4.6). A Mann-Whitney U Test showed that although recovery rates were very different for the two size classes, seeding size did not have a significant effect on recovery rates ($p = 0.08$, Figure 4.8).

Correlation analyses done between recovery rates and seeding-size, showed a highly significant positive correlation between seeding-size and recovery rates at McDougall's Bay (Table 4.7a), a positive but non-significant association at a 95% confidence level at Stilbaai (Table 4.9), and a weak positive association at Gouriqua (Table 4.8a). Both the relatively low values for recovery at Gouriqua and the small

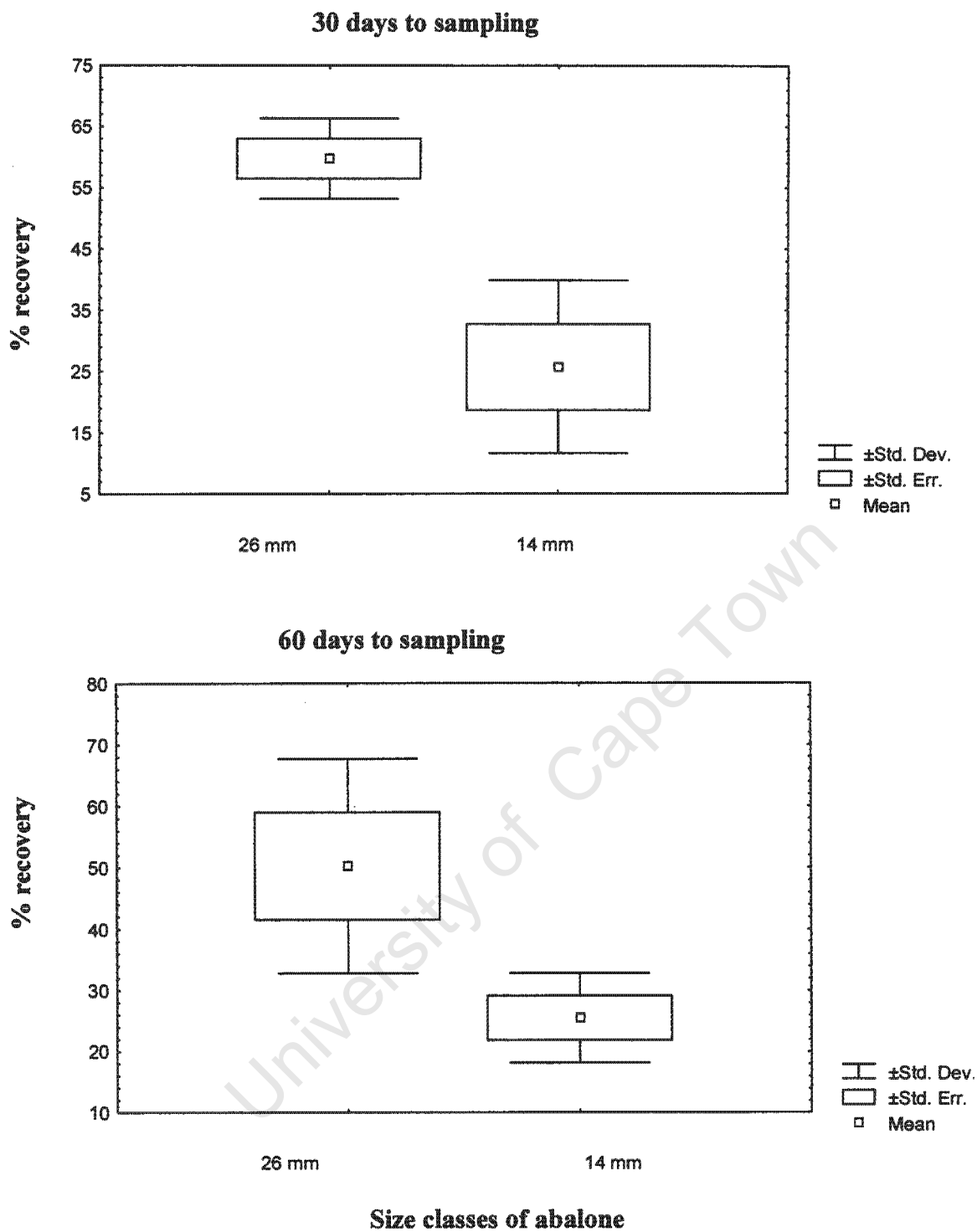


Figure 4.6 Recovery rates of the two size classes of abalone used in the seeding experiments at McDougall's Bay over 30 days ($p = 0.02$) and 60 days to sampling ($p = 0.04$). Mann-Whitney U Tests showed the difference in recovery of the two size-classes to be significant over both periods.

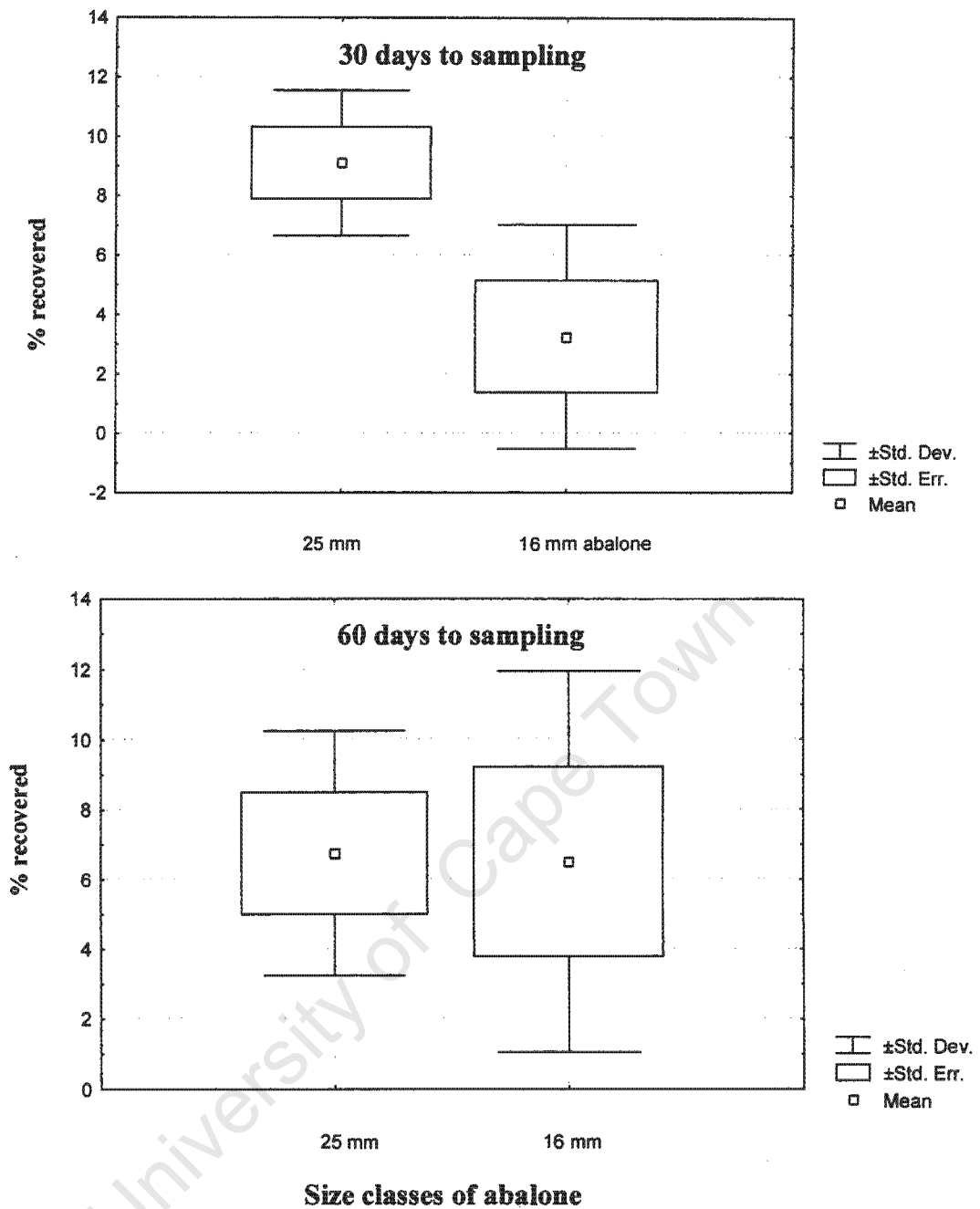


Figure 4.7 Results from Mann-Whitney U Tests showing a significant difference in recovery rates between the two size classes of abalone at Gouriqua for the four sites sampled after 30 days, $p = 0.04$, top figure, and the sites sampled after 60 days, where there was no significance difference in recovery ($p = 1.00$), bottom figure.

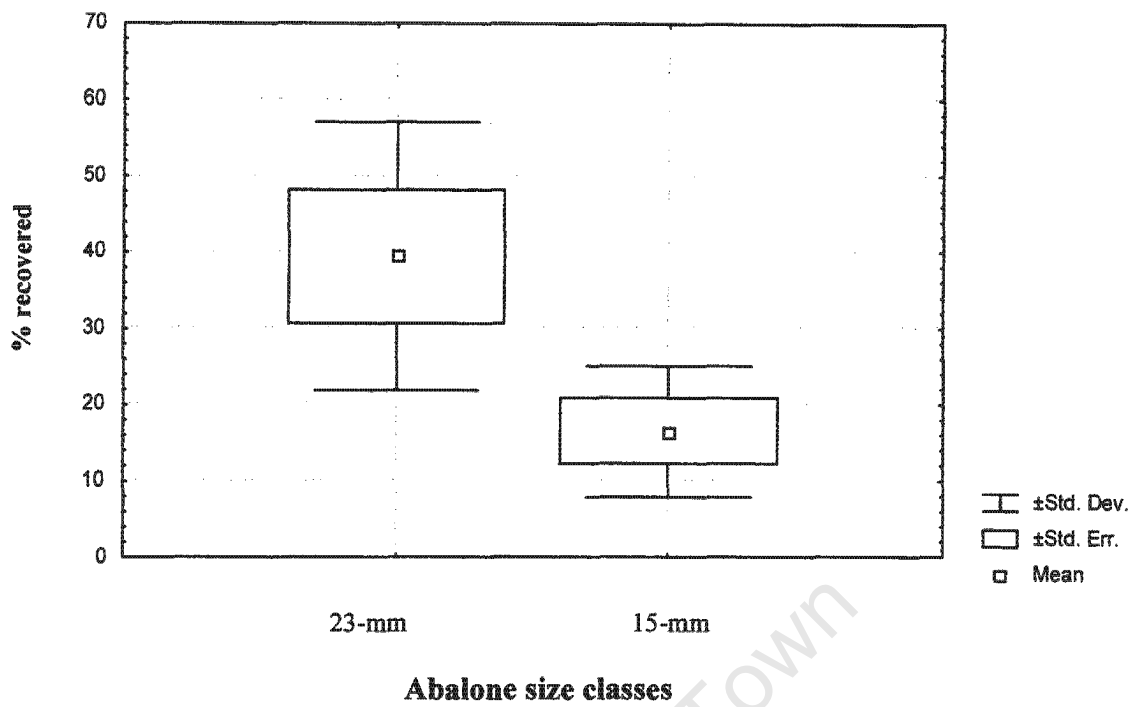


Figure 4.8 Results from a Mann-Whitney U Test showing that seeding size did not make a significant difference in the recovery rate of juvenile abalone over four months in the Stilbaai experimental area, $p = 0.08$.

data set from Stilbaai may have affected these results. The comparisons between seeding sizes were considered in the context that abalone released from the same seeding module were exposed to the same environmental and habitat conditions and could, as a result, be compared to each other.

The seeding experiments with the 45-mm abalone resulted in recovery rates of between 64 and 100% (Tables 4.15, 4.16). A Mann-Whitney U Test showed that the period to sampling had no significant effect on recovery rates (Figure 4.9). The average recovery rates for both periods were very high, 92% and 72% for the 30-day and 60-day periods, respectively. Of the animals recovered, 70% were within one meter of the release point. Thus, most animals had not moved more than one meter over a 60-day period. Over the same period the average size had increased from 45.7 mm (SD ± 2.85) to 47.3 mm (SD ± 4.9), an average increment of approximately 0.8 mm per month.

Using the sighting probabilities mentioned by Shepherd (1998), weighting the recovery rate figures for the different-sized abalone in the experiments did not alter the fact that there was a significant difference in recovery rate between the different-sized animals. Searching efficiency during the recovery stages of the experiments was shown to be high, reflected in Figure 3.3, where time elapsed between seeding and sampling had no significant effect on the total number of abalone found, suggesting that abalone were found outside the release modules just as easily as they were found inside. If there was doubt about the efficiency of the searches and the recovery rates, the use of sighting probabilities would have been essential.

Table 4.15 Environmental conditions at the time of seeding and at the time of recovery for each site in the McDougall's Bay experiments involving 45-mm abalone. Swell height was consistently <1.5 m at all sites during seeding.

Site	Seeding date	Season	Depth (m)	Recovery date	Season
1	14 May 2000	Autumn	2-3	17 Jun 2000	Winter
2	14 May 2000	Autumn	2-3	17 Jun 2000	Winter
3	14 May 2000	Autumn	2-3	17 Jun 2000	Winter
4	14 May 2000	Autumn	2-3	17 Jun 2000	Winter
5	14 May 2000	Autumn	2-3	15 July 2000	Winter
6	14 May 2000	Autumn	2-3	15 July 2000	Winter
7	14 May 2000	Autumn	2-3	15 July 2000	Winter
8	14 May 2000	Autumn	2-3	15 July 2000	Winter

Table 4.16 Habitat attributes in relation to recovery rate for 45-mm abalone at McDougall's Bay. At each site 25 animals were released by hand. Sampling occurred after 33 days (Sites 1 to 4) and after 68 days (Sites 5 to 8). None of the recovered abalone appeared to utilize urchins for refuge; the average urchin density in the experimental area was 8.22 urchins m⁻², SD ±1.66.

Site	Recovery rate (%)	Site	Percentage of area consisting of boulder with diameter				% cover crustose corraline algae
			>50 cm	30-50 cm	<30 cm	% area exposed	
1	76	1	30	30	5	35	48.75
2	96	2	40	20	10	30	42.50
3	96	3	60	25	5	10	40
4	100	4	60	15	5	20	35
5	80	5	60	10	10	20	40
6	76	6	60	10	20	10	28.7
7	64	7	65	5	10	20	46.25
8	84	8	75	5	5	15	31.25

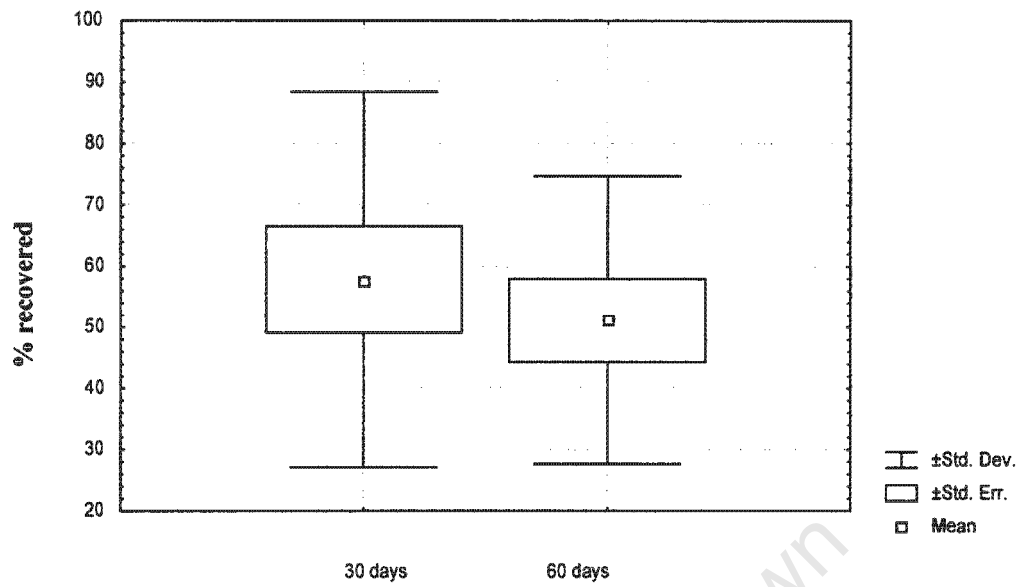


Figure 4.9 Results of a Mann-Whitney U Test showing no significant difference in recovery rates between sites that had been sampled after 30 days and 60 days for 45-mm animals seeded in McDougal's Bay, $p = 0.11$.

4.4 DISCUSSION

Hypothesis 3. There is a significant positive correlation between under-boulder habitat and recovery rates of seeded juvenile abalone.

When defining the attributes of a successful seeding site several factors must be kept in mind. One is the complexity of a three-dimensional habitat made up of layered rocks, and the potential refuge that this may provide. Theoretically, under-boulder habitat, whether it is under a large boulder or a small boulder, should have the same or similar qualities. The difference will be in the abundance of under-boulder habitat associated with the different-sized boulders. The smaller the rocks, the higher the surface area and the more cracks and crevices available per unit area. If under-boulder habitat is the optimum habitat for juveniles, this should be reflected in a positive association between recovery rates of juvenile abalone and a habitat consisting of small boulders. This was only shown to be true in the correlation analyses done with the McDougall's Bay data, where recovery rates correlated positively and significantly with habitat comprising boulders with a diameter less than 30 cm (Tables 4.7a, b). The use of selectivity indices also showed a preference for the smallest class of boulder by the 14-mm abalone (Table 4.11). For the 26-mm abalone the association was less clear, both with respect to the correlation analysis and the selectivity index analysis. The correlation analyses showed a stronger (but non-significant) positive association between recovery rates and habitat comprising boulders with a diameter of less than 30 cm, while the selectivity index analysis shows the abalone had a preference for boulders 30–50 cm. The correlation analysis done on the data involving the 45-mm abalone at McDougall's Bay (Table 4.10) showed a positive (but

non-significant) association between recovery rates and habitat comprising boulders 30–50 cm in diameter. The selectivity index analysis, however, showed the abalone had the greatest preference for the large-boulder habitat (Table 4.11). These contradictory results could be due to the very small data set for this set of experiments. The results from the Gouriqua experiments were also confusing. The correlation analyses showed a negative (but non-significant) association between recovery rates and boulders <30 cm, and a positive association between recovery rates and habitat comprising boulders >30 cm for abalone of both size classes (Tables 4.8b, c). The selectivity index analyses shows the opposite. Preference by both size class of abalone is shown to be positive for habitat comprising boulders <30 cm (Table 4.11). It is possible that the negative association between small boulders and recovery rates relating to the Gouriqua experiments may be a reflection of the fact that small boulders may not provide adequate shelter in very shallow areas exposed to high surf energy.

The use of both the correlation analysis and the selectivity index analysis is influenced by the size of the data set. The McDougall's Bay experiments generated the largest data set and experiments there showed the most consistent results. Although the relationship concerning habitat selection and habitat type are far from clear, there is ample evidence that under-boulder habitat does provide shelter to seeded abalone, and that this shelter can influence recovery rates. In this study, this habitat provided shelter to juvenile abalone ranging from 8 to 45 mm in length for up to 120 days.

The amount of exposed area (sea floor, or large boulders) was consistently (but non-significantly) negatively correlated with abalone recovery rates. The lack of clear-cut correlation can be attributed to the relationship between the percentage of area that is exposed and the characteristics of the rest of the site. A very large boulder would be classified as exposed due to its size, while it may have the potential to house a large number of abalone beneath it. While the relationship between sheltered and exposed area could be used as a simple measure of habitat suitability, the site would have to be investigated for other specific characteristics that could provide habitat. Although the relationship between the amount of crustose coralline algae and recovery rate was insignificant in these experiments, naturally occurring juvenile abalone and urchins are found predominantly on encrusting corallines. The movement of sand and general substratum, as a result of strong currents, is a major and obvious cause of mortalities in natural and seeded abalone (Tegner 1992, 2000). Coralline algae may be an indicator of reef or rock surfaces that are relatively clean of macroalgae, providing abalone with secure footing and space to move, and a source of nutrition, both of which are important to juvenile abalone (Shepherd 1990, 1998, Shepherd et al. 2000). It appeared that juvenile abalone avoided the bottom of the sea floor, perhaps because of sand and shale movement (Table 4.14).

The hypothesis that there is a positive correlation between the complexity of boulder habitat and the recovery (and therefore potential survival) of seeded juvenile abalone has been accepted with reservation (Figure 1.4). The non-significant negative correlation between exposed area and recovery of juvenile abalone at McDougall's Bay, Stilbaai and Gouriqua indicates that shelter is important to the recovery of seeded juveniles; and although it is difficult to draw clear conclusions about the

specific size of boulder that will provide optimum habitat, there appears evidence that boulders can provide adequate shelter for some seeded juvenile abalone. If under-boulder habitat is important to juvenile abalone (Shepherd 1972, Shepherd & Turner 1985, Tegner & Butler 1985, McShane 1991, Schiel 1993, Shepherd 2000) then experiments that are designed to determine urchin-utilization and seeding-size effects, must be done under standardized environmental and physical conditions in order for comparisons to be made. In summary, Hypothesis 3 (Figure 1.4) is supported by several lines of evidence derived from the experiments at three different sites.

Hypothesis 2. There is a significant positive correlation between the density of urchins and seeded juvenile abalone.

The relationship between seeded juvenile abalone and urchins must be seen in the context of the following:

1. The density of urchins at the seeding sites.
2. The abundance of suitable habitat at the seeding sites. Habitat that can provide juvenile abalone with shelter, under boulders, in cracks and crevices would be selected as suitable seeding habitat according to the criteria that were established in the introduction and in the chapters that followed.
3. The ability of the seeded abalone to utilize alternative habitat enabling them to survive both predation and rough sea conditions.

The urchin exclusion experiments showed that the recovery rate of abalone at seeding sites where all the urchins had been removed did not differ significantly from data for sites at which the urchins were not removed (Figure 4.3). Initially this seems to contradict entirely the findings by many authors (e.g. Kojima 1981, Tarr et al. 1996, Day 1998, Rogers-Bennet and Pearse 1998, Day & Branch 2000b, Day & Branch in press, Scott et al. in prep.) who have suggested that urchins are important to the survival of juveniles of some species of abalone. Furthermore, the correlation analyses from the other McDougall's Bay experiments (Tables 4.7a, b, c), and the selectivity indices analyses from both the urchin exclusion experiments and the other McDougall's Bay experiments (Tables 4.12, 4.13), showed a positive selection by seeded abalone for urchins. This also seems to contradict the result of the urchin exclusion experiments done in McDougall's Bay, and enforces the findings of Day and Branch (2000b, in press). However, if abalone are surviving when they cannot utilize urchins, it means that either they are big enough to be able to live without protection (which is not the case here), or there is adequate alternative habitat for them to utilize. The selectivity analyses and the correlation analyses for the McDougall's Bay experiments show that there is a positive relationship between urchin density and abalone recovery, and that there seems to be a positive selection by abalone for urchins. However, densities of urchins in the bay are relatively low. The urchin densities reported by Day and Branch (in press) in the south-western Cape span 28–55 m⁻², much higher than those recorded in the Kleinsee to Koningnaas, McDougall's Bay and Gouriqua experimental areas (0–12 urchins m⁻²). Also, the experiments by Day and Branch (in press) were done in areas where the percentage cover of habitat that could be considered suitable for juvenile abalone, was on average 25%. This included under-boulder habitat, cracks and crevices. In contrast, the

McDougall's Bay and Gouriqua experiments were done in areas where the suitable habitat was estimated at 50%, and the amount of exposed area offering no shelter was <20% (Tables 4.1, 4.2, 4.3). The preliminary experiments done at Kleinsee to Koningnaas (see Chapter 2) were done in areas where the average percentage cover of shelter was intermediate, 33% (Table 2.2). Based on the findings in this series of experiments, and the comparison made between the current data and those from Day and Branch (in press), it could be suggested that poor site selection was responsible for low recovery rates in the initial experiments, since a definite relationship between the utilization of urchins and the utilization of other suitable habitat has been otherwise indicated. When suitable seeding sites provide physical shelter, the utilization of urchins seems not as important as it is in areas where very little suitable habitat exists.

The relationship between abalone size and urchin utilization remains unclear. The experiments by Day and Branch (2000a, b, in press) have shown that both abalone recruits (<3 mm) and juveniles (3–35 mm) utilize urchins for shelter. In the experiments done at McDougall's Bay there was little evidence of a difference in utilization or selectivity between the two abalone size classes examined (~15 mm and ~25 mm). However, in later experiments with 45-mm abalone the abalone were cryptic in their behaviour with none of them utilizing urchins for refuge. Again, these experiments were done in areas where urchin densities were low (8.2 urchins m⁻², SD ±1.66), and the average size of the abalone was greater than animals used in the experiments done by Day and Branch (in press). The recovery rates shown in Figure 4.4 reflect the impact that seeding under rough sea conditions has on recovery rates. The effect of rough water and strong currents was stronger than that of either the

presence of urchins or the time elapsed between seeding and sampling. This emphasizes the point that even if the habitat is selected as suitable, the physical conditions under which seeding takes place are of paramount importance.

The experiments at Gouriqua showed a significant negative association between recovery of seeded abalone and the abundance of urchins (Tables 4.8a, b, c). Although this may be a result of low recovery rates or the size of the data set, the relatively low urchin density in the Gouriqua area may have contributed to the result. Low urchin density seems to be the norm in shallow Eastern Cape subtidal areas (B. Godfrey, Rhodes University, pers. comm.). In unpublished surveys done in Cape Recife there was little evidence of any relationship between urchins and both natural and seeded *H. midae* juveniles (B. Godfrey, Rhodes University, pers. comm.).

Apart from providing shelter, urchins trap drift kelp (Day & Branch, in press). If juvenile abalone live beneath urchins they may benefit from this source of food as well as finding protection. This is abundantly clear when observing the masses of drift kelp trapped on urchins. However, within the context of seeding sites, the advantage of the shelter provided by urchins, for abalone greater than 14-mm in size, becomes negligible. Approximately 8% of seeded animals utilized urchins for cover in the McDougall's Bay experiments. The experiments done at Gouriqua showed approximately 0.5% of the seeded abalone utilized urchins, and none of the naturally occurring juvenile abalone were seen utilizing urchins as cover. The presence of sea cucumbers and sea urchins may indicate potential habitat for juvenile abalone, but their absence does not necessarily indicate lack of abalone habitat.

The experiments did not investigate abalone larvae or juvenile abalone smaller than those used in the seeding experiments, nor their relationships with encrusting coralline algae or urchins. It is quite possible that urchins play a vital role in the successful survival of these earlier stages. The lifecycle stage at which juvenile abalone are seeded plays an important role in determining which other species will be needed to facilitate survival. With respect to selecting seeding sites for ranching, the presence of urchins has been shown to be insignificant. The link between long-term recovery rates of artificially reared juvenile abalone and the presence of urchins still needs to be quantified. Whether or not a habitat of layered boulders removes any long-term requirements that abalone might have for urchins, still needs to be established. The hypothesis that urchins have a positive effect on the survival of seeded abalone has been rejected, at least within the context of areas where there is an abundance of suitable under-boulder habitat.

Results from the McDougall's Bay experiments show that there was a significant negative association between exposed habitat and urchin densities (Table 4.7a). Results from the Gouriqua experiments, however, showed a positive relationship between urchin density and habitat comprising boulders with a diameter of less than 30 cm in diameter (Table 4.8a). In the case of Stilbaai, there was a significant negative association between urchin density and boulders <30–50 cm (Table 4.9). As stated above, the urchin densities in these experimental areas, as well the Kleinsee-Koingnaas coastal area were relatively lower than those in the south-western Cape areas where Day and Branch (in press) did their work. Day (1998) showed that urchin density was highest in cracks and crevices, as opposed to on flat and vertical rock faces. Table 4.14 shows that 38% of all abalone utilizing urchins in the

Namaqualand experiments were found on vertical surfaces, and 45% were found under boulders, indicating that urchins and abalone utilize the same habitat. Good abalone habitat is also good urchin habitat and visa versa. In areas where there is an abundance of urchins it is quite possible that abalone will also be able to utilize the urchins as a habitat, but this is not necessarily the case. (The small data sets from Stilbaai and Gouriqua may have influenced the results). The relationships between urchins and sea cucumbers, and between abalone and sea cucumbers, were found to be non-significant in the Gouriqua area. Between urchins and abalone the relationship was significantly negatively correlated (Table 4.8a). There is no doubt that under-boulder habitat is good sea cucumber habitat, but no quantifiable relationship between sea cucumbers and either urchins or abalone could be found. The process of natural recruitment would play a key role in the abundance of each of these species. Recruitment failure of one species in an area over a specific period will mean that no animals of a specific age will be found until a new cohort has recruited successfully. The absence of quantifiable relationships between different species must be viewed in this context. Sea cucumbers may indeed inhabit areas that are suitable for either abalone or urchins, but a quantifiable relationship can be detected only if both species are present in sufficient numbers at the same time. Both urchins and sea cucumbers may still be viewed as indicators of suitable habitat for juvenile abalone, even if their numbers are not correlated.

Hypothesis 5. There is significant positive correlation between increased seeding size and the survival of seeded juvenile abalone.

The relationship between seeding size and potential short-term recovery rate seems clear with respect to the McDougall's Bay experiments (Figure 4.6). Although correlations were not significant in the Stilbaai experiments or the Gouriqua experiments (Figures 4.7 and 4.8), there appears to be overall justification to accept the hypothesis. (Again this must be seen within the context of seeding abalone in suitable sites.) A range of factors that are not consistent with the Namaqualand experiments, including seeding depth and exposure to direct wave action, have likely influenced the Gouriqua results. Consequently, these factors may have influenced the recovery rate by affecting dispersal, which may have in turn changed the ease with which the abalone could be detected. The topic of dispersal and the interpretation of recovery data are discussed in Chapter 5.

The recovery rate for 45-mm abalone seeded in McDougall's Bay were very high (Tables 4.15 and 4.16). This enforces the positive correlation between seeding size and recovery and survival rates. In this case it was clear that dispersal was insignificant and, thus, it is possible to equate recovery rates with survival rates.

The initial expectation that the smaller abalone would exhibit stronger selection for urchins than would bigger abalone, was not quantified (Table 4.13). It may be that smaller abalone have a greater need for protection than larger abalone, and this could be reflected in their association with urchins. It could also be reflected, however, in

their association with under-boulder habitat. The scale of the experiment was not fine enough to draw conclusions regarding either aspect of habitat utilization.

Observations of the release modules in McDougall's Bay verified the ease with which smaller animals were washed into the water column when boulders were disturbed. Many abalone simply released themselves without being touched by divers. Several of the sites showed up to 60% losses within one week. Initial mortalities were high and may account for a large proportion of total mortality (Tegner & Butler 1985, Olla & Davis 1998, Shepherd et al. 2000, Tegner 2000). It seems that mortalities in smaller seeded animals may be caused by an inability to handle strong water currents and disturbances. Naturally occurring juvenile abalone have also been seen to release themselves when they have been disturbed (Rob Tarr, MCM, pers. comm.), but this is no longer true when the animals become larger. Farm-reared animals do not need to develop the ability to withstand strong currents while they are in hatchery tanks, and animals may need time to adjust to water movements after being placed into the sea (Olla & Davis 1998). The larger animals used in the experiments showed a completely different response while sampled. They seemed more resilient to being disturbed and, in some cases, removing them caused shell damage because they were lodged so securely. Increasing seeding size and both the muscle and shell strength of the juveniles may decrease the time taken by the juveniles to adapt to their new environment after seeding (Munro & Bell 1997, Olla & Davis 1998, Shepherd et al. 2000). There is clear evidence that hatchery-raised abalone suffer elevated mortalities for many months after seeding because they lack the appropriate behavioural responses to predators (Olla & Davis 1998). However, this is reflected in a range of seeding sizes and has not been linked to seeding size (Shepherd 2000). Although there

is some discrepancy regarding the effect of size on recovery rates of seeded *Haliotis rufescens* and *H. fulgens* from the USA (Tegner 2000), the results with *H. midae* in the case of the McDougall's Bay experiments concur with the findings of both Japanese and Australian researchers. Japanese research indicated best results from seeding with a minimum size of 30 mm, combined with the correct choice of refuge or seeding site for *H. discus* (Munro & Bell 1997, Masuda & Tsukamoto 1998). Australian research has shown that both abalone size and abundance of predators play an important role in the recovery rate of seeded *Haliotis* spp. (Shepherd 1998). There was also an indication that size influences recovery in experiments with *H. midae* done by Sweijd et al. (1998). In that work, two batches of different-sized animals were placed at the same site at two different times. Over a six-month period the larger, 14-mm animals, showed a 39.2% recovery rate, compared to a 27.8% recovery rate for 8-mm animals. Interpreting this result is difficult because the release modules were set down at different times, so that environmental conditions may have differed, but the result does support the hypothesis that seeding-size affects recovery.

The relationship between abalone seeding size and recovery rate is, however, not a simple one. Both muscle strength and shell thickness increase with increasing size; both factors can affect survival after seeding. Seeding is a traumatic event, usually incurring high initial mortality. In the case of *H. midae*, it may be possible to address this through correct site selection and selection of appropriately sized animals. The transition from short-term recovery rate to long-term recovery rate and growth needs to be investigated. While there is ample evidence that size plays a role in recovery rates, there are few data to show whether or not significant differences in habitat utilization occur among different-sized abalone, or why size sometimes appears to

play such an important role in their recovery. If survival is determined by habitat, then an optimum habitat can be identified for smaller abalone, and under the right environmental conditions seeding even small abalone may result in relatively high survival rates. If, on the other hand, survival is determined by other factors that are age- or size-related and habitat selection is only of secondary importance, then seeding below some threshold size will yield consistently low recoveries. If there is such a threshold size, experiments to determine it will have to be done in very controlled conditions. Treatments would need to be replicated under conditions where all environmental factors are constant, and in which the stock of juveniles would have to be of comparable quality.

The fact that the sites used for 45-mm animals yielded such high recovery rates and such low dispersal patterns, indicated a potentially high survival rate for animals seeded at this size class in this particular habitat. The fact that the larger animals did not move away from the specific habitat also indicates that the habitat suited these relatively large individuals. The natural adults found at Gouriqua occurred in the same size class and were found in the same habitat. It should be noted, however, that in the wild, adult *H. midae* occur at depths of up to 30 m (Tarr 1995), and they can move extensively. The results of the present experiment merely suggest that suitable juvenile habitat can also suit larger animals. Ample anecdotal and observational evidence indicates that adults are often found in very shallow water in the inter-tidal zone (B. Godfrey, Rhodes University, pers. comm.).

Ranking potential seeding sites

In ranking factors that play the most important role in optimising recovery rates for seeded juvenile abalone along the Namaqualand coast, the most important appears to be site selection. While the relationship between boulder size and under-boulder habitat may not be expressed as a clear linear relationship, it seems boulder habitat is crucial. The most common feature of the sites selected for the McDougall's Bay and Gouriqua experiments was a low percentage cover of exposed area. In these areas the exposed habitat was approximately 11% and 8% respectively, whereas the average exposed area for the Kleinzee-Koingnaas experiments was 21.5%. The relatively small amounts of sheltered habitat were also reflected in the highly variable recovery rates from the initial experiments described in Chapter 2. The relationship between dispersal and recovery and the impact of high-energy surf action on seeded juveniles needs to be further investigated; in this context, the experiments at Gouriqua are interpreted and regarded as preliminary. One of the aspects that most needs to be addressed is that of seeding density relative to the density of juvenile densities that eventually move into natural habitat. There is evidence from the experiments at Gouriqua experiments that the density of surviving juveniles is related to exposure and depth. The detection of surviving juveniles in turn is related to dispersal.

Given suitable habitat, seeding size will, to a large extent, determine potential recovery and survival rates. The seeding experiments at McDougall's Bay and Stilbaai (Tables 4.4, 4.6) showed that season had little impact on recovery rates. More important was the effect of sea conditions during and after seeding. Because the aim was to optimise survival, and considering the high cost of producing abalone, seeding

during bad sea conditions was avoided. When comparing the Stilbaai sites and the results of the seeding experiments there it is important to note that the percentage of exposed habitat exceeded 20%. Stilbaai is more exposed to wave action than were the McDougall's Bay sites. This is reflected in the average survival rates for both size classes of abalone used in the experiments. At McDougall's Bay the average recovery rate for the 14-mm abalone was 21% and 55% for the 26-mm abalone; in Stilbaai the recovery rates were 16% and 39%, respectively. The data sets for Stilbaai were small, and the sampling period was 120 days, as compared to 30 and 60 days at McDougall's Bay. While the degree of exposure to wave action was not quantified, the sites at Stilbaai are not protected by an outside reef as are the sites at McDougall's Bay. The most sheltered site in the Kleinzee-Koingnaas experiments was Site 7 (Table 2.2); it lay behind a small section of reef that protected it from all but the most extreme seas. Recovery rate from this site was high. Sampling period will play a role in recovery rates: the longer abalone are in the sea, the greater the chance that they can be preyed upon, or that some other environmental factor will come into play to reduce survival and recovery. However, the experiments which compared sampling after 30 days or 60 days showed that given similar and suitable habitat, period to sampling had no significant effect on recovery rate. This was most apparent in data for the urchin exclusion experiments at McDougall's Bay (Figure 4.4), where differences in recovery between two sampling periods were probably attributable to differences in sea conditions at the time of seeding. Whereas evidence from the other experimental areas may be circumstantial, the results from the urchin exclusion experiment (Figure 4.4) show negative effects from seeding in unfavourable sea conditions.

Site selection, seeding size and sea conditions are the most important factors that need to be addressed by a potential ranching operation. Although it was outside the scope of this thesis to measure the effect of predation or the densities of predators, predation must be considered in context. If suitable habitat is a measure of providing cover and shelter against predation, then the abundance and quality of suitable habitat must be a central issue when considering sites for seeding (Shepherd 1990). It is evident from the experiments thus far that site selection is the prime variable in determining the degree of abalone recovery. Other variables must be measured against this criterion. Whether the differences in recovery rate between localities are a reflection of differences in the intensity of predation or a measure of habitat suitability is not yet certain (Shepherd 1990). Placing abalone in unsuitable habitat forces them to move and face exposure. The extent to which they must re-locate will be reflected in mortality due to predation. Again, dispersal will be site-related. High dispersal may reduce the detection of surviving seeded abalone, biasing the relationship between recovery and survival. Measuring dispersal is therefore important, and is addressed in the following chapter.

CHAPTER 5.

INVESTIGATING DISPERSAL

5.1 INTRODUCTION

In interpreting of data with respect to abalone recovery rates, the existence of dispersal patterns and potential survival have been contentious issues since the beginning of work on abalone seeding (Rogers-Bennet & Pearce 1998, Shepherd et al. 2000). The relationship between recovery rate and survival is directly related to dispersal and density. The relatively high recovery rates recorded in the first experiments done along the Namaqualand coast were extrapolated as minimum survival rates (Sweijd et al. 1998). The relatively low recovery rates from the initial experiments undertaken in the present study caused concern about the reliability of recovery data and the extent to which dispersal had taken place. If dispersal is the reason for low recovery rates, it should be possible to show that dispersal has taken place. Of course, low recovery rates cannot be interpreted as proof of high dispersal rates without evidence. The initial experiments (Chapter 2) yielded low recovery rates and limited evidence of dispersal; most of the recovered animals were found inside the release modules or within a few meters of them. Later experiments at McDougall's Bay yielded higher recovery rates and limited evidence of dispersal. Finally, the experiments at Gouriqua, in turn, yielded relatively low recovery rates but evidence of high dispersal patterns. Thus, was there a difference in dispersal between the different experimental areas? If dispersal of seeded animals at various sites occurs, can recovery rates be used to indicate survival rates with any degree of confidence? To determine this, the specific hypothesis that there was a significant difference in

abalone dispersal between the Gouriqua and the McDougall's Bay sites was tested (Hypothesis 6, Figure 1.4).

5.2 METHODS

5.2.1 Dispersal patterns

From all the McDougall's Bay experiments, and the Gouriqua experiments using animals between 10–30 mm, the dispersal distance for each of the recovered abalone were recorded (Chapter 4). Dispersal distance was recorded for all the abalone that were found. At all sites, exhaustive destructive searches were done in concentric circles until no more abalone were found. Data for all three size classes (45-mm, 26-mm and 14-mm) seeded at McDougall's Bay were compared separately, and then the two smaller size classes from both the Gouriqua and McDougall's Bay were compared to each other (Table 5.1). A Chi² analysis (Everitt 1977) was performed on the data in which all distances >2 m were combined. The adjusted residuals for the contingency tables were recorded for analysis and interpretation (Table 5.1).

5.2.2 Site attributes

The goal of the analysis was to determine if there was any significant difference in dispersal between the two sites, and, if so, to attempt to explain it. The Gouriqua sites were in shallow water (≤ 1 m), and exposed to direct wave action, in contrast to the McDougall's Bay sites which were in relatively deeper, calmer water (≤ 4 m). The effect of depth, in itself, may be highly significant, although unquantified. To

Table 5.1 Chi² analysis and adjusted residuals analyses of dispersal data from McDougall's Bay and Gouriqua; a) shows the results of comparing three size classes of abalone at McDougall's Bay (Chi² from complete set = 5.9, df = 4, $p < 0.21$) and b) shows the results of comparing two size classes at McDougall's Bay and at Gouriqua (Chi² from complete set = 168.5, df = 6, $p < 0.0001$). Absolute adjusted residuals (Adj. res.) are significant if ≥ 1.96 at $p = 0.05$ for both sets of analyses. (The expected frequencies = (row total * column total) / grand total).

Site			1 m	2 m	3 m
a) Three size classes at McDougall's Bay					
McDougal's Bay	45 mm	Observed	139	24	5
		Expected	139.8	25.3	2.9
		Adj. res.	-0.2	-0.3	1.3
	25 mm	Observed	539	87	11
		Expected	530	95.8	11.2
		Adj. res.	1.5	-1.5	-0.1
	14 mm	Observed	224	52	3
		Expected	232.2	42	4.9
		Adj. res.	-1.5	2.0	-1.0
b) Smaller size classes from both Gouriqua and McDougall's Bay					
McDougall's Bay	25 mm	Observed	539	87	11
		Expected	507.0	112.0	17.9
		Adj. res.	5.2	-4.3	-2.8
	14 mm	Observed	224	52	3
		Expected	222.1	49.1	7.9
		Adj. res.	0.3	0.5	-2.1
Gouriqua	25 mm	Observed	13	17	12
		Expected	33.4	7.4	1.2
		Adj. res.	-8.0	4.0	10.3
	14 mm	Observed	16	19	2
		Expected	29.5	6.5	1.0
		Adj. res.	-5.6	5.5	1.0

determine if there were other significant differences in the physical structure of the seeding sites a Mann-Whitney U Test was used to compare the average percentage abundance of each of the categories of boulder size described in Chapters 2 and 4 (for a listing see Table 5.2).

5.3 RESULTS

At both Gouriqua and McDougall's Bay, no seeded animals were recovered >5m away from the seeding modules. At McDougall's Bay, by far the majority of seeded juveniles in both size classes were recovered <1 m from the seeding module; at Gouriqua they were found to be more evenly dispersed over a larger area (Table 5.1).

5.3.1 Dispersal patterns in McDougall's Bay

Pooling the distances that abalone moved into 1-m intervals and applying a Chi² analysis (Table 5.1), yielded a non-significant difference between observed and expected frequencies for the three different size classes of abalone seeded in McDougall's Bay. The adjusted residual analyses also yielded non-significant results for all groups except one size class: 14-mm abalone were significantly over-represented in the 2-m distance interval (Table 5.1). The results of the test show that this may be due to random effects. Within the context of a similar seeding environment, for these size classes (45-mm, 25-mm and 14-mm), there is no indication that dispersal of seeded abalone will be affected by seeding size.

Table 5.2 Physical attributes of the general seeding sites. A Mann-Whitney U Test showed no significant difference between the superficial physical appearance of the two general experimental sites with respect to boulder size and exposed areas, except for boulders <30 cm in diameter. An asterisk indicates significance at $p \leq 0.05$.

Site attributes (boulder diameter)	Namaqualand experimental area % cover	Gouriqua experimental area % cover	<i>p</i> -value
> 50 cm	42.39	35.00	0.46
30 - 50 cm	25.43	26.88	0.33
< 30 cm	15.54	25.00	0.047 *
Exposed area	16.63	11.88	0.11
Depth (m)	2	0.625	

5.3.2 Dispersal patterns in McDougall's Bay as compared to those found at Gouriqua

Data for the two smaller size classes of seeded abalone from both Gouriqua and McDougall's Bay, yielded highly significant departures from expected frequencies ($\text{Chi}^2 = 168.5$, $p = 0.0001$, Table 5.1). More interesting were the results shown by analysis of the adjusted residuals, a positive value indicating a higher actual value than expected and a negative value indicating a lower than expected value (Table 5.2b). In the McDougall's Bay experiments the analyses showed positive values within the first distance interval (1 m from the release module) for the 25-mm abalone, and significant negative values for the 2- and 3-m intervals. Whereas the 14-mm abalone showed more signs of dispersal (non-significant), they were significantly under-represented in the 3-m distance interval. The Gouriqua abalone of both size classes were significantly under-represented in the 1-m interval, and significantly over-represented in the 2-m interval. For the 25-mm abalone this was also the case in the 3-m distance interval. All the Gouriqua data showed a significantly lower concentration of abalone around the release module than expected and higher than expected numbers further than 1 m from the module, indicating a definite pattern of dispersal.

There seemed to be little difference in dispersal pattern between the different size classes of abalone at Gouriqua, as most of the values being significant at $p = 0.05$.

5.3.3 Site attributes

The percentage cover of boulders of differing diameter and amount of exposed area showed a significant difference between the two areas in the percentage cover of boulders <30 cm, with the habitat at Gouriqua comprising 25% boulders <30 cm, and the Namaqualand area 15% (Table 5.2). In addition, two definite differences in terms of physical description were depth (relatively shallow at Gouriqua) and surf impact (the Gouriqua experiments were carried out in the surf zone).

5.4 DISCUSSION

A number of factors can influence recovery rates of seeded juvenile abalone. One is the complexity of the substratum, and another is dispersal. The concept of dispersal and its potential effect on recovery and survival are addressed in the discussion, but not the complexity of the substratum to the extent that it may affect recovery rate. Obviously a complex substratum full of cracks and crevices may yield a low recovery rate even though the abalone may still survive in the seeding area. There are conflicting reports on the conditions for dispersal of both juvenile and adult experimental abalone (Tegner & Butler 1985, Tegner 2000). Perhaps dispersal is site-specific and affected by a range of factors that include habitat, the condition of the abalone before and after handling and the general seeding environment, for example water depth and sea conditions. Tegner and Butler (1985) found clear evidence of dispersal among seeded juveniles to well beyond the experimental site. Surveys that yield positive results with respect to evidence of dispersal as well as a range of recovery rates, as opposed to experiments in which recovery rates are

recorded with no evidence of either dispersal or lack of dispersal, allow for more valid equations to be constructed between recovery rates and potential survival. When exhaustive destructive sampling yielded no more juvenile abalone during experiments in this study, it was assumed that the abalone had not dispersed, but that they had died. This assumption was made because no evidence could be found of active dispersal over time in the Port Nolloth experiments. The Gouriqua experiments, however, yielded evidence of active dispersal.

Considering that the data sets were small, especially for Gouriqua, where recovery rate was relatively lower than at McDougall's Bay, the hypothesis that a significant difference existed between Gouriqua and McDougall's Bay with respect to dispersal of seeded juvenile abalone was accepted (Hypothesis 6, Figure 1.4). This considers the likelihood of fine-scale variation in physical topography among the sites in and between the different experimental areas (Branch et al. 1987). The extent of dispersal and density at the time of recovery will be directly related to the concentrations in which animals were seeded, and ultimately to their survival rate. Dependant on available habitat, seeding concentrations coupled with a range of survival rates require varying degrees of dispersal to accommodate the seeded abalone in terms of space (Shepherd 1990). To evaluate the potential survival rate of seeded abalone from recovery rate, it is necessary to know to what extent dispersal has taken place. If all the seeded animals can be located, recovery and survival are equal. If recovery is low and evidence suggests that dispersal has not taken place, survival can be interpreted to be low. However, if recovery is low and there is evidence that dispersal has taken place, it could be suggested that survival rates were higher than recovery rates because high dispersal may lead to a diver not recovering all the surviving abalone.

The evidence suggests that dispersal was low in McDougall's Bay, for animals of all seeded sizes. This may indicate that site selection was good, and the animals did not have to move (Shepherd 1990). In the preliminary Kleinzee-Koingnaas sites recovery rates were low, and repetitive exhaustive searches yielded no abalone or evidence of dispersal. This suggests that low recovery rates indicated low survival rates. Whether this was as a result of inferior site selection, or adverse environmental conditions at the time of seeding, cannot be inferred from the data. However, the data from Gouriqua showed consistently low recovery rates (Chapter 4), and consistent patterns of dispersal. Some form of dispersal had taken place at Gouriqua; in that case, low recovery rates did not necessarily mean low survival rates.

Dispersal patterns at Gouriqua were different to observations at McDougall's Bay and the other Namaqualand sites. The Gouriqua experiments were all conducted in shallow water, with most of the release modules set in <1 m of water at low tide, and exposed at spring low tide. The inter-tidal gradient there dropped an average of 1 m over a distance of 20 m out to sea. Thus, the gradient was low and the release modules were in the zone in which wave action was greatest. The McDougall's Bay and other Namaqualand sites were in deeper water. The McDougall's Bay experiments were conducted in an area where the gradient was also very low, but water depth was 1–4 m. The experiments were protected from direct wave action; strong currents and adverse sea conditions could enter the bay, but only the most severe swells resulted in direct wave action inside the bay.

If habitat is as important as the results of the study indicate, it is reasonable to assume it is because the actual physical habitat (e.g. boulders) play a part in providing protection against both predation and adverse environmental factors (Shepherd 1990). Table 5.2 shows the difference in the abundance of boulders <30 cm in diameter between the Gouriqua area (25%) and at Namaqualand (15%). There was a significant positive correlation between the recovery rates of juveniles in the McDougal's Bay area and the abundance of boulders this size (Tables 4.7a, b). Conversely, in the Gouriqua area there was a negative correlation (non-significant) between recovery and boulders <30 cm (Tables 4. 8a, b, c). Table 4.11 shows that there was positive selection by both size classes of juvenile abalone for boulders <30 cm, and the same was shown for the smaller (15-mm) size class of abalone at McDougall's Bay, whereas the larger (26-mm) abalone from McDougal's Bay showed the strongest selection for boulders 30–50 cm in diameter.

Aspects of the results seem to be in direct contrast with each other. However, when seen in the context of both what recovery rate actually means and given evidence of dispersal, the results are less contradicting. Juvenile abalone from both experimental areas were shown to be actively selecting small boulders; this may be only because small boulders provide under-boulder habitat that may not be provided by larger boulders at that specific site. Recovery rate does not necessarily indicate the long-term suitability of a site, unless the recovery rate is established over a long-term period. The fact that the abalone at Gouriqua showed evidence of dispersal while at the same time showing active selection for the small boulders, may be a reflection of density-dependent factors that are influenced by both depth and wave or surf action, among other factors. Dispersal may have been a product of abalone moving to place

themselves in better sites within the small-boulder habitat, to optimize site utilization, and to decrease initial seeding density. No measurement was made of dispersal direction; however, dispersal appeared random, with movement taking place in all directions. There were no indications that the juveniles were moving, for example, to deeper water. Wild juveniles were also found in very shallow water, utilizing small boulders. In the case of Gouriqua, it appears that dispersal may have taken place to optimize density, and not necessarily to acquire better habitat. (On a small scale this is the same as dispersal to optimize habitat, if the description of habitat suitability includes food availability relative to conspecific densities.) Stocking density and seeding density relate directly, not only to physical habitat, but also to the availability of food, in which respect the two areas are vastly different (Introduction, Baird et al. 1986, Sweijd et al. 1998). The low numbers of naturally occurring abalone, juvenile and adult, may be an indication that food is limiting at Gouriqua and, as a result, dispersal of the experimental animals would have been essential for survival. The same seeding density was used in the McDougal's Bay and Stilbaai experiments, but in both these cases dispersal was not evident. In summary, reliable interpretation of recovery data requires, at the very least, knowledge of available habitat, food availability and patterns of dispersal of seeded abalone.

CHAPTER 6.

QUANTIFYING THE DYNAMICS AND THE ECONOMICS OF SEEDED ABALONE POPULATIONS

6.1 INTRODUCTION

The overall goal of the study have been to investigate the factors that may influence potential abalone ranching in areas along the South African coast where no natural stocks exist, and to determine the optimal size at which abalone should be seeded (assuming that size limitations at harvesting are market driven and not limited by law). The target set for potential ranching, as recommended by Port Nolloth Sea Farms management, was to harvest abalone once they reached a mass of 300-g. The viability of a seeding operation is influenced by the financial tradeoff between the cost of raising juveniles to a specific size and the benefits derived from the differential survival rates of seeded populations in different areas. To factor ecological parameters and economic parameters of importance into a cost-benefit analysis, a simple spreadsheet model was developed using population number and biomass calculations for a single cohort of abalone over a period of 10 years (Fielding 1995, Jennings et al. 2001). Contemporary population dynamics equations and the structure of a standard yield-per-recruit model were utilized. The effect of fishing was excluded because no natural stocks of abalone occur in the area being considered for ranching; as a result actual yield-per-recruit was not calculated. Mortality was also not assumed to be constant for all age classes in the model. Harvesting was modelled to take place at an age when the abalone had reached a mass of 300-g, and it was assumed that all abalone in that cohort would be available for removal. In the model, the number

seeded determined initial population number, and no natural recruitment was incorporated. It is possible that seeded abalone may become reproductively active if they are not harvested before they reach sexual maturity and if environmental conditions are favourable. However, there is no evidence to support this possibility on the Namaqualand coast. Although the possibility was not factored into the simulations done in this chapter, potential for natural recruitment is not disregarded. If natural recruitment should ever take place, it will mean reduced seeding can maintain consistent yield, reducing input-costs. However, the possibility of natural recruitment in the future, does not affect present input-costs. Mortality was the driving force in the model; an estimate of mortality was derived from considering initial seeding-induced mortality and longer-term differential mortality. Long-term differential mortality incorporates all aspects of natural mortality. The effect of predation and other density-dependent factors are not modeled separately, since it was assumed that these factors were reflected in the differential survival rates used in the model. The model was created according to the premise that seeding operations would only take place in areas containing suitable habitat for juvenile abalone. Experimental data from Chapter 4 were used to develop the model.

This chapter is divided into two parts: 6A deals with the population dynamics of seeded populations of *H. midae*, and 6B with the economics of seeded populations, based on the parameters derived in part 6A.

The specific hypothesis tested in section 6A (Hypothesis 7, Figure 1.4), states that within the context of suitable seeding sites, seeding-induced mortality plays a greater role in determining population survival than age-specific differential mortality; and,

as a result, increased seeding size will increase long-term survival by reducing total mortality. In other words, increasing seeding size in a specific seeding site will result in a decrease in total mortality (Z). As a corollary to this hypothesis, the maximal economic returns relative to size at seeding were modelled in section 6B.

Even though accurate differential mortality data are not available for ranched *H. midae* at present, commercial seeding experiments are taking place in South Africa. The ability to explore ecological limitations in terms of population survival may assist the decision-making process and minimize unnecessary risk.

6A1. QUANTIFYING THE DYNAMICS OF SEEDED POPULATIONS

Following a literature search and consultation with research scientists (C. Moloney, MCM, pers.comm.), a simple spreadsheet model was developed to consolidate biological data collected from current seeding experiments and research on wild abalone species (Schiel 1993, Fielding 1995, Heppel & Crowder 1998, Hilborn 1998, Wilson et al. 1998, Jennings et al. 2001).

Broadcast spawners, such as abalone, produce large numbers of juveniles relative to those that ultimately survive to adulthood; differential survival in such species is accepted as represented by a curve that follows the general shape of curve B in Figure 6.1. The curve depicts a trend in which survival per age class at first increases with age, then reaches a plateau as the animals mature, and finally begins to decrease as senescence takes effect (Shepherd & Johnson 1991, McNamarra & Johnson 1995, Ebert 1999). Although differential survival data are available for some species of

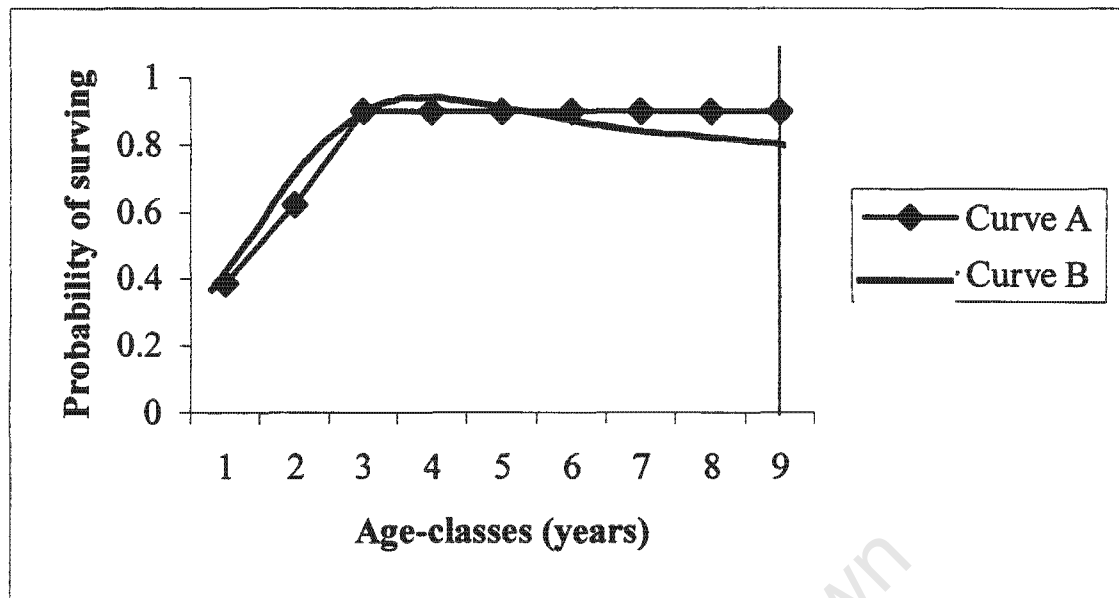


Figure 6.1 Graph showing the general shape of the differential survival curve (Curve A) produced by the model (see Figure 6.4) to represent survival of a cohort of abalone over time. Curve B is a hypothetical curve that generally describes an increasing probability of surviving to the next cohort, a plateau is reached before senescence begins to set in. Given the growth parameters used in this model, harvesting could take place before the age of 10 years, and senescence was not considered to be a factor at this age (Tarr 1993, 1995).

abalone (Shepherd & Johnson 1991, Masuda & Tsukamoto 1998), at present, data are not available for *H. midae*. Because differential survival is age-, and hence, size-related, growth rate plays an integral part in mortality, influencing the rate at which an abalone reaches a larger size class, and the rate at which population biomass increases. There are limited data available about growth of seeded *H. midae* populations in South Africa (Sweijd et al. 1998), but growth rate has been documented for a number of natural populations (Tarr 1993, 1995). These growth rates have been applied to the prediction of rates of return in the economic section of this chapter.

Age-specific differential mortality and survival (DS) and seeding-induced mortality and survival (IS) were handled separately. Results of the experiments in Chapters 3 and 4 suggested that the seeding process results in substantial immediate mortality that is a direct result of the seeding process. Seeding-induced mortality, either due to handling stress or the rate at which behavioural adaptation takes place to accommodate natural environmental factors, is size- and age-related (Chapter 4, Tegner & Butler 1985, Schiel 1993, Tarr 1995, Sweijd et al. 1998, Shepherd et al. 2000, Tegner 2000).

Under natural circumstances, annual recruitment and differential mortality determine population size at any given time. Annual recruitment provides a population's initial age class every year and differential mortality acts on the population as a whole. In a seeded population of abalone, there is no natural annual recruitment. The seeding number provides the recruits, while seeding-induced mortality and the natural process of differential mortality then act upon the seed. Seeding-induced mortality can be

reduced by improving handling techniques and site selection, and increasing size at release. However, the environmental factors that have a more long-term effect on the differential mortality rates in a population generally lie outside the scope of human influence, except that sites can be chosen to minimize adverse factors. These are also the factors about which the fewest data exist. When determining total mortality, the impact of initial mortality and differential mortality can be separated from each other to some extent—for example by changing the length of the period between seeding and sampling. The shorter the period between release of seed and sampling, the more influential the effects of seeding-induced mortality appear. The longer the period between seeding and sampling, the stronger the effect of long-term differential mortality rates.

6A.2 METHODS

6A.2.1 Description of the model

The survival of individuals over time can be modeled in a variety of ways. One is to use a decaying exponential equation with one parameter (Sparre & Venema 1992, Shepherd & Johnson 1991, Fielding 1995, Ebert 1999, Jennings et al. 2001). In this work, such a deterministic, age-structured model was developed which could generate a range of differential survival scenarios and a range of average Z values (Ebert 1999). According to this model population number every year is determined by a Z value calculated by the probability of an abalone surviving that year. As the abalone gets older that probability value can either stay constant, or it can increase by a factor that has been predetermined (Table 6.1, Formula 2), with the proportional increase in

Table 6.1 Sensitivity analyses of driving variables for 14-mm and 26-mm abalone, with an initial seeding number of 1 000 000 abalone. A) Simulations wherein initial (post-seeding) survival was kept constant and differential survival was increased by the factor shown per age class. B) Initial survival was increased in each simulation (as shown) while differential survival was increased by a constant factor of 1.1. In both sets of simulations n was calculated for a population consisting of 10 age classes, and total mortality (Z) was calculated as an average for all 10 age-classes. Both 24% and 56% are experimental recovery rates (Chapter 4).

Simulation	14-mm abalone Initial survival kept constant at 24%			26-mm abalone Initial survival kept constant at 56%		
A	Differential survival factor	Average Z	n	Differential survival factor	Average Z	n
1	1.1	-1.05	46	1.1	-0.26	84349
2	1.21	-0.69	1831	1.21	-0.20	148805
3	1.331	-0.52	8204	1.331	-0.18	179678
4	1.4641	-0.44	17367	1.4641	-0.17	197646
5	1.61051	-0.39	27619	1.61051	-0.16	216956
B	Differential survival kept constant at 1.1					
	Initial survival	Average Z	n	Initial survival	Average Z	n
1	0.24	-1.05	46	0.56	-0.26	84349
2	0.2904	-0.86	311	0.626	-0.20	144580
3	0.31944	-0.76	806	0.68	-0.17	200171
4	0.351384	-0.66	2091	0.75	-0.14	266352
5	0.386522	-0.57	5357	0.82	-0.12	317685

survival being equal to a proportional decrease in mortality. An average Z value was calculated from the Z value that was used in each age class to determine the number of abalone alive in each of the 10 cohorts.

The number of abalone seeded initiated the simulation of population decline; and the number alive at the end of each time period was calculated using the following formula:

$$N_t = N_0 e^{(-Zt)} \quad (\text{Formula 1})$$

where

N_t is the number of survivors from a cohort attaining age t

N_0 is the cohort number at time zero or original number

Z_t is the instantaneous mortality coefficient or total mortality rate at time t, and t is time.

The value of Z used in each time period was calculated by the formula:

$$Z = \ln (N_t / N_0) \quad (\text{Formula 2})$$

The probability of surviving, (N_t / N_0) , for the first year becomes the probability of surviving the actual seeding operation itself (designated IS, 0.24 for 14-mm abalone and 0.56 for 26-mm abalone in Table 6.1). In consecutive years, the probability of

surviving the first year was 0.24, in the second year that was multiplied by 1.1, in the third year the product result in year two was again multiplied by 1.1. Thus, in this simulation, the probability of survival increased by a factor of 1.1 per year. For the 26-mm abalone the initial probability of survival was 0.56. In the second year this was multiplied by 1.1, in the third year the second year product was again multiplied by 1.1. In simulation 2 (Table 6.1A) the probability of survival per age class increased by the factor 2.21 per year. Table 6.1A lists the factors used in each simulation for both size-classes of abalone. Thus, Z , was a combination of seeding-induced and natural mortality, and did not include any fishing mortality.

Shell length (SL) was calculated using the Von Bertalanffy growth equation (Tarr 1995, Fielding 1995, Ebert 1999, Jennings et al. 2001):

$$L_t = L_\alpha (1 - e^{(-K(t-t_0))}) \quad (\text{Formula 3})$$

where

L_t is the length of abalone at time t

L_α is the theoretical maximal length

K is the growth coefficient that is a measure of the rate of approach to the maximum size, and

t_0 is the theoretical age when length is zero.

A shell length-breadth relationship was used to determine shell breadth (SB) from SL (Tarr 1993):

$$\text{Shell length} = \frac{\text{Shell breadth (mm)} + 11.59 \text{ mm}}{0.193} \quad (\text{Formula 4})$$

A mass-breadth relationship was used to determine abalone whole wet mass from SB (Tarr 1993):

$$\text{Whole mass (g)} = 0.002 \text{ SB (mm)}^{2.614} \quad (\text{Formula 5})$$

The populations were modeled up to the time of harvest, i.e. when the individual abalone reached a mass of 300-g, and became commercially suitable for harvest. Natural mortality incorporates a number of factors, including the effects of predation, availability of food, space and other density-dependent factors, together with a range of environmental factors. The larger the value Z , the more rapidly a specific cohort of individuals will decline in number over time. The probability of survival is the value that determines the percentage of animals that have survived a specific time period (in this case one year). This probability of survival may change as an abalone ages: As a result, a cohort will have a range of differential probabilities of survival (DS, Table 6.1) impacting on it as it ages. Differential survival rates that are specific to cohorts of different ages determine the mortality coefficient, or total mortality, denoted as Z (Formula 1, Siddeek & Johnson 1990, Shepherd & Johnson 1991, Sparre & Venema 1992, Ebert 1999, Figure 6.1). Survivorship is the cumulative effect of differential

survival rates over time. Survivorship can also be expressed as a rate if the actual population numbers are known. This rate indicates the rate of decrease in population size over time from the original population size (i.e. recruitment or seeding number) until the time in question. The survival rate on the other hand indicates the decrease in population size over a specific time period for a specific age class only. Hence, survivorship is the cumulative effect of survival rates. Survival per age class can increase as a cohort ages, as assumed in the case of abalone (i.e. the animal has less chance of dying as it gets older). Survivorship, however, cannot increase.

Age class periods were equal in length of time to the first time period, and all subsequent time periods were equal in duration to the first period. The first time period was taken to be one year; as a result, all simulations in this work were done in time periods of one year. Survivorship or cumulative survival per age class was calculated by multiplying the survival per age class of a specific year by the previous year's figure. The product then became the cumulative survival or survivorship value for that year.

6A.2.2 Assumptions made to develop the model

1) Differential mortality rates were developed using the assumption that percentage mortality per age-class decreased by a constant factor in consecutive age classes to reach a defined plateau (Figure 6.1). Maximum survival of any age class could be 90% of the previous age class. Average mortality is taken by the Marine and Coastal Management Branch of the Department of Environmental Affairs (MCM) to be approximately 11% for all size classes of natural abalone stocks (C. Moloney, MCM,

pers. comm.). This would mean that an average of 89% of abalone survive in each age class every year, yet the maximum survival per age class figure of 90% was used to simplify the assumptions made while developing the model. Maximum cumulative survivorship cannot exceed 81% per age class if differential survival per age class is never greater than 90%.

2) Differential mortality per age class included all limiting factors that effect survival, including density-dependence, carrying capacity, predation, etc. No fishing mortality takes place on the Namaqualand coast. Populations were modeled up to the time of harvest, no harvesting would take place before this time, and at this stage the total population that has reached a defined size would be available for harvest.

3) There is no natural recruitment taking place into the seeded population, and the effect of fishing has an impact only when harvesting takes place. There is no existing abalone fishery on the Namaqualand coast because there are no natural stocks of abalone there.

4) The effect of senescence was disregarded (Figure 6.1). It was assumed that harvesting would take place no more than 10 years after seeding. Based on growth data, senescence does not begin to effect the population before that (Tarr 1995, Sweijd et al. 1998).

5) The relationship between differential survival and differential growth has not been quantified for seeded populations of *H. midae*. Although growth will affect the rate at which a cohort reaches a specific size, it will also have an effect on the rate at which differential survival changes. Growth within abalone populations is also highly variable. This relationship has not been included in the model, for the sake of simplicity and because there are no data to test this relationship for seeded populations.

An increase in growth rate of an individual abalone would increase its chance of surviving as it ages; it would not affect the initial post-seeding survival (IS) rate. The extent to which the entire population is affected by an increased growth rate would determine to what extent harvesting can take place earlier, as well as the number of animals that will have survived to a given size (or mass) when harvesting occurs. The effect would be similar to the effect of a factor increasing the survival per age class. Exactly what the increase would be is not known. For the purpose of this study it was assumed that the effects would be similar in extent to those exhibited by changes in survival per age class, as shown in the sensitivity analysis (Section 6A.2.4). Average growth rates were used because it was assumed that the entire cohort behaves in the same way. In the cost-benefit analyses more than one growth rate was used, and it was assumed that the entire cohort attains the same size at the same time. This was done both for simplicity's sake and because there are at present no data available concerning these relationships for seeded abalone.

6A.2.3 Investigating the range of potential differential mortality regimes (Z)

Although a range of differential mortality rates may exist for any species in different habitats, this model was restricted to only one approach, one in which survival per age class increased from an initial post-seeding value (IS) to a maximum value of 90% over time. The curve for survival per age class produced by this approach, together with a hypothetical curve B, is demonstrated in Figure 6.1. Size-specific differential mortality rates and the gradient of the curve, or the value of instantaneous mortality rate (Z) for the species from different sites are not known for seeded animals of this

species (Chapter 4, Schiel 1993, Shepherd et al. 2000, Tegner 2000).

6A.2.4 Sensitivity analysis of the model with regard to survival regime and initial survival

It was necessary to test the behaviour of the model in relation to the two driving variables, i.e. seeding-induced mortality and differential mortality. To do this, the model was run for 10 years, with an initial seeding number of 1 000 000, at the end of which population number in year 10 was noted (value n in Table 6.1).

Two general scenarios were used to test the sensitivity of the model to the two driving variables (Table 6.1). In scenario A, initial survival (IS) was 24% for the 14-mm abalone, and 56% for the 26-mm abalone. In each of five simulations, differential survival was increased per consecutive age-class (or cohort) by factors of 0.1 (Table 6.1A). In other words, for the both the 14-mm and 26-mm abalone the differential survival values were increased by a factor of 1.1, 1.21, 1.33, 1.46 and 1.61. These probabilities of survival were used to calculate Z factors for each cohort these were in turn used in Formula 1 to calculate number of abalone surviving in each cohort, and total population (n). An average Z value for each population was also calculated (Table 6.1). In the scenario B (Table 6.1B) differential survival (DS) was kept constant at 1.1 for both the size-classes of abalone, while initial survival was increased by a factor of 0.1 per simulation. In other words, for 14-mm abalone the initial survival figures used were 0.24, 0.29, 0.32, 0.35 and 0.39. For the 26-mm abalone the initial survival figures used were 0.56, 0.63, 0.68, 0.75 and 0.82.

6A.2.5 Investigating specific total mortality values (Z) for two sizes of seeded abalone

In two series of simulations, differential survival rates were used in which survival per age class was increased in consecutive cohorts by the factor shown as differential survival in simulations 1 to 5 (Table 6.1) per age class. In each simulation the factor was increased by a factor of 0.1 from the one used in the previous simulation. Initial survival figures were based on experimental data (Chapter 4), 24% being the initial survival rate for 14-mm animals, and 56% the rate for 26-mm animals. Average Z values were calculated for each differential survival simulation (Table 6.1). One initial seeding batch of one million abalone was allowed to run the course of the model to a market size of 300 g (including shell), which is approximately 120 mm in shell length (Table 6.2). The length of time that this takes is determined from the growth rate used in each specific simulation. In this case, experimental growth data and growth data for naturally occurring abalone from the south-west and west coast of South Africa was used (Table 6. 2, Tarr 1993, 1995).

In this study, a range of growth rates was determined for seeded abalone, both juvenile and adult (Table 6.3). In cases where increments are represented by growth periods shorter than one year, average annual increments were calculated (Figure 6.2). These growth rates have been compared to a range of growth rates reported for naturally occurring populations of *H. midae* from a number of different sites (Tarr 1995). Standard Von Bertalanffy growth curves are commonly used to determine growth parameters for different species of abalone (Shepherd & Johnson 1991, Shepherd et al. 1995, Tarr 1995, McNamara & Johnson 1995, Shepherd et al. 1995,

Table 6.2 Von Bertalanffy growth parameters used in the model (Tarr 1993, 1995). All parameters are from data on abalone along the south-western and west coast of South Africa. A large portion of the broodstock used to breed juveniles for the ranching experiments in Port Nolloth come from Robben Island. K is the growth coefficient, and L_{∞} is the theoretical maximum length that the abalone can attain.

Data set	K (s.e.)	L_{∞} (s.e.)
Robben Island	0.249 (0.012)	163.29 (3.23)
Betty's Bay	0.186 (0.008)	172.76 (2.37)
Danger Point	0.092 (0.021)	210.32 (28.66)

Table 6.3 Original data showing the range of growth rates for experimental abalone seeded along the Namaqualand coast, showing growth increments, the size class of the animals at time of seeding, the season in which they were seeded, and period of time at sea.

Growth rates						
Size class (mm)	n	Period (days)	Growth increment mm month ⁻¹ (mm)	Season	Date in	Date out
8 to 10	33	128	0.4	Summer	10 11 98	1 04 99
12 to 20	60	184	1.2	Summer	7 07 98	7 02 99
17 to 25	60	199	1.2	Summer	31 10 98	18 05 99
25 to 26	100	40	1.5	Spring	28 07 99	8 09 99
27 to 28	162	60	0.5	Summer	6 09 99	4 11 99
45 to 47	31	60	0.6	Winter	25 05 00	25 07 00
57 to 129	17	417	1.5	Year- round	13 07 98	01 09 99

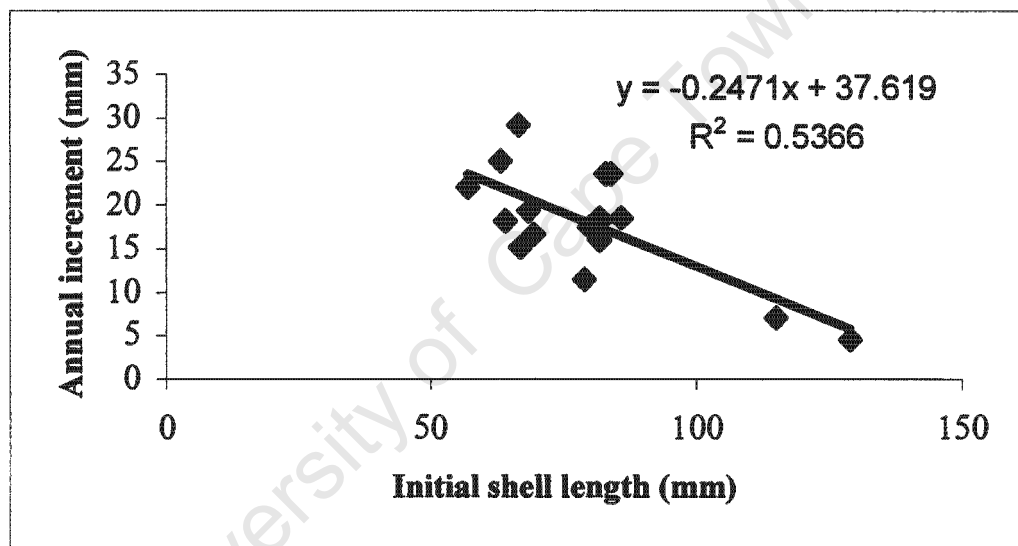
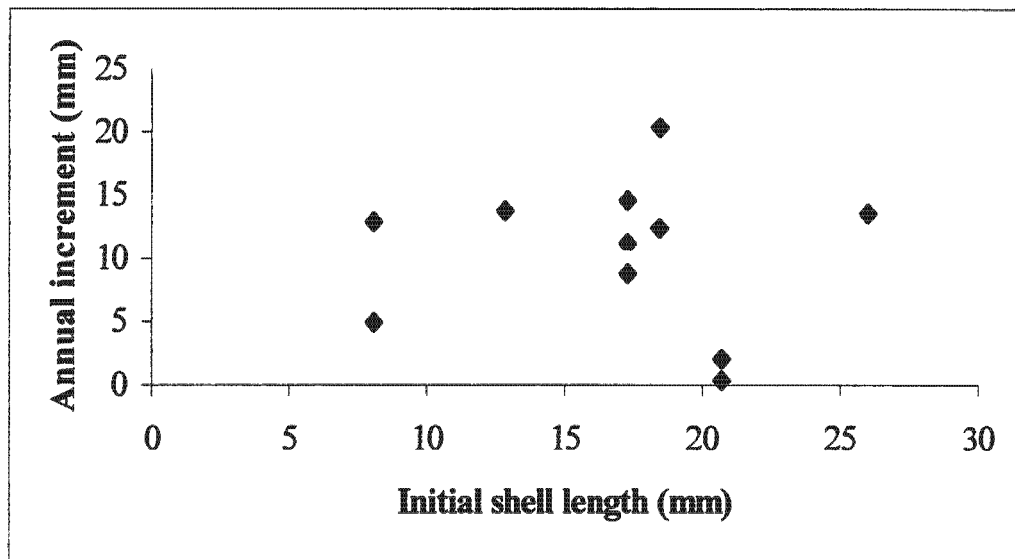


Figure 6.2 Annual growth increment curves generated from original data for abalone planted on the Namaqualand coast during the present study. The top graph depicts smaller abalone (<20 mm shell length), and the bottom graph for adult abalone; the solid line in the bottom graph is a linear trend line.

Ebert 1999). Annual increments calculated for the different-sized abalone used in this experiment showed increments in smaller abalone that were in the same range as that of larger abalone (Figure 6.2). There is no clear evidence that the size increments for abalone smaller than 50 mm in length are consistently larger than those for abalone greater than 50 mm. There may be a number of reasons for this, including stress, environmental factors and genetic factors attributable to the specific broodstock used to produce the seed. As a result, the growth parameters from the data of Tarr (1995) have been used to model growth in seeded abalone populations. Using the three different sets of growth parameters from Table 6.2 (Tarr 1993, 1995), total growth until harvest would be attained after an average minimum period of between 7 and 9 years if 14-mm abalone were seeded. (A mass-length curve measured for a range of experimental abalone that had been in the sea at Kleinsee for up to 13 months shows that a mass of 300 g is reached at a length of approximately 120 mm; see Figure 6.3. This concurs with published data by Tarr 1993, 1995).

Data from Tarr (1993, 1995) were used to determine the time to harvest from seeding. Growth data for juvenile farm animals were used to determine the difference in time spent in grow-out tanks on the farm before seeding the two size-classes (14-mm and 26-mm). Juvenile growth is often best expressed by linear equations (Shepherd & Johnson 1991). As a result, using an average growth rate in the range of 1.5 mm per month, as measured at Port Nolloth for farm-reared juveniles, it was determined that it would take approximately 9 months for 14-mm juveniles to reach 26 mm. To compensate for this in the economic cost-benefit part of this chapter (6B), the 26-mm abalone are foreseen as harvested one year earlier than the 14-mm abalone.

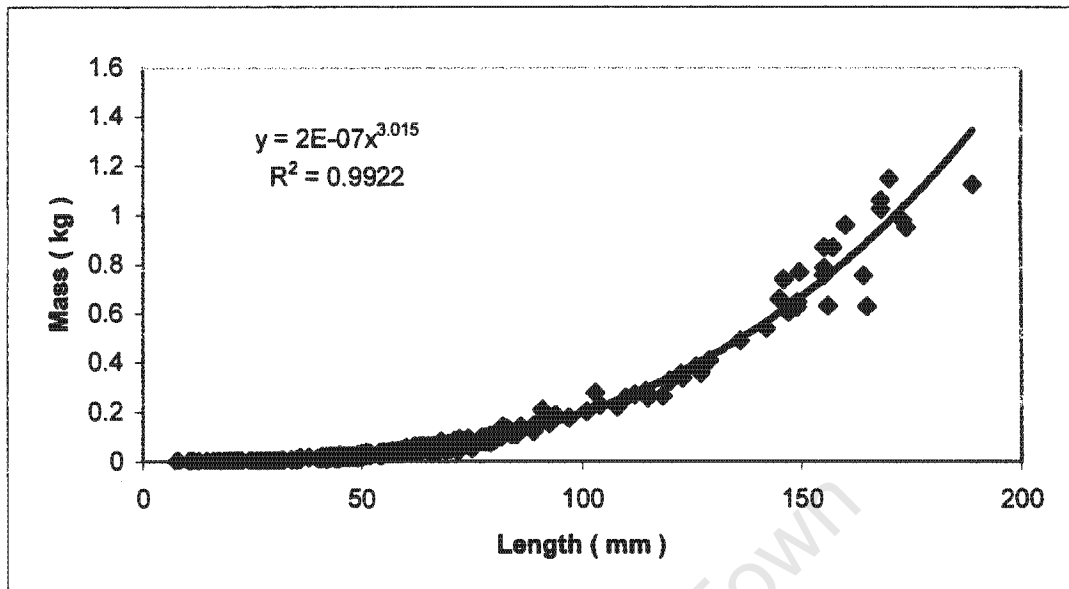


Figure 6.3 Mass-length curve for *Haliotis midae* plotted from measurements of animals used in the Namaqualand experiments. Original data were used in conjunction with published data to compile estimates of growth and mass at time of harvest to be used in the model (Table 6.2).

6A.2.6 Determining the extent of seeding-induced mortality over time

It was necessary to determine whether or not a 30-day period could be regarded as sufficient time for the effects of seeding-induced mortality to have dropped to a level of no significance. To do this, average recovery rates after 30 days for the three different size classes used in Chapters 3 and 4 (14 mm, 26 mm and 45 mm) were compared with recovery rates for the same size classes after 60 days. The seeding experiments were done in what was visually assessed as similar habitat and under similar environmental conditions, in an attempt to better standardize both biological and physical conditions. The recovery rates from the two time periods were compared using a Mann-Whitney U Test.

6A.3 RESULTS

6A.3.1 Differential survival regimes

Figure 6.4 shows curves for the extreme range of survival per age class generated by the model, given a specific initial population size set at 1 000 000.

6A.3.2 Sensitivity analysis

Both driving variables, i.e. seeding-induced mortality and differential mortality, had an influence on the model output in terms of the rate of population decrease. The increase in initial survival due to 26-mm abalone being used as compared to 14-mm abalone, is almost double. However, the impact that this doubling in initial survival

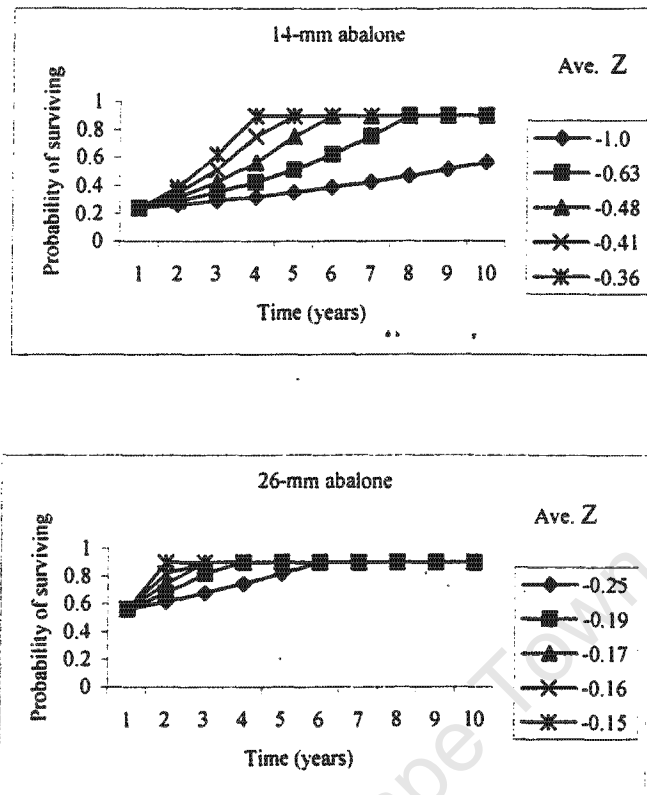
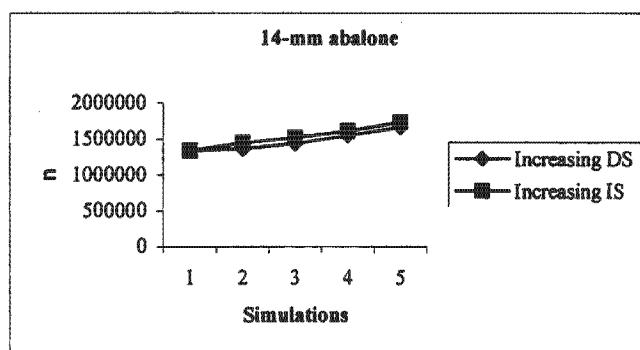


Figure 6.4 Probability of survival per age class as generated by the model when differential survival per age class was increased by the factor shown in simulations 1 to 5 (see Table 6.1), beginning with an initial post-seeding survival probability of 0.24 for 14-mm and 0.56 for 26-mm abalone. The top graph shows the range of curves generated for the smaller 14-mm animals and the lower graph those for the larger 26-mm animals. The simulations assumed a time span of 10 years which was considered short enough to rule out increased mortality rate per age class due to senescence. The average values for total mortality (Z) that were generated in each simulation are given to the right of each legend; these can be related to the differential survival factors in Table 6.1.

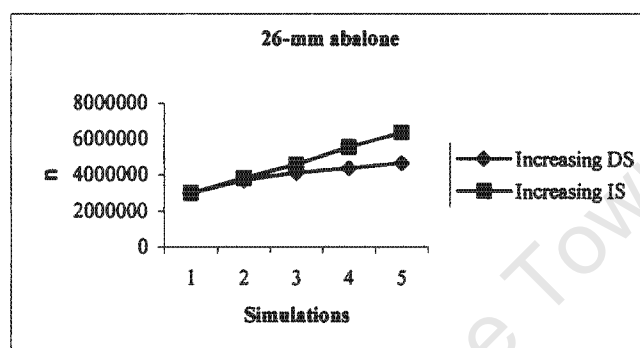
has on the extent to which a population declines over time is exponential (Figure 6.5). Although small increases in initial survival appear to have little effect, larger increases seem to have a strong impact. The increase in initial survival is also reflected by differential survival. Since the model is designed to build on initial survival to develop a differential survival regime. The model shows that seeding-induced mortality and survival have a very strong effect on recovery rates over the short-term and, as a result, influence long-term recovery and total Z , a reflection of what was seen experimentally.

6A.3.3 Determining the extent of seeding-induced mortality over time

When a comparison was made between experiments having a 30-day seeding-to-sampling period and a 60-day seeding-to-sampling period, a Mann-Whitney U Test showed no significant difference between recovery rates for the set of experiments done at McDougall's Bay (with animals of average size 14-mm, 26-mm and 45-mm) (Figure 6.6). A period of 30 days is thus assumed to be sufficient for a seeded population of *H. midae* to stabilize after initial seeding-induced mortalities have taken place. In other words, seeding-induced mortality may be complete within 30 days. In the first annual time period, only a very small percentage of total mortality will be as a result of differential mortality, and the greater part will be the result of seeding-induced mortality. According to the results, a seeded population that has been in the water longer than 30 days can be safely assumed to be driven by the same natural environmental factors that will affect a natural population in the same site and habitat.



a)



b)

Figure 6.5 Results of sensitivity analyses for two size classes of abalone, a) 14-mm and b) 26-mm average length. The curves marked as Increasing DS (differential survival) in both graphs, show the effects of increasing DS by a factor of 0.1 for each simulation, from an initial value of 1 for both size classes. In each simulation initial survival (IS) was kept at 0.24 for the 14-mm abalone and 0.56 for the 26-mm abalone. The Increasing IS curves show the effects of increasing initial survival by a factor of 0.1 for each simulation, starting with an initial value of 0.24 for the 14-mm abalone and 0.56 for the 26-mm abalone. In each simulation DS was kept constant at 1.1; n was calculated as total population number for a population consisting of 10 age-classes, aged 1 to 10 years. In both graphs the effect of increasing initial survival is depicted in terms of increasing differential survival by the same factor. The proportional increase between the two curves in the bottom graph is larger than that in the upper graph because of the exponential increase in initial survival of the 26-mm abalone as compared to the 14-mm abalone.

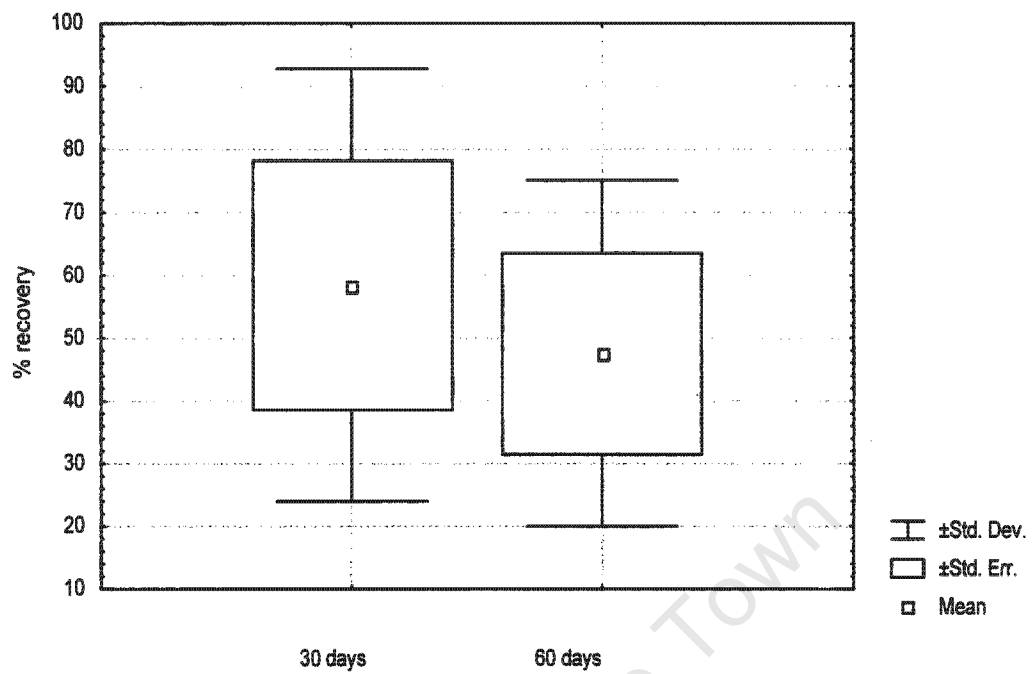


Figure 6.6 Recovery rate of abalone sampled after 30 days and 60 days. Differences were not significant (Mann-Whitney U Test, $p = 0.60$). Data were pooled for three size classes (14-mm, 25-mm and 45-mm).

6A.3.4 Investigating specific total mortality values (Z) for two sizes of seeded abalone

The average Z values shown in Figure 6.4 are a result of the combination of seeding-induced mortality and long-term mortality. Under the same ecological conditions, determined by the factor increase in survival per age class (Figure 6.4), Z was shown to be smaller for 26-mm abalone as compared to 14-mm abalone. (As a point of reference-a probability of survival of 90% is equal to a Z value of -0.105, if the probability of survival remained constant at 90% over a number of consecutive years, the average Z value would be -0.105).

In summary, when investigating the population dynamics of a seeded abalone population using the population parameters described in this section of the chapter, initial survival, which is a direct effect of seeding size, is shown to be the most important factor that drives population decline over time. Although there are no existing data concerning natural differential survival probabilities, increasing seeding size will result in higher population numbers. Short-term initial survival plays a significant role over the long-term, regardless of differential survival.

6A.4 DISCUSSION

The model was designed to investigate the dynamics of a single population of abalone based on contemporary knowledge of the dynamics of abalone populations in general. The ultimate goal would be to generate sufficient experimental data so that modelling could be based on accurate differential mortality and initial survival figures. At this

stage, this is not possible. However, a choice based on scientific facts could be made between realistic and unrealistic options. Indications from this study, and those reported in the contemporary literature, are that differential mortality decreases with age, i.e. survival increases, until senescence sets in. Davis (1995) estimated survival of juveniles in artificial habitats to be 32% after one year and 24% after two years. Tegner and Butler (1985) found a 21% planting mortality that could be directly attributed to seeding, and an overall seed mortality of 43%, with no significant difference in recovery rate shown among abalone of different sizes. These authors stressed the effect of habitat and environmental conditions at time of seeding and the variability in mortality between sites. In New Zealand a series of seeding experiments resulted in annual mortality rates that ranged from 27.6 to 98.8%, with values for instantaneous mortality ranging from 0.323 to 4.44 (Schiel 1993). Again the emphasis was on identifying the characteristics of suitable seeding sites to optimize recovery and survival. In seeding experiments from Tasmania done with 7-month-old abalone, seeding-induced mortality was calculated to be approximately 20% in the first two days, with an instantaneous mortality coefficient over a one-year period at 1.8. This was substantially higher than that recorded for wild populations of abalone (Shepherd et al. 2000). Seeding experiments done with juveniles in artificial habitats, also in Tasmania, showed lower instantaneous mortality than abalone released into natural habitat (Shepherd et al. 2000). Again habitat and site selection were emphasized in terms of their impact on total mortality, to the extent that artificial rather than natural habitats were regarded as a better option to optimize survival; seeding-induced mortality would account for a large percentage of the first year's mortality, and differential mortality would account for the decrease in

mortality of the seeded population in the second year (Shepherd et al. 2000). The average Z values generated by differential survival and initial survival for the different-sized seed abalone (Figure 6.4), and the proportional difference in total population shown in Table 6.1, show the impact that initial survival has compared to differential survival. As a result, Hypothesis 7 (Figure 1.4), stating that seeding-induced mortality is the most important component of total mortality (Z), was accepted.

The high initial survival figures in the simulation have the effect of reducing total mortality (Z); furthermore, regardless of initial numbers, increasing seeding size has been shown to maximize long-term survival by reducing total mortality (Z) (Table 6.1). Mortality is age- and size-related because environmental and biological factors affect abalone of different sizes in different ways. As a result, Z can be manipulated by seeding size. Within this context, if a hypothetical value of Z exists for one specific area, and a relatively higher hypothetical Z value exists for another area, smaller abalone should be seeded in the area with the relatively lower Z value, and bigger abalone in the area with the higher Z value. Z can be interpreted as a risk factor because it is directly related to animal size and to the environmental and biological attributes of an area. Although the total Z values for seeded populations are not known, it is possible to model returns within specific economic constraints using hypothetical Z values. Importantly, seeding size is a parameter that can be controlled by management, and so used to maximize survival by decreasing Z .

The percentage survival curves in Figures 6.4 clearly show that it is possible for theoretical curves to converge at some point. If only a point value is known, very little

can be determined about the dynamics of the population. To model production accurately, it is recommended to have a good idea of the differential mortality regime acting in that specific habitat. The goal of objective-driven research should, in this case, be to determine the most realistic mortality regimes in given situations.

Appropriate experimental data applied to models can allow the analysis of a ranching project's feasibility before any financial input is made, these should be continually developed as more biological data become available (Heppel & Crowder 1998, Hilborn 1998, Wilson et al. 1998). It is essential to understand the concept of differential mortality and survival before any predictions can be made about the success of seeding programs. In a long-term (18-year) monitoring exercise on a discrete natural population of *Haliotis laevis* Shepherd (1990, 1998) showed instantaneous mortality coefficients for abalone ≥ 3.5 years to range from 0.02 to 0.86, with a mean of 0.38 (s.e. 0.06). This shows the extent to which mortality can vary, even with respect to older animals. The model in this study has generated average Z values over a number of years in a very simplistic manner. While these values may safely fall within the range that has been calculated for wild populations (albeit for another species), Z values must be regarded as representative of reality only if they represent long-term averages.

To determine economic implications in different scenarios (see section 6B), simulations used for the economic cost-benefit analyses were done using a combination of experimental and natural growth data (Tarr 1995, Sweijid et al. 1998).

6B.1 QUANTIFYING THE ECONOMICS OF SEEDED POPULATIONS

One of the underlying themes of the model described in section 6A is that a trade-off exists between expected initial mortality (or survival) of seeded juveniles (which is size specific and growth-related) and the cost of producing juvenile abalone of different size classes. One goal in developing the model was to attempt to quantify this relationship. Economic constraints cannot alter ecological parameters, and the interpretation of production figures based on parameters such as fluctuating exchange rates and market prices must bear this in mind. In all the simulations carried out here, it is assumed that the populations of different-sized abalone are seeded under comparable environmental conditions; as a result, results from the different simulations can be compared to each other.

6B.2 METHODS

6B.2.1 Cost-benefit analysis to show the effect of seeding size

The survival regimes and the harvest strategies described in part 6A.2.5 (Figure 6.4, Table 6.1) were considered while undertaking economic analyses to investigate seeding strategies. Experimental and growth data from natural west-coast abalone populations were used in these analyses (Tarr 1993, 1995).

The cost-benefit analysis was developed using the initial post-seeding survival figures (IS) obtained from the experimental seeding of both 14-mm and 26-mm abalone, the range of differential survival rates (DS) given in Figure 6.4 and Table 6.1, and the

present market price for abalone. Purchase prices of R1 per animal for 14-mm animals and R4 per animal for 26-mm animals, and a selling price of R210 per kg for 300-g abalone were used (prices obtained from Port Nolloth Sea Farms). The financial prices are not of cardinal importance in the analysis, but will influence the absolute levels of profit or loss. More important are the relationship between size-at-seeding, the potential returns and how these data are interpreted. An initial population figure for seeding of 1 000 000 was selected for the cost-benefit analysis. Because the decisions and skills of management will impact to a great extent on the monthly overheads of a business, and because there are various ways of releasing abalone into the sea, the cost of planting and the cost of harvesting have been included in the purchase and selling price of the abalone. (At present there are experiments underway to determine the feasibility of placing seed without a seeding module (B. Godfrey, Rhodes University, pers. comm.)).

If survival is a factor of size, and this is age related, then growth rate will have a compounding effect on total mortality (Z). The variability of growth rates between populations and within populations affects both survival and biomass production. This compound effect has not been incorporated into the model used here, both for the sake of simplicity, and because the relationship between a change in growth rate and a change in factor Z is not understood. The relationship will affect the rate at which a population declines in number over time, and the proportion of each cohort that can attain a specific size by a specific time. However, it has been assumed that the effects of the relationship are consistent within each of the size classes used in the simulation. The possible effects of growth were incorporated into the model by using three different sets of growth parameters, according to data available for *H. midae* in the

south-western and western Cape (Tarr 1993, 1995, Table 6.2). Two of these sets, from Robben Island and Betty's Bay, yielded the same time for abalone to reach a size of 300 g whole wet mass. As a result, the Danger Point and Robben Island data sets were used as two extremes (Table 6.2). Furthermore, when comparing the time to harvest for the two different size classes of abalone (14-mm and 26-mm), the time to harvest was shortened by one year in each case where the larger abalone were being modelled. This is based on the growth of abalone raised in grow-out tanks in Port Nolloth which showed that it took approximately 9 months for 14-mm abalone to reach 26 mm. Average Z values determined from the model were calculated from time of seeding to the time of harvesting (9 years for the 14-mm Danger Point abalone, 7 years for the 14-mm Robben Island abalone, 8 years for the 26-mm Danger Point abalone and 6 years for the 26-mm Robben Island abalone).

6B.2.2 Cost-benefit analysis using opportunity costs

It is necessary at this stage to look at the results compiled in Table 6.4, and to note that when the growth parameters from the Danger Point data set were used for the smaller abalone (14-mm), the lowest differential survival factor to turn a profit was 1.4641 (average $Z = -0.44$). When the growth parameters from Robben Island data were used on the same size-class, a relatively larger profit was shown by using the same survival factor (average $Z = -0.53$). For the larger abalone (26-mm), a profit was shown for all the differential survival factors; however, the higher the factor, the higher the profit. In short, the differential survival factor of 1.4641 (resulting in an average $Z = -0.18$ for the 26-mm abalone, utilizing Danger Point growth parameters, and an average $Z = -0.20$ for the 26-mm, utilizing Robben Island growth parameters)

Table 6.4 Cost-benefit analyses relating to seeding with 14-mm or 26-mm abalone. A range of differential survival rates are reflected in the value for total mortality (Z), and a range of different growth rates are reflected in time to harvest (Danger Pt. and Robben Is. growth parameters are given in Table 6.2). The larger abalone were harvested one year earlier than the smaller abalone. Z values are calculated as an average over the period between seeding and harvesting. (Note Z values are lower for the larger abalone as compared to the smaller abalone under the same ecological parameters). Higher growth rates result in higher Z values relative to those generated by lower growth rates. Purchase price of 14-mm abalone was R1 and 26-mm abalone R4. Selling price was R210 kg⁻¹.

	Time to Harvest (years)	Seeding Size (mm)		Factor by which differential survival per age class increases per year				
				1.1	1.21	1.331	1.4641	1.61501
(Danger Pt.)	9	14	Harvest (kg)	25	627	2810	5949	9540
			Profit (R)	-0.99	-0.87	-0.41	0.25	1.0
			(million)					
			<i>Ave. Z</i>	<i>-1.04</i>	<i>-0.69</i>	<i>-0.52</i>	<i>-0.44</i>	<i>-0.39</i>
(Robben Is.)	7	14	Harvest (kg)	127	922	4135	8754	13922
			Profit (R)	-0.97	-0.81	-0.13	0.84	1.9
			(million)					
			<i>Ave. Z</i>	<i>-1.14</i>	<i>-0.86</i>	<i>-0.64</i>	<i>-0.53</i>	<i>-0.47</i>
(Danger Pt.)	8	26	Harvest (kg)	25543	45602	54411	59852	65699
			Profit (R)	1.4	5.5	7.4	8.6	9.8
			(million)					
			<i>Ave. Z</i>	<i>-0.28</i>	<i>-0.21</i>	<i>-0.19</i>	<i>-0.18</i>	<i>-0.16</i>
(Robben Is.)	6	26	Harvest (kg)	37458	66083	79793	87773	96348
			Profit (R)	3.9	9.9	12.8	14.4	16.2
			(million)					
			<i>Ave. Z</i>	<i>-0.34</i>	<i>-0.25</i>	<i>-0.22</i>	<i>-0.20</i>	<i>-0.18</i>

was the absolute minimum that would yield any profit if the smaller abalone were seeded and if the growth rate was favourable. Therefore, this factor is used in the next section, since it places the simulation with a meaningful economic context.

The experiments with 45-mm animals in Chapter 4 resulted in high recovery rates that could be directly equated with high survival rates. An analysis was done in which the opportunity costs and the potential benefits were calculated for 26-mm and 45-mm animals, making an assumption that money to purchase the animals had to be borrowed at a fixed rate. Differential survival per year was increased by a factor of 1.4641, and the respective initial survival rate for the 26-mm (56%) and 45-mm (86%) animals from Chapters 4 and 5 were used. The growth parameters from the Robben Island study were used because much of the broodstock at Port Nolloth Sea Farms is from there, and because Robben Island is further up the west coast and closer to the Namaqualand coast than Danger Point. In each case the model was run to produce approximately 88 tonnes of export size abalone. Based on the average growth rate used in the previous cost-benefit analysis, this was attained after 6 years starting with 26-mm animals, and after 5 years starting with 45-mm animals (growth rates from Tarr 1993, 1995). The initial population number to produce 88 tonnes over 6 years for the 26-mm abalone was 1 000 000. The model was manipulated to determine what number of 45-mm abalone would be required to produce 88 tonnes of 300-g abalone over 5 years. The time taken to produce this mass of abalone, and the cost of borrowing the purchase price for the seed abalone at a compounded interest rate of 10%, were used to determine costs. The benefits were calculated as the difference between the selling price and the compounded cost of purchase (seeding and harvest costs were not considered separately, but were included in the cost of

purchase). For the purpose of the analysis, the cost of purchasing 26-mm animals was set at R4 per animal and the cost of the 45-mm animals was set at R4 initially and increased until the benefit relative to that of seeding the 26-mm abalone was the same; this occurred at approximately R8.20 per abalone. Benefits were calculated by multiplying the mass produced (88 000 kg) by US \$35 kg⁻¹ and then by a conversion rate of R10 to the US \$, (totaling R 30.8 million). The difference between benefit and production (or purchase) costs for each scenario determined benefit.

6B.3 RESULTS

6B.3.1 Cost-benefit analysis showing effects of seeding size

Table 6.4 shows the results of a cost-benefit analysis if seeding with 14-mm and 26-mm abalone under a range of mortality rates (Z), and then harvesting after different time periods depending on the growth parameters used. The analysis shows that under the same ecological conditions, the average Z values generated by the model are lower for the larger 26-mm abalone than for the smaller 14-mm abalone. The analysis also shows that the Z values are higher when faster growth rates are used and when harvesting takes place over a shorter time period, as seen when comparing Z values from the simulations using growth parameters from the Robben Island and Danger Point data sets (Table 6.4). This is caused by the shorter time span between seeding and harvesting, and the effect that initial seeding-induced mortality has on the calculation of average Z . However, while the average Z values generated by the model for a specific size class may be higher as a result of higher growth rates (e.g. from Robben Island), higher growth rates yield relatively higher biomass figures

when compared to potential yield generated by lower growth rates (e.g. from Danger Point). The 26-mm animals were theoretically harvested one year earlier than the 14-mm animals. Table 6.4 shows that the smaller abalone were only economically viable when Z was ≤ -0.53 using the growth parameters from Robben Island and ≤ -0.44 using the growth parameters from Danger Point. Use of the Danger Point growth rates resulted in relatively lower potential biomass yields when compared to the potential yields generated when using the Robben Island growth rates. On the other hand, the higher initial survival figures for the 26-mm abalone yielded positive economic results regardless of which of the two sets of growth parameters were used. The effect of lower total Z values, as reflected by the 26-mm abalone, show that initial survival (a direct effect of seeding size) plays a very dominant role in determining the decline in population number over time.

The optimal situation, as shown by the simulation utilizing the 26-mm abalone (Table 6.4), is a combination of both lower total Z values generated by larger juveniles, and relatively high growth rates, as shown by the simulations using the growth parameters from Robben Island. The 26-mm abalone are shown to be viable within the specified economic parameters, with total Z values as low as -0.16 , and total yield depending on the growth parameters used.

6B.3.2 Cost-benefit analysis using opportunity costs

Using the growth parameters from Robben Island, the time-to-harvest for the 26-mm animals is 6 years and 5 years for the 45-mm animals (Tables 6.4 and 6.5, Tarr 1993, 1995). Using a compound interest rate of 10% for borrowed money, the benefits

Table 6.5 Cost-benefit analysis using a selling price of R30.8 million per harvest of approximately 88 tonnes for each size class. A purchase prices of R4 and R8.2 are shown for the 45-mm animals. This is the maximum purchase price for which seeding with 45-mm abalone is as profitable as seeding with the smaller, 26-mm, abalone.

Time to harvest (years)	Size class	No seeded	Cum. purchase price (million Rand)	Benefit (million Rand) (Selling price- purchase price)	Profit ratio (Benefit/ purchase price)
6	26-mm	1 000 000	@ R4 = 6.4	24	3.8
5	45-mm	535 000	@ R4 = 3.1	27.7	8.8
5	45-mm	535 000	@ 8.2 = 6.4	24	3.8

produced are shown in Table 6.5. The cost-benefit analysis shows that at the quoted prices, with an interest rate of 10%, the 26-mm animals are viable at a purchase price of R4. In this scenario, only 535 000 45-mm abalone were required to produce approximately 88 tonnes of 300-g abalone over 5 years, as compared to the 1 000 000 26-mm abalone that were required to produce the same mass of 300-g abalone over 6 years. The 45-mm animals could also be viable, depending on the purchase price. At any price ranging from R4 to R8.20 it is more profitable to use 45-mm animals than 26-mm abalone. With purchase prices >R8.20 there is no benefit relative to the 26-mm animals (Table 6.5). The profit ratio figures in Table 6.5 show the extent to which the relatively high initial survival rate of 45-mm abalone (84%), its effect on total Z, and a favourable purchase price can improve profit ratios. The average total mortality values generated by the simulations using the two size classes of abalone ($Z = -0.12$, $SD \pm 0.03$ for the 45-mm abalone, and $Z = -0.20$, $SD \pm 0.19$ for the 26-mm abalone) reflect the degree that mortalities, which can be translated into opportunity cost, are influenced by seeding size.

6B.4 DISCUSSION

Through a simple cost-benefit analysis of seeding with the two smaller size classes of abalone (Table 6.4), the model showed that within the economic constraints defined here, it is not economically viable to seed juvenile abalone 14-mm in size unless total Z is lower than -0.44 if projected growth rate is similar to that from Danger Point data, and -0.53 if the growth rate is similar to that from Robben Island data. On the other hand, 26-mm abalone would prove economically viable, even under less-favourable growth conditions. Although seeding larger abalone can increase

growth conditions. Although seeding larger abalone can increase survival rate over a specific time period, increased growth rate optimizes biomass production.

In short, the longer a cohort of abalone spends time at sea, the longer the period of time that the effect of Z can impact on it. If the initial population number is relatively low, such as it was in experiments with 14-mm abalone, and the growth parameters are also relatively low, such as those from Danger Point, a large proportion of the population may have died by the time the abalone are large enough to harvest. A combination of relatively high initial population numbers, such as in experiments here with 26-mm abalone, and relatively high growth parameters, such as those for Robben Island, will yield optimal results. The model clearly showed an exponential increase in potential yield in terms of biomass, for larger seed animals as compared to smaller seed animals, regardless of economic parameters. This is the most important aspect of this exercise and justifies accepting Hypothesis 7 (Figure 1.4), which states that increasing seeding size plays the dominant role in increasing survival and decreasing total mortality. This appears to be a realistic reflection of what happens under natural conditions (Schiel 1993, Shepherd et al. 2000, Tegner 2000). Experimental results (Chapter 4) have shown an exponential increase in the survival of juvenile abalone with increasing seeding size. In terms of the model, the difference in potential yield was caused by both the strong effects that initial survival has on the model's output, and by the speed at which survival reaches a maximum of 90%. Although experimental evidence suggests that both adults and juveniles may survive well in the same habitat (Chapter 5), this may not always be the case. Seeding must be done in an area where both initial mortalities and long-term mortalities are as low as possible.

The cost-benefit analysis using opportunity costs (Table 6.5) indicates that, although ecological factors determine the value of Z and, as a result, the biomass generated over a specific period, economic parameters and not ecological viability determine economic viability. Ecological viability, in this case, means the extent to which a population declines over time. A seeded abalone population will, in theory, be harvested and replenished on an ongoing basis, and natural recruitment will be replaced by replenishment. Economic viability means financial returns are high enough for management to continue the process. This process will be driven by economic parameters, such as exchange rates and market prices. Ecological viability will determine to what extent the population does in fact decrease. If natural recruitment does begin to take place as a result of broodstock becoming established in an area following seeding, then ecological viability takes on another meaning entirely. Then, the concept of minimum viable population size and population growth as a result of both seeding and natural recruitment will come into play. Although there is no indication that natural recruitment will take place along the Namaqualand coast, the potential for this to happen is not disregarded as it may play a role in the future. However, natural recruitment was not incorporated into the model.

According to the model, by the time the 14-mm animals have reached harvesting size, approximately 90% of the initial seeded number have been lost, in contrast to 60% and 40% for the 26-mm and the 45-mm animals, respectively. However, due to the exponential increase in survival as size is increase to 26 mm, and considering the cost of purchasing 45-mm animals, the model shows that, above a certain price for seed abalone, it is not viable to use animals larger than 26 mm. The very low values of average Z generated by the model for the 45-mm animals (-0.12 , $SD \pm 0.03$) and

26-mm abalone (-0.20 , $SD \pm 0.19$), indicate that, within the context of suitable habitat, seeding these sizes of abalone should result in relatively low rates of population decline over time. However, the cost of production, i.e. economic parameters, will determine an economic threshold that will influence the choice of seeding-size (Table 6.5). A dimension of the model that needs to be considered is the rate at which differential survival reaches the defined maximum of 90%. This influences the model's outcome, particularly with respect to larger animals, to the extent that at some point no extra benefit will be derived from increasing initial survival figures for animals that already have initial survival figures close to 90%. This is reflected in the experimental data from Port Nolloth, when 45-mm abalone seeded in McDougall's Bay showed survival close to 100% over 60 days. These results may be an indication that, excluding the inevitable ultimate effects of senescence, survival per age class for mature *H. midae* may be in the region of 90% or more.

Production and purchase prices are variable, just as the interest rate and potential survival rate are variable. As a result, the actual production figures used in the cost-benefit analysis should not be seen as absolute. Rather, they provide a relative means of comparing different scenarios.

In any potential ranching or stock-enhancement project, production costs that are too high relative to gain, will not allow continuation of the project. Potential increase in yield, as a result of increasing seeding size, has limits because of rising costs and these must be quantified to allow accurate analysis. This model has allowed an insight into the limitations set by natural processes, such as mortality rate, before the production process has begun (Schiel 1993, Hilborn 1998, Moksness et al. 1998).

Production costs can be much lower than the quoted purchase prices and optimizing potential income would mean producing or purchasing low-cost abalone seed. A trade-off not only exists between supply and demand in terms of the market price of abalone, but also between market price and the seeding strategy and site characteristics of the project concerned. Abalone ranching production costs must be seen to include both the negative effect of initial seeding mortalities and the negative effect of the potential differential mortality rates, reflected in total mortality (Z). The influence that these two variables have on the potential viability of a ranching project, and the lack of experimental data concerning these variables, emphasizes the need for empirical research in this field. Every seeding exercise, and its analysis, must be seen as multi-dimensional. Each site is different and must be evaluated accordingly. By accumulating data from different sites and compiling these data a quantified understanding of successful seeding operations will begin to emerge.

As stated previously, the relationship between the variability in intra-population growth rates for *H. midae*, and its impact on the variability in Z , has not been built into the model. The extent to which the model has simplified growth rates and mortality coefficients justifies the use of the model to predict trends but not exact values.

Interpreting the ecological attributes of suitable seeding sites, and the biological implications of seeding size, influences the analysis of economical modelling and the interpretation of results. As soon as ecological constraints or limiting factors are recognized, their effect on the economic model must also be accepted. The results from the study so far indicate strongly that there are both minimum and maximum

ecological thresholds with respect to survival rates and seeding sizes. Results have also shown that within the ecological parameters associated with a specific seeding area, management can manipulate the value of Z by altering seeding size. These thresholds will be affected by the specific characteristics of each area, and rather must be seen as indicators of a range of values that can be utilized by managers. While management options and skills are variable to a large degree, restraints set by the ecological factors that drive the system are much more rigid. A better understanding of the ecological factors associated with abalone ranching will mean better decision-making and better utilization of financial, natural and economical resources.

Many marine invertebrates appear to have constant survival rates once they pass the early juvenile phase, and so the survival rate is often no different for a 5- or a 50-year-old individual (Ebert 1999). Abalone, once they have become emergent, exhibit this type of life pattern until they become senescent. It is also this general emergent-age-class, on which most analyses on growth, stock abundance and survival rates are done. Juveniles, regardless of whether they are seeded or recruit naturally, are far more difficult to find and to study on a large scale. While survivorship of natural emergent populations of abalone can give an indication of what to expect from seeded abalone once they have reached the emergent phase, the biggest challenge is to quantify and optimize seed survival in the earlier cryptic phase. It is in this cryptic phase that survival is most variable and in which growth rates are the highest and extremely variable. The simplistic approach taken in this chapter, with respect to the relationship between growth and survival, camouflages an otherwise complex relationship that will be highly variable, and also definitely influenced by seeding habitat. It is easier to identify potential trends than it is to attempt to make exact

projections with respect to growth rates and recovery rates. The assumptions made in this chapter are again applied in the work described in the next chapter where the model was used to investigate assumptions made when predicting yield for a potential ranching area.

University of Cape Town

CHAPTER 7.

DETERMINING POTENTIAL YIELD OF SEEDING SITES

7.1 INTRODUCTION

As abalone ranching along the Namaqualand coast develops, understanding production and its benefits to the local economy will motivate investors. Due to the close association between *H. midae* and the kelp species *Ecklonia maxima*, kelp distribution and biomass has been used as an indicator for abalone biomass (Tarr 2000, Sampson et al. 2001). Using GIS techniques, Sampson et al. (2001) estimated the surface area of patches of kelp along a stretch of Namaqualand coastline from approximately 20 km north of Port Nolloth, to approximately 44 km south (Figure 3.1). In total, the length of coastline where kelp was recorded was 41 km, and the average width of the kelp bed perpendicular to the coastline was approximately 50 m. Using commercial Total Allowable Catch (TAC) figures (Stuttaford 1998), and the associated recorded kelp surface area from TAC areas (Figure 1.2), Sampson et al. (2001) estimated a potential total sustainable abalone biomass of approximately 1000 kg per ha of kelp. Of this, 55% is regarded as meeting legal harvestable size (shell length >137 mm, whole wet mass in shell approximately 0.5 kg), or 0.057 kg of legal-sized abalone per m² of kelp. This equates to approximately 0.11 legal-sized abalone m⁻², or about 108 tonnes of abalone over 188 ha or 1 880 000 m² of kelp. These predictions rely on the close association of abalone with typical west-coast kelp habitat (Tarr 2000, Dichmont et al. 2000). The method of estimation assumes the following:

1. Surface area of kelp equates to surface area of habitat suitable for adult abalone.
2. Habitat suitable to allow successful recruitment and successful development of all lifecycle stages from recruitment to adulthood is present, or else exists close enough to the kelp beds to allow successful recruitment into the kelp bed.
3. The degree of aggregation of abalone in the kelp beds is similar to other areas for which potential yield has been calculated (Douros 1987, McShane 1991, McShane 1992, Hart et al. 1997, Hart & Gorfine 1997, Dichmont et al. 2000, Tarr 2000).
4. The TAC is a true indication of the abalone production for that specific area (Tarr 2000, Dichmont et al. 2000).
5. The environmental factors that determine abalone production in the TAC area will be similar in the area in which potential yield is being calculated.

For the purpose of this chapter, the above assumptions pertaining to the environmental factors relating to abalone production and aggregations of abalone are acceptable. Both kelp and abalone exist in the TAC areas and, in a general sense, it has been shown that they do, or can, exist in the experimental ranching areas on the Namaqualand coast. The TAC yields originate from the entire TAC area and, as a result, the aggregatory behaviour of abalone is incorporated into estimates of abalone abundance and the relationship between their abundance and kelp. If this relationship is used to predict yield in other kelp beds, then aggregatory patterns are automatically assumed to be similar in the potential abalone-producing areas. Certain environmental factors determine both kelp and abalone production. Kelp is an established part of the Namaqualand coastal ecosystem, a fact that motivated the concept of introducing abalone to this area. The assumption is also acceptable based on the experiments and

the hypotheses that were tested in Chapter 4. The assumptions equating kelp habitat to habitat suitable for both abalone recruitment and juvenile development (as opposed to adult survival) are both crucial and open to debate. From personal observations made while diving along the Namaqualand coast, it was noticed that many kelp beds do not have habitat that corresponds to suitable habitat for seeding juvenile abalone as identified in the research. Since potential ranching yield will be the result of a successful seeding operation, success is the result of a combination of adequate site selection, the seeding of optimal-sized abalone and favourable long-term environmental conditions. No matter how suitable environmental conditions may be for adult abalone, ranching is founded on juvenile habitat.

TAC figures and catch per unit effort are not regarded as flawless measures of sustainability (Dichmont et al. 2000); the question of illegal harvests and the highly aggregatory behaviour of *H. midae* are increasingly considered in adaptive approaches to the management of the species in South Africa. However, TAC figures are an indication of minimum yield per area of natural stock. In this context, TAC figures are used here to make predictions concerning ranching yields along the Namaqualand coast.

In a sense, the seeding process replaces the process of natural recruitment. Natural mortality and an exponential population decline beginning with the larval stage through to an established juvenile population in a naturally recruiting population, can be significantly altered by successfully seeding. The overall objective of the study has been to identify the criteria that determine suitable seeding sites and the conditions under which seeding should take place. The results and hypotheses tested in the thesis

indicate that in typical west-coast kelp habitat on the Namaqualand coast, under-boulder habitat is the most important aspect of seeding sites. Thus, three factors must be considered by a potential seeding operation:

1. The area and size of the seeding site (suitable juvenile habitat).
2. The number of seed that will be used, given optimal seed size and condition (Chapters 4 and 6).
3. Prevailing environmental conditions (ensuring sufficient survival for the enterprise to be viable).

This allows a bottom-up approach to determining potential yield. It also allowed a further investigation of the model-generated dynamics developed in the previous chapter. By using the 1 888 000 m² area selected by Sampson et al. (2001), the potential yield of 0.11 abalone per m² of kelp bed (207 680 abalone), and the assumption that kelp habitat in some way equates with habitat suitable for juvenile abalone, it is possible to investigate the required seeding density under different differential survival regimes. In other words, it is possible to determine which values of total mortality (Z), associated with a seeding size of approximately 26-mm, are required to generate the potential yield predicted by Sampson et al. (2001). Based on the results from Chapters 4 and 6, 26-mm was selected as the optimal seeding size for juvenile abalone.

In the model, Z -values are an indication of mortality as a result of seeding-induced mortality together with subsequent natural mortality (Chapter 6). The initial seeding density used in the model can be regarded as the seeding density of 26-mm abalone in

suitable habitat that will result in a pre-harvest density of approximately 0.11 legal-sized abalone m^{-2} . The relationship between surface area of kelp and suitable juvenile seeding habitat is not known. However, a sustainable relationship between kelp surface area and habitat suitable for natural recruitment, must exist to allow viable commercial harvest areas such as the present TAC areas. This principle introduces the assumption that kelp beds in non-TAC areas will be able to support introduced populations of abalone. It is the same principle that needs to be further investigated in order to predict potential abalone yield along the Namaqualand coast.

7.2 METHODS

The model developed in Chapter 6 was used in this chapter. Based on the outcome of the seeding-size and cost-benefit analyses done in Chapters 4 and 6, 26-mm abalone were selected for the simulated seeding operation. The growth parameters relating to a Robben Island data set (Tarr 1993, 1995, Table 6.2) were used. The average time taken for an abalone to reach the legal mass was estimated at 9 years. Initial population numbers were manipulated for the range of differential survival factors shown in simulations (Table 6.1) until the number of abalone that reached legal size (after 9 years) resulted in a density of approximately 0.11 abalone m^{-2} over an area of 1 888 000 m^2 (Sampson et al. 2001). Initial population number and average total Z were recorded for each simulation beginning with 26-mm abalone (Table 6.1).

An increased growth rate would mean that harvest size can be reached sooner, and also that survival per age class would increase, as the abalone became bigger. However, the variability of growth rate within a population, and the relationship

between changing growth rates and survival per age class is not known for seeded abalone. While it is acknowledged that variation in growth rate will impact on variation in survival per age class, the effect has not been incorporated into this model.

7.3 RESULTS

Table 7.1 summarizes the results from simulations done to determine the number of seed (average length 26-mm) required to produce a pre-harvest density of 0.11 abalone m^{-2} (Sampson et al. 2001). For the set area, 1 888 000 m^2 , the required seed number decreased from 2.22 million with an average Z of -0.25 to 0.86 million with an average Z of -0.15. The higher the total mortality, the higher the number of seed that were required to yield the same biomass. The profit ratios show that the ratio between seeding costs and selling costs increases as total Z decreases.

The data presented in Table 7.1 must be considered in two contexts. First, there is the ecological context where both seeding and natural mortality determine Z , and so determine the rate of population decline over time. In this case, Z is a result of differential mortality and not variation in growth rate. On the scale of the simulations, the Z factor does not change as the proportion of suitable seeding habitat decreases, nor is it affected by economic parameters. Z is variable over time and related to numerous environmental factors (see previous chapters), and it is specific to a seeding area. As previously discussed, the only impact that management can make on Z is through selection of suitable sites and optimum seeding sizes. The second context in which the results can be interpreted is an economic one. Economic parameters are

Table 7.1 Number of seed abalone (26-mm) needed to produce the same average density of legal-sized abalone ($0.11 \text{ abalone m}^{-2}$) calculated for the commercial TAC areas (Sampson et al. 2001). In each case the simulation was done for an area of $1\,888\,000 \text{ m}^2$. Average Z values indicate the average total mortality indicated in the simulation when using specific differential survival factors. The cost price of 26-mm abalone was set at R4 each. The selling price for the abalone was R19.44 million in all cases. Profit ratios show the relationship between the cost of seed and selling price. In each simulation harvest size was reached after 9 years (Tarr 1993, 1995).

Simulation (see Table 6.1A)	Average Z (constant IS of 0.56)	Seed number (million)	Cost of seed (million R)	Profit ratio (selling price/ purchase price)	Pre-harvest density of legal (0.5 kg) abalone (207 680 abalone) (m^{-2})
1	-0.25	2.22	8.9	2.2	0.11
2	-0.19	1.25	5	3.9	0.11
3	-0.17	1.04	4.16	4.7	0.11
4	-0.16	0.95	3.8	5.1	0.11
5	-0.15	0.86	3.44	5.7	0.11

highly variable and market-driven. The economic parameters that drive decision-making cannot influence ecological parameters, or at least only function within the ecological parameters that determine population numbers. Favourable economic parameters may allow risk-taking even in the presence of unfavorable ecological constraints, such as less than ideal seeding habitat or bad sea conditions.

Within the economic parameters described here (26-mm abalone seeded at R4 each, and sold at R 180 kg⁻²) a Z value of -0.25 generates a profit-ratio of ≈ 2.2 . In other words, even within the most unfavourable differential survival scenario modelled, the profit-ratio was positive (a ratio of 1 would signify break-even). This suggests that if seeding 26-mm abalone in suitable habitat results in total Z values in the range modelled (i.e. -0.25 to -0.15), the numbers required to seed enough 26-mm abalone to yield the relative pre-harvest densities found in the TAC areas, will result in a favourable cost-benefit ratio. For example, even an average Z value of -0.25 was not high enough to cause less than positive returns.

7.4 DISCUSSION

Within the context of a seeding operation, rate of total mortality (Z) can be seen as an indicator of risk due to total mortality. It is not possible to calculate a Z value beforehand for natural (existing) circumstances. Rather, one must model a situation and derive a Z value from that; if the Z value is higher than a specific value, the yield will not exceed break-even levels. It is only possible to manipulate Z by identifying those criteria that could increase survival. Several criteria have been identified in the

previous chapters; the results may be utilized in attempting to determine potential yield, from the time of initiation of the seeded population up to the time of harvesting.

To predict potential yield from a seeding operation one must determine:

1. The area in which seeding is going to take place, and the seeding density.
2. The area in which harvesting is going to take place and the potential pre-harvest density of harvestable abalone.
3. The relationship between initial seeding density and pre-harvest density (or total mortality Z).

From a practical point of view, the most fundamental aspect of predicting the potential yield of an abalone ranching area is choosing the seeding site and understanding how well the site meets the criteria for suitable seeding habitat. Without this knowledge it may be possible to equate kelp surface area to some degree with suitable habitat for adult abalone, but it is not possible to foresee the results of a seeding operation. Certain kelp beds may not offer suitable seeding habitat. And, ultimately, the area of suitable seeding habitat must be linked to the decline in number of seeded abalone between seeding and harvesting.

Research is still at a “what if” stage in regard to both identifying all the conditions that will benefit *H. midae* seeding operations and maximise potential yield. It is not possible to use conventional effort-based stock-assessment models to determine potential yield for seeding operations that must still be initiated. Recruitment in abalone has been shown to be highly variable, both with respect to the relationship

between the numbers of broodstock and recruits and with respect to area and time (Tegner 1985, Shepherd 1990, McShane 1992, Slattery 1992, Shepherd 1998, Tegner 2000, Shepherd 2000). Possibly, seeding juvenile abalone may cause a relative decrease in variation of their rate of survival as compared to wild juvenile abalone.

Although seeding area, seeding density, initial survival and survivorship and growth are all variable, they are each linked in determining potential yield. Seeding is not the beginning of an open-ended production line, it is part of a regulated system, which may be highly variable with respect to ecological factors that contribute to the system but which is definite in outcome. The effect of density-dependence has been shown to be pronounced in post-settlement *Haliotis rubra*, such that mortality increases with an increase in density (McShane 1991). In the species *H. laevigata* and *H. scalaris*, mortality in juveniles aged 2–8 months was shown to be density dependent. As the animals aged from 8 months to 3–4 years, mortality became either independent of density (Shepherd 1998), or, in some cases, density dependent (Shepherd 1990). There is also evidence of density-dependent mortality among pre-recruits (Shepherd 1990). Although several studies have indicated the strong effect that density dependence has on the survival of pre- and post-settling abalone (and, consequently, on seeded juveniles) there is also evidence that space limitation has a definite impact on some abalone species. Dourous (1987) has shown that dense populations of adult *H. cracherodii* are characterized by secondary substratum use, as they stack on top of each other in a facultative response to space limitation. *H. midae* is regarded as showing a high degree of aggregatory behaviour, and this behaviour and the degree to which aggregation takes place are affected by fishing (Dichmont et al. 2000)—another indication of density dependent behaviour.

The process that determines average densities of abalone at different lifecycle stages is complex, and it is difficult to determine which stage most determines population number at time of harvest. Total population could be restricted by recruitment, or it could be a result of density-dependent factors affecting adults. These factors will change, both short term and long term. For example, they may range seasonally as a result of food availability, or over a longer time period as a result of global warming and increased water temperatures.

To model a population using survival data and growth parameters is a reasonably simple task. Once an acceptable model has been developed it is possible to investigate patterns and trends in populations. However, to be able to use a model to predict values that are realistic, the parameters used in the model and the mechanics of the model must be reliable. The model developed in this thesis can be used to show trends and relationships between variables such as seeding size and survival and seeding and harvest figures. It cannot generate absolute values. The model uses a combination of experimental survival data and hypothetical differential survival scenarios resulting in a range of total mortality rates (Z). Within the economic parameters described here (26-mm abalone seeded at R4 each, and sold at R180 kg⁻²) a Z value of -0.25 generates a profit-ratio of ≈ 2.2 . In this context, the model suggests that if total mortality (Z) was lower than -0.25, ranching in this area would be viable (the profit ratio of 2.2 for a Z value of -0.25 suggests that even if Z were slightly higher, ranching would still be viable). Data from the short-term survival experiments are interpreted only as that, but the combination of these data together with long-term differential survival scenarios can give indications of actual long-term survival. The

Table 7.1 are a fundamental part of the acceptance of the model output. A range of total mortality rates have been calculated for other species of *Haliotis* and these can be compared to those generated by the model (Tables 6.1, 7.1). A long-term study on *H. laevis* showed total mortality coefficients for wild abalone older than 3.5 years that ranged from 0.02 to 0.86 per annum (Shepherd 1990). Total mortality for juveniles less than 8 months old was calculated between 0.05 and 0.4 per month, while for older abalone 8 months to 4 years, total mortality ranged from 0.2 to 3.2 per year (Shepherd 1998). It is clear from the results of these long-term studies, that under natural conditions, total mortality rates (Z) for abalone, including emergent adults, are highly variable. The Z values generated by the model must be seen within the context of a highly variable environment in which natural Z factors will differ from year to year and from site to site. Environmental factors that drive Z are almost exclusively beyond the control of management, except for decisions made about seeding-size and site selection. Those decisions will determine to what extent seeding-induced mortality and natural mortality will influence population numbers over time. This must be kept in mind when predicting potential yield.

Recovery rates have been reported for different abalone species in different habitats in the United States, New Zealand, Japan and Australia (Tegner & Butler 1985, Tegner 2000, Shepherd et al. 2000). The long-term results of Japanese seeding projects are difficult to incorporate into the context of seeding juveniles into natural habitat. In Japan there is extensive harvesting of other marine species, including some that predate on juvenile abalone, abalone yield must be regarded in this context (Tegner & Butler 1985, Tegner 2000). In a two-dimensional world, with survival per age class a consistent and constant figure, the relationship between seeding density and harvest

density would be straightforward. In reality there is a diverse range of environmental factors that affect this relationship. In South Africa there is also a serious problem with respect to the amount of abalone that are removed illegally, as well as doubt about the accuracy of estimates regarding the actual size of the areas in which abalone recruitment and harvesting is taking place.

To compare natural stocks and the potential of ranched stocks a fundamental comparison has to be made between shallow subtidal habitat from both areas, with an account of kelp biomass and substratum topography being most important. The Namaqualand coast and the areas from which the TACs were taken both have an abundance of kelp. It has been assumed that food is not a limiting factor in either of the two areas. This is not an assumption that can be made absolutely, and areas will have to be evaluated individually.

All the experimental sites in McDougall's Bay and Stilbaai were done in kelp beds. The survival rates for seeded abalone in McDougall's Bay correlated most with the amount of boulders <30 cm in diameter, which comprised approximately 16% of the McDougall's Bay area and approximately 13% of the Stilbaai area (Tables 4.1, 4.2 and 4.3). While the Spearman Rank Order Correlation analyses used in Chapter 4 indicate more precise results, it can be generally assumed that, areas with boulders <50 cm could provide shelter for young abalone. Using the percentage cover estimates done at experimental seeding sites ranging from Kleinsee to McDougall's Bay, the average occurrence of boulders with a diameter <50 cm was approximately 40% within the seeding sites. If the figures for the area consisting of boulders <30 cm are used as an indication of the substratum description for the rest of the area around

Port Nolloth, it means that suitable seeding area comprises less than 25% of the kelp bed area. The most important conclusion from this portion of the work may be that to attempt to predict potential yield, it is necessary to have an understanding of the ecological processes that drive total mortality (Z) and essential to have accurate measurements of suitable habitat size.

It is possible to develop realistic limits against which ecological processes can be measured. In a sense, abalone seeding is an ecological process that can be measured. The scale at which seeding takes place, and the extent to which variables can be simplified and assumed to be constant between areas, determines the extent to which estimates can be considered realistic. The density-dependence of juvenile abalone, and the understanding that there is variability in the survival of different age classes of abalone, allows for realistic scenarios to be developed and evaluated.

The relationship between adult habitat and suitable juvenile habitat should be further investigated. The Eastern Cape of South Africa supports populations of *H. midae* in areas where kelp beds are negligible (Introduction, Chapter 4). Then, how can one predict yield of seeding operations in areas where there are no kelp beds? One of the common denominators in otherwise diverse areas where *H. midae* occurs seems to be juvenile habitat. The abundance of habitat suitable to juveniles and the density-dependent factors that drive recruitment will place a limit on maximum recruitment rate regardless of the broodstock number or favourable environmental factors. In seeding operations such habitat will play a determining role in potential yield.

CHAPTER 8.

GENERAL CONCLUSIONS

8.1 SUMMARY OF EXPERIMENTAL RESULTS

Seven hypotheses tested in the course of the study are listed in Figure 8.1 and the most important results that determined the acceptance or rejection of the hypotheses are summarized in Figure 8.2. The general hypothesis that the Namaqualand coast can support those stages of the lifecycle of *H. midae* needed for successful ranching is largely based, on the acceptance of a specific hypotheses that small boulder habitat provides essential shelter to seeded juvenile abalone. The selectivity analyses (Figure 8.2) show the importance of habitat with boulders <50 cm to abalone 14–26 mm, both at Gouriqua and Port Nolloth. The presence of urchins seemed to have an insignificant effect on the survival of juvenile abalone 14–26 mm in size, even though they showed a positive selection for them (Figure 8.2), thus site selection could rather be based on the presence of boulders <50 cm in diameter. The effect of increasing seeding size on both initial post-seeding survival and the subsequent long-term effect of differential mortality on total Z , may clearly determine the benefits associated with combining suitable habitat and the seeding of abalone ≈ 25 mm. In short, the viability of potential ranching operations will depend on appropriate site selection, seed quality and size selection, a favourable differential mortality rate (reflected in Z), and favourable economic conditions. Of these, site selection, seed quality and seed size can be controlled by management. Hence, the most fundamental concept behind ranching is that one needs to understand the local ecological system and the limiting factors within it.

PO as a small rock

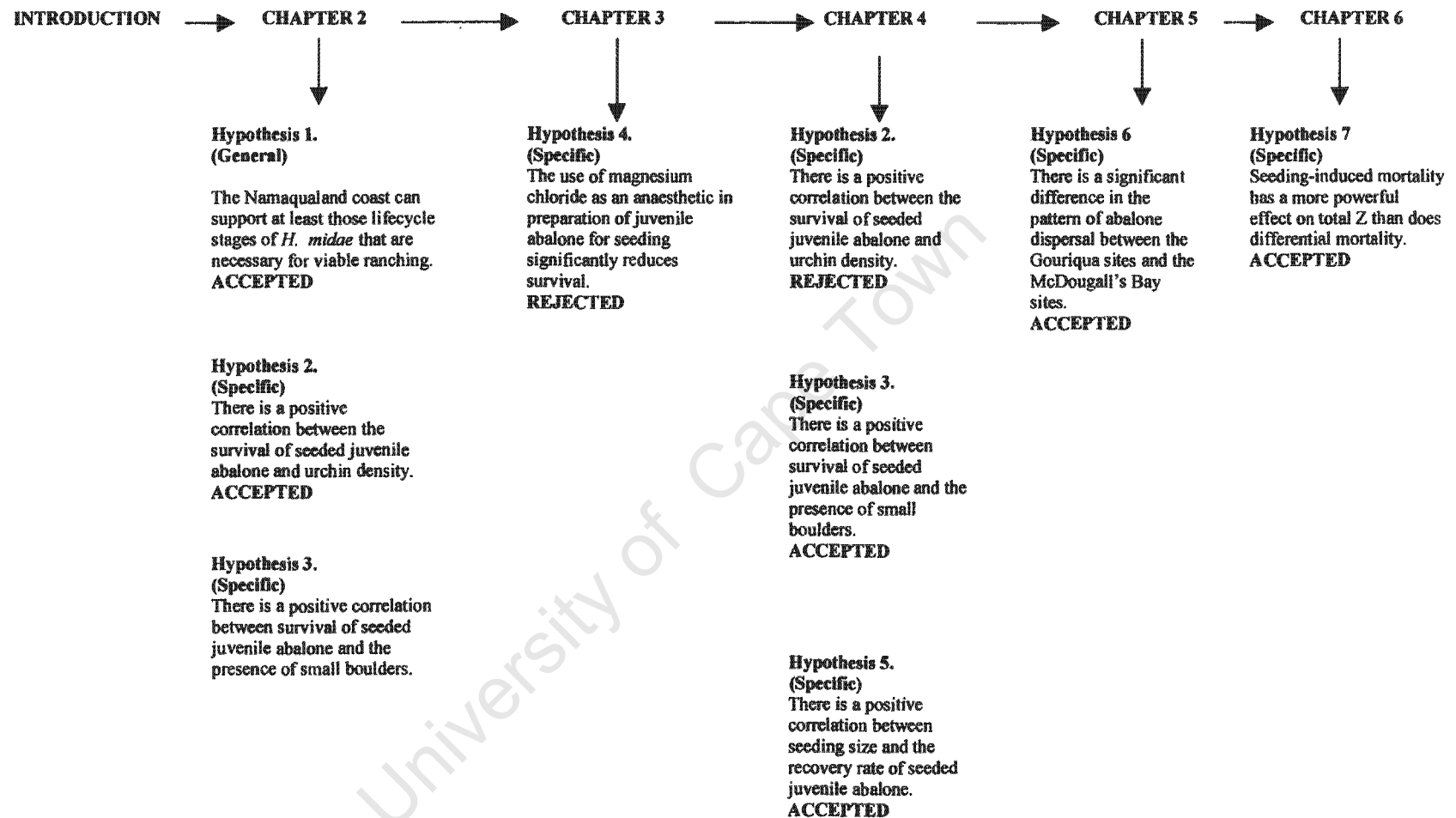
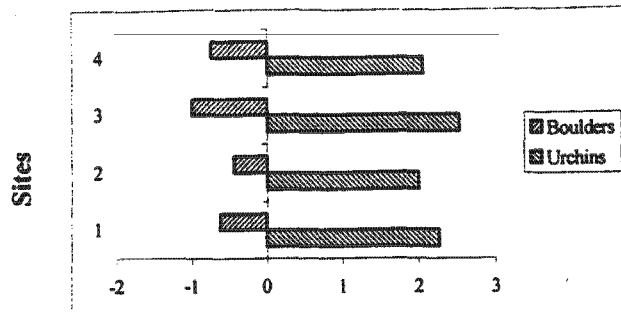
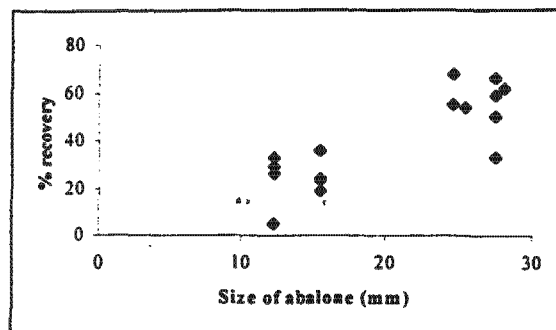


Figure 8.1 Flow chart showing the development of hypotheses based on seeding experiments described in Chapters 2, 3, 4, 5 and 6. See Figure 8.2.

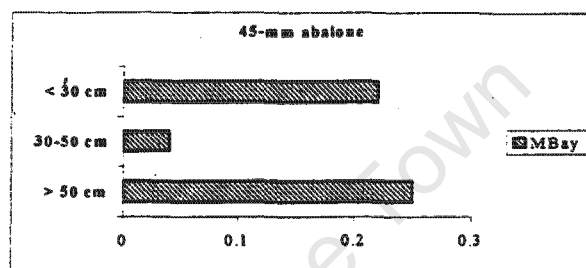
Boulder categories



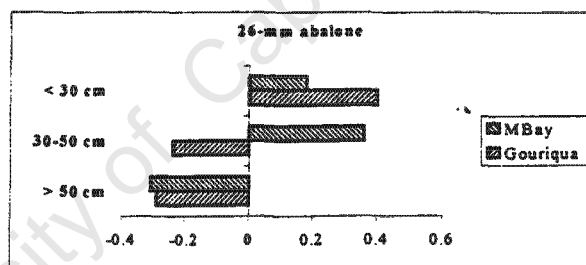
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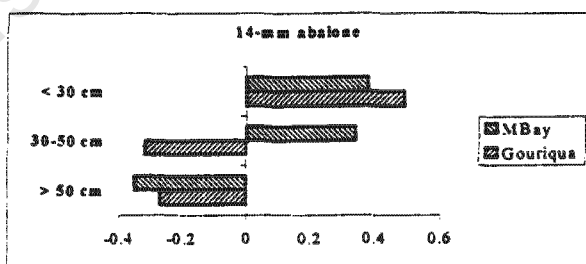
B



C



D



E

Selectivity index ($\text{Log}_{10}W$)

Figure 8.2 Summary of the selectivity analyses showing: A) the extent to which 14-mm abalone selected for urchins in McDougall's Bay, B) the effect of seeding size on recovery rate, and C, D and E) the extent that abalone in different size-classes selected boulders of different size classes. At McDougall's Bay the 14-mm abalone selected boulders <30 cm and 30-50 cm, the stronger selection being for smaller boulders. At Gouriqua the 14-mm abalone selected <30 cm boulders. At McDougall's Bay the 26-mm abalone also selected both <30 cm and 30-50 cm, in this case, however, the larger abalone made the stronger selection for the larger boulders, while abalone at Gouriqua selected only boulders <30 cm. The 45-mm abalone showed the strongest selection for boulders >50 cm.

8.2 ECOLOGICAL LIMITING FACTORS

Ecological limiting factors that have a direct influence on seeded juvenile abalone, and that can be quantified regardless of the financial implications, are as follows:

8.2.1 Physical condition of the site with respect to boulder size and amount of exposed area

Boulder size and abundance and the amount of exposed area in experimental sites at McDougall's Bay, Stilbaai and Gouriqua were quantified in Chapters 4. Results showed that wherever it was possible to differentiate between degrees of cover and boulder size, the most important factor was whether or not there was an abundance of cover. Areas that are marginal in this respect should not be used. The experiments recorded in Chapter 4 and the experiments reported by Day and Branch (in press), strongly indicate that the relationship between urchin density and juvenile abalone may be influenced by the amount of exposed habitat. When physical shelter is limited, protection provided by urchins may be vital for the survival of juvenile abalone (Day & Branch in press). In my experiments, however, removal of urchins had no effect on degree of recovery of seeded juvenile abalone because there was an abundance of shelter in the form of rock cover. This emphasizes the importance of site selection and the concept of approaching a seeding operation with a holistic point of view, taking as much into consideration as possible. Site selection would have to include habitat required by adult abalone. While certain ecological requirements are specific for juvenile abalone with respect to habitat, larger abalone may have habitat requirements

that are not met by sites that are suitable for seeding juveniles. Seeding sites that do not have the potential to support both juvenile and adult abalone, would in effect seriously limit potential ranching or enhancement projects.

8.2.2 General ocean conditions at the time of seeding and immediately afterwards

Although ocean conditions were not quantified directly, evidence presented in Chapters 2 and 4 suggests that surf action and strong ocean currents, combined with the movements of sand, crushed shell material and shale, have a direct effect on the survival of seeded juvenile abalone. This influence is probably of greatest importance at or shortly after, seeding and is most likely to affect short-term seeding-induced mortality rather than long-term differential mortality. The experiments at McDougall's Bay and Gouriqua showed that although deeper water countered the effect of direct surf action, depth did not prevent strong currents from adversely affecting seeding sites.

8.2.3 Size of abalone at seeding

The size-experiments described in Chapter 4 showed that abalone seeding size has a direct effect on recovery rate and potential survival rate of seeded abalone. Seeding size also has a direct effect on the habitat selected by the seeded abalone, the presence or absence of urchins may still affect the recovery of very small abalone (below the size range used in my experiments). As a result, site selection based on the abundance

of boulders may be incorrect if seeding sizes outside the range in these experiments are used.

Ecological factors that have been addressed, and partially quantified, include boulder size, exposure to surf action and adverse sea conditions and size at seeding. Disregarding other less tangible factors, and assuming that there is an abundance of boulders <50 cm in diameter at all sites selected as being suitable, it is possible to construct a hypothetical three-dimensional set of constraints that can direct decision-making with respect to selecting seeding areas and seed size (Figure 8.3). Smaller animals can be seeded in protected areas, and larger animals should be seeded in more exposed areas. However, each site must be evaluated with respect to physical attributes of the substratum, ocean conditions and suitable seeding times. In general, economic returns will be greater when seeding with ≈ 25 -mm abalone than with ≈ 14 -mm abalone.

8.2.4 Food and growth

None of the experiments attempted to quantify the availability of macroalgal species that may provide food for seeded populations. Based on the abundance of typical west-coast kelp-bed habitat along the Namaqualand coast, food is not considered a limiting factor to abalone ranching. However, when seeding areas where natural stocks occur, it cannot be assumed that food will not be a limiting factor. There, low abalone densities may be an indication of low levels of food. This may also be the case in marginal areas, or in areas where environmental factors have changed to the extent that natural abalone have decreased in numbers.

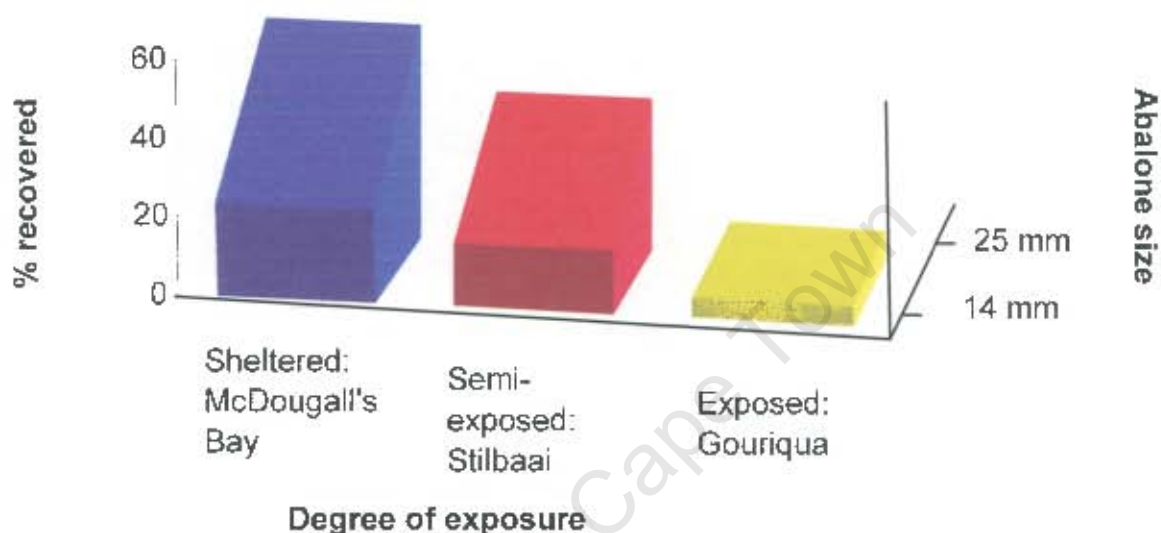


Figure 8.3 Three-dimensional graph showing some quantifiable factors that can facilitate the selection process and potential outcome of a seeding site. The percentage recovery and the seeding size are based on experimental data; degree of exposure is based on unquantified observations of sites. Exposure means the extent to which adverse ocean conditions, such as swells and currents, will affect the site, during and immediately afterward seeding. Depth is another factor that will determine the degree of exposure. Gouriqua is regarded as a site having extreme exposure, Stilbaai as a semi-protected one and McDougall's Bay as protected. Within the different areas, sites were selected according to boulder size and abundance to ensure that seeded abalone had the potential to survive.

A range of growth rates and parameters reported for *H. midae* (Tarr 1993, 1995, Fielding 1995) are attributed in part to water temperatures and in part to diet. Diet is determined by the variable abundance of different algal species in areas with naturally occurring stocks of *H. midae*. The abalone that occur east of Cape Agulhus have been shown to be smaller at sexual maturity and to grow relatively faster than those that occur to the west (Fielding 1995, Tarr 1995). The spreadsheet model developed in Chapter 6 used growth parameters relating to abalone from the south-western Cape (Tarr 1995). These growth parameters are from areas with slightly varying temperatures, but where the predominant algal species is *Ecklonia maxima* (forming typical west-coast kelp beds, Sweijd et al. 1998). As a result, the effect of temperature on growth may over-shadow the more subtle effects of algal biomass and diet. No doubt, diet influences growth in abalone, and the growth rate of seeded abalone is determined by a combination of ecological factors which include the availability of different algal species. Until long-term growth data are collected from abalone seeded along the Namaqualand coast, growth parameters from *H. midae* along the south-western coast must be used (Tarr 1995, Sweijd et al. 1998).

8.3 HANDLING AND STOCKING CONSTRAINTS

Handling large numbers of juvenile abalone can be problematic since stress in abalone is associated with touching and packing. The anaesthetic experiments conducted in Chapter 3 showed that, magnesium chloride, in the prescribed doses, can be used to anaesthetize juvenile abalone packed for seeding; however, it is my opinion that the use of anaesthetic should be avoided. More research is needed on the long-term

effects of this anaesthetic on the behaviour of juvenile abalone released into the ocean.

The method of seeding and the choice of using modules or releasing the abalone by hand (scattering them either above the water or directly over the substratum), determines, to a large extent, the density of seeded juveniles in a specific area. In present experiments in the Eastern Cape, abalone are released by hand over areas approximately 50m x 50m, to achieve densities between 10 and 20 abalone m⁻² (unpublished original data). These experiments may reveal whether or not seeding in low densities is more favourable than releasing abalone from modules, since the juveniles would not have to disperse to compensate for over-crowding, and as a result, would not be exposed to predation while moving (see also Shepherd 2001). More research on seeding techniques will help to resolve certain logistical problems that face abalone ranchers.

8.4 MANAGEMENT CONSTRAINTS

Commercial abalone quotas in South Africa are set by the government, and vary year-by-year with respect to both the size and allocation of harvest quotas. Partly because of dissatisfaction with quotas and allocations, but mainly due to greed and inadequate enforcement, poaching has become as great a threat to abalone stocks as it is for many natural resources on land and in the oceans (Craik 1994, Vega et al. 1994, De Alessi 1995, Caddy 1999). The experimental concession granted by the South African government to Port Nolloth Sea Farms allows exclusive rights to seeding and harvesting abalone along a 60-km stretch of coastline in Namaqualand. This right can

be regarded as a form of territorial user right in fisheries (TURF). While experimental, it establishes a shift from open-access user rights in the fishing industry, to new paradigms in marine resource management (Stephenson 1995, Surtida 1998, Caddy 1999). Port Nolloth Sea Farms are sole owners of the stock in the designated area, and this sets a precedent that may have long-term implications for abalone stocks in South Africa, both seeded and natural. The potential harvest from a 60-km zone is nearly equivalent in both tonnage and potential income to that from the present commercial harvest enterprises in the country. The stock belongs to a small group of people with strong motivation to manage the resource and to protect their investment. The potential exists for a broodstock to develop that may recruit naturally. If that happens, ownership of the natural recruits must be determined. Any abalone that develop along the Namaqualand coast will be the result of the seeding operation and the justification for sole ownership can be argued on these grounds. Although there are no current costs to securing exclusive use of the sea bed for abalone ranching, this may change in the future, influencing input costs and potential benefits.

The concept of ownership will constitute a fundamental difference between seeded stocks and natural stocks. Already the South African government has granted two other experimental concessions, on a much smaller basis, that allow seeding experiments in areas with natural stocks. Sole ownership of all abalone in such areas is problematic. The concept of ownership and vested interest due to financial benefits has long been hailed as a proven method of ensuring sustainable utilization of renewable resources (Craik 1994, Vega et al. 1994, De Alessi 1995). Ample evidence of this exists with respect to terrestrial conservation. The management of marine resources will become a more complicated issue if abalone quotas become private

property and transferable as an asset from one "owner" to another. The allocation of natural resources in a country as socially complex as South Africa must be seen in the context of the sociopolitical environment in which those resources exist. The evolution of the sociopolitical system in the country will require that resource management systems evolve at the same tempo. It is quite possible that the allocation of private property rights, for seeding and harvesting abalone in the vicinity of Port Nolloth, is a first step in that direction. The success of private ventures that involve stock enhancement may also motivate the government to invest revenue received from the commercial abalone industry in stock-enhancement research. There is a growing trend worldwide to manage marine resources with this approach, and there is ample evidence to suggest that abalone has the potential to lend itself to this approach (Emmet & Jamieson 1988, Grimes 1998, Hilborn 1998, Howell et al. 1999).

8.5 CONSERVATION IMPLICATIONS

The development of seeding technology as an option to mitigate the radical decrease in natural *H. midae* stocks will be governed by a set of financial and economic constraints that is far removed from those that govern a commercial operation. The values attached to the protection of a species mature as it becomes more apparent that short-term financial gain has caused massive degradation of both habitat and species diversity worldwide (Carr & Reed 1993, Munashinge 1994, De Alessi 1995). For the reintroduction or enhancement of broodstock in areas where traditional commercial fisheries have provided an important source of employment and income, the price of both research and seeding can be much higher than what is acceptable in a commercial ranching scenario. The time scale over which such a project is evaluated

should not be as limited as that over which a commercial seeding operation is evaluated, as the time needed to ensure that natural recruitment is taking place after seeding may require many years.

In terms of conservation, the values attached to ecosystems and species can be so diverse and innovative that the concept of financial costs moves into a completely different sphere (Cacha 1994, Craik 1994, Munashinge 1994). The potential effects of introducing *H. midae* to Namaqualand where it does not currently exist, needs careful consideration. *H. midae* is capable of attaining extremely high densities and biomass (Tarr 2000) and could transform the dynamics of the shallow, coastal ecosystem if seeding occurs.

The valuation of biodiversity, in itself, has increased motivation to spend money and energy on research into the reintroduction of species. Research into seeding technology and stock enhancement of *H. midae* needs to move into the realm of conservation and species protection (Shepherd & Brown 1993). This will facilitate research into aspects of abalone recruitment and population dynamics that are of little interest to commercial ranchers, but will aid enhancement of natural stocks and restoration of functioning broodstock. There is potential for the establishment of broodstock areas that can act as refugia for a heavily exploited resource, if those refugia are protected (Duggan & Davis 1993, Tegner 1993, Shepherd & Brown 1993, Shepherd et al. 2001). Seeding technology can be used to establish broodstock areas. However, this can only be done if those areas are actually protected and if the source of abalone broodstock is genetically acceptable. The establishment of new, naturally recruiting populations will allow investigation into the population dynamics, meta-

population theory and what constitutes a minimum viable population as it applies to this species (Shepherd & Brown 1993). Such data could provide valuable insight into the long-term conservation of the species.

The high variability in survival rates for different species of *Haliotis* has led some researchers to speculate that seeding for economic gain will, in general, not prove viable, whereas seeding to enhance declining stocks for conservation purposes is more often regarded as feasible and important (Shepherd et al. 2000, Tegner 2000).

8.6 POTENTIAL RANCHING YIELD

Financial restraints and implications limit the commercial viability of a ranching program. Each project should be evaluated with respect to specific goals, be it short-term financial gain, or long-term ecological gain. It is quite possible for a seeding site to experience high survival of seeded juveniles, while the ranching project itself is not economically viable. It is also quite possible, perhaps predictable, that some ranching projects will fail as a result of poor management. Economic expectations and ecological realities are strongly linked, ecological realities need to be understood before economic expectations can be formulated.

Yield varies according to the abundance of suitable habitat. Each potential abalone ranching site must be individually evaluated and predictions must be area-specific. The results from this study and data from contemporary literature reveal that mortality of juvenile abalone, both natural and seeded, is site-specific and highly variable. To a large extent, this is also true for adult abalone (Shepherd 1990, Schiel 1992, Schiel

1993, Shepherd 1998, Shepherd et al. 2000, Tegner 2000). Potential yield projections based on habitat suitability and the abundance of food (Sampson et al. 2001) must also consider seeding habitat, growth rates and survival of juvenile abalone. Juveniles have to be seeded, survive and grow to harvestable size to complete the ranching process.

The spreadsheet models developed in this thesis show that, given suitable habitat, long-term yield depends to a large extent on the size of seeded juveniles. Increased initial survival achieved by seeding with larger abalone results in lower long-term total mortality rate. Prevailing economic constraints determine the choice made by management with respect to seeding size. The relationship between ecological parameters and economic ones must be considered holistically by potential managers.

By recognizing a dynamic relationship between ecological factors and economic factors, it is possible to design an abalone-seeding programme in which seeding and harvesting strategies yield optimal results.

8.7 FUTURE RESEARCH

Although this thesis has addressed a number of basic concepts specific to ranching *H. midae*, there are a number of topics of research that have been identified as being important in the general context of abalone ranching and potential stock enhancement:

1. The higher the initial survival of seeded juveniles, the greater the number of abalone with the potential to reach maturity. With this in mind, the potential effect of pre-release conditioning of juvenile abalone, both in terms of their capability to

adapt to the effect of stronger water currents than those experienced in the hatchery tanks, and to develop the ability to identify and respond to predators found in the wild, are crucial aspects that need to be investigated.

2. Optimal habitat-related stocking densities for abalone of different sizes, and efficient means of seeding vast numbers of abalone in appropriate stocking densities are important factors in the context of minimizing seeding costs.
3. Site-specific spatial/abundance relationships between the habitat required by juvenile abalone and habitat suitable for adult abalone, and the extent and pattern of dispersal between habitats undertaken by growing abalone require investigation. Specifically with regard to *H. midae*, this will facilitate potential estimates of yield in designated ranching areas along the Namaqualand coast.
4. Extensive research is required with respect to the potential release of fertilized abalone larvae. Successful larval release technology would have major beneficial implications for stock enhancement and commercial ranching.
5. A serious level of concern has been raised about the effect that releasing hatchery-reared juvenile abalone will have on genetic population structure of wild abalone. This is an internationally valid question, and whereas technology has been developed and used for a number of years to determine the genetic structure of wild abalone, this technology needs to be used to address the concept of large-scale releases of selectively bred abalone into the oceans.
6. With regard to *H. midae*, there is a need for extensive investigation into the population dynamics of the species, particularly with regard to differential mortality. In this context, seeding experiments need to be conducted over extended time periods, to determine to what extent and over what time periods

artificially reared abalone released into the wild follow patterns of mortality exhibited by natural populations.

These concepts are valid for most species of abalone, and although there may be species-specific differences, the development and exchange of scientific knowledge on an international scale is essential. This exchange has brought research on *H. midae* in South Africa to the point that it is today and must continue, particularly in view of the financial and institutional limitations that prevail in this country. Despite these limitations, however, research in South Africa has made its own unique contributions to the art of ranching abalone.

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University of Cape Town