USING SHELL MORPHOLOGY TO CHARACTERISE ABALONE POPULATIONS ACROSS MULTIPLE SPATIAL SCALES

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Declaration

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Abstract

Many sedentary marine invertebrates have a fine-scale (100s m) population structure that complicates their conservation and management. This is a consequence of the limited information on the boundaries between component populations and the biological variability among them. Blacklip abalone (*Haliotis rubra*) form discrete populations many of which are 'stunted' with individuals reaching a maximum length less than those in adjacent areas. A range of morphological measurements from samples of stunted and 'non-stunted' *H. rubra* collected from sites spread across broad (10s km) and fine (100s m) spatial scales in southern South Australia. In addition, information on the growth, size at maturity and fecundity of *H. rubra* was obtained from these same sites. The ratio between shell length and shell height showed clear and significant differences among samples from stunted and non-stunted sites. The fine-scale morphometric collections suggested that stunted populations existed at smaller spatial scales compared to those for non-stunted populations. Spatial variation in these key life history parameters could primarily be attributed to differences between stunted and non-stunted sites. Relationships between each of these parameters and the ratio between shell length and shell height were also examined. The spatial patterns in morphology and biology were highly correlated suggesting that shell length:shell height ratio can be used as a simple 'morphometric marker' to distinguish among populations of abalone and identify their biological characteristics.

The detection of differences *H. rubra* morphology among variable environments cannot determine whether these differences represent a plastic response to the local environment, or whether morphology is genetically fixed. A reciprocal transplant experiment was used to test whether stunted *H. rubra* are the result of a plastic response to the environment or fixed genetic trait. Furthermore, environmental factors that affect food availability were related to differences in morphology. Morphological plasticity was confirmed as the mechanism causing morphological variation in *H. rubra*. Individuals transplanted to sites with non-stunted *H. rubra* grew significantly faster when compared to stunted controls, while individuals transplanted to stunted sites grew significantly slower compared to non-stunted controls. It is suggested that these differences are related to resource availability with areas limited in food supply

resulting in stunted populations and areas with abundant food resulting in non-stunted populations.

To reduce the risks of over-fishing and localised depletion of *H. rubra*, management units (MUs) that encompass individual populations need to be determined and then managed according to their life-history characteristics. Potential MUs in the South Australian abalone fishery were identified from the broad-scale, spatial distribution of stunted and non-stunted populations of *H. rubra*, by applying the morphometric marker to commercial shell samples. Key life-history parameters of the *H. rubra* populations within the potential MUs were estimated using relationships between this marker and *H. rubra* biology. Data from fine-scale systematic sampling by commercial fishers were used to validate spatial patterns observed from the more broadly distributed commercial catch samples. The location, distribution and size of potential MUs were largely inconsistent with that of current management. The locations of two MUs were consistent across the broad- and fine-scale datasets with the fine-scale samples being more informative for identifying a potential boundary between these. These results suggest that this morphometric marker can used as a tool for the spatial management of abalone fisheries by simply and inexpensively inferring key biological parameters for individual populations and identify the boundaries among these based on these differences. This approach is among the first to provide a practical means of more closely aligning the scales of assessment and management with biological reality for sedentary marine invertebrates.

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Finally I would like to commemorate all of the abalone that unwittingly sacrificed themselves for this project. I hope this research contributes to this species living long into the future!

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Chapter 1: General Introduction

Many marine species exist as demographically isolated populations across their geographic range (Berryman 2002; Sponaugle et al. 2002; Taylor and Hellberg 2003; Cowen et al. 2006). This complex population structure has been most commonly recognised in sedentary invertebrates that have limited larval dispersal and form individual populations, across multiple spatial scales, which often vary greatly in their life-history parameters (McShane et al. 1988a; Orensanz and Jamieson 1995; Smith and Rago 2004; Orensanz et al. 2005; Prince 2005; Temby et al. 2007). Effective conservation and management of these species requires knowledge of the spatial scale of connectivity among these component populations and their individual life-history characteristics (Cowen et al. 2006). However, a lack of appropriate, spatially-resolved data describing population structure has hindered this process, leaving management regimes operating over large spatial scales (Leiva and Castilla 2001; Castilla and Defeo 2005; Prince 2005). Failure to manage these species at appropriate spatial scales has resulted in many of them becoming serially depleted, with stock collapses occurring in some extreme cases (Tegner et al. 1996; Perry et al. 2002; Orensanz et al. 2004).

Abalone (genus *Haliotis*) are a typical group of sedentary invertebrates, having numerous 'local' populations that vary in their life-history characteristics across their geographic range (McShane et al. 1988a; Prince 2005; Naylor et al. 2006; Temby et al. 2007). However, this highly complex population structure has rarely been taken into account during their management (Shepherd and Brown 1993; Prince 2005). Since the 1960's the world production of abalone has declined by more than 60% (Tegner 1993; Kojima 1995; Karpov et al. 2001; Prince 2005) with some species currently close to extinction (Tegner et al. 1996; Hobday et al. 2001). Along with poaching, this failure to manage abalone fisheries sustainably has probably been a result of the discrepancy between the spatial scales of management compared to that at which abalone populations exist (Prince 2005).

Historically, abalone fisheries have been managed at regional spatial scales (100–1000s km, McShane et al. 1994a; Prince 2005). However, increasing evidence suggests that abalone resources are comprised of many, small (100-1000s m), self-

recruiting populations (McShane et al. 1988b; Prince et al. 1988a; Temby et al. 2007; Saunders et al. 2008) with highly variable life history characteristics (Nash 1992; McShane et al. 1994b; Worthington and Andrew 1997; Prince 2005). Regional scale management does not account for this variability among populations, leaving them vulnerable to serial depletion (Shepherd and Brown 1993; Prince 2005). For example, due to the spatial variability in abalone growth rates, size limits dictated by average regional growth expose fast-growing populations to excessive fishing effort (Prince and Shepherd 1992). These populations can become serially depleted, causing local extinctions, all within the 'safe keeping' of regional management (Shepherd and Brown 1993; Prince 2005).

The blacklip abalone (*Haliotis rubra*, hereafter referred to as blacklip) is the most common species taken in Australian abalone fisheries and constitutes almost half of the global, wild capture, commercial abalone harvest (Conod et al. 2002). Blacklip have many characteristics in their life cycle that suggests this species forms local, self-recruiting populations across its geographic range: larval dispersal is restricted because the pelagic phase is brief (3 to 7 days between egg fertilisation and settlement competency; McShane 1995); spawning occurs during periods of little water movement (Prince et al. 1987; Shepherd et al. 1992a); larvae are benthic an thus experience reduced flows in the benthic boundary layer (Denny and Shibata 1989; Boxshall 2000); and they inhabit complex reef habitat that is likely to entrain larvae (McShane 1992). Blacklip also show substantial spatial variation in life history patterns (Nash 1992; McShane et al. 1994b; Worthington and Andrew 1997; Prince 2005) resulting in the presence of so-called 'stunted' populations of blacklip that have a slower growth rate and/or a smaller maximum size compared to adjacent populations (Shepherd and Cannon 1988; Nash 1992). Stunted populations typically form dense aggregations in sheltered areas with lower wave exposure (McShane and Naylor 1995a). It is suggested that abalone in these areas grow more slowly, compared to individuals in more exposed habitats, as a result of the lower water movement providing less food in the form of drift algae (Day and Fleming 1992; Shepherd and Steinberg 1992; McShane and Naylor 1995a). However, it is unknown whether these morphological differences are a result of a plastic response to the local environment or whether it reflects a genetically fixed trait (Worthington et al. 1995a). To determine whether this morphological variability is a result of genetic divergence

rather than adaptive phenotypic plasticity, these differences must persist in a reciprocal transplant experiment (Swain and Foote 1999).

Like most abalone species, management of blacklip fisheries occurs over broad spatial scales (McShane et al. 1988b; Worthington and Andrew 1997; Prince 2005) exposing fast-growing component populations to a higher risk of overexploitation. In response to this complex population structure, the spatial scale of management in the Southern Zone of the South Australian abalone fishery (SZ) was reduced through the introduction of four, separately managed, 'fish-down' areas (FDAs) within which the blacklip populations are considered stunted. These areas were formally introduced during 1994/95 and within them blacklip are harvested at a minimum legal length of 110 mm shell length (SL), 15 mm smaller than that in the remainder of the fishery. Nevertheless, despite these relatively 'novel' management arrangements, it is widely acknowledged that the FDAs do not encompass all of the stunted populations of blacklip in this fishery, and their current size and locations ensures they also contain populations of 'non-stunted' blacklip. However, obtaining information on the boundaries between component populations and their individual life-history characteristics is impeded by the difficulties of collecting demographic data at a variety of spatial scales (Prince 2005; Naylor et al. 2006).

The most common method that has been employed to identify blacklip population structure has been the analysis of genetic divergence among hypothesised populations (Brown 1991; Huang et al. 2000; Conod et al. 2002; Temby et al. 2007). However, these studies have typically shown genetic differences at scales of 100s km which is larger than would be expected given their larval dispersal capabilities (Prince et al. 1987; McShane et al. 1988b; Temby et al. 2007). The inferences made from genetic studies on population structure are probably a result of < 1% of larvae, per generation, being required to be exchanged between component populations to maintain genetic homogeneity (Slatkin 1985). This number is demographically trivial because recruitment events that act to sustain populations typically consist of orders of magnitude more individuals (Palumbi 2003; Miller and Shanks 2004). This problem is further compounded by the extended longevity of abalone and high temporal variability in successful recruitment resulting in historical patterns of genetic connectivity being maintained (Hancock 2000). Consequently, to identify populations

of blacklip that are ecologically distinct it is pertinent that other methods are used so as not to underestimate the degree of population structure present (Miller and Shanks 2004).

An alternative approach is identification of separate populations based on spatial variability in morphology (Cadrin 2005). This method, which relies on the relationship between morphology and the growth and maturation rates of individuals, is ideally suited to species that have easily-measurable, hard-body parts that reflect their ontogenetic history. Discrimination among populations can be achieved by identifying spatially distributed samples with similar morphology (Cadrin 2005; Cadrin and Silva 2005). The substantial spatial variation in blacklip morphology (McShane et al. 1988a; Worthington et al. 1995a; Worthington and Andrew 1997; Prince 2005; Prince et al. 2008) suggests that this may be an effective method for identifying component blacklip populations. This approach has the added benefit of potentially being able to estimate the specific life-history characteristics of these populations because of the strong links between morphology and biology (Cadrin 2005).

However, identifying and managing individual blacklip populations provides the additional challenge of revising the current management framework to one that explicitly requires reductions in the spatial scale of management (Meester et al. 2001; Prince and Hilborn 2003; Wilen 2004; Castilla and Defeo 2005; Prince 2005; Naylor et al. 2006). Adoption of fine-scale management necessitates consideration of the limitations of the data available, as well as the requirements for effective (and efficient) management and compliance arrangements both within, and across, any new units of management identified. The number of individual populations of blacklip could potentially be very large in any given fishery and would probably exceed the number of that can realistically be assessed and managed by a Government Agency without the associated costs becoming prohibitive (Prince 2005). In other sedentary invertebrate fisheries that have successfully implemented fine-scale management, the approach has been to rely heavily on extensive collaboration and an increase in the responsibility and accountability of all stakeholders (Castilla and Fernandez 1998; Leiva and Castilla 2001; Defeo and Castilla 2005; Orensanz et al. 2005; Prince et al. 2008).

This thesis is focussed around developing practical, cost-effective methods that can provide information on the size and biological characteristics of blacklip populations to assist with the necessary move towards finer scale management of this species. This was achieved by identifying spatial variability in shell morphology among component populations as well as identifying the links between shell morphology and biology.

Chapter 2 investigated the potential for identifying a 'morphometric marker' that could be used as a tool to discriminate between stunted and non-stunted populations of blacklip in the southeast of South Australia. This was achieved by examining the spatial variability in the morphology of blacklip among stunted and non-stunted sites at broad (10s km) and fine (100s m) spatial scales within this region. The morphometric marker developed was applied to the fine-scale samples of blacklip to assess the spatial extent of stunted and non-stunted populations.

In Chapter 3 the spatial variability in the growth, size at maturity and fecundity among populations of blacklip was investigated in the southeast of South Australia. This was achieved by collecting biological information from stunted and non-stunted sites at broad (10s km) and fine (100s m) spatial scales within this region. Further, to assess whether spatial variation in morphology was reflected in the biological variation, the strength of the relationships between key biological parameters and the simple morphometric marker developed in Chapter 2 was examined. This enabled evaluation of the utility of the morphometric marker to infer biological characteristics among blacklip populations.

Chapter 4 assessed whether the spatial variability in the morphology of blacklip was a plastic response to the local environment or a genetically fixed trait by reciprocally transplanting individuals between stunted and non-stunted sites at three locations in south eastern South Australia. It was predicted that if morphology is a plastic trait that varies in response to environmental factors, then (1) stunted blacklip transplanted to non-stunted sites will grow more quickly than those re-placed in their native site, (2) non-stunted blacklip transplanted to stunted sites will grow more slowly than those re-placed in their native site and (3) transplanted individuals will have similar growth rates to those placed in the recipient site. In addition, information was acquired on

environmental factors relating to food availability to improve interpretations on spatial variation in morphology.

In Chapter 5 the morphometric marker developed in Chapter 2 was used to identify potential management units (MUs) in the SZ by determining the broad-scale, spatial distribution of stunted and non-stunted populations of blacklip in the fishery. Potential MUs, containing separate blacklip populations, were identified and their key biological parameters estimated using the relationships developed in Chapter 3 between the morphometric marker and blacklip biology. Data from fine-scale, systematic sampling by commercial fishers in one of the principal SZ fishing areas were used to confirm the spatial patterns observed in the morphometric marker from the broadly distributed commercial catch samples.

The thesis is concluded by a general discussion in Chapter 6 that synthesises the information from the previous chapters and suggests some directions for future research.

1.1 Notes on chapter style

Each of Chapters 2-5 is written in a style suitable for publication in a scientific journal and they are therefore written in plural. Consequently, they can be read as individual papers, but I have maintained a logical progression of ideas so that each chapter contributes towards a thesis of reasoning. All figures and tables are embedded in the text while the references occur at the end of the thesis.

Each chapter is preceded by a preamble that describes the content of the chapter and its relationship to the other chapters, the publication status at the time of submission and the contributions of the co-authors.

Preamble to Chapter 2

Chapter 2 presents data identifying a 'morphometric marker' that was able to discriminate among component abalone populations. Sampling was done at multiple spatial scales in south-eastern South Australia to assess the spatial extent of abalone populations at both broad- and fine-spatial scales in this region.

This chapter was published in the journal *Marine and Freshwater Research* in 2008 (vol. 59: 32-40), with myself as senior and corresponding author and Stephen Mayfield and Andrew A. Hogg (SARDI Aquatic Sciences) as co-authors. It is, therefore, written in plural. Permission from the publisher (CSIRO Publishing http://www.publish.csiro.au/nid/127/issue/4117.htm) to reproduce this manuscript herein has been granted (see Appendix A).

Contributions and signatures of authors

THOR M. SAUNDERS

Sampled, analysed, and interpreted all data, wrote manuscript as senior and corresponding author.

Signed:…… Date:…….

STEPHEN MAYFIELD

Supervised development of research, data interpretation and manuscript evaluation

Signed:…… Date:…….

ANDREW A. HOGG

Assisted with the sampling and collation of data.

Signed:…… Date:…….

Chapter 2: A simple, cost-effective, morphometric marker for characterising abalone populations at multiple spatial scales

Abstract: The ability to identify and separately manage component populations is becoming increasingly important in guarding against overexploitation of many marine species. Blacklip abalone (*Haliotis rubra*) form isolated populations with variable life history characteristics as a result of the heterogeneous areas they inhabit. Many of these populations are 'stunted', reaching a lower maximum shell length compared to those in adjacent areas. We obtained a range of morphological measurements from samples of stunted and 'non-stunted' *H. rubra* collected from sites spread across broad (10s km) and fine (100s m) spatial scales in southern South Australia. The ratio between shell length and shell height showed clear and significant differences among samples from stunted and non-stunted sites. The morphometric collections from the sub-sites suggested that stunted populations existed at smaller spatial scales (up to 400 m) compared to that for non-stunted populations (at least 1000 m). The 'morphometric marker' developed in this study has the potential to be used as a tool to rapidly and cost-effectively identify individual populations that can then be managed separately. Our approach is applicable to other species of abalone as well as other sedentary invertebrates with limited larval dispersal.

2.1 Introduction

Fine-scale population structure is common in many inshore marine species because they are structured by static coast scapes (Sponaugle et al. 2002; Strathmann et al. 2002; Swearer et al. 2002; Orensanz et al. 2005). This is particularly the case for sedentary invertebrates with limited larval dispersal for which the stocks tend to be highly structured across small spatial scales (Orensanz et al. 2005; Sponaugle et al. 2002; Strathmann et al. 2002). Aggregations of such species form discrete populations, which are more or less isolated from conspecifics by reproduction and migration (Berryman 2002), often with variable life history parameters (McShane et al. 1988a; Orensanz and Jamieson 1995; Withler et al. 2003; Orensanz et al. 2005). The high degree of population structuring in these species has been historically unrecognised in their management leading to serial depletion of populations and in

many cases stock collapse (Tegner et al. 1996; Perry et al. 2002; Orensanz et al. 2005). This is because acquiring information on the boundaries between separate populations and identifying the demographic variability among these is impeded by the difficulties of tracking minute larva (Swearer et al. 2002; Gilg and Hilbish 2003) and the high costs of collecting biological information across a range of spatial scales (Prince 2005).

The study of morphometric variation among populations may offer a cost-effective tool with which to identify separate populations of marine species (Cadrin 2005). While this approach has been commonly used (Cadrin 2000; Kong et al. 2007), spatial patterns in morphology may be environmentally induced, and not reflect demographically isolated units (Swain and Foote 1999; Swain et al. 2005). However, the highly localised populations formed by sedentary invertebrates with limited larval dispersal are likely to exist at similar scales to this environmental variation, making studies on morphology an extremely useful tool for population identification. In addition, morphological differences among populations are likely to indicate differences in growth and maturation (Cadrin 2005), and can potentially provide biological information to support their effective management (Cadrin and Friedland 1999).

Abalone are a typical group of sedentary invertebrate species with limited larval dispersal that have numerous discrete populations often within metapopulations across their geographical extent (Prince 2005; Morgan and Shepherd 2006). These populations often differ in their biology and morphology (Shepherd and Hearn 1983; McShane et al. 1988a; Worthington et al. 1995a; Worthington and Andrew 1997; Tarbath et al. 2003; Tarbath 2003) resulting in the presence of so-called stunted areas of abalone that have a slower growth rate and/or a smaller maximum size compared to adjacent populations (Shepherd and Cannon 1988; Nash 1992). Stunted populations typically form dense aggregations in sheltered areas with lower wave exposure (McShane and Naylor 1995a). It is suggested that abalone in these protected areas grow more slowly compared to individuals in more exposed habitats as a result of lower water movement providing less food in the form of drift algae (Day and Fleming 1992; Shepherd and Steinberg 1992; McShane and Naylor 1995a). However, density-dependent processes may also contribute to relatively lower rates of growth in

stunted areas (Emmett and Jamieson 1988; McShane and Naylor 1995b; Dixon and Day 2004) compared to other fished populations.

The current broad-scale (100-1000s km of coastline; McShane et al. 1994a) management of most abalone fisheries fails to account for the finer scale variability in population structure evident in abalone stocks leaving fast growing populations prone to over-fishing and slower growing populations under utilised (Strathmann et al. 2002; Prince 2005). In response to this localised variability, the spatial scale of management in the South Australian abalone fishery has decreased steadily since 1985. Notably, in the Southern Zone of this fishery (SZ) there are four separately managed, 'fish-down' areas (FDAs) within which the blacklip abalone (hereafter referred to as blacklip) populations are considered stunted. These areas were formally introduced during 1994/95 following *ad hoc* fishing at a variety of minimum legal lengths (MLL) between September 1989 and October 1994 (Tyrer 1995; Mayfield et al. 2007). Collectively, the FDAs have a separate total allowable commercial catch (TACC) that is harvested at a MLL of 110 mm shell length (SL), 15 mm smaller than that in the remainder of the fishery. Nevertheless, despite these relatively 'novel' management arrangements it is widely acknowledged that FDAs do not encompass all of the stunted populations of blacklip in this fishery and their large size ensures they also contain populations of non-stunted blacklip.

Studies on the spatial variability of abalone morphology have shown differences among sites separated by as little as 200 m (Breen and Adkins 1982; McShane et al. 1988a; McShane et al. 1994b; Worthington et al. 1995a). Consequently, phenotypic variation in morphometric traits may be an effective method for discriminating among stunted and non-stunted abalone populations. Here, we investigated the potential of identifying a morphometric marker that could be used as a tool to discriminate between stunted and non-stunted populations of blacklip in the SZ. This was achieved by examining the spatial variability in the morphology of blacklip among stunted and non-stunted sites at broad (10s km) and fine (100s m) spatial scales within the fishery. The morphometric marker developed was applied to the fine-scale samples of blacklip to assess the spatial extent of stunted and non-stunted populations. These data were also used to evaluate the suitability of current management arrangements, particularly in one of the current FDAs.

2.2 Methods

2.2.1 Study site

This study was conducted in the Southern Zone (SZ) of the South Australian abalone fishery. The SZ includes all coastal waters of South Australia east of Meridian 139°E, with the exception of the Coorong and waters inside the Murray River mouth. After consultation with divers and licence holders, all of the sites were distributed in the waters between Beachport and the SA/Vic border (Figure 2.1).

2.2.2 Broad-scale

Data to evaluate the broad-scale variation in morphology were obtained from eight sites (Gerloffs Bay (GB), Ringwood Reef (RR), Acis Reef (AR), Red Rock Bay (RB), Salmon Hole (SH), Number 2 Rocks (No2), Middle Point (MP) and Cape Northumberland (CN)) distributed along 100 km of coastline. The first four sites were located in areas with stunted blacklip while the latter four were in areas with non-stunted blacklip (Figure 2.1). Stunted and non-stunted sites were selected on the basis that they represented two common growth forms in the SZ and other abalone fisheries so the development of a morphometric marker would have to at least have the ability to separate abalone from these sites. Furthermore, these sites were also chosen for the fact they were regularly targeted by commercial fishers. Between 120 (SH) and 236 (GB) blacklip were collected from each of these sites between October 2004 and January 2005 (see Table 2.1 for sampling details).

2.2.3 Fine-scale

To assess finer scale patterns in blacklip morphology, GB and MP were re-sampled in conjunction with the collection of additional samples from sub-sites located approximately 150 (GB150, MP150), 400 (GB400, MP400) and 1000 m (GB1000, MP1000) from each of these sites (Figure 2.1). GB and MP were chosen for re-sampling as blacklip from these sites showed substantial differentiation in morphology. In addition, information on the spatial extent of stunted populations in GB and non-stunted populations in MP was important for these sites as they receive the most effort from commercial fishers. These sub-sites were determined by moving the prescribed distance along a randomly selected compass bearing from the original site whereupon divers were deployed to locate the nearest aggregation of blacklip.

Between 134 (MP) and 187 (GB150) blacklip were collected from GB and MP and each of the six sub- sites during May 2006 (Table 2.1).

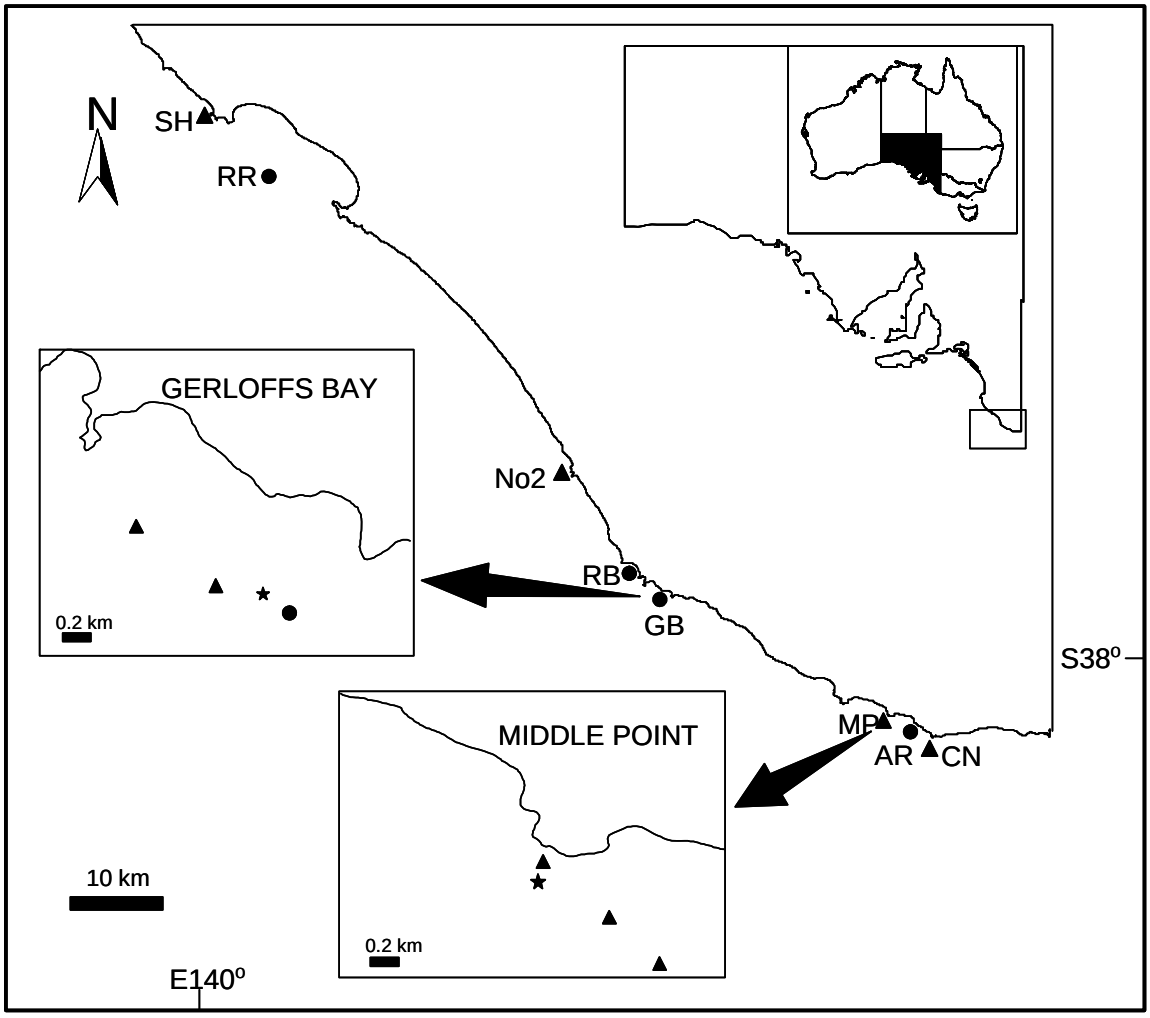

Figure 2.1: Map of study area with the locations of the broad-scale sites: Salmon Hole (SH), Ringwood Reef (RR), Number 2 Rocks (No2), Red Rock Bay (RB), Gerloffs Bay (GB), Middle Point (MP), Acis Reef (AR) and Cape Northumberland (CN). Insert maps show the location of the sub- sites within GB and MP. Stars indicate the location of the broad-scale site in these areas. Circles and triangles represent stunted and non-stunted sites, respectively.

2.2.4 Morphometric sampling

At all sites samples of blacklip were collected using SCUBA within approximately a 10 × 10 m area. Divers moved haphazardly among aggregations of blacklip and collected every individual within each of these. This methodology would have provided a relatively unbiased sample of the size range of blacklip present as samples

were typically collected from 3 to 4 aggregations. A strictly random approach to sampling would have relied on identifying all of the aggregations within each site and would have been difficult to achieve given the time limitations of SCUBA diving. Numerous 'morphometric measurements' including shell length, shell width, shell height, shell weight, shell volume and whole wet weight were obtained from each blacklip collected. All of the linear shell measurements were obtained using vernier callipers to 0.1 mm (Tissot 1988) and weight measurements were obtained using an electronic balance to 0.1g. Shell volume was measured by sealing the respiratory pores with a latex glove, filling the shell with water and then weighing the water from the shell.

Table 2.1: Blacklip morphometric data collection summary from the broad and fine-scale sites in the SZ. Gerloffs Bay 1 and Middle Point 1 indicate the re-sampled broad-scale sites.

Site	Latitude	Longitude	Date	n	Size range (mm)
Acis Reef	38°02.8' S	140°37.9'E	31/10/2004	215	15-147
Cape Northumberland	38°03.6' S	140°39.7'E	31/10/2004	173	39-159
Gerloffs Bay	37°55.7' S	140°24.4'E	11/02/2005	236	27-122
Middle Point	38°02.5' S	140°37.0'E	31/10/2004	128	30-170
No 2 Rocks	37°48.8' S	140°19.5'E	27/11/2004	168	11-158
Red rock Bay	37°54.6' S	140°23.2'E	28/11/2004	131	28-148
Ringwood Reef	37°31.9' S	140°02.6'E	17/10/2004	203	37-141
Salmon Hole	37°29.2' S	139°59.8'E	17/10/2004	120	51-167
Gerloffs Bay 1	37°55.7' S	140°24.4'E	23/05/2006	153	49-124
Gerloffs Bay 150	37°55.8' S	140°24.2'E	23/05/2006	187	53-130
Gerloffs Bay 400	37°55.7' S	140°24.5'E	23/05/2006	162	49-160
Gerloffs Bay 1000	37°55.4' S	140°23.9'E	23/05/2006	167	48-145
Middle Point 1	38°02.5' S	140°37.0'E	21/05/2006	134	54-156
Middle Point 150	38°02.4' S	140°37.0'E	26/05/2006	164	50-151
Middle Point 400	38°02.6' S	140°37.3'E	21/05/2006	138	74-153
Middle Point 1000	38°02.9' S	139°37.5'E	26/05/2006	161	71-158

2.2.5 Data analysis

As a result of the considerable variation in shell length among sites (Table 2.1, Figure 2.2), shell width and shell height were transformed by dividing shell length with each of these variables to provide an index that was independent of shell length. The effect of shell length on the rest of the morphometric measures was removed by using the

relationship described by (Thorpe 1975) that adjusts each variable to that expected for the overall mean shell length. In addition, this transformation removed the non-linearity of these relationships, satisfying the assumptions underlying the PCA (Quinn and Keough 2002). Furthermore, only blacklip greater than 90 mm shell length were used due to the similarity of juvenile morphology among sites (Figure 2.2). The morphometric data included in the multivariate analysis were shell length/width (SL:SW ratio), shell length/height (SL:SH ratio), shell weight (SWt), shell volume (SV) and whole weight (WW). Principal components analysis (PCA) was then used to reduce the dimensionality of the transformed morphometric data.

Thereafter, discriminant function analysis (DFA) was used to determine which morphometric character contributed most to the observed variation among sites. This was achieved by including all the variables in the analysis initially and then proceeding in a backwards fashion of removing the variable with the lowest 'F-to-remove' value. This value for a variable indicates its statistical significance in the discrimination between groups, that is, it is a measure of the extent to which a variable makes a unique contribution to the prediction of group membership. The discriminant function (DF) was developed from the retained variable with the highest 'F-to-remove'. The success of the discrimination among sites was assessed by determining the proportion of the various groups of blacklip that were correctly assigned to their respective site of origin. The assumptions of linearity between relationships of the variables for the PCA and homogeneity of the within-group variance-covariance matrices for the DFA (Quinn and Keough 2002) were met through the above transformations of the data.

To assess the suitability of using the SL:SH ratio as a morphometric marker to differentiate among sites ANOVA was used with site as a random factor. Tukey's HSD *post hoc* tests were conducted to assess where the differences existed. Plots of residuals against group means revealed that these data satisfied the assumptions of normality and homogeneity of variance (Quinn and Keough 2002). Statistica ver. 6.1 (StatSoft, www.statsoft.com) was used for all ANOVA and DFA, whereas PC-ORD (McCune and Mefford 1999) was used to conduct the PCAs.

2.3 Results

2.3.1 Broad-scale

Blacklip from the stunted sites tended to have higher and heavier shells compared to those in non-stunted sites while the rest of the morphometric measures tended to overlap between the two classifications (Figure 2.2). Outputs from the PCA showed that blacklip from Acis Reef and Red Rock Bay, and from Cape Northumberland, Middle Point and Number 2 Rocks exhibited similar morphometric characteristics (Figure 2.3). Blacklip from Salmon Hole tended to separate from the other non-stunted sites while blacklip from Gerloffs Bay and Ringwood Reef grouped separately to the other sites (Figure 2.3). Further, the PCA reduced the number of axes from 5 to 2 as the first two axes explained almost 95% of the variation.

The DF, based on the SL:SH ratio (Table 2.2) further supported these results. Samples of blacklip from Gerloffs Bay, Salmon Hole and Ringwood Reef showed high levels of 'correct classification' (>60%; Table 2.3). However, lower proportions (<40%) of samples from Red Rock Bay, Middle Point and Cape Northumberland classified correctly, primarily due to these sites overlapping with others (Figure 2.3).

The SL:SH ratio differed significantly among sites ($F_{7,772}$= 37.65; p= <0.0001) with the Tukey's HSD tests revealing significant differences between stunted and non-stunted areas. Furthermore, within non-stunted areas, Cape Northumberland had a significantly lower SL:SH ratio compared to the other sites (Figure 2.4). These data suggest that a SL:SH ratio >3.25 reflects blacklip from non-stunted populations and <3.25 reflects blacklip from stunted populations.

2.3.2 Fine-scale

Blacklip had higher shells that were heavier in both shell and whole weight in GB and GB150 compared to the other sub-sites (Figure 2.2). This variability was reflected in the PCA outputs as samples from these two sites tended to group away from those of the other sub-sites (Figure 2.5). Again this variability was a result of differences in the SL:SH ratio that contributed most to the variability observed (Table 2.2). However, the DFA showed that GB and GB150 had low levels of correct classification as a result of samples from these two sites overlapping in the PCA (Table 2.4, Figure 2.5).

MP1000 had the highest level of correct classification (62.8%) as it tended to group away from the other sites that all overlapped strongly (Table 2.4, Figure 2.5).

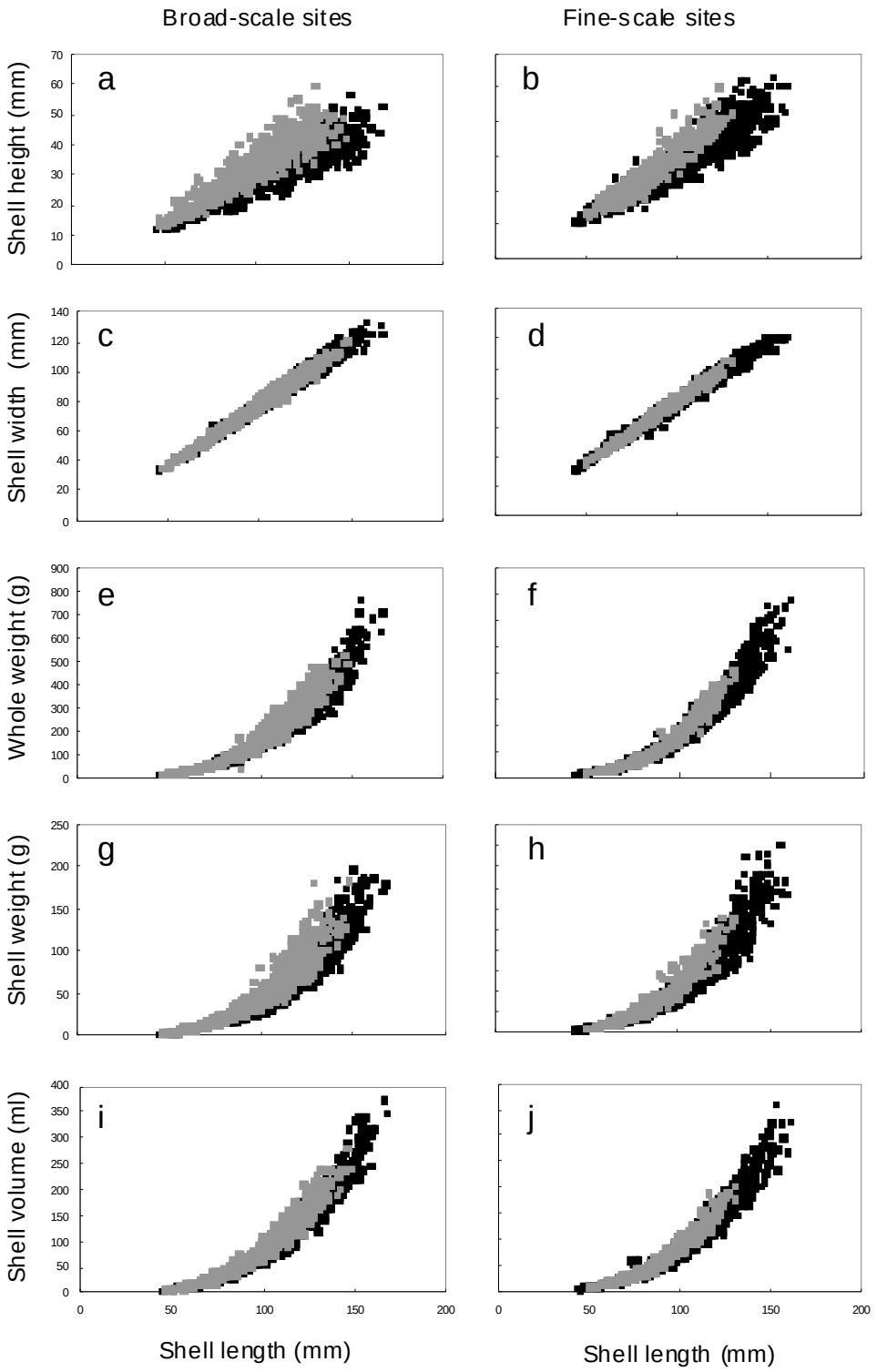

Figure 2.2: Relationships of a-b/ shell height, c-d/ shell width, e-f/ whole wet weight, g-h/ shell weight and i-j/ shell volume against shell length for all sites. Grey= data from stunted sites; black= data from non-stunted sites.

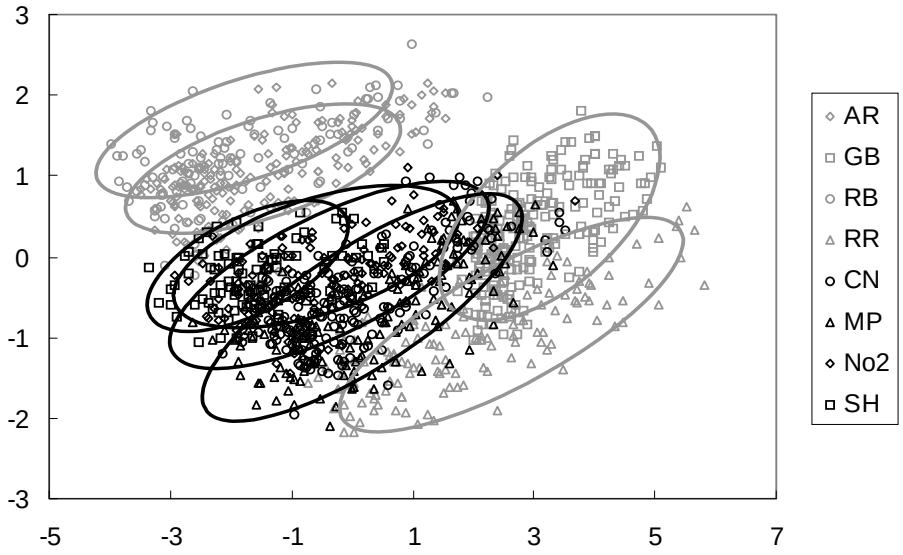

Figure 2.3: Ordination of the PCA on the morphometric characteristics from each of the eight broad-scale sites. Black and grey symbols indicate abalone from non-stunted and stunted sites respectively. Ellipses indicate 95% confidence intervals.

The SL:SH ratio varied significantly among sites ($F_{7,601}$= 23.5; df = 7; p= <0.0001). In Gerloffs Bay, the Tukey's HSD test revealed that GB and GB150 had a significantly lower SL:SH ratio compared to the other sites while MP1000 had a significantly lower SL:SH ratio compared to the other sites in Middle Point (Figure 2.6). Application of the 3.25 SL:SH ratio value identified above suggests blacklip at GB and GB150 are stunted while blacklip at the remainder of these sites are non-stunted. These results suggest that the spatial extent of the stunted blacklip population in Gerloffs Bay is up to 400 m compared to 1000m for the non-stunted population in Middle Point.

Table 2.2: Summary outputs from the Discriminant Function Analysis on all morphometric characters for all broad-scale and sub-sites. Morphometric characters in bold indicate the discriminant function with the highest F-to-remove value.

Scale	Morphometric character	F-to-remove
Broad-scale	**Length/height**	**58.43**
Broad-scale	Length/width	6.79
Broad-scale	Whole weight	36.65
Broad-scale	Shell weight	7.23
Broad-scale	Shell volume	40.37
Fine-scale	**Length/height**	**44.63**
Fine-scale	Length/width	3.63
Fine-scale	Whole weight	33.71
Fine-scale	Shell weight	29.77
Fine-scale	Shell volume	24.57

Table 2.3: Outputs from the discriminant function analysis examining the percentage of successful discrimination among sites based on the SL:SH ratio for each of the eight broad-scale sites.

Site	Percent correct	AR	CN	SH	MP	No2	GB	RB	RR
Acis Reef	47.6	70	24	9	3	11	15	13	2
Gerloffs Bay	60.2	8	16	0	0	3	59	1	11
Red Rock Bay	31.8	30	14	2	2	3	7	28	2
Ringwood Reef	63.8	2	3	0	1	3	17	3	51
Cape Northumberland	36.5	30	57	4	23	25	12	3	2
Middle Point	36.8	13	26	10	43	18	4	2	1
No 2 rocks	27.7	0	32	13	32	38	14	0	8
Salmon Hole	64.7	3	4	55	2	17	1	2	1
Total	**44.2**	**156**	**176**	**93**	**106**	**118**	**129**	**52**	**78**

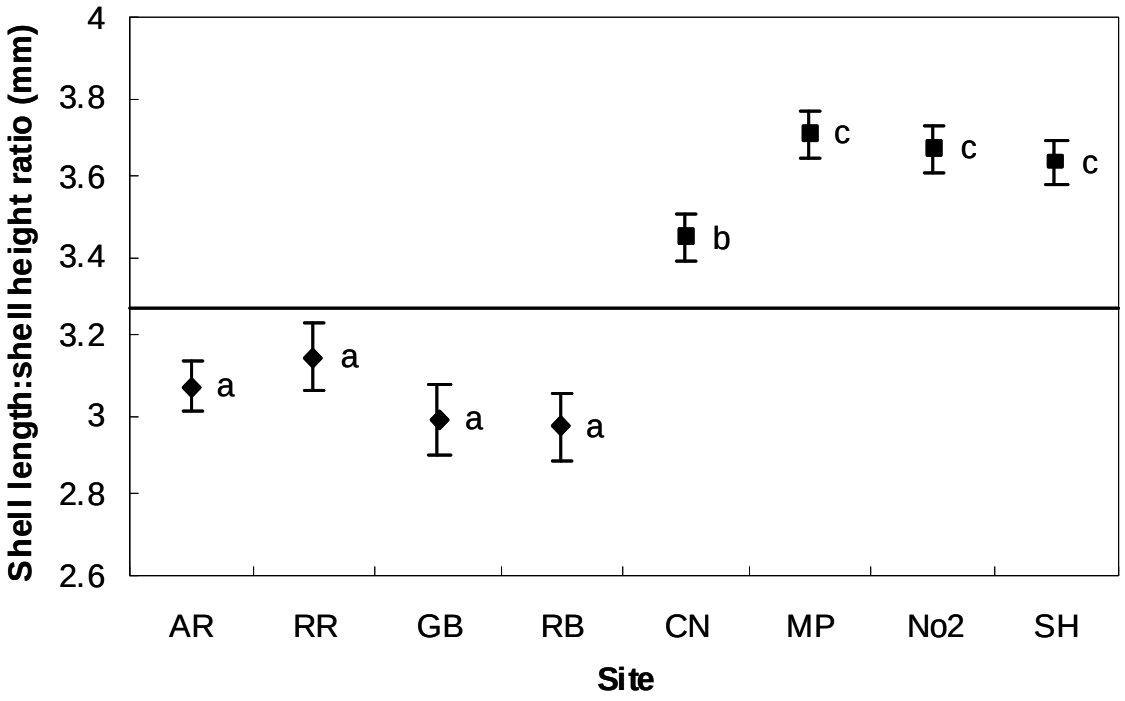

Figure 2.4: SL:SH ratio for all abalone measured from the broad-scale sites. Stunted and non-stunted sites are represented by diamonds and squares respectively. Letters indicate groups classified by the Tukey's HSD test. Horizontal line indicates SL:SH ratio value that separates stunted from non-stunted sites. Error bars are ±1 SE.

2.4 Discussion

The collection of morphometric data across both broad and fine spatial scales enabled identification of a simple morphometric-marker to distinguish between stunted and non-stunted blacklip populations. The substantial, small-scale spatial variation in

morphology of blacklip observed in this study was most evident in differences in the SL:SH ratio of individuals among sites. The DFA revealed that this ratio was primarily responsible for the variation observed in the PCA among sites and was consistent across broad and fine spatial scales. The spatial differentiation in the morphology of blacklip we have observed here is probably a result of spatial variability in environmental factors acting at broad and fine-spatial scales. However, blacklip morphology has been shown to vary at the finest spatial scales measured (Worthington et al. 1995a). Given that the dispersal of blacklip probably only occurs at scales of 10-100s m (Prince et al. 1987), populations formed under these conditions, that are demographically isolated from conspecifics, exist at very fine spatial scales (Temby et al. 2007) and would be similar to that at which environmental variability operates. Consequently, we argue that the SL:SH ratio is likely to be a useful tool for differentiating among separate blacklip populations.

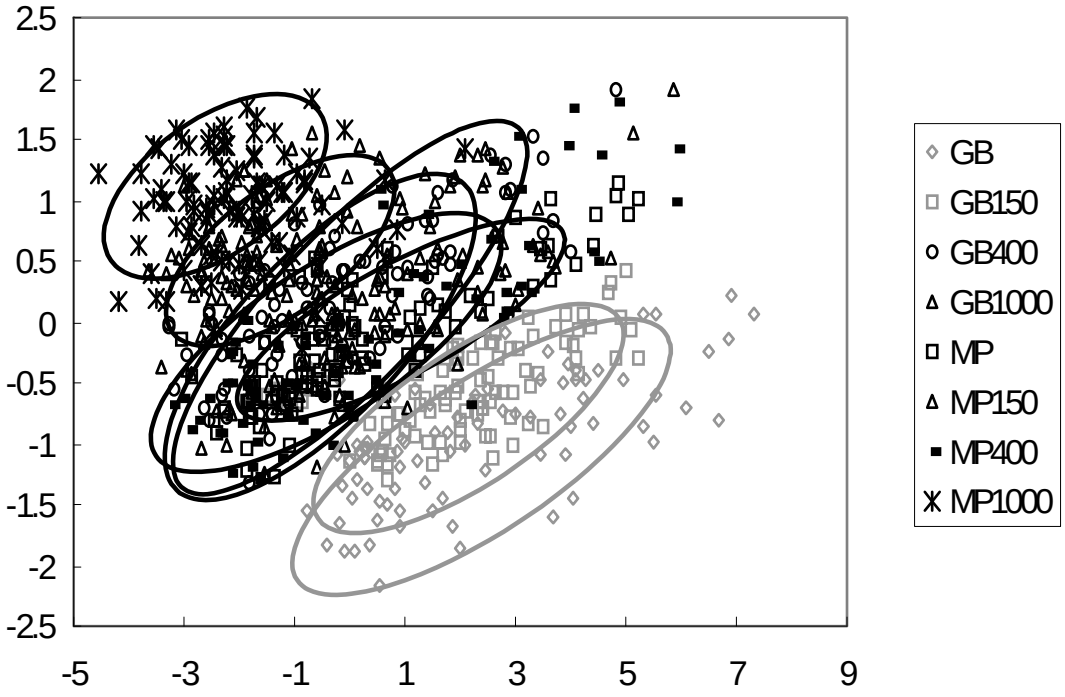

Figure 2.5: Ordination of the PCA on the morphometric characteristics from GB, MP and the six sub-scale sites. Black and grey symbols indicate abalone from non-stunted and stunted sites respectively. Ellipses indicate 95% confidence intervals.

Table 2.4: Outputs from the discriminant function analysis examining the percentage of successful discrimination among sites based on the SL:SH ratio for GB and MP broad-scale sites and the six sub-sites.

Site	Percent correct	GB	GB150	GB400	GB1000	MP	MP150	MP400	MP1000
GB	40.0	22	25	0	3	1	0	0	4
GB150	48.5	14	32	0	14	0	3	1	2
GB400	38.5	1	1	20	15	0	6	6	3
GB1000	62.8	2	5	7	49	0	5	9	1
MP	5.6	0	3	1	6	4	19	26	12
MP150	56.1	0	2	6	5	1	46	14	8
MP400	54.1	2	1	3	6	5	13	53	15
MP1000	54.1	3	4	1	4	7	5	15	46
Total	**46.3**	**44**	**73**	**38**	**102**	**18**	**97**	**124**	**91**

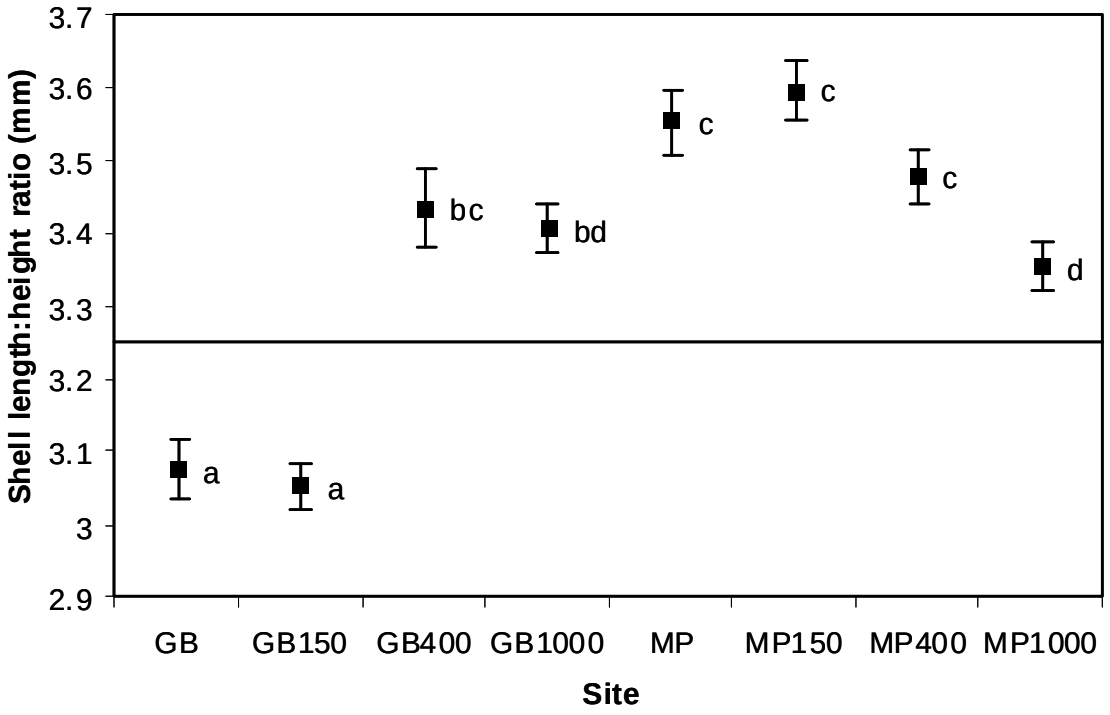

Figure 2.6: SL:SH ratio for all abalone measured from GB, MP and the six sub-sites. Letters indicate groups classified by the Tukey's HSD test. Horizontal line indicates SL:SH ratio value that separates stunted from non-stunted sites. Error bars are ±1 SE.

Broad-scale differences in morphology were greatest between sites in stunted areas compared to non-stunted areas, with a SL:SH ratio of 3.25 separating all of the stunted and non-stunted sites. However within the non-stunted sites, Cape Northumberland had a significantly lower SL:SH ratio compared to the others

suggesting blacklip from this site may comprise an intermediate morphological classification between the two we have presented here. The fact that the SL:SH ratio was able to identify this variability indicates that it is a sensitive measure of morphometric differentiation among populations. The morphometric samples collected at finer scales revealed that the stunted population of blacklip in Gerloffs Bay occupied a smaller area compared to the non-stunted one in Middle Point. Stunted samples of blacklip were only found within 400 m of the original GB site while all of the samples within 1000 m of the MP site were classified as non-stunted. Consequently, these data suggest that the scale of differentiation between stunted and non-stunted populations ranges from up to 400 m (Gerloffs Bay) to at least 1000 m (Middle Point). These results might imply that the population at Middle Point could potentially extend to 10's – 100's km if similar values of the SL:SH ratio were observed continuously over this range. However, the mixture of stunted and non-stunted populations among the broad-scale sites suggests that the environmental conditions that are probably causing the variability in the ratio are acting at finer scales. In addition, the population at Middle Point is probably nearing its boundary at this distance as MP1000 had a significantly lower SL:SH ratio compared to the other sites in Middle Point. Alternatively, blacklip in MP1000 could represent the beginning of a separate population within Middle Point that is an intermediate classification similar to that of Cape Northumberland above.

These results are supported by those in previous studies where abalone inhabiting areas of slower rates of growth tend to have heavier, wider and higher shells compared to those located in areas with faster growth rates (Breen and Adkins 1982; McShane et al. 1988a; Tissot 1988; Worthington et al. 1995a). Breen and Adkins (1982) found slower growing *H. kamatsakana* populations could be differentiated on the basis of shell height. Similarly, in NSW, Worthington et al. (1995a) found that slower growing blacklip populations had significantly wider shells. In their study, shell height was not measured and could also have potentially separated these populations. However, neither of these studies collected samples of abalone at appropriate spatial scales to identify the spatial extent of separate populations. Our data, in combination with these studies, suggest that the principles underpinning the morphometric marker we have developed may be more broadly applicable to other abalone fisheries.

While the SL:SH ratio was able to discriminate between stunted and non-stunted populations of blacklip in the SZ so was the variability in shell length. The blacklip in all of the non-stunted sites had substantially greater shell lengths compared to those in stunted sites. However, using shell length as a tool to discriminate between these populations is problematic as non-stunted populations that are heavily fished will have very few large blacklip and the length frequencies will be similar to stunted populations that are unfished. Nevertheless, length frequencies of populations in conjunction with the SL:SH ratio would be extremely useful in discriminating between 'lightly fished' and stunted populations. Lightly fished populations could potentially be classified as stunted according to the SL:SH ratio as they tend to have many larger blacklip that have reached their maximum size and have grown substantially in shell height due to their age (Prince et al. 2008). Given that these populations will still have a higher average shell length compared to that for stunted populations, length frequency distributions for each of these populations would reveal this difference.

Patterns of morphometric variation among populations are also likely to indicate differences in growth and maturation rates (Cadrin 2005) which will determine how they respond to exploitation (Wells and Mulvay 1995). Therefore, for the purpose of fishery stock assessment, morphologically distinct populations should be modelled and managed as separate management units (Cadrin and Friedland 1999; Cadrin 2000; Cadrin 2005). While this has been attempted in the SZ with the implementation of FDAs, where stunted stocks of blacklip were thought to exist, the boundaries of these fishing areas were based on ease of geographical identification due to the limited information on the extent of these populations. The location and boundaries of these FDAs can now be re-considered by using the morphometric marker we have developed as a tool to ensure they encompass only stunted blacklip. For example, data presented here suggest that FDA 4, which encompasses all of Gerloffs Bay, could be reduced in size to exclude non-stunted blacklip. Further, two sites (Acis Reef and Red Rock Bay) not located in any of the current FDAs were classified as stunted indicating the potential for additional FDAs across the SZ. In addition, our data indicate that non-stunted blacklip may exist as larger populations compared to stunted blacklip. Consequently, management units for the former could potentially be much larger in size compared to those for the latter. However, further morphometric

samples of blacklip are required to determine the consistency, and confirm the location and extent of the stunted and non-stunted populations across this fishery. If individual populations of abalone can be identified using this approach, then managing these separately on this basis would assist in guarding against serial depletions of abalone stocks.

The development of this approach provides a cost-effective tool to provide a wealth of data, through the measurement and analysis of shell samples to inform changes (i.e. a reduction) in the spatial scale of abalone management. This is timely as the concept of finer scale management of abalone fisheries has effectively become the orthodox position (Naylor et al. 2006) but its application has been restricted by the inability to gather detailed demographic data at useful spatial scales (Prince 2005; Naylor et al. 2006). Thus, use of the morphometric marker developed in this study provides an opportunity to bridge the traditional disconnect between scales of ecological variation and fisheries management. While these ideas are particularly pertinent for abalone given their history of stock collapse, fine-scale population structuring is common for most sedentary invertebrates and probably for many teleosts and chondrichthyans (Prince 2005). Consequently, developing a morphometric marker may be able to assist with the conservation and management of many marine species.

Preamble to Chapter 3

Chapter 3 presents data linking biological variability among abalone populations to the simple 'morphometric marker' that can be used as a tool to discriminate among abalone populations developed in Chapter 2. Sampling was conducted at multiple spatial scales across south-eastern South Australia to assess whether these linkages were consistent at both broad-and fine-spatial scales.

This chapter was published in the journal *Marine Ecology Progress Series* in 2008 (vol. 366:75-89), with myself as senior and corresponding author and Stephen Mayfield (SARDI Aquatic Sciences) as co-author. It is, therefore, written in plural. Permission from the publisher (Inter-Research, www.int-res.com) to reproduce this manuscript herein has been granted (see Appendix A).

Contributions and signatures of authors

THOR M. SAUNDERS

Sampled, analysed, and interpreted all data, wrote manuscript as senior and corresponding author.

Signed:…… Date:…….

STEPHEN MAYFIELD

Supervised development of research, data interpretation and manuscript evaluation

Signed:…… Date:…….

Chapter 3: Predicting biological variation using a simple morphometric marker in the sedentary marine invertebrate *Haliotis rubra*

Abstract: Many sedentary marine invertebrates have a fine-scale (100s m) population structure that complicates their conservation and management. This is a consequence of the limited information on the boundaries between component populations and the biological variability among them. Blacklip abalone *Haliotis rubra* form discrete populations, many of which are 'stunted' with individuals reaching a maximum length less than those in adjacent areas. In the present study, we obtained information on the growth, size at maturity and fecundity of *H. rubra* from stunted and 'non-stunted' populations spread across broad (10s km) and fine (100s m) spatial scales. Relationships between each of these key population parameters and a simple 'morphometric marker' based on the relationship between shell length and shell height were also examined. Variation in broad-scale growth and size at maturity could primarily be attributed to differences between stunted and non-stunted sites. Within the stunted site, growth and size at maturity were substantially different over distances >150 m. However, within the non-stunted site these parameters tended to be similar across 1000 m. While the lowest fecundities tended to be in the stunted sites, there was significant overlap among all sites. These spatial patterns in biology were highly correlated with the spatial variability observed in a simple morphometric marker. These results suggest that this morphometric marker can be used as a tool for the spatial management of abalone fisheries by cheaply inferring key biological parameters for individual populations and identifying the boundaries among these based on these differences.

3.1 Introduction

It is becoming increasingly evident that many sedentary marine invertebrates demonstrate fine-scale population structure across their range (Strathmann et al. 2002; Orensanz et al. 2005). These individual populations are isolated from conspecifics by reproduction and migration (Berryman 2002) and often vary in their life-history parameters, typically as a consequence of environmental variability (McShane et al. 1988a; Orensanz & Jamieson 1995; Steffani and Branch 2003; Orensanz et al. 2005).

While this variability has long been recognised, the spatial scale at which it exists is poorly understood, due to biological data being typically collected from study sites that inadequately represent the variation that occurs across the distribution of the species (Prince 2005). The lack of appropriate data to inform marine scientists and managers has resulted in many of these species becoming serially depleted across their range, with stock collapses occurring in some extreme cases (Tegner et al. 1996; Perry et al. 2002; Orensanz et al. 2005). Thus, while there is a clear need to acquire information on the biological variability among separate populations, this process has been restricted by the high costs and difficulties of collecting these data across the required range of spatial scales (Prince 2005).

The collection of morphometric data may offer a cost-effective alternative for inferring key biological parameters for individual populations. This is a result of patterns in morphometric variation reflecting differences in growth, maturation rates and fecundity, as body form is a product of ontogeny (Begg et al. 1999a; Cadrin 2005). For example, individuals in populations characterised by slower growth tend to be smaller in body form, mature at smaller sizes and produce less eggs compared to those in populations with faster growth (Worthington and Andrew 1997; Campbell and Ming 2003; Campbell et al. 2003). If biological variability can be linked to a simple morphometric measure, inferring the biology of a species at appropriate spatial scales, using morphological variability as a surrogate becomes practicable. In addition, these relationships enable spatial variability in morphology to be used to identify separate populations of these species (Cadrin and Silva 2005; Saunders et al. 2008) based on their different biological characteristics. While this approach has been commonly used in teleosts (Worthington et al. 1995b; Berg et al. 2005; Cadrin and Silva 2005), it can be applied to sedentary marine invertebrates that have easily measurable, hard body parts that reflect their ontogenetic history. Although these morphological characteristics may be environmentally induced (Swain and Foote 1999; Alunno-Bruscia et al. 2001; Swain et al. 2005), the highly localised populations formed by sedentary invertebrates with limited adult movement and larval dispersal are likely to exist at similar scales to this environmental variation.

Abalone (Genus *Haliotis*) are a typical sedentary invertebrate species, having numerous discrete populations across their range (Prince 2005; Morgan and Shepherd

2006) that often differ in their biology and morphology (McShane et al. 1988a; Worthington et al. 1995a; Worthington and Andrew 1997; Tarbath 2003). This variability commonly results in the presence of so-called stunted areas of abalone that have a slower growth rate and/or a smaller maximum length compared to adjacent populations (Nash 1992; Wells and Mulvay 1995). Stunted populations typically form dense aggregations in sheltered areas with lower wave exposure (McShane and Naylor 1995a). It is suggested that abalone in these protected areas grow more slowly, mature at smaller sizes and produce fewer eggs compared to individuals in more exposed habitats (Shepherd et al. 1991; Wells and Mulvay 1995; Worthington and Andrew 1997; Campbell et al. 2003). This variability is considered to be primarily a result of lower water movement providing less food in the form of drift algae (Day and Fleming 1992; Shepherd and Steinberg 1992; McShane and Naylor 1995a). However, density-dependent processes, or genetic variability, may also contribute to relatively lower rates of growth in stunted areas, compared to other fished populations (Emmett and Jamieson 1988; Dixon and Day 2004).

The current broad-scale (100 to 1000s km; McShane et al. 1994a) management of most abalone fisheries fails to account for the finer-scale variability in their population structure, leaving fast-growing populations prone to over-fishing and slower-growing populations underutilised (Strathmann et al. 2002; Prince 2005). In response to this localised variability, the spatial scale of management in Australian abalone fisheries has decreased substantially over recent years. Notably, in the Southern Zone of the South Australian abalone fishery (SZ), separately managed, 'fish-down' areas (FDAs), within which the abalone populations are considered stunted, were introduced between 1989 and 1994. Despite these attempts to reduce the spatial scale of management, it is widely acknowledged that the current management areas still encompass numerous populations of abalone that vary in their life-history parameters. To overcome this challenge, stakeholders in the Victorian Western Zone abalone fishery use a qualitative assessment of the shape (flat or domed) and appearance (i.e. clean or fouled) of shells from commercial catches to aid reef-specific assessment (Prince et al. 2008). This has led to increasingly complex spatial management of the resource, with current management arrangements including reef-specific catch limits and minimum legal lengths. However, these assessments of shell shape and appearance need to be calibrated with key biological parameters to ensure

that individual populations of abalone are being managed on the basis of their biological characteristics.

Obtaining biological information for individual populations of abalone is unlikely to be achievable by traditional research methods, given the high costs of conducting tag–recapture and reproductive studies across the scale of current fisheries. However, the substantial spatial variation in abalone morphology (Breen and Adkins 1982; McShane et al. 1994b; Worthington et al. 1995a; Saunders et al. 2008) may offer a proxy through which biological variability among populations can be inferred. For example, Saunders et al. (2008) identified a simple morphometric marker, based on the ratio of shell length to shell height (SL:SH ratio), that was able to differentiate between stunted and non-stunted populations in the SZ. The authors suggest that the populations formed by the limited dispersal of abalone larvae were likely to exist at similar spatial scales to the variability observed in the SL:SH ratio. Consequently, linking this simple measure to key biological parameters has the potential to enhance the utility of the morphometric marker as a tool to support finer-scale spatial management of abalone fisheries.

In the present study, we investigated the spatial variability in the growth, size at maturity and fecundity among populations of the blacklip abalone *Haliotis rubra*, hereafter referred to as blacklip, in the SZ. This was achieved by collecting biological information from stunted and non-stunted sites at broad (10s km) and fine (100s m) spatial scales within this fishery. Further, to assess whether spatial variation in morphology was reflected in the biological variation, we examined the strength of the relationships between key biological parameters and a simple morphometric marker (Saunders et al. 2008). This enabled evaluation of the utility of this morphometric marker to infer biological characteristics among blacklip populations.

3.2 Methods

3.2.1 Study site

The present study was conducted in the SZ, which includes all coastal waters of South Australia east of Meridian 139° E, with the exception of the Coorong and waters inside the Murray River mouth. Data to evaluate the spatial variation in rate of growth, size at maturity and fecundity were obtained from 8 sites: Gerloffs Bay (GB), Ringwood Reef (RR), Acis Reef (AR), Red Rock Bay (RB), Salmon Hole (SH),

Number 2 Rocks (No2), Middle Point (MP) and Cape Northumberland (CN) distributed along ~100 km of coastline. These were the same sites used in Saunders et al. (2008), and the morphometric data from that study revealed that the first 4 sites contained stunted blacklip while the latter 4 contained non-stunted blacklip (Figure 3.1). Using these sites allowed for the direct comparison between spatial patterns in blacklip biology and morphology. To assess finer-scale patterns in blacklip biological parameters, GB and MP were re-sampled in conjunction with the collection of additional samples from sub-sites located ca. 150 (GB150, MP150), 400 (GB400, MP400) and 1000 m (GB1000, MP1000) from each of the 2 sites (see insets, Figure 3.1).

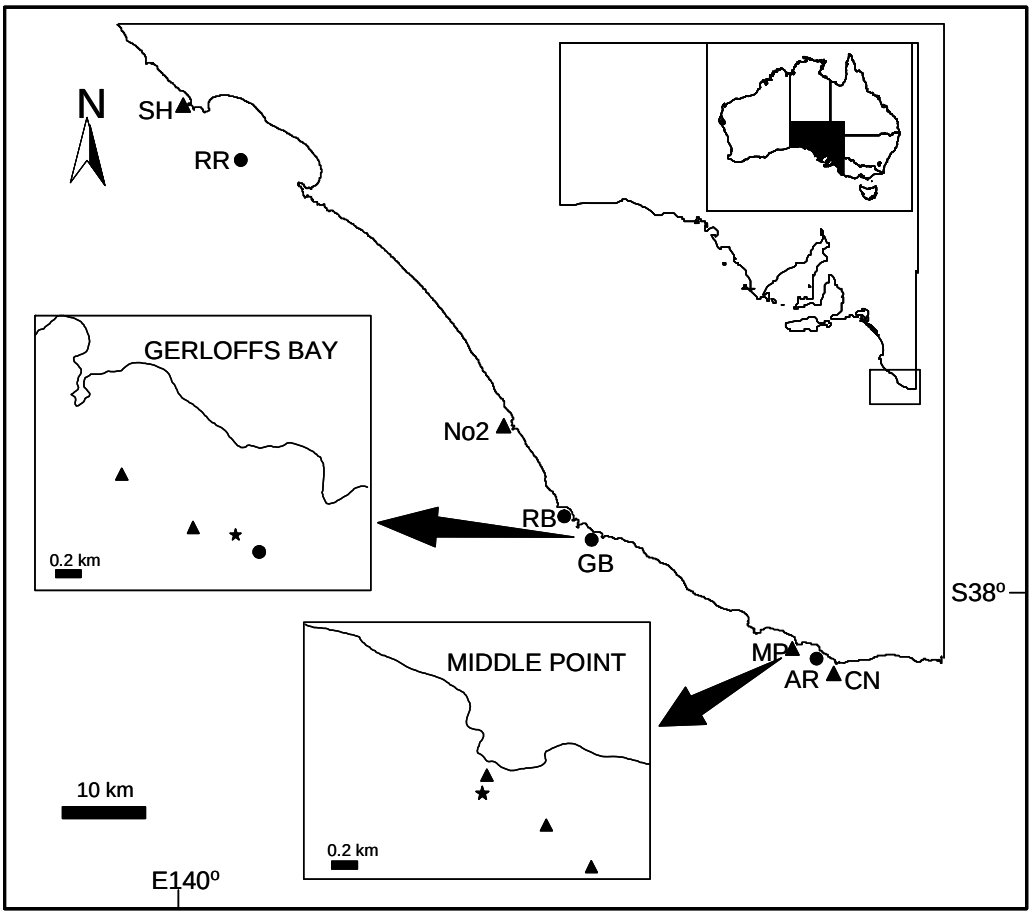

Figure 3.1: Map of study area with the locations of the broad-scale sites: Salmon Hole (SH), Ringwood Reef (RR), Number 2 Rocks (No2), Red Rock Bay (RB), Gerloffs Bay (GB), Middle Point (MP), Acis Reef (AR) and Cape Northumberland (CN). Inset maps show the location of the sub- sites within GB and MP. ★: broad-scale site in these areas. ▲:non-stunted and ●:stunted sites.

GB and MP were chosen for re-sampling as blacklip from these sites showed biological traits that were typical of stunted and non-stunted populations, respectively. The sub-sites were determined by moving the prescribed distance along a randomly selected compass bearing from the original site, whereupon divers were deployed to locate the nearest aggregation of blacklip.

3.2.2 Growth

Between 368 (SH) and 404 (RR) blacklip were tagged at each of the 8 broad-scale sites between November 2004 and January 2005. This process required that they be removed from the water to tag and measure the length of individuals to the nearest 0.5 mm before they were replaced in the area from where they were collected. Individuals were collected in a haphazard manner to obtain a representative sample of the size range present in each site. Small (12 mm), individually numbered, plastic disc tags were attached to blacklip by fixing a nylon rivet to the proximal pore hole of each shell (Prince 1991). These individuals were then recaptured and re-measured for SL during January and February 2006. Recaptures from the GB and MP sites were returned to the site from which they were recaptured so that growth data could be collected at these sites during the same time period as the sub-sites. At the sub-sites, between 158 (GB1000) and 288 (GB150) blacklip were tagged and measured as described above between January and May 2006 and were recaptured and re-measured between November 2006 and April 2007 (Table 3.1).

3.2.3 Size at maturity

Between 120 (SH) and 256 (GB) blacklip (>30 mm SL) were collected by SCUBA divers from the broad-scale sites between October 2004 and February 2005. Blacklip show high levels of gonad present between October and April in the SZ (Mayfield et al. 2002), so the blacklip sampled during the present study should not have their size at maturity skewed to higher size classes as a result of having recently spawned. In addition, between 131 (MP150) and 187 (GB150) blacklip were collected between December 2006 and January 2007 from the sub-sites within GB and MP (Table 3.1). Each blacklip was measured and the reproductive state (immature, male or female) determined macroscopically, based on gonad colour (immature- brown, male- creamy and female- pale green; Shepherd and Laws 1974).

Table 3.1: Tagging data used to determine growth and collection data used to determine the size at maturity and fecundity of blacklip at all sites. Gerloffs Bay 1 and Middle Point 1 indicate the broad-scale sites that were re-sampled along with the sub-sites.

	Tagging data						Collection data		
Site	Date tagged	No. tagged	Size range tagged	Date recaptured	No. re-captured	Size range recaptured	Date collected	No. collected	Size range collected
Acis Reef (AR)	11/11/2004	398	34-148	21/01/2006	65	67-148	31/10/2004	215	15-147
Cape Northumberland (CN)	26/11/2004	396	21-148	06/02/2006	75	60-148	31/10/2004	173	39-159
Gerloffs Bay (GB)	29/01/2005	402	28-124	05/02/2006	58	41-124	11/02/2005	256	27-122
Middle Point (MP)	10/11/2004	399	38-167	21/01/2006	59	38-167	31/10/2004	128	30-170
Number 2 Rocks (No2)	27/11/2004	398	41-164	20/01/2006	97	75-166	27/11/2004	168	11-158
Red Rock Bay (RB)	03/12/2004	397	60-150	20/01/2006	74	78-150	28/11/2004	131	28-148
Ringwood Reef (RR)	25/11/2004	404	36-147	19/01/2006	63	55-147	17/10/2004	203	37-141
Salmon Hole (SH)	13/12/2004	368	54-181	19/01/2006	76	85-181	17/10/2004	120	51-167
Gerloffs Bay 1 (GB1)	29/01/2006	58	41-124	22/11/2006	39	36-112	04/01/2007	153	49-124
Gerloffs Bay 150 (GB150)	16/05/2006	288	37-142	16/04/2007	34	37-120	04/01/2007	187	53-130
Gerloffs Bay 400 (GB400)	17/05/2006	179	63-160	25/04/2007	45	63-149	10/01/2007	162	49-160
Gerloffs Bay 1000 (GB1000)	16/05/2006	158	41-186	16/04/2007	32	53-160	10/01/2007	168	48-145
Middle Point 1 (MP1)	21/01/2006	59	75-156	13/04/2007	28	63-154	10/12/2006	135	48-156
Middle Point 150 (MP150)	26/04/2006	207	53-160	13/04/2007	70	61-161	10/12/2006	131	44-150
Middle Point 400 (MP400)	27/04/2006	201	49-155	14/04/2007	35	57-140	10/12/2006	138	59-153
Middle Point 1000 (MP1000)	26/04/2006	209	40-152	13/04/2007	51	56-141	10/12/2006	161	50-158

3.2.4 Fecundity

The entire visceral mass of ca. 30 mature female blacklip were retained from the size-at-maturity samples from all sites. Individuals ranged in size from 55 to 157 mm SL. To preserve the visceral mass for subsequent egg counting, each sample was labelled and preserved in 100% ethanol for at least 1 mo.

Following preservation, the ovary was excised from the entire visceral mass and weighed to the nearest 0.01 g. Estimates of the no. eggs g^{-1} of ovary were obtained from 3 sub-samples taken from 3 regions of the gonad (tip of the conical appendage, top of the body whorl, and anterior gonad; after Wells and Keesing 1989). Subsample wet weights ranged from 0.4 to 2.5 mg. Each sub-sample was separated, and the eggs flushed into a plankton-counting chamber with 70% ethanol and counted using a dissecting microscope at 40× magnification. The total number of eggs for each blacklip was calculated by multiplying the average no. of eggs g^{-1} of ovary by the total weight of the ovary.

3.2.5 Data analysis

To test for differences in rates of growth among sites, an analysis of covariance (ANCOVA) was carried out on the regression slopes of annual growth rate against length at tagging.

The percentage of mature blacklip was determined for individual 5 mm size classes. These data were fitted to a 2 parameter logistic curve (after Schnute and Richards 1990) of the form:

$$P(L) = (1 + e^{-(L - L_{50})/\delta})^{-1}$$

Where $P(L)$ represents the proportion of mature blacklip from length class L, L_{50} the length at 50% maturity and δ the steepness of the ogive. The model parameters were estimated by minimising the negative binomial likelihoods. The confidence intervals for L_{50} were determined using profile likelihood methods (Haddon 2001). Likelihood ratio tests were used to test for differences in L_{50} among sites.

Egg no. $ind.^{-1}$ was log transformed and differences among the slopes and y-intercepts of the resultant linear relationships (log egg no. = m(SL) + c where m is the slope and

c the intercept on the y-axis) were investigated using ANCOVA. Site was a random factor and SL a covariate for these analyses.

Given the assumption of ANCOVA that the covariate is similarly distributed between treatments for each analysis (Quinn and Keough 2002), data were truncated to examine the robustness of the test. Truncating the growth or log transformed fecundity data did not alter the significance of the test, so all data were retained in the analyses. To determine where the significant differences lay between factors, Student's t-tests on adjusted means were calculated for each combination of factors with a sequential Bonferonni adjustment of significance levels to correct for multiple testing (Quinn and Keough 2002).

Each biological parameter (residuals of growth, L_{50} and residuals of fecundity) was plotted against the average SL:SH ratio for each of the broad-scale and sub-site samples. The average growth residuals were calculated by using multiple linear regression for the 8 broad-scale sites. The residuals from this analysis indicated whether a shell was longer or shorter than expected compared to the average growth relationship. Residuals were calculated in the same way for the sub-sites. This residual analysis was used in a similar way on the log transformed fecundity relationship among sites. The maximum likelihood estimates calculated for L_{50} above were used in these plots. Relationships among these variables were investigated through Pearson's correlation analyses.

3.3 Results

3.3.1 Growth

There was a significant linear relationship between SL at tagging and rate of growth at all sites, with larger individuals growing more slowly compared to smaller ones (Table 3.2, Figs. 3.2 and 3.3). There was significant variation among the broad-scale sites (ANCOVA, $F_{7,533} = 20.05$, $p < 0.0001$). This variation was primarily a result of blacklip in the non-stunted sites (CN, MP, No2 and SH) having significantly higher rates of growth when compared to those in stunted sites (AR, GB, RB and RR, Figure 3.2). Furthermore, among the non-stunted sites, blacklip in No2 and SH, had significantly faster rates of growth compared to CN and MP (Figure 3.2). There was also significant variation among the blacklip tagged within GB (ANCOVA, $F_{3,145}$ =

8.84, p < 0.0001) and MP (ANCOVA, $F_{3,179}$ = 22.9, p < 0.0001). Multiple comparisons revealed that blacklip in GB, GB150 and MP1000 had significantly slower rates of growth compared to the other sites (Figure 3.3).

Table 3.2: Sample size (n), correlation coefficient (r) from the relationship between blacklip shell length (SL) at tagging and annual growth rate for all sites. Values for a and b represent the constants for this linear relationship. For site definitions see Table 1. p < 0.001 for all sites.

Site	n	a	b	r
AR	62	0.212	27.12	-0.921
CN	75	0.217	30.07	-0.885
GB	58	0.157	18.84	-0.855
MP	59	0.225	32.01	-0.904
No2	82	0.225	36.01	-0.845
RB	74	0.184	24.27	-0.858
RR	63	0.191	24.49	-0.916
SH	76	0.257	39.98	-0.898
GB1	39	0.114	15.61	-0.527
GB150	31	0.060	11.98	-0.381
GB400	44	0.239	34.75	-0.813
GB1000	33	0.169	28.26	-0.669
MP1	28	0.225	31.34	-0.937
MP150	70	0.333	47.66	-0.898
MP400	35	0.296	39.85	-0.816
MP1000	51	0.268	38.12	-0.784
SH	39	0.114	15.61	-0.527

3.3.2 Size at maturity

Among the broad-scale sites, the likelihood ratio test revealed that the shell length at 50% maturity (L_{50}) was generally significantly lower for blacklip in stunted compared to non-stunted sites (Figure 3.4). The exception was RB which had a similar L_{50} compared to those for most of the non-stunted sites (Figure 3.4). In addition, SH had a significantly higher L_{50} compared to all of the other sites (Figure 3.4). There were also differences in L_{50} within Gerloffs Bay as a result of GB and GB150 having significantly lower L_{50} compared to the other sites (Figure 3.5). At Middle Point, L_{50} at MP1000 was significantly lower compared to the rest of the sites in this area (Figure 3.5).

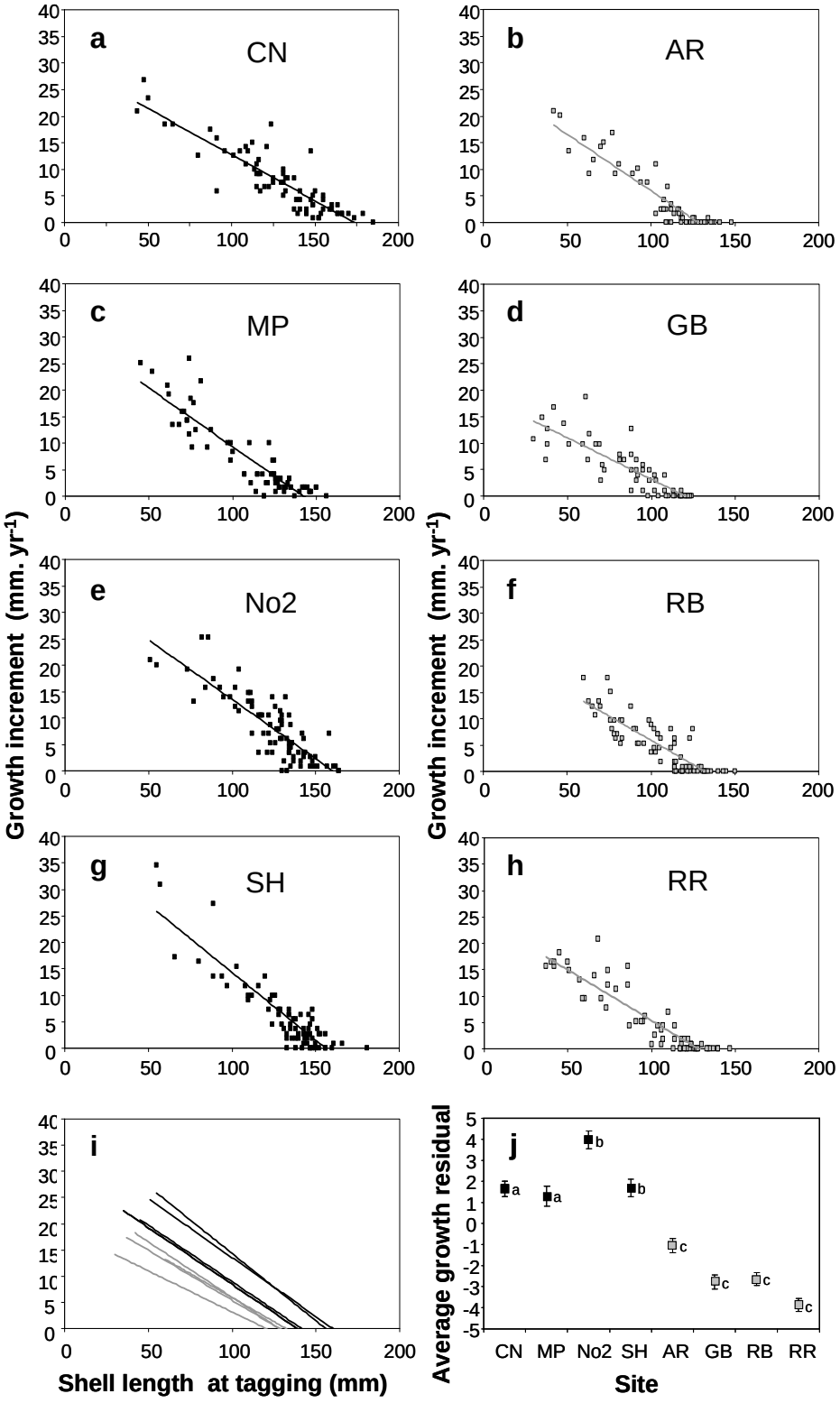

Figure 3.2: (a–h) Relationship between shell length (SL) at tagging and growth increment for blacklip at the broad-scale sites. (i) The trend lines for each of these relationships and (j) the average growth residuals for all sites. Letters in (j) indicate similar groups classified by the multiple comparisons. Black and grey symbols indicate non-stunted and stunted sites respectively. Error bars indicate ± SE.

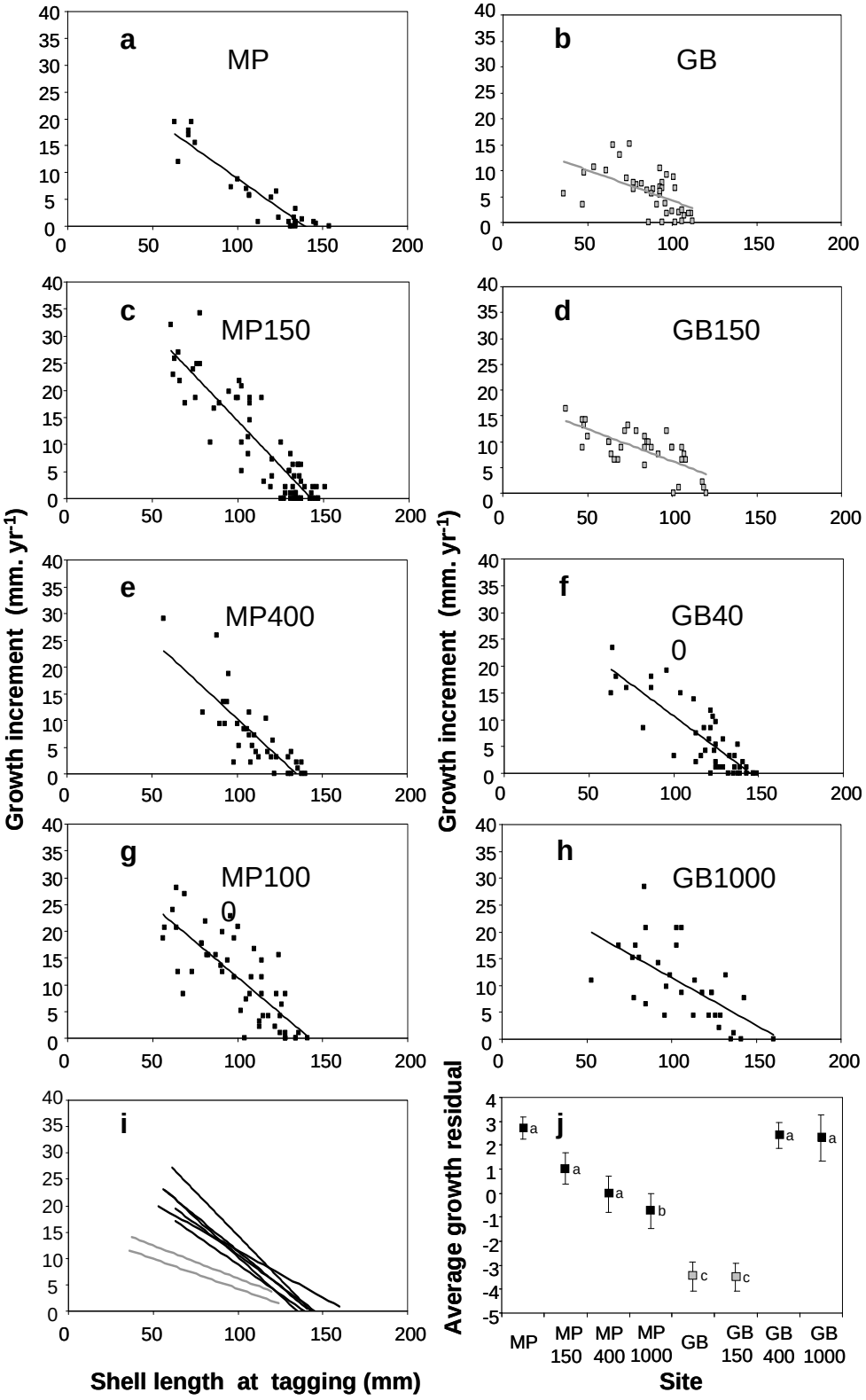

Figure 3.3: (a–h) Relationship between shell length (SL) at tagging and growth increment for blacklip at the MP and GB broad-scale sites and sub-sites. (i) The trend lines for each of these relationships and (j) the average growth residuals for all sites. Letters in (j) indicate similar groups classified by the multiple comparisons. Black and grey symbols indicate non-stunted and stunted sites, respectively. Error bars indicate ±1 SE.

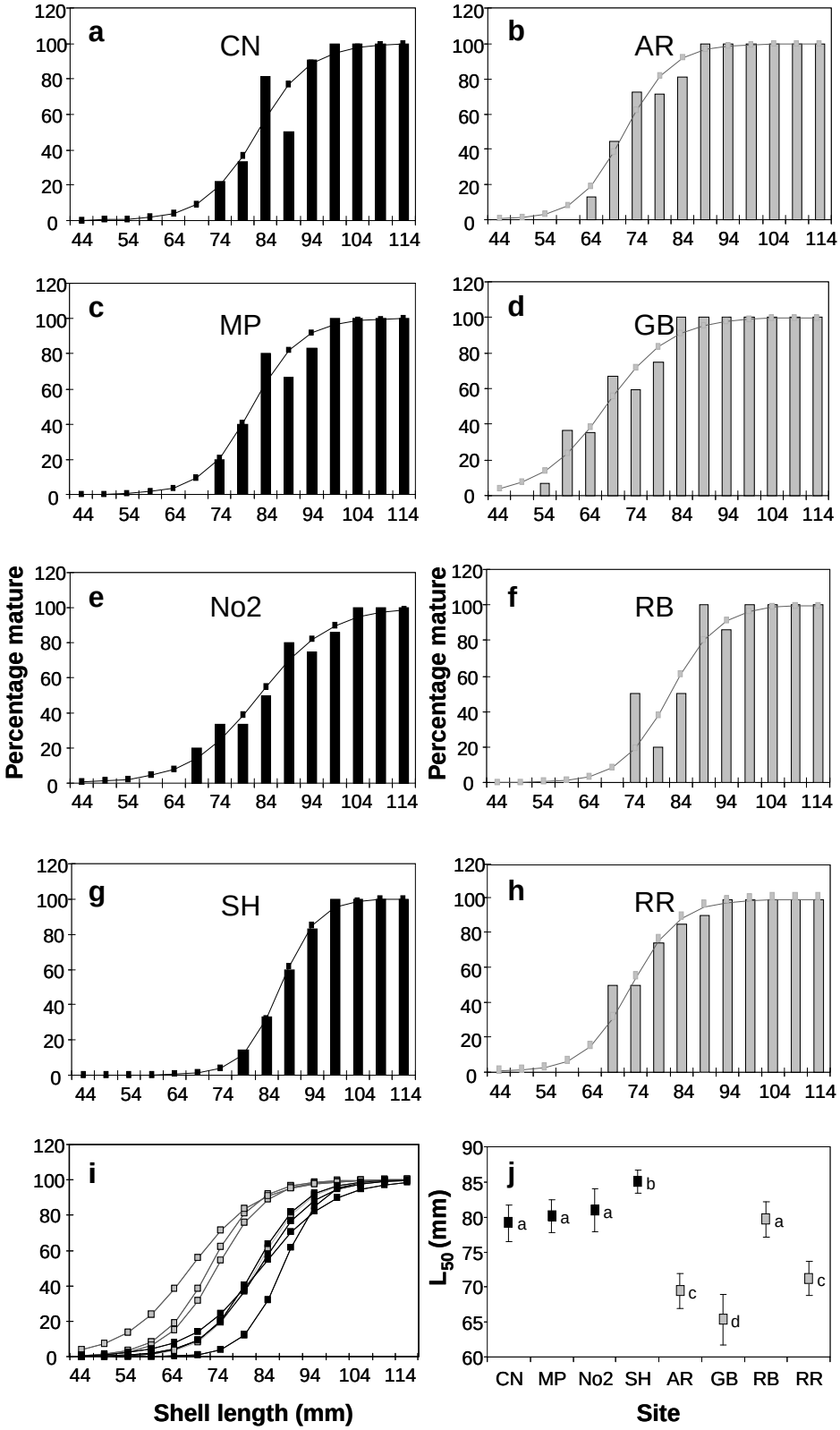

Figure 3.4: (a–h) Percentage blacklip mature within each size class at the broad-scale sites. (i) The trend lines for each of these relationships and (j) the estimates of L50 for all sites. Letters in (j) indicate similar groups classified by the likelihood ratio test. Black and grey symbols indicate non-stunted and stunted sites, respectively. Error bars indicate 95% CI.

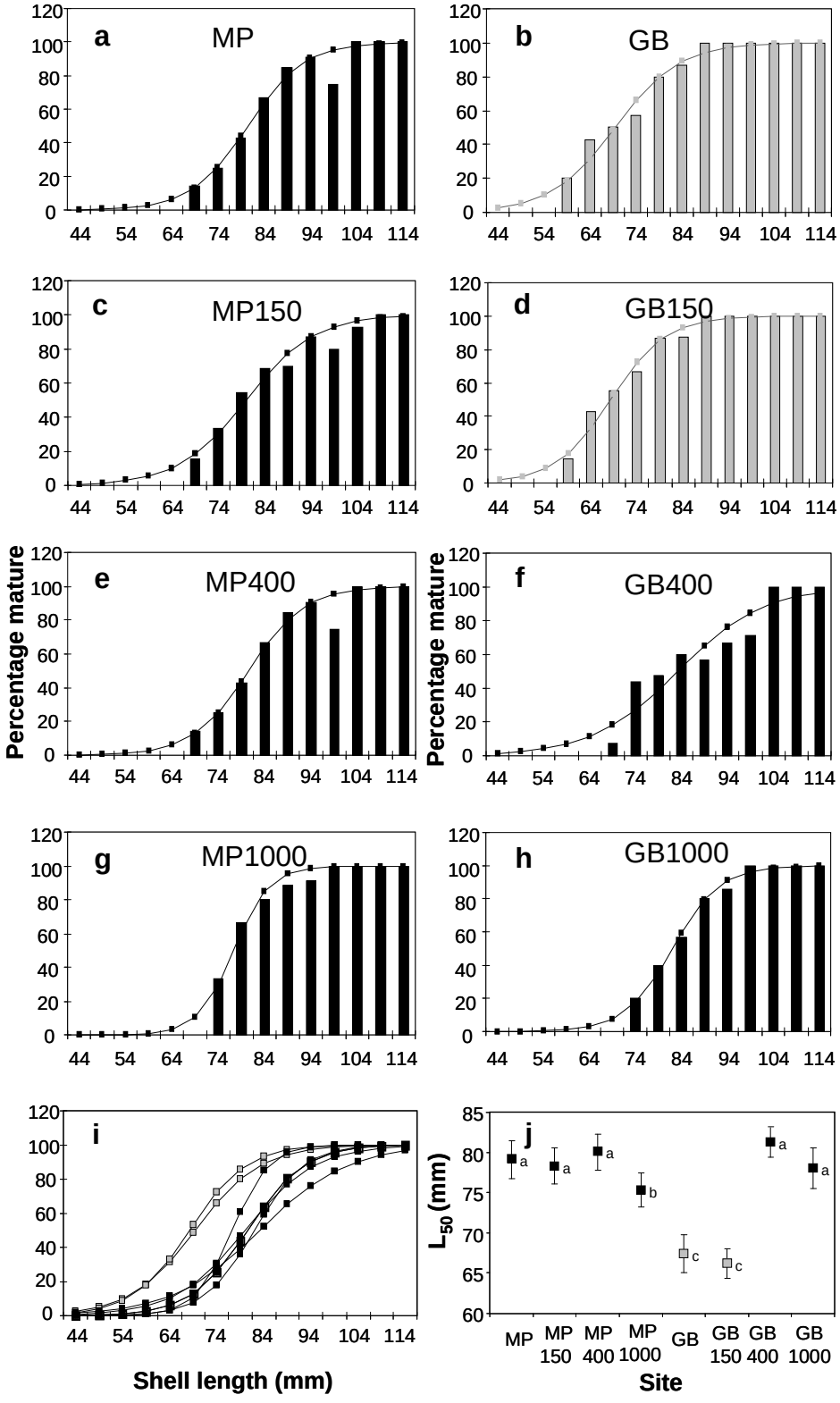

Figure 3.5: (a–h) Percentage blacklip mature within each size class at the MP and GB broad-scale sites and sub-sites. (i) The trend lines for each of these relationships and (j) the estimates of L50 for all sites. Letters in (j) indicate similar groups classified by the likelihood ratio test. Black and grey symbols indicate non-stunted and stunted sites, respectively. Error bars indicate 95% CI.

3.3.3 Fecundity

Samples among the broad-scale sites showed significant variability in fecundity (ANCOVA, $F_{7,254} = 2.31$, $p < 0.03$). However, the multiple comparisons revealed that these were a result of blacklip within GB and RB having significantly lower fecundity compared to the other sites rather than differences between stunted and non-stunted sites (Figure 3.6). There were also significant differences in the fecundity of blacklip within GB (ANCOVA, $F_{3,82} = 6.00$, $p < 0.001$) and MP (ANCOVA, $F_{3,80} = 4.41$, $p < 0.01$). Multiple comparisons revealed that blacklip in GB and GB150 and MP1000 had significantly lower fecundity compared to the other sites (Figure 3.7).

3.3.4 Relation of biology to morphology

The correlation analysis revealed significant positive relationships between the SL:SH ratio and growth (broad-scale sites: $r^2_7 = 0.646$, $p < 0.01$; sub-sites: $r^2_7 = 0.753$, $p < 0.005$), L_{50} (broad-scale sites: $r^2_7 = 0.579$, $p < 0.02$; sub-sites: $r^2_7 = 0.856$, $p < 0.001$) and fecundity (broad-scale sites: $r^2_7 = 0.453$, $p < 0.05$; sub-sites: $r^2_7 = 0.514$, $p < 0.05$; Figure 3.8). Furthermore, when the data from the broad-scale and sub-sites were combined, there were significant correlations between the SL:SH ratio and each of the biological parameters (growth: $r^2_{15} = 0.682$, $p < 0.001$; L_{50}: $r^2_{15} = 0.651$, $p < 0.001$; fecundity: $r^2_{15} = 0.419$, $p < 0.005$; Figure 3.8).

3.1 Discussion

The collection of information on growth, size at maturity and fecundity across both broad (10s km) and fine (100s m) spatial scales demonstrated that these parameters vary at both of these scales. Moreover, we were able to demonstrate that these parameters were significantly correlated to a simple morphometric marker (Chapter 2; Saunders et al. 2008). The spatial variability in the biology of blacklip observed is likely a result of fine-scale spatial variability in environmental factors (Swain et al. 2005). However, the dispersal of blacklip probably only occurs at scales of 10 to 100s m (Prince et al. 1987). Therefore, populations formed under these conditions exist at very fine spatial scales (Temby et al. 2007) and would be similar to that at which environmental variability operates (Saunders et al. 2008). Consequently, the morphometric marker could provide a valuable tool to aid fine-scale management of abalone fisheries by inferring the key biological parameters of individual populations and through using this information to discriminate among these.

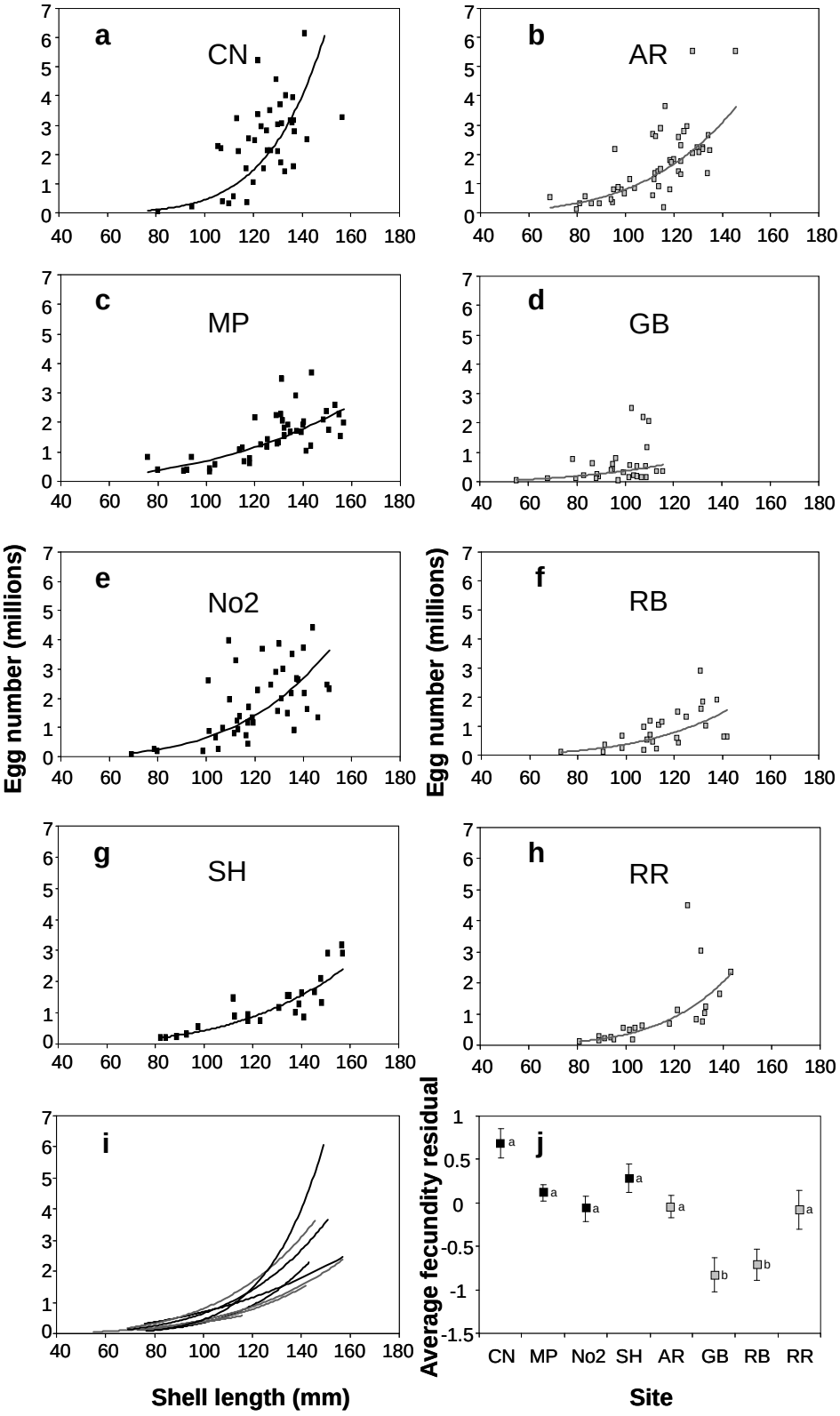

Figure 3.6: (a–h) Relationship between no. eggs ind.$^{-1}$ and shell length (SL) for blacklip at the broad-scale sites. (i) The trend lines for each of these relationships and (j) the average fecundity residuals for all sites. Letters in (j) indicate similar groups classified by the multiple comparisons. Black and grey symbols indicate non-stunted and stunted sites, respectively. Error bars indicate ±1 SE.

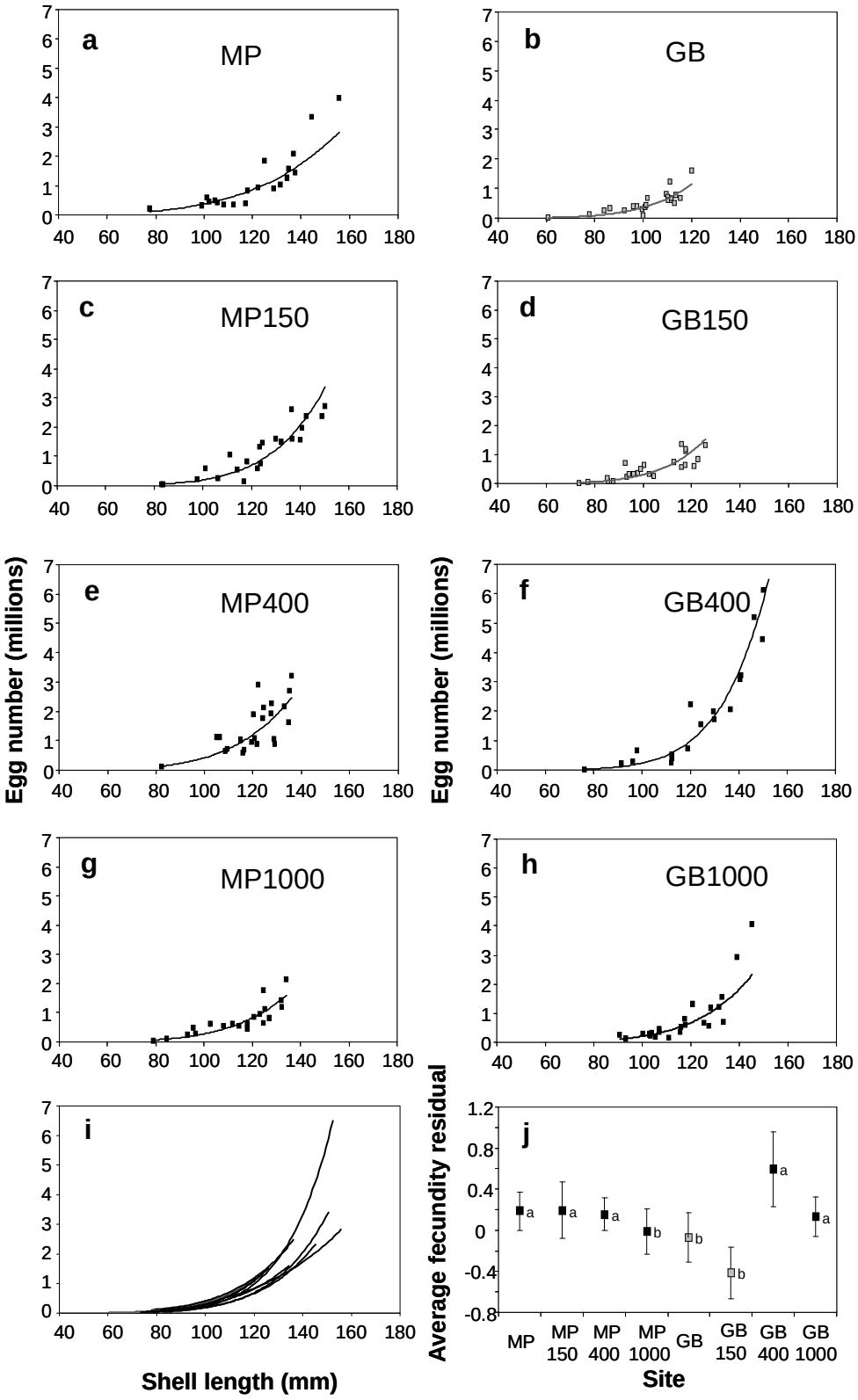

Figure 3.7: Relationship between no. eggs ind.$^{-1}$ and shell length (SL) for blacklip at the MP and GB broad-scale sites and subsites. (i) The trend lines for each of these relationships and (j) the average fecundity residuals for all sites. Letters in (j) indicate similar groups classified by the multiple comparisons. Black and grey symbols indicate non-stunted and stunted sites, respectively. Error bars indicate ±1 SE.

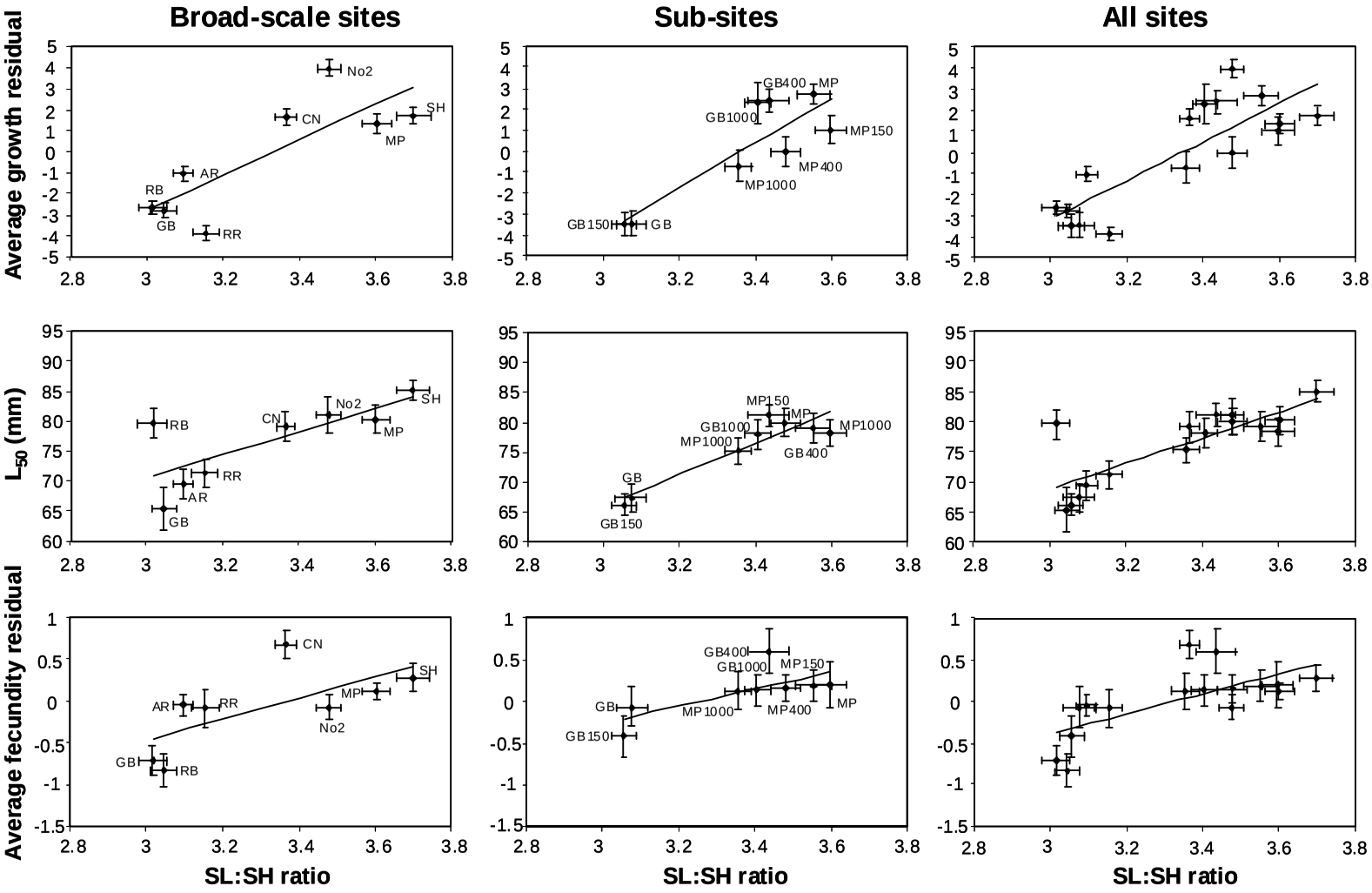

Figure 3.8: Relationship between the SL:SH ratio and average growth residuals, estimates of L_{50} and average fecundity residuals for the broad-scale sites, sub-sites and all sites combined. Error bars indicate ± 1 SE for growth and fecundity residuals and 95% confidence intervals for estimates of L_{50}.

The substantial spatial variation in growth that we observed for blacklip in the SZ appears to be characteristic of abalone populations worldwide (McShane et al. 1988a; Day and Fleming 1992; Worthington et al. 1995a). Differences in growth among the broad-scale sites were primarily determined by the site being within a stunted or non-stunted area. Within GB, the stunted pattern of growth was only observed within 400 m of the original site; the sites beyond this distance had significantly higher growth rates that were similar to those in the non-stunted sites. In contrast, growth patterns of blacklip in MP were consistent across a broader area, to at least 1000 m from the original site. These differences are likely to be attributed, in part, to blacklip in stunted sites being exposed to lower food availability as a result of less water movement and hence less drift algae compared to non-stunted populations (McShane et al. 1988a; Day and Fleming 1992; Worthington et al. 1995a). Furthermore, higher densities of conspecifics may have also contributed to differences in the rate of growth among sites (Dixon and Day 2004), as abundances of blacklip were ca. 7 times greater within stunted sites compared to those in non-stunted (Chapter 4). In addition to these factors, genetic variability among populations may be influencing the growth of abalone (Worthington et al. 1995a). To delineate how these environmental or genetic factors contribute to this observed spatial variation in growth, reciprocal transplant experiments need to be conducted (Swain and Foote 1999).

The spatial variability in size at maturity closely matched that observed for growth. At broad spatial scales, sites that contained stunted blacklip generally had a smaller size at maturity compared to those in non-stunted sites. The exception to this was the blacklip in one stunted site (RB) where they grew slowly but matured at a similar size to individuals in the non-stunted sites. Anecdotal evidence from fishers suggests that blacklip in this area grow quickly, but this manifests itself in changes in shell width and height as opposed to length. Importantly, within GB and MP the spatial variability in size at maturity mimicked that for growth. These results are unsurprising as growth rate reflects both individual size at age and the rate at which that size is attained and will affect size/age of maturity for individuals (Begg et al. 1999a; Cadrin 2005). Indeed, these patterns in growth and size at maturity are commonly observed in abalone populations in Tasmania (Tarbath 2003), New South Wales (Worthington and Andrew 1997), Victoria (McShane et al. 1988a) and elsewhere in South Australia

(Shepherd and Hearn 1983). These observations are probably a result of maturity being related to age, with blacklip in stunted areas maturing at the same age, but at a smaller size, compared to those in non-stunted areas (Shepherd and Laws 1974; Prince et al. 1988b; Shepherd et al. 1991; Nash 1992; McShane and Naylor 1995a). However, as we have no data on the age of individual blacklip in the present study, the observation of smaller size at maturity at stunted compared to non-stunted sites may reflect plasticity in the life-history strategy of blacklip among these areas (McAvaney et al. 2004; Naylor et al. 2006).

Among the broad-scale sites, the stunted sites that exhibited the lowest growth rates (GB and RB) all had the lowest levels of fecundity; however, the stunted sites that had slightly higher growth rates tended to have similar levels of fecundity compared to those in the non-stunted sites. Nevertheless, within GB and MP the spatial patterns in fecundity were consistent with those observed for growth and size at maturity. Similar spatial variability in growth and fecundity have been observed, with abalone generally producing fewer eggs in stunted compared to non-stunted areas (Shepherd et al. 1992b; Wells and Mulvay 1995; Campbell et al. 2003). The fact that fecundity was not as tightly linked to growth, when compared to size at maturity, is probably due to the substantial individual variation that was observed in egg-count data in the present study. This variability is most likely caused by the low sample sizes not accounting for the highly variable timing and duration of spawning of blacklip (Shepherd and Laws 1974). Consequently, at the time of collection all blacklip may have appeared to be fully gravid, despite some individuals having spawned and only having a fraction of their eggs.

The spatial variability in the biology of blacklip we have observed at multiple scales in the SZ was not unexpected, as it has been documented in numerous studies in Australia and elsewhere around the world. However, we have taken the identification of this variability in the SZ three additional steps forward. Firstly, we have demonstrated that growth, size at maturity and fecundity tend to co-vary together across these spatial scales. Previous studies have typically focussed on the spatial variability of these parameters in isolation. Secondly, we were able to identify the scale at which biological variability exists within 2 locations in the SZ. In GB, populations of blacklip that exhibited stunted characteristics (low growth, small size at maturity and low fecundity) were observed to occupy an area of ca. 400 m

compared to 1000 m for the non-stunted population of blacklip in MP. Thirdly, and most importantly, we have demonstrated that the SL:SH ratio developed previously (Chapter 2; Saunders et al. 2008) is highly correlated to key life-history parameters among populations of blacklip at both broad (100s km) and fine (100s m) spatial scales. Therefore, even though the biological classifications of the populations we have examined were not always consistent, these strong relationships allow for the biological characteristics of other populations of blacklip to be inferred simply and inexpensively by applying the SL:SH ratio to spatially resolved, commercial-catch samples. These results provide further evidence for the utility of the SL:SH ratio to aid fine-scale management of abalone fisheries. Not only can it provide information on the boundaries of separate populations (Saunders et al. 2008), but it can also be used to estimate the growth, size at maturity and fecundity for any population based on the relationships developed in the present study. Consequently, the assessment of samples from across the SZ fishery will ultimately enable blacklip populations to be mapped, with fine-scale systematic sampling facilitating determination of the boundaries of individual populations within and between these areas. The biological information inferred by the SL:SH ratio could then be used to assign individual populations of blacklip with appropriate size limits that reflect their biological characteristics.

The present study provides an important step towards practical implementation of fine-scale management strategies for abalone fisheries. Identifying the strong correlation between a simple morphometric marker and estimates of key biological parameters provides a potential tool to infer biological variability among populations of abalone and to separate them on this basis. Obtaining this information by traditional research methods remains challenging due to the high costs of obtaining demographic data at appropriate spatial scales. Thus, use of the morphometric marker provides a simple, cost-effective opportunity to bridge the traditional disconnect between scales of ecological variation and fisheries management. While this approach is particularly pertinent for abalone, given their stock structure and history of sudden collapse, it could also be applied to many other sedentary invertebrates that have fine-scale population structure and easily measurable hard-body parts that reflect their ontogenetic history. Consequently, being able to predict biological variation using a morphometric marker is broadly applicable and can assist with the conservation and management of many marine species.

Preamble to Chapter 4

Chapter 4 uses a reciprocal transplant experiment to assess whether the spatial variability observed in blacklip biology and morphology in Chapters 2 and 3 is a genetically fixed or phenotypically plastic trait. The data from Chapter 4 suggests that spatial variation in morphology and biology of blacklip is a result of a plastic response to environmental factors that were related to food availability.

This chapter has been accepted for publication and is currently in press in the journal *Marine Biology*. This manuscript included myself as senior and corresponding author and Sean D. Connell (University of Adelaide) and Stephen Mayfield (SARDI Aquatic Sciences) as co-authors. It is, therefore, written in plural. Permission from the publisher (Springer/Kluwer Academic Publishers, www.springeronline.com) to reproduce this manuscript herein has been granted (see Appendix A).

Contributions and signatures of authors

THOR M. SAUNDERS

Sampled, analysed, and interpreted all data, wrote manuscript as senior and corresponding author.

Signed:…… Date:…….

SEAN D. CONNELL

Supervised development of research, data interpretation and manuscript evaluation

Signed:…… Date:…….

STEPHEN MAYFIELD

Advised on aspects of research and manuscript evaluation

Signed:…… Date:…….

Chapter 4: Differences in abalone growth and morphology between locations with high and low food availability: morphologically fixed or plastic traits?

Abstract: Many species of sedentary marine invertebrates exhibit large spatial variation in their morphology that allow them to occupy a broad geographic distribution and range of environmental conditions. However, the detection of differences in morphology among variable environments cannot determine whether these differences represent a plastic response to the local environment, or whether morphology is genetically fixed. We used a reciprocal transplant experiment to test whether 'stunted' blacklip abalone, (*Haliotis rubra*) are the result of a plastic response to the environment or fixed genetic trait. Furthermore, we related environmental factors, that affect food availability (density of abalone, water movement, algal cover, and reef topography), to differences in growth and morphology. Morphological plasticity was confirmed as the mechanism causing morphological variation in *H. rubra*. Individuals transplanted to sites with 'non-stunted' *H. rubra* grew significantly faster when compared to stunted controls, while individuals transplanted to stunted sites grew significantly slower compared to non-stunted controls. The growth response was greater for individuals transplanted from non-stunted to stunted sites, suggesting that the environmental stressors in morphologically stunted habitat are stronger compared to locations of faster growing morphology. We propose that these differences are related to resource availability whereby low algal cover and topographic simplicity results in stunted populations, whereas high algal abundance and topographic complexity results in non-stunted populations.

4.1 Introduction

Morphological variation is common among sedentary marine invertebrates and has generally been attributed to being a plastic response to stressors in the local environment (Lively 1986; Johannesson et al. 1990; Robles and Robb 1993; Trussell 1996; Steffani and Branch 2003). However, morphological variability may also be caused by genetic differences among individuals as a result of historical selective pressure for a particular morphotype, or a combination of both phenotypic plasticity and genetic differences (Etter 1996; Luttikhuizen et al. 2003; Swain et al. 2005).

Identifying whether the morphological variability in sedentary invertebrates is a plastic or fixed trait provides useful information on whether these species form separate, localised populations or more broadly-distributed, mixed populations that are responding to local environmental conditions. In addition, the ability for these species to change their body form in response to environmental variability affects species interactions and the structure of communities (Raimondi et al. 2000; Miner et al. 2005).

Abalone are typical of sedentary invertebrates that show strong variability in morphology at both broad and fine spatial scales (Breen and Adkins 1982; Worthington et al. 1995a; Prince et al. 2008; Saunders et al. 2008). This variability commonly results in areas of reef inhabited by stunted abalone that are smaller in body form with typically shorter shells that are higher, wider and thicker compared to abalone in adjacent areas (Breen and Adkins 1982; Shepherd and Hearn 1983; Wells and Mulvay 1995). Stunted abalone typically occur in dense aggregations on reefs that are sheltered from the prevailing swell (McShane and Naylor 1995a). It has been suggested that the stunted morphology exhibited by abalone in these areas is a plastic response to receiving less food, in the form of drift algae, compared to conspecifics in more exposed areas (Day and Fleming 1992; Shepherd et al. 1992a; McShane and Naylor 1995a).

Translocation of stunted abalone to habitats where non-stunted abalone occur has been shown to significantly increase growth rate (Emmett and Jamieson 1989; McShane and Naylor 1995b; Dixon and Day 2004). In all of these studies it was suggested that the increased growth of stunted abalone was a result of a plastic response to more favourable environmental conditions, specifically a greater abundance and/or higher quality of food available. However, because none of these studies included a fully reciprocal transplant experiment, it is difficult to interpret the role of genetic variation as a cause of spatial differences in growth and morphology among locations. Indeed, the only genetic study on abalone where samples were collected at appropriate ecological scales, revealed genetic differences at spatial scales that are similar to the observed variability in morphology (Temby et al. 2007; Saunders et al. 2008). Consequently, morphological variability in abalone may be a fixed genetic trait rather than a plastic response to environmental factors.

To distinguish between models of morphologically plastic and fixed traits we reciprocally transplanted blacklip abalone (*Haliotis rubra*, hereafter referred to as abalone) between stunted and non-stunted sites at three locations in South Australia. It was predicted that if morphology is a plastic trait that varies in response to environmental factors, then (1) stunted abalone transplanted to non-stunted sites will grow more quickly than those re-placed in their native site, (2) non-stunted abalone transplanted to stunted sites will grow more slowly than those re-placed in their native site and (3) transplanted individuals will have similar growth rates to those placed in the recipient site. In addition, we acquired information on environmental factors related to food availability to improve interpretations of spatial variation in growth and morphology.

4.2 Methods

4.2.1 Study site

The study was conducted in the south east of South Australia in the waters between Beachport and Port Macdonnell (Figure 4.1). Reciprocal transplants of blacklip were replicated in three locations: Ringwood Reef, Gerloffs Bay and Jones Bay (Figure 4.1). These locations are known to contain both stunted and non-stunted blacklip populations based on commercial divers' observations that were validated by measurements of ratios of shell length to shell height (see Saunders et al. 2008) taken in this study (Figure 4.2).

4.2.2 Reciprocal transplant experiment

To assess whether sites chosen for the reciprocal transplant contained stunted or non-stunted abalone ~ 100 abalone were collected from each area using the sampling method described in Saunders et al. (2008). Briefly, the shell length (SL) and shell height (SH) were measured for each abalone and the average ratio between these (SL:SH ratio) was plotted for each site. Sites with a SL:SH ratio > 3.25 were considered to be non-stunted while sites with a SL:SH ratio < 3.25 were deemed to be stunted (after Saunders et al. 2008). The samples of abalone collected revealed that each location had a non-stunted and stunted site as classified by the SL:SH ratio value (after Saunders et al. 2008; Figure 4.2). Consequently, these sites were considered suitable for the reciprocal transplant experiment.

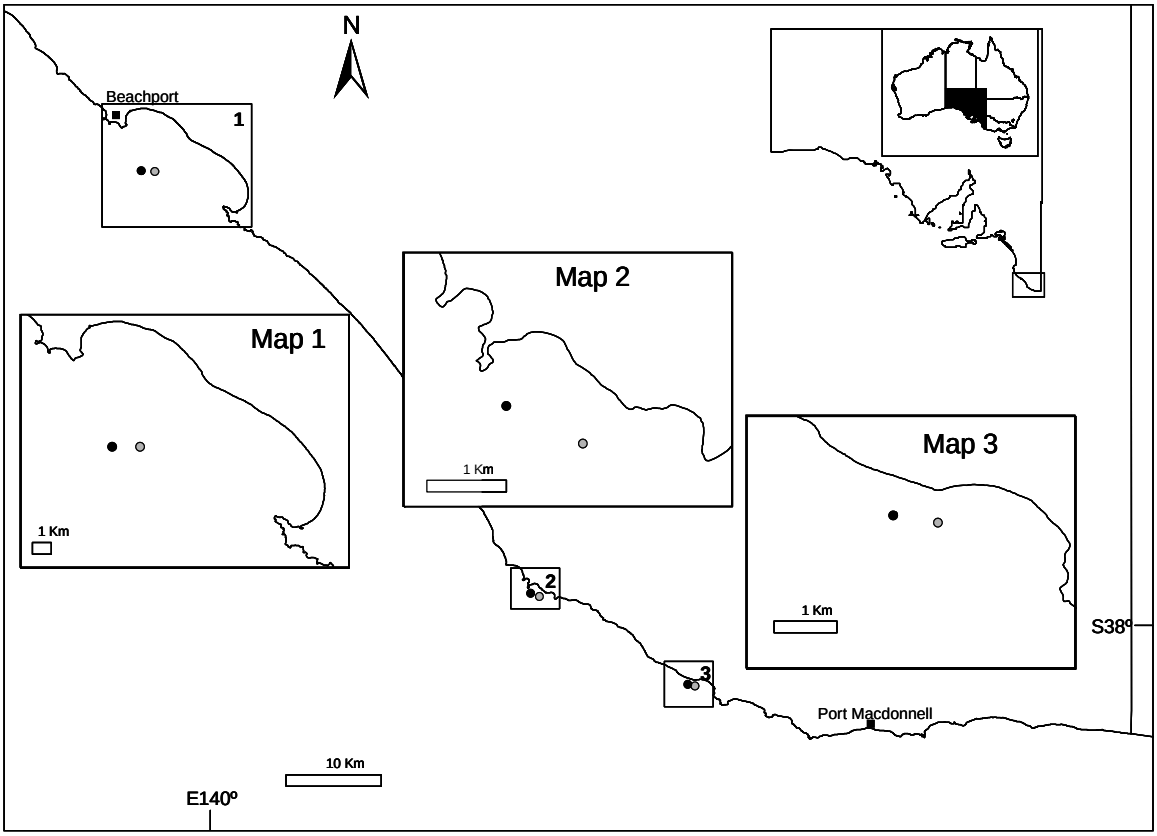

Figure 4.1: Map of study area showing the sites where the translocations were conducted, within Australia and South Australia. Inserts show map 1 Ringwood Reef, map 2 Gerloffs Bay and map 3 Jones Bay. Black and grey markers indicate non-stunted and stunted sites respectively.

During February and March 2006, between 66 (Jones Bay) and 116 (Ringwood Reef) juvenile abalone were collected from non-stunted sites and between 70 (Jones Bay) and 110 (Ringwood Reef) from stunted sites using SCUBA. These collections were obtained from an approximately 5 × 5m area within each non-stunted and stunted site. To remove the effect of size on the growth and morphology of abalone, only individuals that ranged between 90 and 110 mm SL were used for this experiment. While abalone showed morphological differentiation between the non-stunted and stunted sites at these sizes (individuals from stunted sites exhibiting higher shells at a given length compared to those in non-stunted sites), this size range selected was the only one for which there were sufficient numbers of abalone among all sites to achieve an interpretable result.

All abalone were tagged using small (12 mm), individually numbered, plastic discs attached to the shell by fixing a nylon rivet to the proximal pore hole (Prince 1991).

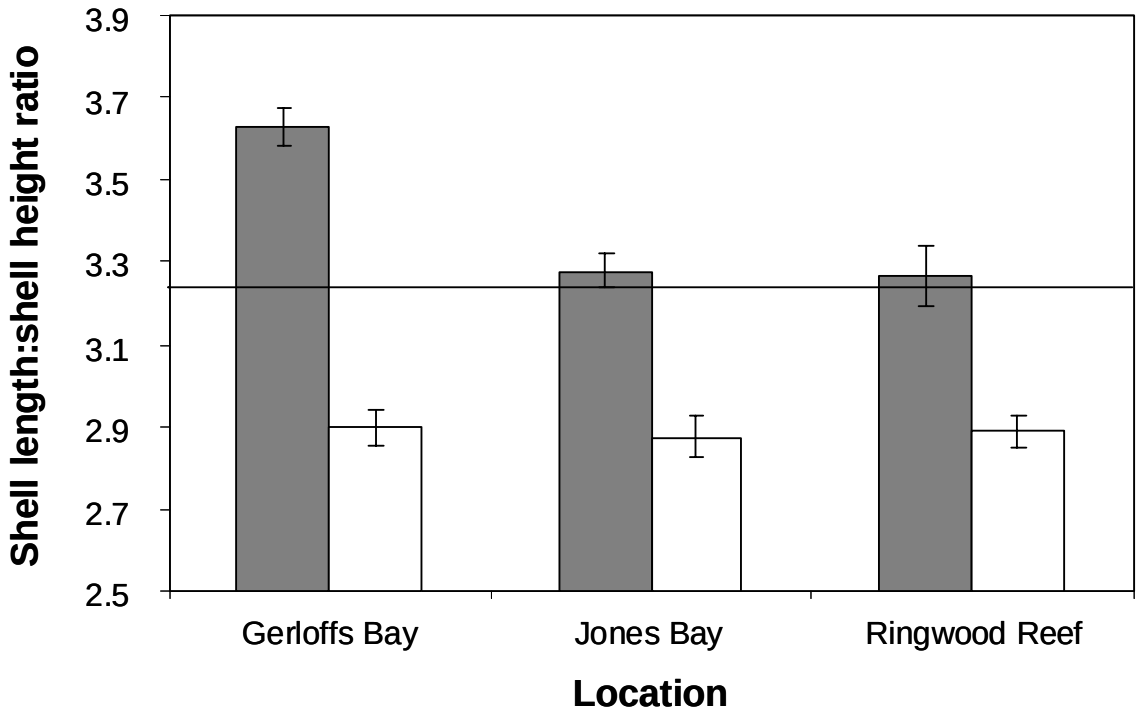

Figure 4.2: Mean SL:SH ratio of abalone samples in non-stunted and stunted sites for all three locations. Horizontal black line indicates the SL:SH ratio that separates non-stunted and stunted populations (after Saunders et al. 2008). Error bars indicate ± 1 SE.

The translocation process required all abalone be removed from the water. Consequently, all tagging and measuring of individuals was conducted aboard the research vessel. To minimise the stress incurred by the abalone in this process all individuals were; carefully removed from the substrate so they did not receive any cuts or bruising, suspended in fresh seawater in mesh bags over the side of the research vessel during tagging and translocated between sites in fish bins full of fresh seawater. All abalone were measured for SL to the nearest 0.5 mm during the tagging process. Spatial variation in abalone morphology has been shown to be strongly related to growth differences in the shell length of individuals (Breen and Adkins 1982; McShane et al. 1988a; Worthington et al. 1995a; Saunders and Mayfield 2008). Consequently, growth in shell length was used as a surrogate for testing hypotheses about the spatial variation in abalone morphology because changes in this measure occur over time scales that were manageable for this experiment. Within each location, half of the tagged abalone obtained from the 'non-stunted sites' were replaced back at their native site (= non-stunted controls (NSC)) and half were transplanted into the recipient stunted site (= non-stunted translocated (NST)). The reciprocal experiment was carried out on individuals collected from stunted sites

(stunted controls (SC) and stunted translocated (ST)). Tagged abalone were subsequently recaptured and remeasured from each site after at least 6 months at liberty (September and October 2006).

4.2.3 Measurements of blacklip density, topography, water movement and algal cover

Estimates of abalone density were obtained in each site within each location by counting all individuals within five 25 × 2 m transects that were systematically distributed within a 25 m^2 area. In addition, the water depth was recorded every 2.5 m along each transect using a dive computer, thus providing a total of 50 measurements. Each measurement was converted into a substrate relief value by subtracting it from the mean depth of the transect. Reef topography was then described as an average of substrate relief for each site. Abalone density and reef topographic data were obtained during October and November 2006.

Estimates of benthic water motion were obtained by deploying hemispherical gypsum blocks in each area. These blocks were made of CSR® casting plaster of Paris ($CaSO_4$ ½H_2O) at a mixture of 5:1 plaster and distilled water. Each block was made to a weight of 34 ± 0.01 g using the same method employed by Jokiel and Morrissey (1993). Each block was glued to a 70 × 100 mm lead ingot base for application. Eight blocks were deployed in each site for all locations during March 2008 and were retrieved after ~ four days on the bottom. Eight identical control blocks were placed in separate insulated containers containing 30 l of seawater over the same time period. At the end of the measurement period, all blocks were allowed to air-dry to a constant weight before they were reweighed. During deployment, all blocks were placed on flat, rocky substratum that was similar among sites. Blocks were placed adjacent to the tagged individuals in a south westerly direction that faced the prevailing swell. Estimates of mean water velocity over four days were obtained using relationships between the dissolution of blocks exposed to moving water, compared to those in still water, as developed by Jokiel and Morrissey (1993). In addition, the maximum water velocity was obtained at each site by the use of dynamometers consisting of spring scales that recorded drag measurements that were converted into water velocities using the calibration curves provided by Bell and Denny (1994). Three dynamometers were simultaneously deployed adjacent to the plaster blocks in all sites.

Estimates of algal cover were obtained from each site by placing a $1m^2$ quadrat every 10 m along four 100 m lines that ran from the NE edge of the site towards the prevailing swell (SW). Estimates of percentage cover were recorded for the species of red (*Asparagopsus armatus* and *Plocamium* sp.) and brown algae (*Cystophora* sp. and *Macrocystis augustifolia*) that are the main constituents of abalone diet (Shepherd 1973; Day and Fleming 1992; Shepherd et al. 1992a; Guest et al. 2007).

4.2.4 Data analysis

The design of the reciprocal transplant experiment tested the following predictions: (1) abalone translocated between growth areas will differ in growth rate from individuals replaced within their native site (i.e. a plastic response: NST < NSC and ST > SC) and (2) non-stunted abalone will grow faster than stunted individuals regardless of the site they are in as a result of their different growth histories (NSC > ST and NST > SC). A 3 factor ANOVA with location (random factor), history (fixed factor) and treatment (fixed factor) was used to test these predictions with *a priori* planned contrasts (Day and Quinn 1989) to test for differences in growth rate between treatments (i.e. NSC vs NST, SC vs ST, NSC vs ST, and SC vs NST).

A two factor ANOVA with location (random factor) and site (fixed factor) was used to assess the variability in substrate relief, abalone density, water velocity, maximum water velocity and percentage algal cover among sites and locations. Tukey's HSD tests were used *post hoc* to assess where significant differences existed. All these environmental factors were plotted against the mean growth in SL for both non-stunted and stunted sites for each location. Relationships among the environmental factors and abalone growth in SL were investigated through Pearson's correlation analyses. The relationships among the environmental factors measured would have been ideally assessed by a multiple linear regression. However, the nature of the growth data prohibits the use of this technique as each tagged abalone that was recaptured would require individual environmental data. To acquire this amount of information within the weather periods available would have been logistically impossible.

4.3 Results

4.3.1 Reciprocal transplant experiment

Transplanted abalone grew faster when transferred to non-stunted sites and slower when transferred to stunted sites compared to individuals re-placed into their native site (ST > SC, NSC > NST, Figure 4.3; significant History × Treatment interaction, Table 4.1). In addition, differences in growth were detected between individuals with different growth history, independent of whether they were transplanted or replaced into their native site (non-stunted > stunted; significant History effect; Figure. 4.3, Table 4.1). This difference was caused by the control abalone in non-stunted sites growing at a faster rate compared to conspecifics translocated there from stunted sites (NSC > ST). However, abalone translocated from non-stunted to stunted sites grew similarly to stunted controls (NST = SC). The significant interaction of Location × History × Treatment suggests that differences in growth between transplanted abalone and their neighbouring controls varied among locations (Figure 4.3, Table 4.1).

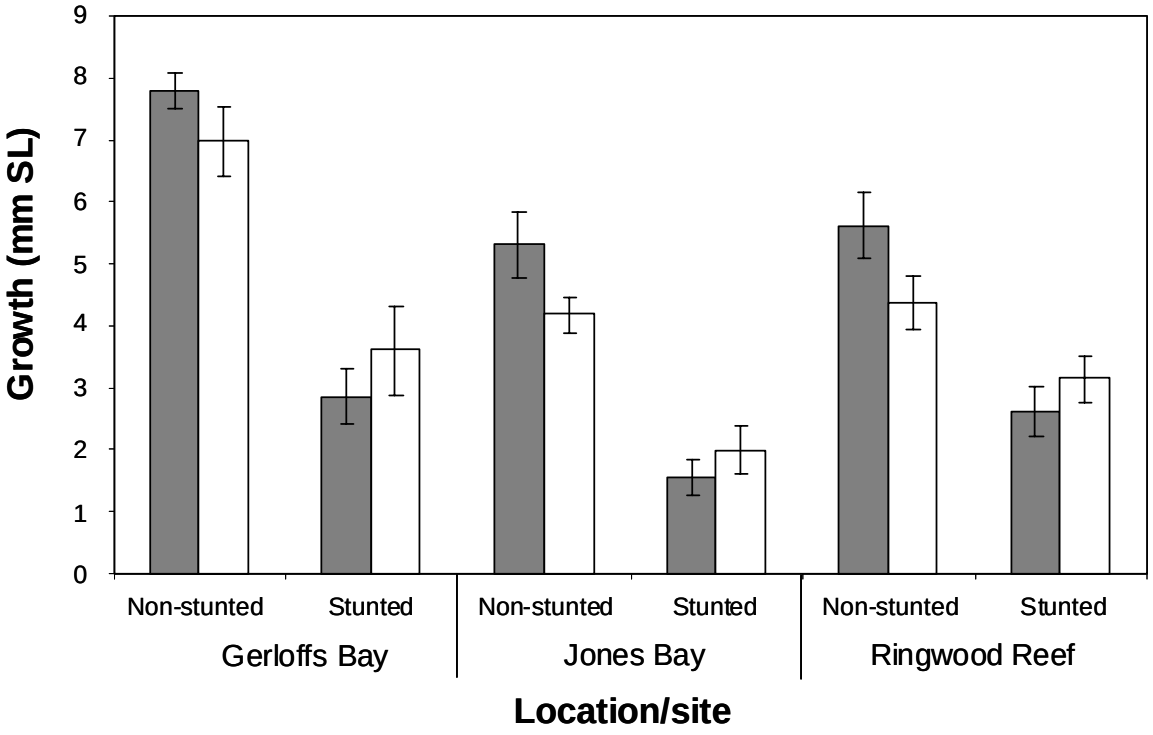

Figure 4.3: Mean growth (mm SL) standardised for six months for abalone for all non-stunted and stunted sites. Grey and clear bars specify native control and translocated abalone, respectively. Error bars indicate ± 1 SE.

Table 4.1 Results of the three-way ANOVA with planned contrasts testing for differences between abalone growth, for the transplant treatments: non-stunted controls (NSC), stunted to non-stunted sites (NST), stunted controls (SC) and stunted to non-stunted sites (ST). The experiment was done at 3 locations (Location) where abalone with a non-stunted or stunted growth history (History) were transplanted to the reciprocal or replaced in their native site (Treatment).

	df	MS	*F*	*P*
Location	2	64.28	2.10	*NS*
History	1	29.95	121.88	***
Treatment	1	2.79	3.87	*NS*
Location×History	2	0.07	0.01	*NS*
Location×Treatment	2	0.56	0.03	*NS*
History×Treatment	1	433.54	22.44	*
NSC vs NST	1	239.60	59.28	***
SC vs ST	1	194.20	48.05	***
NSC vs ST	1	24.54	6.07	*
SC vs NST	1	7.53	1.86	*NS*
Location×History×Treatment	2	20.03	4.96	**
Error	195	4.04		

NS Non-significant ($P > 0.05$)
*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

4.3.2 Spatial variability in environmental factors

Non-stunted sites had significantly higher substrate relief (ANOVA: $F_{1,290} = 447.9$, $p < 0.001$; Figure 4.4a), water velocity (ANOVA: $F_{1,41} = 96.3$, $p < 0.001$; Figure 4.4c) and percentage algal cover (ANOVA: $F_{1,234} = 76.3$, $p < 0.02$; Figure 4.4e) compared to stunted sites. In contrast abalone densities were significantly higher in stunted compared to non-stunted sites (ANOVA: $F_{1,149} = 363.1$, $p < 0.001$; Figure 4.4b). The Tukey's HSD test revealed that the non-stunted sites at Gerloffs Bay and Ringwood Reef had the highest substrate relief and percentage algal cover, while the stunted sites at Gerloffs Bay and Ringwood Reef had the highest densities of abalone (Figure 4.4). The non-stunted site at Jones Bay had the highest time averaged and maximum water velocity, although the latter was not significantly different as a result of the small sample size and high variability among the dynamometer readings (Figure 4.4d).

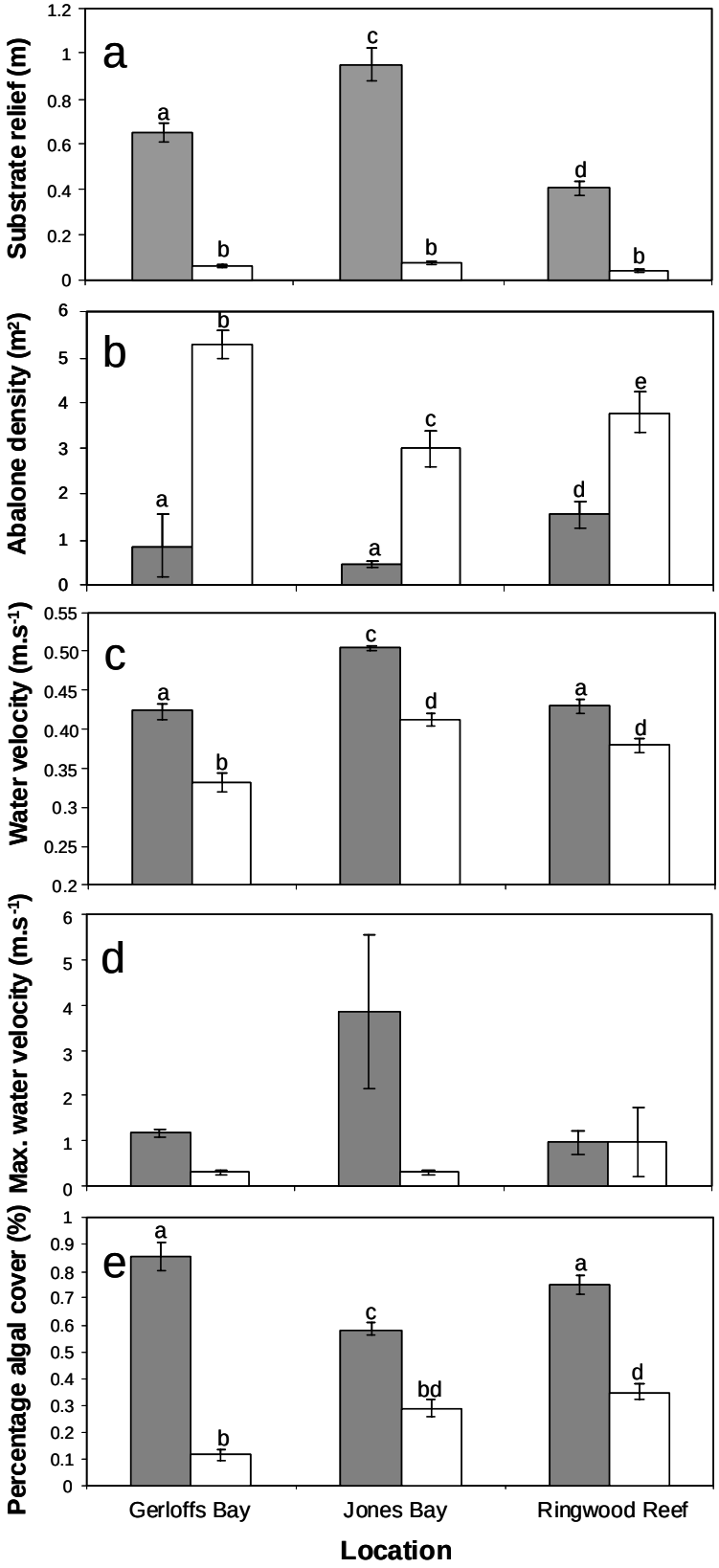

Figure 4.4: Mean values for (a) substrate relief, (b) density of abalone, (c) water velocity, (d) maximum water velocity and (e) percentage algal cover in non-stunted and stunted sites within each location. Grey and clear bars specify non-stunted and stunted sites, respectively. Letters signify similar groups classified by the Tukey's HSD test. Error bars indicate ± 1 SE.

4.3.3 Relationship between growth and environmental factors

Growth was significantly, positively correlated to substrate relief ($r_5 = 0.778$, $p < 0.05$; Figure 4.5a) and percentage algal cover ($r_5 = 0.870$, $p < 0.02$; Figure 4.5e) but not to time averaged water velocity ($r_5 = 0.358$, $p > 0.2$; Figure 4.5c) or maximum water velocity ($r_5 = 0.127$, $p > 0.5$; Figure 4.5d). In addition, the negative correlation between growth and abalone density was also non-significant ($r_5 = 0.663$, $p > 0.05$; Figure 4.5b).

4.4 Discussion

The reciprocal transplants revealed that the variability in the growth and morphology of abalone is a result of a plastic response to environmental factors. Reef topography and algal cover were positively correlated with higher growth rate of abalone, and both factors relate to the availability of food in the form of drift algae. Abalone translocated from high to low areas of food availability showed a stronger response in growth compared to their reciprocal transplants. Consequently, this study provides the first experimental evidence to support the theory that spatial variation in abalone growth and morphology is a plastic response to localised environmental conditions, which are probably related to food availability, rather than genetic differences between conspecifics.

Transplanted abalone grew differently to their native site controls indicating that growth and morphology was the result of a phenotypic response to their local environment. However, abalone from non-stunted sites had faster growth rates compared to stunted individuals independent of the site they inhabited. This result was expected as the juvenile abalone used in this experiment were already morphologically differentiated. Consequently, the difference in growth between individuals with varying growth history is probably a result of an age effect on growth, resulting in stunted abalone growing more slowly because they are older compared to non-stunted individuals (Johnson and Black 1998; Dixon and Day 2004; Prince et al. 2008). However, among treatments, non-stunted abalone only had faster growth rates within their native site suggesting the environmental stressors in stunted areas are strong enough to influence growth, independent of the growth history of individuals.

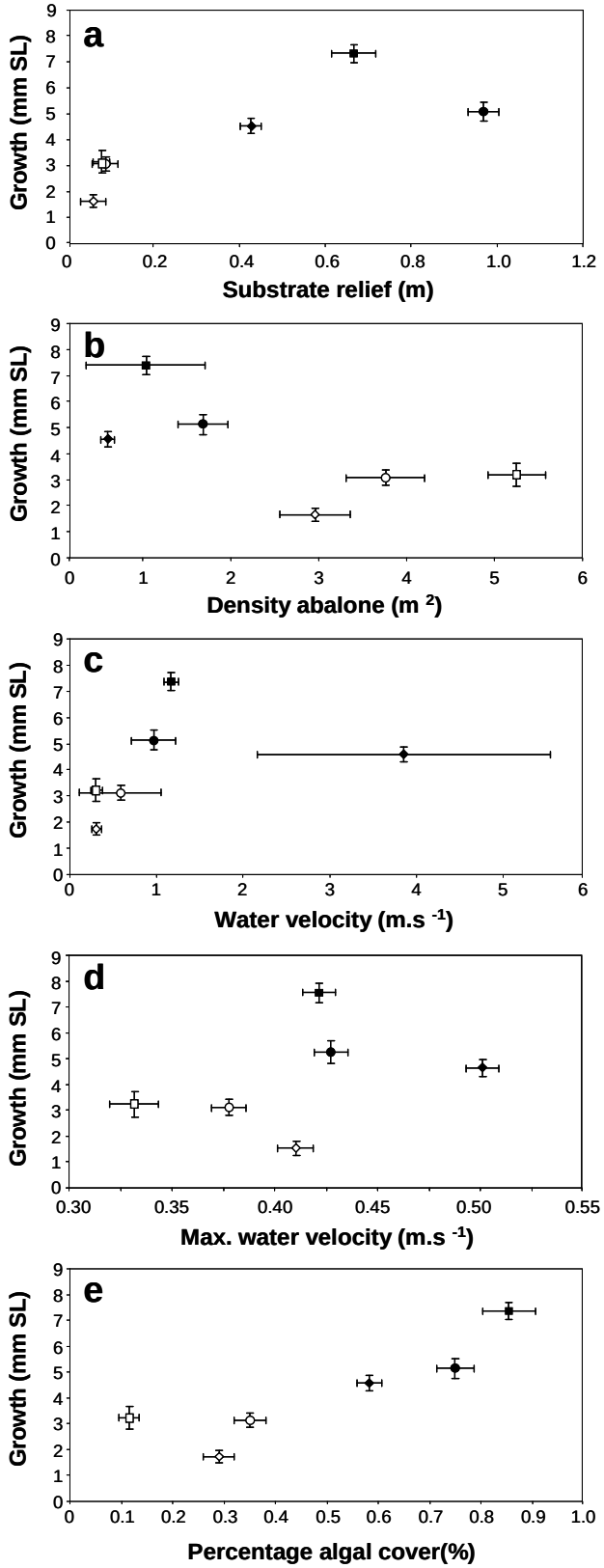

Figure 4.5: Relationships between growth and (a) substrate relief, (b) density of abalone, (c) water velocity, (d) maximum water velocity and (e) percentage algal cover in non-stunted (black symbols) and stunted sites (white symbols) within all locations. Squares, diamonds and circles indicate samples from Gerloffs Bay, Jones Bay and Ringwood Reef respectively. Error bars indicate ± 1 SE.

Higher algal abundance has often been suggested as a factor promoting increased growth in abalone (Shepherd and Hearn 1983; Shepherd et al. 1992a; Dixon and Day 2004). However, both algal abundance and bottom topography were strongly correlated to abalone growth, and both factors may be used as proxy's to estimate spatial variation in the availability of food in the form of drift algae. Bottom topography has rarely been used to explain differences in abalone growth, but we propose that areas with complex vertical reef topography would act as a natural trap for drift algae compared to reef with a simpler vertical structure. Consequently, we predict that abalone inhabiting topographically complex reef are exposed to a greater volume of drift algae compared to individuals on simpler reef structures.

Increased water flow has been shown to enhance the food supply for many invertebrates, including abalone (McShane and Naylor 1995a; Ebert 1996; Steffani and Branch 2003; Donovan and Taylor 2008). It is suggested that the continual churning action of the ocean on algal canopies in exposed areas results in regular supplies of drift algae compared to sheltered habitat (McShane et al. 1988a). There was, however, no significant correlation between water movement and abalone growth in the current study. This result is related to non-stunted abalone in one location (Jones Bay) exhibiting slow growth rates despite being exposed to maximum water velocities more than three times greater than observed at any other site. Indeed, the correlation between water movement and feeding has only been shown to exist up to a threshold level that, when exceeded, results in a decrease in abalone growth rate due to the metabolic costs of holding onto the substrate and the limited opportunities to feed (Shepherd et al. 1973; Donovan and Taylor 2008).

Studies on the effect of density on abalone growth have shown variable results. Dixon and Day (2004) showed that *Haliotis laevigata* growth increased significantly in aggregations where densities were reduced by 50% compared to control aggregations left at natural densities. In contrast, McShane and Naylor (1995b) found no significant differences in growth of *H. iris* between enclosures at natural and ~ 50× natural densities. The authors argued that the opportunistic feeding on drift algae by abalone does not promote significant competition for food among individuals. Similarly, there was no significant correlation between abalone growth and density in the current study. While there was a negative relationship between growth and density it was

apparent that the environmental factors relating to food availability (algal cover and topography) were influencing the significance of this relationship. The sites with the highest food availability had the highest growth but not the lowest densities (Gerloffs Bay and Ringwood Reef non-stunted) while the site with the lowest food availability had the lowest growth but not the highest density (Jones Bay stunted). To test the effect of density on growth independent of food availability, experiments need be conducted that vary densities and control for topography, algal abundance and water flow.

The short, high morphology exhibited by stunted abalone is probably related to individuals in these areas having a very low growth in SL as a result of receiving limited amounts of food in the form of drift algae (McShane et al. 1988a; Day and Flemming 1992; Shepherd and Hearn 1992). The increase in SL relative to SH is probably related to increases in SH being a natural product of age and abalone in stunted areas being comparatively older than their non-stunted conspecifics (Prince et al. 2008). In contrast, the long, flat, morphotype exhibited by non-stunted abalone is probably related to individuals being exposed to higher water velocities and this shell shape would offer less drag resistance (Johnson and Black 2000; Steffani and Branch 2003). However, the results from the reciprocal transplant experiment indicate that the limited availability of food experienced by stunted abalone provides a stronger morphological response than the greater water velocities experienced by non-stunted individuals. These observations suggest that plasticity in morphology of abalone may operate under similar constraints as those well known in benthic algae. That is, the stressors associated with extreme environmental conditions drive rapid changes to morphology (i.e. towards those individuals that survive in their environments), whereas in less stressful environments they are not so influential (Fowler-Walker et al. 2006).

The phenotypic plasticity we observed suggests that abalone populations occur at broader scales than the spatial variation observed in abalone morphology. Indeed, genetic studies on abalone have found genetic similarity in this species across spatial scales ranging from 10’s - 100’s km (Brown 1991; Huang et al. 2000; Conod et al. 2002). However, these same studies suggest gene flow and larval dispersal distances in excess of those inferred from empirical field studies and hydrodynamic modelling

of dispersal (McShane et al. 1988b; Prince et al. 1988a). These conflicting results are probably due to relatively little genetic exchange being required to maintain genetic homogeneity in populations that are otherwise ecologically distinct and genetic models may underestimate the degree of population structure present (Palumbi 2003; Miller and Shanks 2004). Indeed, it is suggested that abalone exist as a series of discrete populations across their geographic range at scales of 10's to 100's m and management of this species should occur at similar spatial scales to ensure the sustainability of these individual populations (Prince 2005; Saunders et al. 2009).

In conclusion, this study suggests that variability in abalone growth and morphology is a result of a plastic response to the local environment, rather than being genetically fixed. We suggest this morphological variability is a response to varying levels of food as a function of supply and availability (e.g. short-high shells in low algal cover and low relief vs long-flat shells in high algal cover and high relief). Furthermore, the results also suggest that the more stressful the environment (e.g. low food availability) the stronger the growth response in abalone. Such morphological variation in response to resource availability may enable benthic populations to occupy a wide range of habitats that vary in environmental stress and resource availability.

Preamble to Chapter 5

Chapter 5 presents data applying the morphometric marker developed in Chapter 2 to spatially resolved commercial abalone shell samples to identify potential units of management consisting of individual populations of abalone. Further, fine-scale, systematic sampling of commercial shell samples was used to more accurately determine the boundaries between adjacent abalone populations. The relationships between blacklip biology and morphology developed in Chapter 3 were used to estimate the biological characteristics of these populations.

This chapter was published in the journal *ICES Journal of Marine Science* in 2009 (vol. 66:305-314), with myself as senior and corresponding author and Stephen Mayfield and Andrew A. Hogg (SARDI Aquatic Sciences) as co-authors. It is, therefore written in plural. Permission from the publisher (Oxford University Press, www.oxfordjournals.org) to reproduce this manuscript herein has been granted (See Appendix A).

Contributions and signatures of authors

THOR M. SAUNDERS

Sampled, analysed, and interpreted all data, wrote manuscript as senior and corresponding author.

Signed:…… Date:…….

STEPHEN MAYFIELD

Supervised development of research, data interpretation and manuscript evaluation

Signed:…… Date:…….

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Assisted with the sampling and collation of data.

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Chapter 5: Using a simple morphometric marker to identify management units for abalone fisheries

Abstract: Managing stocks of sedentary marine invertebrates is complicated by the highly structured populations they form. Blacklip abalone (*Haliotis rubra*) form isolated populations with variable life history characteristics. Many of the populations are 'stunted', attaining a lower maximum size than those in adjacent areas. To reduce the risks of over-fishing and localized depletion, management units (MUs) that encompass individual populations need to be determined, then managed according to their life history characteristics. Here, potential MUs in a South Australian abalone fishery were identified from the broad-scale, spatial distribution of stunted and 'non-stunted' populations of blacklip abalone, by applying a morphometric marker to commercial shell samples. Key life history parameters of the populations within the potential MUs were estimated using relationships between the morphometric marker and blacklip abalone biology. Data from fine-scale systematic sampling by commercial fishers were used to validate spatial patterns observed from the more broadly distributed commercial catch samples. The location, distribution, and size of potential MUs were largely inconsistent with those of current management. The locations of two MUs (in Gerloffs Bay) were consistent across the broad- and fine-scale datasets, with the fine-scale samples more informative for identifying a potential boundary between them. The disparity between these data and current management arrangements are highlighted, and approaches for modifying them are discussed. This approach is among the first to provide a practical means of more closely aligning the scales of assessment and management with biological reality for sedentary marine invertebrates.

5.1 Introduction

The importance of considering demographic differences among populations to manage against over-fishing and localized depletion has long been recognized (Begg et al. 1999b), and has led to the concept of identifying management units (MUs). These MUs can be defined as demographically independent populations that should be managed and monitored separately (Taylor and Dizon 1999; Martien and Taylor 2003). Fundamental to the successful development of MUs is the ability to discriminate among component populations and, subsequently, to manage each on the

basis of their biological parameters and associated productivity (Taylor and Dizon 1999; Bergenius et al. 2005; Defeo and Castilla 2005).

The recognition of fine-scale stock structure and a consequent desire to develop MUs has perhaps been most common for a range of sedentary marine invertebrates, including abalone (Prince 2005; Naylor et al. 2006), sea urchins (Prince and Hilborn 2003; Perry et al. 2002), and scallops (Smith and Rago 2004). Typically, such species have limited larval dispersal and form individual populations, across multiple spatial scales, which often vary greatly in their life history parameters (Orensanz and Jamieson 1995; Orensanz et al. 2005; Temby et al. 2007). However, a lack of appropriate, spatially-resolved data describing population structure has hindered the development of MUs, leaving management regimes operating over large spatial scales (Leiva and Castilla 2001; Castilla and Defeo 2005; Prince 2005).

Abalone (genus *Haliotis*) are typical of these sedentary species, in that they constitute many discrete populations across their geographical extent (Nash 1992; Prince 2005). The populations are highly variable in life history characteristics (McShane et al. 1988a; Worthington et al. 1995a; Worthington and Andrew 1997), with many containing stunted abalone that have slower growth and/or a smaller maximum size than abalone in adjacent populations (Nash 1992; Wells and Mulvay 1995). As with most sedentary marine invertebrates, the current broad-scale (more than 100s-1000s of km of coastline; McShane et al. 1994a) management of abalone fisheries fails to account for this fine-scale population structure. This leaves fast-growing, non-stunted populations prone to over-fishing, and slow-growing, stunted populations under-utilised (Strathmann et al. 2002; Prince 2005). Identification of appropriate MUs, which reflect abalone population structure, could overcome this problem.

The most common method that has been employed to identify the population structure for abalone has been the analysis of genetic divergence among hypothesized populations (Hamm and Burton 2000; Conod et al. 2002; Chambers et al. 2006; Temby et al. 2007). However, such studies have typically shown differences at scales larger than would be expected given their predicted larval dispersal capabilities (McShane et al. 1988b; Chambers et al. 2006; Stephens et al. 2006). This discrepancy in the estimated dispersal distances of abalone larvae has probably arisen because ecological studies tend to focus on small spatial scales (i.e. <1 km), whereas genetic

studies have generally sampled at larger scales (10s–100s of km). Therefore, the genetic studies have a limited capacity to support or refute the scale of dispersal identified in field studies (Temby et al. 2007). Moreover, genetic models often underestimate the degree of population structure present, because relatively little genetic exchange is required to maintain genetic homogeneity between populations that are otherwise ecologically distinct (Palumbi 2003; Miller and Shanks 2004).

An alternative approach is to identify separate populations based on spatial variability in morphology (Cadrin 2005). This method relies on the premise that growth and maturation of individuals vary among separate populations and that morphology is strongly linked to these parameters (Cadrin and Silva 2005; Saunders and Mayfield 2008). Consequently, discrimination among populations can be achieved by identifying spatially distributed samples with similar morphology (Cadrin 2005; Cadrin and Silva 2005). The substantial spatial variation in abalone morphology (Breen and Adkins 1982; McShane et al. 1994b; Worthington et al. 1995a; Saunders et al. 2008) suggests that this may be an effective method for identifying appropriate MUs for this group of species. The approach has the added benefit of estimating the specific life history characteristics of these populations because of the strong links between morphology and biology (Cadrin 2005; Saunders and Mayfield 2008).

Notably, Worthington et al. (1995a) used this concept to distinguish among fast- and slow-growing abalone populations in New South Wales using shell width. They found that abalone in slow-growing areas typically had wider shells than conspecifics in fast-growing areas. Accordingly, they suggested that a minimum width limit would allow for increased exploitation of populations of slower growing abalone, by allowing these animals to be collected at shorter lengths than those that grew quickly. More recently, in the western zone of the Victorian abalone fishery, fishing effort has focused on harvesting abalone with domed and fouled shells, on the assumption that regardless of size, these characteristics indicate an older age composition and a correspondingly higher level (approximately 50%) of spawning per recruit (Prince et al. 2008). This method of assessing abalone population health qualitatively by shell shape has led to increasingly complex spatial management of the resource, with current management arrangements including reef-specific catch limits and minimum legal lengths (MLLs). A limitation of this approach is the absence of calibration

between shell shape or appearance and key biological parameters. Saunders et al. (2008) provide a more formal method through development of a quantitative morphometric marker. They demonstrated that such a marker, based on the ratio of shell length to shell height (SL:SH), was able to differentiate between stunted and non-stunted abalone populations in the southern zone of the South Australian abalone fishery (SZ). That marker was subsequently shown to be strongly linked to growth rate, size-at-maturity, and fecundity (Saunders and Mayfield 2008). Therefore, this morphometric marker is potentially a powerful tool for identifying and distinguishing among abalone populations, and for inferring crucial life history characteristics.

The objective of this study was to identify potential MUs in the SZ by determining the broad-scale, spatial distribution of stunted and non-stunted populations of blacklip abalone (*H. rubra*, hereafter referred to as blacklip) in the fishery, through categorising commercial shell samples on the basis of the SL:SH ratio. Potential MUs, containing separate blacklip populations, were identified and their key biological parameters estimated using the relationships between the SL:SH ratio and blacklip biology (Chapter 3; Saunders and Mayfield 2008). Data from fine-scale, systematic sampling by commercial fishers in one of the principal SZ fishing areas were used to confirm the spatial patterns observed in the SL:SH ratio from broadly distributed commercial catch samples. The disparity between these data and current management arrangements are highlighted and approaches for modifying them are discussed.

5.2 Methods

5.2.1 Study site

This study was conducted in the SZ, which includes all coastal waters of South Australia east of Meridian 139°E, with the exception of the Coorong and waters inside the Murray River mouth (Figure 5.1). This fishery operates under South Australian legislation and regulation, which incorporates a formal management plan that controls the fishery by input (*e.g.* limited entry) and output (*e.g.* MLL and quotas) controls.

The fishing season in the SZ extends from 1 September to 31 August. Most (98%) of the total allowable commercial catch (TACC) in the SZ is comprised of blacklip. In 2006/2007 the blacklip TACC was 144 t shell weight. A small amount of greenlip

abalone was also harvested (TACC 6 t shell weight). The TACC for blacklip has generally been stable in recent years and levels of recreation and illegal harvest are considered negligible (Mayfield et al. 2007). The SZ includes four fish-down areas (FDAs) where stunted blacklip are thought to occur (FDA 1: Nene Valley; FDA 2: East of Port MacDonnell: FDA 3: Ringwood Reef; and FDA 4: Gerloffs Bay; Figure 5.1). These are managed separately with a minimum legal length (MLL) of 110 mm shell length (SL), 15 mm smaller than that in the non-FDA. The TACCs in the non-FDA and FDAs in 2006/2007 were 99 and 45 t, respectively (Mayfield et al. 2007).

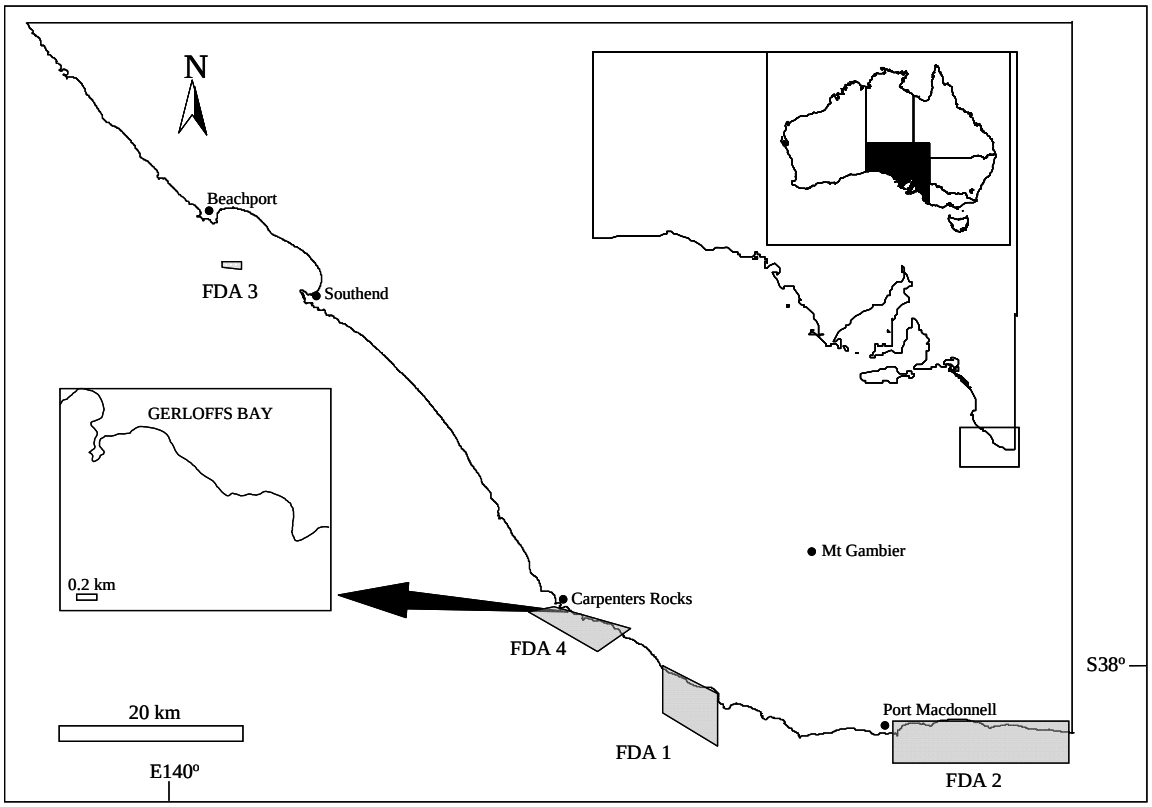

Figure 5.1: Location of the study area within Australia and South Australia. Grey areas indicate fish-down areas (FDAs), and the insert map shows the location of Gerloffs Bay, where the fine-scale commercial abalone shell samples were collected.

5.2.2 Broad-scale spatial distribution of stunted and non-stunted blacklip

Data on the broad-scale, spatial distribution of blacklip populations were obtained from 103 commercial samples, each consisting of at least 50 abalone shells, provided by commercial fishers across the spatial extent of the fishery. Permits were issued to fishers that allowed them to take abalone >110 mm SL from pre-defined fishing areas (based on local commercial fisher knowledge) so that samples could be obtained from populations in the non-FDAs that fail to attain the regulated MLL (i.e. 125 mm SL)

applicable in these areas. Data provided by the commercial fishers included latitude, longitude and depth of sample location. The SL and SH of each shell in all samples was measured, whereafter the mean (± 1 SE) of the ratio between SL and SH (i.e. the morphometric marker, Chapter 2; Saunders et al. 2008) was calculated for each.

A SL:SH ratio value of 3.25 was found to distinguish between stunted and non-stunted blacklip populations (Chapter 2; Saunders et al. 2008). Consequently, this value was used to classify each sample into one of three categories. Samples with an SE < 3.25 were classified as stunted, and those with an SE > 3.25 were classified as non-stunted. The few samples (<10%) where the mean ratio was within 1 SE of 3.25 were classified as 'intermediate'. Pearson's correlation analyses were used to determine whether these categories were related to latitude or longitude.

Preliminary analysis of the data showed that seven (7%) of the blocks classified as stunted contained significantly larger blacklip than expected from the mean and maximum SL of typically stunted samples. This inconsistency is probably indicative of these areas being lightly fished, non-stunted populations with an older age composition and, consequently, shell morphology similar to the stunted populations (Prince et al. 2008). As lightly fished areas will typically have many blacklip with high SL compared with stunted areas, the average maximum SL can be used to differentiate the classifications. The broad-scale samples in Saunders et al. (2008) suggested that the average maximum SL was < 140 mm and > 145 mm for the stunted and non-stunted samples, respectively. Using this information, the following procedure was used: (i) samples classified as non-stunted by the SL:SH ratio remained non-stunted; (ii) samples classified as stunted or intermediate, but with an average maximum SL > 145 mm (from the ten highest shells in SL) were reclassified as non-stunted; (iii) samples classified as stunted with an average maximum SL < 145 mm remained stunted; and (iv) samples classified as intermediate with an average maximum SL < 145 mm remained as intermediate. It is important to note that if the SL:SH ratio classifies a sample as non-stunted, the classification remains, because heavily fished non-stunted areas can have a low maximum SL. Using these rules, seven blocks classified as stunted were reclassified as non-stunted (Figure 5.2).

The locations of each categorised sample were mapped using ArcMap version 9.2. Relationships between sample category and both the current fishing areas and FDAs were evaluated qualitatively. Clusters of samples categorised as stunted and non-

stunted were identified, and used as the basis for indicating the size and location of potential MUs.

5.2.3 Fine-scale spatial distribution of stunted and non-stunted blacklip

To validate the size and location of the potential MUs identified from the broad-scale commercial samples, fine-scale systematic commercial samples were collected by commercial fishers in Gerloffs Bay. That area was selected because it was known to contain both stunted and non-stunted blacklip populations, and it is also one of the principal fishing areas in the SZ, contributing ~50% of the FDA TACC. Systematic sampling was achieved by identifying the outer boundary of the fishing grounds in Gerloffs Bay, then subdividing the fishing area into blocks of 200 × 200 m. The commercial fishers were assigned a series of blocks to sample and were provided with the GPS positions of the corner and centre of each block. In addition, 10 blocks located across the principal fishing ground within Gerloffs Bay were repeat-sampled by four other commercial fishers. The samples from each block consisted of 20-80 blacklip that were all larger than the MLL (110 mm SL). Morphometric data were collected from each shell, and each sample was categorised (stunted, non-stunted, or intermediate), as described above.

Initial analysis of these data suggested that eight (13%) of the blocks classified as stunted and 1 (2%) of the blocks classified as intermediate contained significantly larger blacklip than expected from the mean and maximum SL of typically stunted samples. Using the same procedure as for the broad-scale samples, these blocks were subsequently reclassified as non-stunted (Figure 5.3).

The locations of each categorised sample were mapped as described above. Relationships between sample category and the broad-scale data were evaluated qualitatively. Clusters of samples categorised as stunted and non-stunted were identified, then used as the basis for indicating the size and location of two potential MUs within Gerloffs Bay.

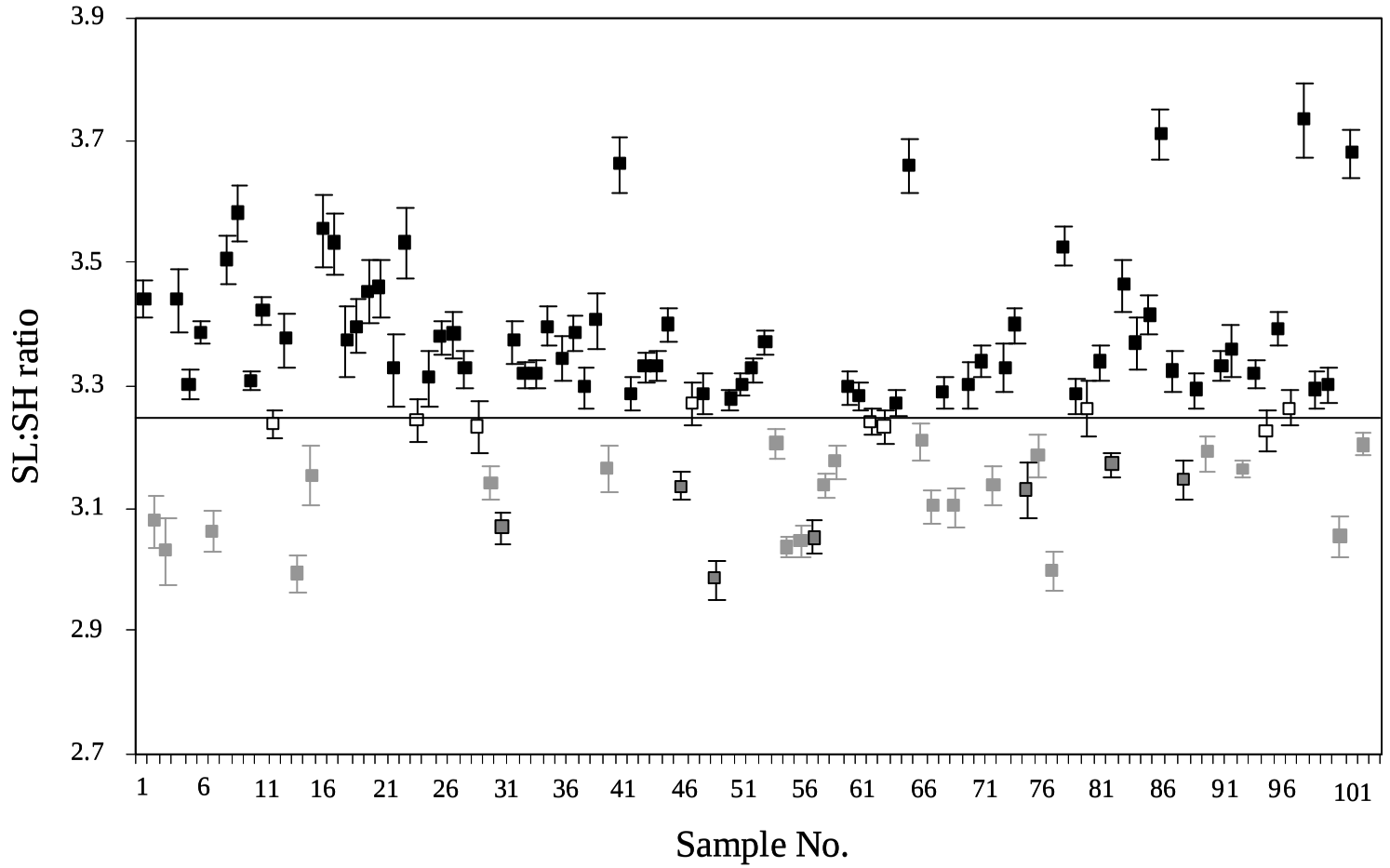

Figure 5.2. SL:SH ratio for each of the commercial abalone shell samples in the SZ. The horizontal line indicates a SL:SH ratio of 3.25, which separates samples of non-stunted (black squares) and stunted (grey squares) abalone. Open squares indicated intermediate samples, where the ± 1 SE bars cross the black line. Dark grey squares signify stunted samples with a mean maximum SL > 145 mm that were subsequently reclassified as non-stunted.

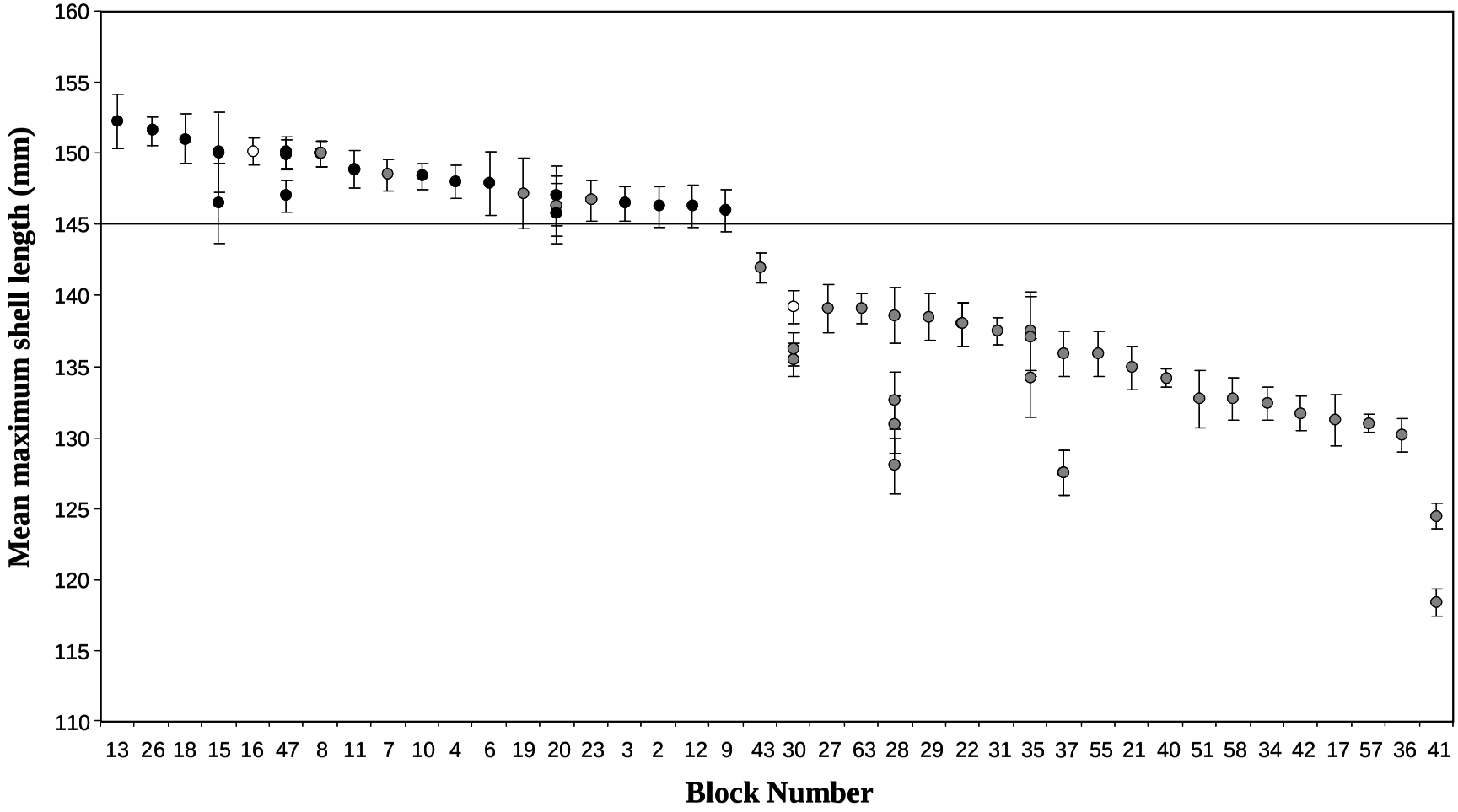

Figure 5.3. Mean maximum SL for each of the systematic samples in Gerloffs Bay. Black, grey, and white circles indicate samples categorized as non-stunted, stunted, and intermediate, respectively. All stunted and intermediate samples above the horizontal line (145 mm SL) were subsequently reclassified as non-stunted. Error bars indicate ± 1 SE.

5.2.4 Estimates of biological parameters for potential MUs

Estimates of the key biological parameters for ten potential MUs were determined by the linear relationships between the SL:SH ratio and growth residuals and L_{50} (after Saunders and Mayfield 2008). These were:

$Gr = -16.99R + 25.30$

and

$L_{50} = 26.18R - 12.51$

Where Gr is the growth residual, R the mean SL:SH ratio, and L_{50} is the SL at 50% maturity. Using these relationships, the value of L_{50} for each potential MU was calculated from the mean estimate of this parameter from the commercial samples within that area. Similarly, the growth residuals were calculated for these samples to predict the rate of growth at L_{50} within each potential MU. This was achieved using the average growth relationship for all sites sampled in Saunders and Mayfield (2008) to determine the growth rate at L_{50}. The growth rate at L_{50} for each potential MU was then calculated by adding (or subtracting) the residual value predicted by the SL : SH ratio of the samples in that area. These relationships were used to estimate increases in SL from L_{50} after 2 and 4 years.

5.3 Results

5.3.1 Broad-scale spatial distribution of stunted and non-stunted blacklip

Using the SL:SH ratio, 73 samples were categorised as non-stunted, 21 as stunted, and 9 as intermediate (Figure 5.2). There were no significant correlations between the SL:SH ratio and either latitude (r_{103}= 0.164, $p > 0.05$; Figure 5.4) or longitude (r_{103} = 0.158, $p > 0.05$; Figure 5.4). This was reflected by the mixture of samples categorised as stunted, non-stunted, or intermediate along the SZ coast (Figure 5.4).

The broad-scale samples were unevenly distributed along the coast (Figure 5.4). Notably, there were several management areas from which either no or very few (<3) samples were obtained. In most cases, commercial catches from those areas are small. In areas with >3 samples there was no consistent sample classification within any of the current management areas, including the FDAs (Figure 5.4). Nevertheless, there were eight locations in the SZ across which the spatially resolved samples were

similarly categorised. These areas with a consistent spatial pattern constituted the basis for identifying the size and location of potential MUs that contain separate blacklip populations. Potential MUs with stunted blacklip included Ringwood Reef, Gerloffs Bay South, and Acis Reef. The MUs with non-stunted blacklip were Salmon Hole, Red Rock Bay, Gerloffs Bay North, Middle Point, and Cape Northumberland (Figure 5.4).

5.3.2 Fine-scale spatial distribution of stunted and non-stunted blacklip

In Gerloffs Bay, samples from 29 blocks were categorised as stunted, 28 as non-stunted, and just one block as intermediate. There were 17 blocks within which no blacklip were found (Figure 5.5). All multiple samples collected within the same block were similarly categorised. These fine-scale data suggested that there were two potential MUs (one stunted and one non-stunted) in Gerloffs Bay. Their locations were consistent with those identified by the broad-scale commercial samples collected from the area (Figure 5.5).

5.3.3 Estimates of biological parameters for potential MUs

Within the potential stunted MUs, estimates of L_{50} ranged between 68 mm (Acis Reef) and 70 mm SL (Ringwood Reef). It was predicted that blacklip from those two populations would grow to between 88 and 91 mm SL and to between 102 and 105 mm SL after two and four years growth, respectively. In contrast, for the potential non-stunted MUs, estimates of L_{50} ranged between 74 mm (Red Rock Bay) and 84 mm SL (Salmon Hole). It was predicted that blacklip at Red Rock Bay would grow to 97 and 113 mm SL, and those from Salmon Hole to 100 and 127 mm after two and four years of growth, respectively (Figure 5.6). The estimates of L_{50} and SL after two and four years for blacklip in the stunted and non-stunted potential MUs in Gerloffs Bay were consistent for the samples collected at both broad and fine spatial scales (Figure 5.6).

5.4 Discussion

Successful application of MU principles is based on an ability to discriminate among component populations and, subsequently, to manage each on the basis of their biological parameters and associated productivity (Taylor and Dizon 1999; Bergenius et al. 2005; Defeo and Castilla 2005). In this study, we were able to identify potential

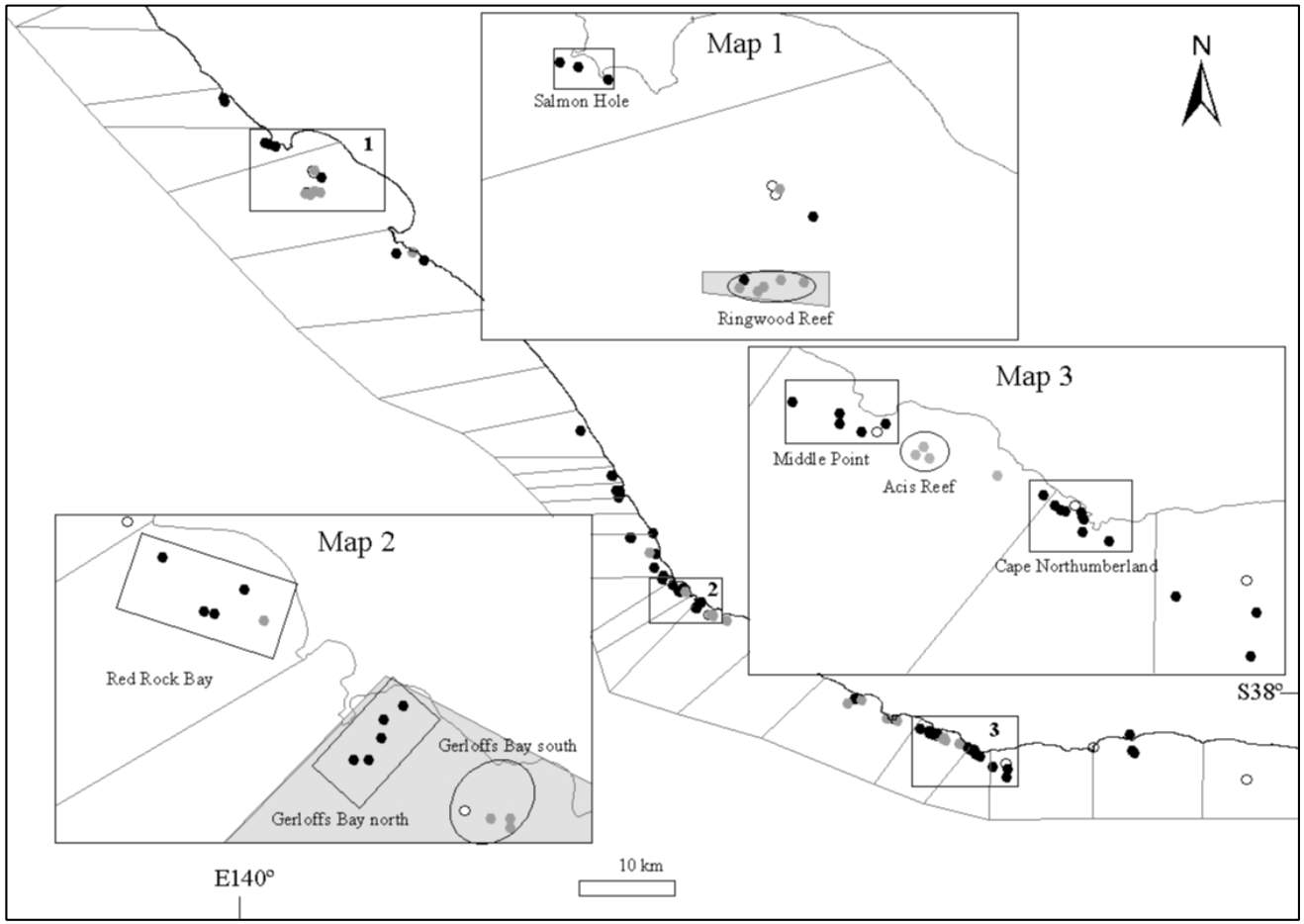

Figure 5.4. Map showing the distribution of commercial shell samples classified into non-stunted (black dots), stunted (grey dots), and intermediate (open circles) categories along the SZ coastline. The insert maps show enlarged sections of coast, with rectangles (non-stunted areas) and ellipses (stunted areas) indicating potential MUs. Grey shading indicates current FDAs, and divisions along the coast show boundaries of the current management areas.

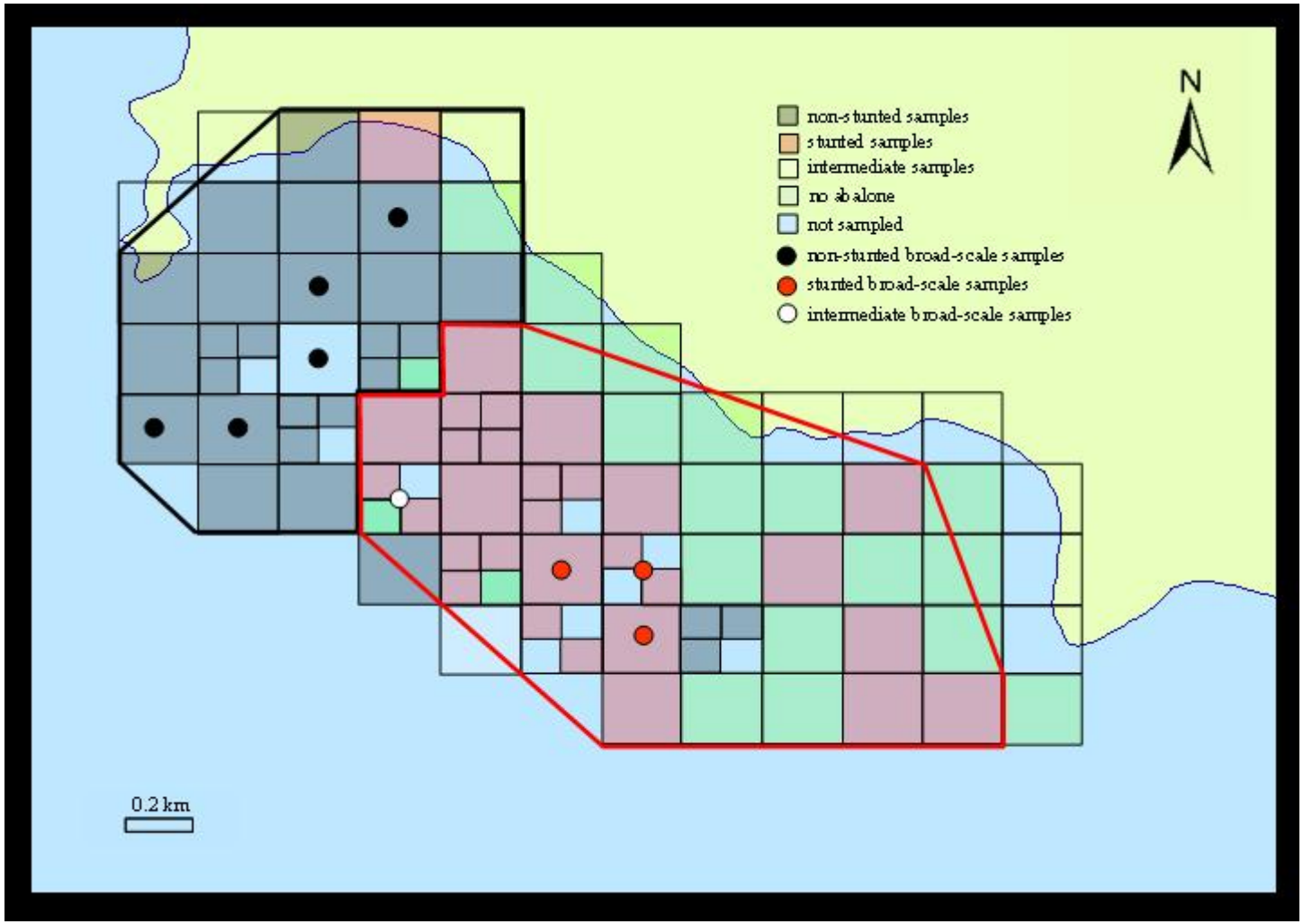

Figure 5.5: Map of Gerloffs Bay, showing the gridded area where fine-scale commercial shell samples were collected. Multiple samples were collected in squares with four divisions. The black and red boundary lines represent the potential non-stunted and stunted MUs in this area.

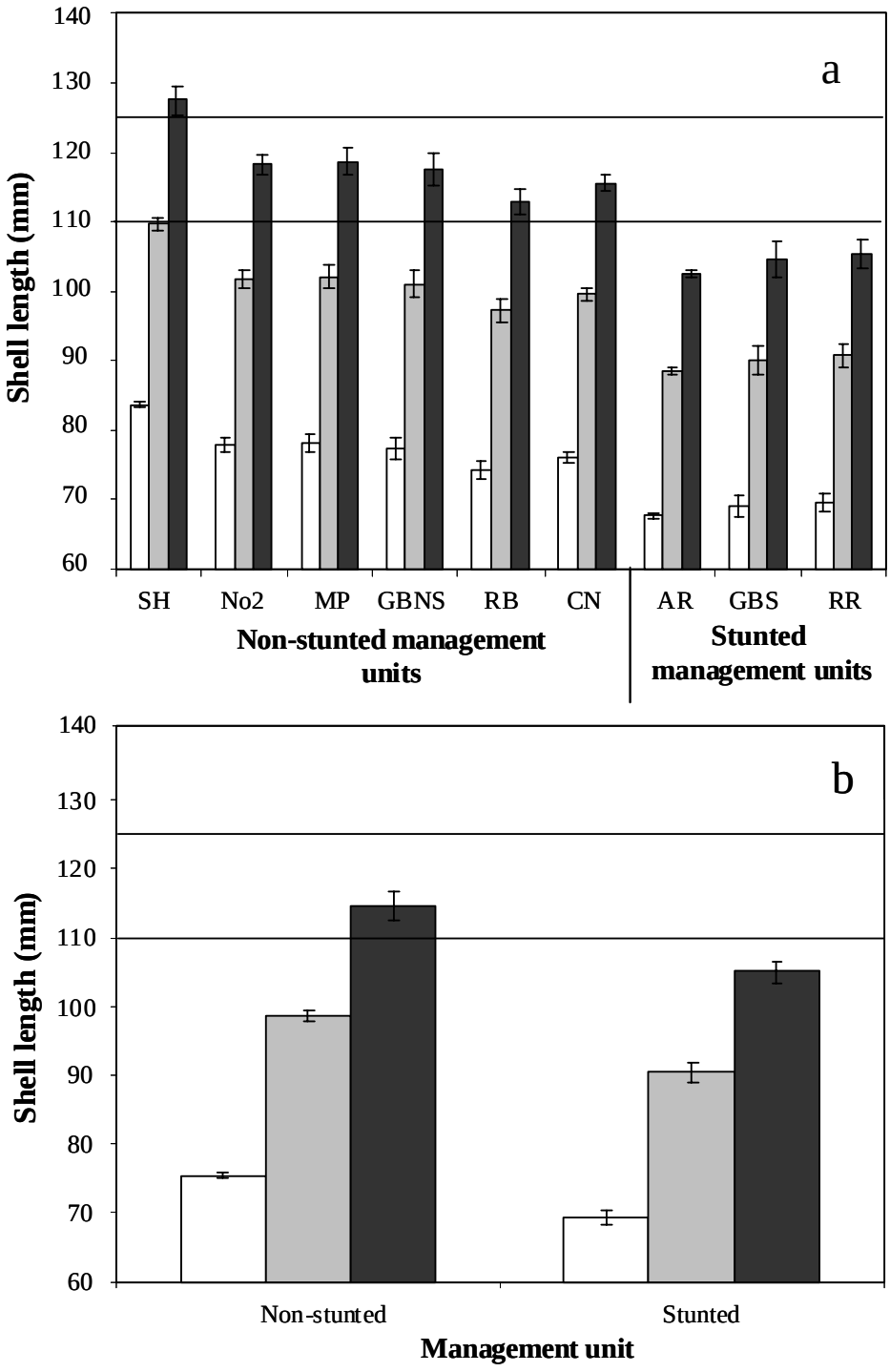

Figure 5.6: Values for L_{50} (white columns), L_{50} + 2 years growth (grey columns), and L_{50} + 4 years growth (black columns) calculated from the SL:SH ratio for the potential MUs identified by (a) broad-scale commercial samples, and (b) fine-scale samples in Gerloffs Bay. Horizontal lines indicate the current MLLs in the SZ. Error bars indicate ± 1 SE.

MUs as a result of the significant spatial variability observed in the SL : SH ratio from commercial shell samples obtained along the SZ coast. Notably, the location,

distribution, and spatial extent of the potential MUs were largely inconsistent with those of the current fishing/management areas, or the FDAs. Importantly, the locations of stunted and non-stunted MUs (in Gerloffs Bay) were consistent across broad- and fine-scale datasets, although the fine-scale samples were more informative for identifying a potential boundary between the two. It is likely that the potential MUs identified represent separate blacklip populations, because these occur at fine spatial scales (10s to 100s of meters; Temby et al. 2007), reflecting limited larval dispersal (Prince et al. 1988a). In addition to identifying the size and location of potential MUs, relationships between the SL:SH ratio and key biological parameters for blacklip permitted estimation of the biological characteristics for the populations within the areas. This data would likely remain unavailable if traditional biological sampling was required to obtain them, but our approach allows for practical determination of MUs, along with their life-history characteristics, at relevant spatial scales.

There was no significant correlation between latitude or longitude and the SL:SH ratio, eliminating the possibility of clines and suggesting that the environmental factors that are probably causing the variability are acting at finer spatial scales (Swain et al. 2005). Relatively consistent spatial patterns in the SL:SH ratio only occurred at the scale of one of the current fishing areas (Red Rock Bay) and one FDA (Ringwood Reef). Although these and the other areas with spatial consistency in the SL:SH ratio could be potential MUs, their sizes and locations require further validation through the collection of fine-scale, systematic, commercial catch samples.

This fine-scale information was obtained from Gerloffs Bay, where the patterns observed from broad-scale sampling suggested the presence of two (one stunted and one non-stunted) potential MUs. Importantly, the fine-scale information revealed two potential MUs in the same area as identified by the broad-scale samples. However, assuming that blacklip in blocks classified as non-stunted or stunted are separate populations, these two potential MUs do not contain uniform blacklip populations. Rather, each is dominated by a large population of stunted or non-stunted blacklip, interspersed with a small population of the alternative morphotype. Although this approach deviates from several central MU principles, the suggested groupings reflect the need for practical implementation of potential MUs. The small pockets of blacklip misclassified in the process do not justify the difficulties and costs that would be associated with managing them independently, given their small contribution to the numbers of blacklip in these areas. For these reasons, some of the other proposed

MUs containing samples of mixed morphology were selected to reflect this practical application of MU principles.

A few of the broad- and fine-scale samples collected contained large blacklip (mean maximum SL > 145 mm) and were classified as stunted by the SL:SH ratio. Anecdotal information provided by the fishers who collected the samples suggested that the reef areas being sampled had not been fished for many years. As a consequence, the large, old blacklip resembled the morphology of smaller, stunted individuals. This is consistent with the suggestion of Prince et al. (2008) that lightly fished areas of reef tend to have many larger abalone that have reached their maximum size and have grown substantially in shell height, shell width, and whole weight due to their age. However, the occurrence of non-stunted, lightly fished populations is likely to be rare in most abalone fisheries, because faster-growing populations are typically heavily exploited (Worthington et al. 1995a; Prince 2005; Prince et al. 2008). Evidence for this infrequency of occurrence is the fact that there were very few non-stunted, lightly fished areas in the current study, and none in the broad- and fine-scale samples of Saunders et al. (2008). Nevertheless, the rule-based approach developed that incorporated the average maximum SL of a sample in conjunction with the morphometric marker provides a formal method to identify samples from lightly fished areas.

The use of the SL:SH ratio to describe potential MUs provides a simple, cost-effective tool to re-consider the management arrangements for blacklip in the SZ so that they better reflect the population structure of the species (Begg and Waldman 1999). Although management is best achieved at spatial scales that reflect the actual population structure of the species, the opportunities to do so for many fisheries are limited by the difficulties and cost of obtaining the information (Begg et al. 1999b). Our data suggest that only one current fishing area and one FDA constitute valid MUs, but that the creation of at least six additional MUs is warranted within the current management areas. These include Salmon Hole, Red Rock Bay, Gerloffs Bay North, Middle Point, and Cape Northumberland, which contain non-stunted blacklip, and Ringwood Reef, Gerloffs Bay South, and Acis Reef, which contain stunted blacklip. Further sampling of the commercial catch, which is relatively easy and inexpensive, is likely to suggest more MUs in future.

Identifying and then discriminating between these MUs constitutes the first step in applying MU principals. Subsequently, the biological characteristics of the blacklip

populations within the MUs need to be estimated to support their appropriate management. One of the most recognized approaches is to use size limits as a tool to ensure adequate reproductive capacity among populations and to reduce the likelihood of recruitment over-fishing (Shepherd et al. 1995). Nash (1992) suggested that 50% of potential spawning production needs to be retained to ensure sustainability in abalone fisheries. Although the growth and fecundity estimates inferred by a morphometric marker value can contribute to estimating retained egg production, other data on natural and fishing mortality, and on length/weight relationships, are required. In the SZ, it was estimated that 95.5 and 79.0% of potential spawning production is retained in non-FDAs and FDAs, respectively (Mayfield et al. 2005). In addition to these high levels of retained egg production, the biological characteristics inferred by the morphometric marker suggest that the blacklip populations in the MUs identified would generally permit >4 spawning seasons after attaining L_{50} under the current size limits (110 mm SL for stunted, 125 mm SL for non-stunted blacklip). A different model is used in the Tasmanian abalone fishery, where size limits are designed to provide abalone with two spawning seasons between L_{50} and the MLL (Tarbath 2003). Applying the Tasmanian approach to the SZ suggests that size limits for the stunted MUs identified could range from 88 to 92 mm SL, whereas those for the non-stunted MUs would need to be substantially larger, between 99 and 110 mm SL. However, there is no empirical evidence to support the use of the Tasmanian model (L_{50} + 2 years), especially as previous assessments on *H. roei* revealed very low levels of retained egg production when the MLL provides only two spawning seasons post-L_{50} (Preece et al. 2004). Hence, it would it would be pertinent to consider the current, more-conservative size limits as a baseline, so that MLLs would guarantee greater levels of retained egg production.

These analyses on retained egg production should also be supported through application of an integrated, length-structured stock assessment model tailored for each MU (Breen et al. 2003; Gorfine et al. 2005; Mayfield et al. 2007). Stock assessment and simulation models incorporating spatial complexity are becoming more common (Holland 2003; Mayfield and Saunders 2008), and they may perform better than when applied at broader scales because they remove the need to aggregate data across component populations (Punt 2003; Naylor et al. 2006). Such an approach would aid the establishment of catch and effort limits within MUs, which are important in a fishery with intensive spatial management (Hewitt et al. 2004).

The regional or zonal scale application of the morphometric marker approach to identify potential MUs and the life history parameters of abalone within them provides additional challenges for management of sedentary marine invertebrates. These arise from the need to combine a wealth of data (and other fishery-related information) into a revised management framework under a new paradigm that explicitly requires reductions in the spatial scale of management (Castilla and Defeo 2005; Prince 2005; Naylor et al. 2006). Adoption of fine-scale management necessitates consideration of the limitations of the data available, as well as the requirements for effective (and efficient) management and compliance arrangements both within, and across, any MUs identified. For example, our data from Gerloffs Bay suggest the need for two MUs within this small area, each of <2 km^2. Should MUs be warranted at this spatial scale throughout the SZ, the potential number of MUs exceeds 100, with each potentially demonstrating unique life history characteristics and hence requiring separate assessment and management (e.g. quotas and size limits). This number of MUs is substantially greater than the number (~30) of reef codes assessed and managed annually in the western zone of the Victorian abalone fishery (Prince et al. 2008). It would also greatly exceed the number of MUs that could realistically be assessed and managed by a Government Agency without the associated costs becoming prohibitive (Prince 2005). Consequently, in other sedentary invertebrate fisheries that have successfully implemented fine-scale management, the approach has been to rely heavily on extensive collaboration and an increase in the responsibility and accountability of all stakeholders (Castilla and Fernandez 1998; Leiva and Castilla 2001; Defeo and Castilla 2005; Orensanz et al. 2005). This collaborative approach to management was also critical in the recent development of 30+ MUs with separate catch and size limits in the western zone of the Victorian abalone fishery (Prince et al. 2008).

New, spatially explicit management policies and recent/novel methods for data collection, synthesis, and analysis will need to be developed to provide an integrated and sound basis for rational, appropriate spatial management of the resources. In most cases, this is likely to require a pragmatic approach, with trade-offs being made between management constraints and biological reality. This was illustrated by the results of the fine-scale sampling in Gerloffs Bay, where the two proposed MUs contained multiple populations with variable life history characteristics. However, our suggested division separates the two main populations and provides two MUs of a size that could feasibly be managed independently. Importantly here, we link

morphology and biology to provide a mechanism that simply, practically, and cost-effectively overcomes the crucial first step of being able to discriminate among, and estimate the biological parameters of, component populations. Without such knowledge, suitable MUs cannot be identified or managed. This approach is not limited to abalone; it is also applicable to many sedentary invertebrate species for which fine-scale, population structures exist.

Chapter 6: General discussion

Many marine species form numerous populations across their geographic range that vary in their spatial extent and life-history characteristics (Begg and Waldman 1999; Sponaugle et al. 2002; Taylor and Hellberg 2003; Bergenius et al. 2005; Cowen et al. 2006). Differences in life-history that characterise a population's local productivity (*e.g.* parameters such as reproduction, recruitment, survival and rates of growth) can outweigh the potential modifying effects of immigration and emigration (Begg and Waldman 1999; Holland 2003). Thus, there is a clear need to identify component populations for effective conservation and management of these species (Cowen et al. 2006). In this thesis, I have developed a 'morphometric marker' that was able to discriminate among separate populations of blacklip abalone (*Haliotis rubra*, hereafter referred to as blacklip) over multiple spatial scales (Chapter 2). Importantly, the morphometric marker was highly correlated to several key life history parameters and so can be used as a tool to identify component populations as well as their individual life history parameters (Chapter 3). While the morphometric variability observed in this study was found to be environmentally induced (Chapter 4), the discrete populations formed by blacklip (Prince et al. 1988a; Temby et al. 2007), probably exist at similar scales to this morphometric variability. Finally, the practical application of the morphometric marker to identify separate populations of blacklip and predict their key life history parameters was demonstrated (Chapter 5).

6.1 Identification and characterisation of blacklip populations using a morphometric marker

Fine-scale population structure is common among many marine species (Sponaugle et al. 2002; Strathmann et al. 2002; Orensanz et al. 2005). These individual populations are isolated from conspecifics by reproduction and migration and often vary in their life history parameters (McShane et al. 1988a; Orensanz and Jamieson 1995; Johnson and Black 2000). It is critical to identify these separate populations and obtain information on the demographic variability among these for effective conservation and management of these species (Cowen et al. 2006). However, acquiring this information has been impeded by the difficulties of tracking minute larvae (Swearer et al. 2002) and the high costs of collecting data on the biological variability of a species across a range of spatial scales (Prince 2005). The study of morphometric variation

among separate populations offers a simple, cost-effective approach to identify separate populations of marine species as well as their individual life history characteristics (Cadrin 2005).

Sampling of morphometric variability at multiple spatial scales revealed that the ratio between shell length and shell height (SL:SH ratio) was able to separate among 'stunted' and 'non-stunted' populations of blacklip (Chapter 2, Saunders et al. 2008). Importantly this morphometric marker was shown to be highly correlated to growth rate, size at maturity and fecundity of blacklip populations (Chapter 3; Saunders and Mayfield 2008). Consequently, these strong relationships allow for the biological characteristics of other populations of blacklip to be inferred, simply and inexpensively, by applying the SL:SH ratio to spatially-resolved, commercial-catch samples. These results provide excellent evidence for the utility of the SL:SH ratio to aid fine-scale management of abalone fisheries. Not only can it provide information on the boundaries of separate populations (Chapter 2; Saunders et al. 2008) but it can also be used to estimate the growth, size at maturity and fecundity for any population based on the relationships developed in the current study (Chapter 3; Saunders and Mayfield 2008). Consequently, the assessment of samples from across abalone fisheries will enable separate populations to be mapped, with fine-scale, systematic sampling facilitating determination of the boundaries of individual populations within these areas. The biological information inferred by the SL:SH ratio could then be used to assign individual populations with appropriate size limits reflective of their biological characteristics.

6.2 Environmental effects on blacklip morphology

The substantial, spatial variation in growth and morphology observed for blacklip appears to be characteristic of abalone populations world-wide (Shepherd and Hearn 1983; McShane et al. 1988a; Day and Fleming 1992; Worthington et al. 1995a). The reciprocal transplant experiment revealed that the variability in the growth and morphology of blacklip is a result of a plastic response to environmental factors. Reef topography and algal cover were both significantly correlated to blacklip morphology, both of which relate directly to the availability of food in the form of drift algae. The stunted and non-stunted morphotypes exhibited characteristics consistent with responses to local food availability, with reef areas limited in food forcing a stronger

response in blacklip growth compared to areas with abundant food. Consequently, this study provides the first experimental evidence to support the theory that spatial variation in abalone growth and morphology is a plastic response to localised environmental conditions, which are probably related to food availability, rather than genetic differences between conspecifics.

A critical assumption for the utility of the morphometric marker as a tool for separating abalone populations is that different populations will exhibit variable morphology. The fact that spatial differences in morphology of blacklip were found to be environmentally induced rather than a fixed genetic trait suggests that abalone populations occur at broader scales than the spatial variation observed in abalone morphology. Supporting this theory are the results from genetic studies on abalone that have found genetic similarity across spatial scales ranging from 55-500 km (Brown 1991; Huang et al. 2000; Conod et al. 2002). However, these same studies suggest gene flow and larval dispersal distances in excess of those inferred from empirical field studies and hydrodynamic modelling of dispersal (McShane et al. 1988b; Prince et al. 1988a). These conflicting results are probably related to genetic models often underestimating the degree of population structure present as < 1% of larvae being transferred per generation is sufficient to maintain genetic connectivity between populations that are ecologically distinct (Palumbi, 2003). Yet, the number of larvae required to sustain populations during recruitment events are several orders of magnitude higher (Miller and Shanks 2004). Indeed, it is becoming increasingly evident that abalone exist as a series of discrete populations across their geographic range at scales of 10s to 100s m (Temby et al. 2007) and management of this species should occur at similar spatial scales to ensure the sustainability of these individual populations (Prince 2005; Saunders et al. 2009). Adding weight to this argument is the fact that new colonists are rarely observed when abalone populations are overexploited (Gruenthal and Burton 2008). Consequently, the highly localised populations formed by blacklip are likely to exist at similar scales to the environmental variability observed, making the morphometric marker an extremely useful tool for population identification.

6.3 Identifying units of management for blacklip using a morphometric marker

The importance of considering demographic differences among populations to manage against over-fishing and localised depletion has led to the concept of management units (MUs), defined as demographically independent populations that should be managed and monitored separately (Taylor and Dizon 1999; Martien and Taylor 2003; Palsboll et al. 2007). Fundamental to the successful development of MUs is the ability to discriminate among component populations and, subsequently, to manage each of these on the basis of their biological parameters and associated productivity (Taylor and Dizon 1999; Martien and Taylor 2003; Bergenius et al. 2005; Defeo and Castilla 2005; Hammer and Zimmermann 2005). However, a lack of appropriate, spatially-resolved data describing population structure has hindered the development of MUs, leaving management regimes operating over large spatial scales (Leiva and Castilla 2001; Castilla and Defeo 2005; Prince 2005). In the majority of cases, management areas are linked to 'non-biological' jurisdictions, typically defined by political and regulatory boundaries (Wilen 2004). Failure to manage these fisheries at appropriate spatial scales has resulted in many of these species becoming serially depleted, with stock collapses occurring in some extreme cases (Tegner et al. 1996; Perry et al. 2002; Orensanz et al. 2004).

The development of the morphometric marker provides a key tool for successful application of MU principles, as it has the ability to discriminate among component populations and, subsequently, to facilitate management of each of these on the basis of their biological parameters and associated productivity (Taylor and Dizon 1999; Martien and Taylor 2003; Bergenius et al. 2005; Defeo and Castilla 2005; Hammer and Zimmermann 2005). Potential MUs were identified from collections of commercial shell samples that were categorised by their morphometric marker value. Notably, the location, distribution and spatial extent of the potential MUs were largely inconsistent with that of the current fishing/management areas in the study area. Importantly, fine-scale systematic sampling in one location was able to delineate two separate populations of blacklip that were adjacent to each other. In addition to identifying the size and location of potential MUs, relationships between the morphometric marker and key biological parameters for blacklip permitted estimation

of their biological characteristics within these areas. These data would likely remain unavailable if traditional biological sampling were required to obtain them.

The regional- or zonal-scale application of the morphometric marker to identify potential MUs and the life-history parameters of individuals within these areas provides new challenges for management of abalone. These arise from the need to combine a wealth of data (and other fishery-related information) into a revised management framework under a new paradigm that explicitly requires reductions in the spatial scale of management (Meester et al. 2001; Prince and Hilborn 2003; Wilen 2004; Castilla and Defeo 2005; Prince 2005; Naylor et al. 2006). Adoption of fine-scale management necessitates consideration of the limitations of the data available, as well as the requirements for effective (and efficient) management and compliance arrangements both within, and across, any MUs identified. Thus, the challenge for all stakeholders – scientists, fishers and fisheries managers – will be to respond through developing new, spatially-explicit management policies and seeking recent/novel methods for data collection, synthesis and analysis to provide an integrated and sound basis for the rational management of these resources. Where the need for fine-scale management has arisen in other invertebrate fisheries there has been a strong emphasis of co-management, so that stakeholders shoulder some of the responsibility for the sustainability of the resource they are exploiting (Castilla and Defeo 2005). This has led to the development of Territory User Rights Fisheries (TURFs) whereby areas of sea bottom are allocated to small fishery organisations that are allowed to harvest species at levels determined to be appropriate by initial biomass surveys (Leiva and Castilla 2001). TURFs are then adaptively managed according to catches by the user group and periodic surveys from research agencies. Recently, a management model has been developed for abalone that has taken a collaborative approach to identifying separate abalone ‘reefs’, the setting of reef-scale size limits based on shell shape characteristics and catch limits based on catch history (Prince et al. 2008). Real-time reporting by fishers after they have dived on a reef then allows for the assessment of whether these catch limits are appropriate (Prince et al. 2008). The morphometric marker developed in this thesis could be incorporated in this process to help identify these separate populations and relevant size limits for each of these. Biomass estimates could be obtained by fishers through conducting abundance surveys in these areas, supported by periodic validation of the estimates by research divers. The biomass that harvested from each population can be determined from a risk framework similar to that developed by Mayfield et al. (2008).

Importantly, the morphometric marker provides a mechanism to simply, practically and cost-effectively overcome the crucial first step of being able to discriminate among, and estimate the biological parameters of, component populations. Without this knowledge, MUs cannot be appropriately developed or managed. The morphometric marker can be applied at any spatial scale to address the observed mix of variability and lack of predictability of the size and location of abalone populations. When used within a suitable management framework, it can provide the necessary information to enable practical reductions in the scale of abalone fishery management, which has previously been hampered by the inability to gather detailed demographic data at appropriate spatial scales.

6.4 Future Research

A critical assumption of the utility of the morphometric maker is that separate abalone populations show variability in their morphology. The empirical evidence provided by hydrodynamic studies (McShane et al. 1988b) and removal experiments (Prince et al. 1987; Prince et al. 1988a) suggests that the scales of abalone populations are similar to the observed morphometric variability (Chapter 2; Saunders et al. 2008). To confirm the degree to which 'morphometric' populations reflect demographic populations, it would be pertinent to conduct experiments similar to those described in the above studies and assess these patterns against spatial variability in the morphometric marker. Hydrodynamic studies would be the most appropriate method to do this comparison, given the difficulties of removing large numbers of adult abalone over large spatial scales. Historically, drift cards have been deployed during known spawning periods of abalone to assess potential larval dispersal of abalone (Tegner and Butler 1985; Guzman-del Proo et al. 2000; Gruenthal and Burton 2008). However, the difficulties of deploying and retrieving drift cards over multiple spatial and temporal scales render this approach unsuitable for broad-scale application. A better approach would be to employ the Lagrangian particle-trajectory models that have recently been employed on abalone (Stephens et al. 2006). Briefly, the predicted dispersal of a passive particle released over abalone habitat is predicted by modelling the net water movement from the site taking into account bathymetry, wind and tidal currents. To enhance the results of the model it is pertinent to understand the larval duration as well as any larval behaviour that may affect dispersal (*e.g.* blacklip larvae tend to be negatively buoyant so are not exposed to surface water movement

(McShane 1992). Stephens et al. (2006) found dispersal distances for *H. iris* of up to 30 km from the release site using this approach. However, the authors did not assess whether the larvae that dispersed these distances would have encountered viable settling habitat. It has been suggested that despite abalone larvae having the potential to disperse over large distances, larval mortality would dilute the numbers to such an extent that distant settlement is unlikely (McShane et al. 1988b). These authors argue that local retention of larvae is attenuated by their entrapment in rock crevices and/or kelp canopies nearby the spawning adults and live out their larval life in these areas.

The morphometric marker should also be tested by applying it to other blacklip fisheries and abalone species. For other blacklip fisheries, this could be as simple as applying the morphometric marker to collections of commercial shell samples with fine-scale systematic samples revealing the location of population boundaries (*e.g.* Chapter 5; Saunders et al. 2009). A small amount of biological data would be required to confirm the linear relationships developed between the morphometric marker and key life history parameters (Chapter 3; Saunders and Mayfield 2008). These relationships could then be then used to predict the biological characteristics of individual populations. Studies on morphology for other abalone species have indicated that shell height may be a good indicator of differences in life-history parameters among separate populations (Breen and Adkins 1982; Wells and Mulvay 1995), so the morphometric marker developed in this thesis may be applicable to many other species of abalone. However, the relationships between morphology and biology would have to be developed separately as life history parameters vary among species (*e.g.* Shepherd and Laws 1974; Shepherd and Hearn 1983). For other sedentary invertebrates, the identification of a suitable morphometric marker could be achieved using similar methodologies as were used in the chapters of this thesis.

6.5 Conclusion

The development of a morphometric marker that can delineate separate abalone populations and characterise their key life-history parameters provides a cost-effective tool and the opportunity to bridge the traditional disconnect between scales of ecological variation and fisheries management. Consequently, these results provide an important step towards practical implementation of fine-scale, management strategies for abalone fisheries. This is timely as the need for finer scale management of abalone

fisheries has been increasingly recognised in recent years but its application has been restricted by the inability to gather detailed demographic data at useful spatial scales. While this approach is particularly pertinent for abalone, given their stock structure and history of sudden collapse, it could also be applied to many other sedentary invertebrates that have fine-scale, population structure and easily-measurable, hard-body parts that reflect their ontogenetic history. Consequently, the capacity to predict biological variation using a morphometric marker appears broadly applicable and may assist with the conservation and management of many marine species.

References

Alunno-Bruscia M, Bourget E, Frechette M (2001) Shell allometry and length-mass-density relationship for *Mytilus edulis* in an experimental food-regulated situation. *Marine Ecology Progress Series* 219: 177-188

Begg GA, Friedland KD, Pearce JB (1999b) Stock identification and its role in stock assessment and fisheries management: An overview. *Fisheries Research* 43: 1-8

Begg GA, Hare JA, Sheehan DD (1999a) The role of life history parameters as indicators of stock structure. *Fisheries Research* 43: 141-163

Begg GA, Waldman JR (1999) An holistic approach to fish stock identification. *Fisheries Research* 43: 35-44

Bell EC, Denny MW (1994) Quantifying wave exposure - a simple device for recording maximum velocity and results of its use at several field sites. *Journal of Experimental Marine Biology and Ecology* 181: 9-29

Berg E, Sarvas TH, Harbitz A, Fevolden SE, Salberg AB (2005) Accuracy and precision in stock separation of north-east arctic and Norwegian coastal cod by otoliths comparing readings, image analyses and a genetic method. *Marine and Freshwater Research* 56: 753-762

Bergenius MAJ, Mapstone BD, Begg GA, Murchie CD (2005) The use of otolith chemistry to determine stock structure of three *Epinepheline serranid* coral reef fishes on the Great Barrier Reef, Australia. *Fisheries Research* 72: 253-270

Berryman AA (2002) Population: A central concept for ecology? *Oikos* 97: 439-442

Boxshall AJ (2000) The importance of flow and settlement cues to larvae of the abalone, *Haliotis rufescens* Swainson. *Journal of Experimental Marine Biology and Ecology* 254: 143-167

Breen PA, Adkins BE (1982) Observations of abalone populations on the north coast of British Columbia, July 1980. Department of Fisheries and Oceans Resource Services Branch, 1633, Nanaimo, British Columbia

Breen PA, Kim SW, Andrew NL (2003) A length-based Bayesian stock assessment model for the New Zealand abalone *Haliotis iris*. *Marine and Freshwater Research* 54: 619-634

Brown LD (1991) Genetic-variation and population-structure in the blacklip abalone, *Haliotis rubra*. *Australian Journal of Marine and Freshwater Research* 42: 77-90

Cadrin SX (2000) Advances in morphometric identification of fishery stocks. *Reviews in Fish Biology and Fisheries* 10: 91-112

Cadrin SX (2005) Morphometric landmarks. In: Cadrin SX, Friedland, KD, Waldmann JR (eds) Stock identification methods: Applications in fishery science. Elsevier Academic Press, London, pp 153-172

Cadrin SX, Friedland KD (1999) The utility of image processing techniques for morphometric analysis and stock identification. *Fisheries Research* 43: 129-139

Cadrin SX, Silva VM (2005) Morphometric variation of yellowtail flounder. *Ices Journal of Marine Science* 62: 683-694

Campbell A, Lessard J, Jamieson GS (2003) Fecundity and seasonal reproduction of northern abalone, *Haliotis kamtschatkana*, in Barkley Sound, Canada. *Journal of Shellfish Research* 22: 811-818

Campbell A, Ming MD (2003) Maturity and growth of the pacific geoduck clam, *Panopea abrupta*, in southern British Columbia, Canada. *Journal of Shellfish Research* 22: 85-90

Castilla JC, Defeo O (2005) Paradigm shifts needed for world fisheries. *Science* 309: 1324-1325

Castilla JC, Fernandez M (1998) Small-scale benthic fisheries in Chile: On co-management and sustainable use of benthic invertebrates. *Ecological Applications* 8: S124-S132

Chambers MD, VanBlaricom GR, Hauser L, Utter F, Friedman CS (2006) Genetic structure of black abalone (*Haliotis cracherodii*) populations in the California Islands and central California coast: Impacts of larval dispersal and decimation from withering syndrome. *Journal of Experimental Marine Biology and Ecology* 331: 173-185

Conod N, Bartlett JP, Evans BS, Elliott NG (2002) Comparison of mitochondrial and nuclear DNA analyses of population structure in the blacklip abalone *Haliotis rubra* Leach. *Marine and Freshwater Research* 53: 711-718

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. *Science* 311: 522-527

Day RW, Fleming AE (1992) The determinants and measurement of abalone growth. In: Shepherd SA, Tegner MJ, Guzman del Proo SA (eds) Abalone of the world: Biology, fisheries and culture. Fishing News Books, Oxford, pp 141-168

Day RW, Quinn GP (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* 59: 433-463

Defeo O, Castilla JC (2005) More than one bag for the world fishery crisis and keys for co-management successes in selected artisanal Latin American shellfisheries. *Reviews in Fish Biology and Fisheries* 15: 265-283

Denny MW, Shibata MF (1989) Consequences of surf-zone turbulence for settlement and external fertilization. *American Naturalist* 134: 859-889

Dixon CD, Day RW (2004) Growth responses in emergent greenlip abalone to density reductions and translocations. *Journal of Shellfish Research* 23: 1223-1228

Donovan DA, Taylor HH (2008) Metabolic consequences of living in a wave-swept environment: Effects of simulated wave forces on oxygen consumption, heart rate, and activity of the shell adductor muscle of the abalone *Haliotis iris*. *Journal of Experimental Marine Biology and Ecology* 354: 231-240

Ebert TA (1996) Adaptive aspects of phenotypic plasticity in echinoderms. *Oceanologica Acta* 19: 347-355

Emmett B, Jamieson GS (1988) Transplant of abalone in Barkley Sound, British Columbia. *Journal of Shellfish Research* 7: 117

Etter RJ (1996) The effect of wave action, prey type, and foraging time on growth of the predatory snail *Nucella lapillus* (L). *Journal of Experimental Marine Biology and Ecology* 196: 341-356

Fowler-Walker MJ, Wernberg T, Connell SD (2006) Differences in kelp morphology between wave sheltered and exposed localities: Morphologically plastic or fixed traits? *Marine Biology* 148: 755-767

Gilg MR, Hilbish TJ (2003) Patterns of larval dispersal and their effect on the maintenance of a blue mussel hybrid zone in south western England. *Evolution* 57: 1061-1077

Gorfine HK, Taylor G, Cleland M, Haddon M, Punt A, Worthington D, Montgomery I (2005) Developement of a spatially-structured model for stock assessment and TAC decision analysis for Australian abalone fisheries. PIRVic, Queenscliff

Gruenthal KM, Burton RS (2008) Genetic structure of natural populations of the California black abalone (*Haliotis cracherodii* Leach, 1814), a candidate for endangered species status. *Journal of Experimental Marine Biology and Ecology*: 47-58

Guest MA, Nichols PD, Frusher SD, Hirst AJ (2007) Evidence of abalone (*Haliotis rubra*) diet from combined fatty acid and stable isotope analyses. *Marine Biology* 153: 579–588

Guzman-del Proo SA, Salinas F, Zaytsev O, Belmar-Perez J, Carrillo-Laguna J (2000) Potential dispersion of reproductive products and larval stages of abalone (*Haliotis* spp.) as a function of the hydrodynamics of Bahia Tortugas, Mexico. *Journal of Shellfish Research* 19: 869-881

Haddon M (2001) Modelling and quantitative methods in fisheries. Chapman and Hall/CRC, Boca Raton

Hamm DE, Burton RS (2000) Population genetics of black abalone, *Haliotis cracherodii*, along the central California coast. *Journal of Experimental Marine Biology and Ecology* 254: 235-247

Hammer C, Zimmermann C (2005) The role of stock identification in formulating fshery management advice. In: Cadrin SX, Friedland KD, Waldmann JR (eds) Stock identification methods applications in fishery science. Elsevier academic press, London, pp 631-658

Hancock B (2000) Genetic subdivision of Roe's abalone, *Haliotis roei* grey (Mollusca: Gastropoda), in South-western Australia. *Marine and Freshwater Research* 51: 679-687

Hewitt RP, Watters G, Trathan PN, Croxall JP, Goebel ME, Ramm D, Reid K, Trivelpiece WZ, Watkins JL (2004) Options for allocating the precautionary catch limit of krill among small-scale management units in the Scotia sea. *CCAMLR Science* 11: 81-97

Hobday AJ, Tegner MJ, Haaker PL (2001) Over-exploitation of a broadcast spawning marine invertebrate: Decline of the white abalone. *Reviews in Fish Biology and Fisheries* 10: 493-514

Holland DS (2003) Integrating spatial management measures into traditional fishery management systems: The case of the Georges Bank multispecies groundfish fishery. *Ices Journal of Marine Science* 60: 915-929

Huang BX, Peakall R, Hanna PJ (2000) Analysis of genetic structure of blacklip abalone (*Haliotis rubra*) populations using RAPD, minisatellite and microsatellite markers. *Marine Biology* 136: 207-216

Johannesson K, Kautsky N, Tedengren M (1990) Genotypic and phenotypic differences between Baltic and North-sea populations of *Mytilus edulis* evaluated through reciprocal transplantations 2. Genetic-variation. *Marine Ecology Progress Series* 59: 211-219

Johnson MS, Black R (1998) Effects of habitat on growth and shape of contrasting phenotypes of *Bembicium vittatum philippi* in the Houtman Abrolhos islands, Western Australia. *Hydrobiologia* 378: 95-103

Johnson MS, Black R (2000) Associations with habitat versus geographic cohesiveness: Size and shape of *Bembicium vittatum philippi* (Gastropoda: Littorinidae) in the Houtman Abrolhos islands. *Biological Journal of the Linnean Society* 71: 563-580

Jokiel PL, Morrissey JI (1993) Water motion on coral reefs - evaluation of the clod card technique. *Marine Ecology Progress Series* 93: 175-181

Karpov KA, Tegner MJ, Rogers-Bennett L, Kalvass PE, Taniguchi IK (2001) Interactions among red abalones and sea urchins in fished and reserve sites of northern California: Implications of competition to management. *Journal of Shellfish Research* 20: 743-753

Kojima H (1995) Evaluation of abalone stock enhancement through the release of hatchery-reared seeds. *Marine and Freshwater Research* 46: 689-695

Kong L, Li Q, Qiu Z (2007) Genetic and morphological differentiation in the clam *Coelomactra antiquata* (Bivalvia: Veneroida) along the coast of China. *Journal of Experimental Marine Biology and Ecology* 343: 110-117

Leiva GE, Castilla JC (2001) A review of the world marine gastropod fishery: Evolution of catches, management and the Chilean experience. *Reviews in Fish Biology and Fisheries* 11: 283-300

Lively CM (1986) Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. *Evolution* 40: 232-242

Luttikhuizen PC, Drent J, van Delden W, Piersma T (2003) Spatially structured genetic variation in a broadcast spawning bivalve: Quantitative vs. Molecular traits. *Journal of Evolutionary Biology* 16: 260-272

Martien KK, Taylor BL (2003) Limitations of hypothesis-testing in defining management units for continuously distributed species. *Journal of Cetacean Research* 5: 213-218

Mayfield S, Hogg A, Saunders TM (2007) Southern Zone abalone (*Haliotis laevigata* & *H. rubra*) fishery. Fishery assessment report to PIRSA Fisheries, F2007/000552-1

Mayfield S, McGarvey R, Carlson IJ, Dixon CD (2008) Integrating commercial and research surveys to estimate the harvestable biomass, and establish a quota, for an unexploited abalone population. *ICES Journal of Marine Science* 65

Mayfield S, Saunders TM, Hogg A, Ward TM (2005) Southern Zone abalone (*Haliotis laevigata* & *H. rubra*) fishery. Fishery assessment report to PIRSA Fisheries. SARDI Aquatic Sciences, Adelaide

Mayfield S, Saunders T, Jones A, Ward TM (2002) Abalone (Southern Zone). Fishery assessment report to PIRSA Fisheries policy group. SARDI Aquatic Sciences, Adelaide

McAvaney LA, Day RW, Dixon CD, Huchette SM (2004) Gonad development in seeded *Haliotis laevigata*: Growth environment determines initial reproductive investment. *Journal of Shellfish Research* 23: 1213-1218

McCune B, Mefford MJ (1999) PCORD: Multivariate analysis of ecological data version 4. MJM Software Design Gleneden Beach, Oregon USA

McShane PE (1992) Early life history of abalone: A review. In: Shepherd SA, Tegner MJ, Guzman del Proo SA (eds) Abalone of the world; biology, fisheries and culture. Fishing news books, Oxford

McShane PE (1995) Recruitment variation in abalone - its importance to fisheries management. *Marine and Freshwater Research* 46: 555-570

McShane PE, Black KP, Smith MG (1988b) Recruitment processes in *Haliotis rubra* (Mollusca, Gastropoda) and regional hydrodynamics in South-eastern Australia imply localized dispersal of larvae. *Journal of Experimental Marine Biology and Ecology* 124: 175-203

McShane PE, Mercer SF, Naylor JR (1994a) Spatial variation and commercial fishing of New Zealand abalone (*Haliotis iris* and *H. australis*). *New Zealand Journal of Marine and Freshwater Research* 28: 345-355

McShane PE, Naylor JR (1995b) Density-independent growth of *Haliotis iris* Martyn (Mollusca, Gastropoda). *Journal of Experimental Marine Biology and Ecology*: 51-60

McShane PE, Naylor JR (1995a) Small-scale spatial variation in growth, size at maturity, and yield- and egg-per-recruit relations in the New Zealand abalone *Haliotis iris*. *New Zealand Journal of Marine and Freshwater Research* 29: 603-612

McShane PE, Schiel DR, Mercer SF, Murray T (1994b) Morphometric variation in *Haliotis iris* (Mollusca, Gastropoda) - analysis of 61 populations. *New Zealand Journal of Marine and Freshwater Research* 28: 357-364

McShane PE, Smith MG, Beinssen KHH (1988a) Growth and morphometry in abalone (*Haliotis rubra* Leach) from Victoria. *Australian Journal of Marine and Freshwater Research* 39: 161-166

Meester GA, Ault JS, Smith SG, Mehrotra A (2001) An integrated simulation modelling and operations research approach to spatial management decision making. *Sarsia* 86: 543-558

Miller JA, Shanks AL (2004) Evidence for limited larval dispersal in black rockfish (*Sebastes melanops*): Implications for population structure and marine-reserve design. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1723-1735

Miner BG, Sultan SE, Morgan SG, Padilla DK, Relyea RA (2005) Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution* 20: 685-692

Morgan LE, Shepherd SA (2006) Population and spatial structure of two common temperate reef herbivores: Abalone and sea urchins. In: Kritzer JP, Sale PF (eds) Marine metapopulations. Elsevier Academic Press, Burlington, pp 205-234

Nash WJ (1992) An evaluation of egg-per-recruit analysis as a means of assessing size limits for blacklip abalone (*Haliotis rubra*) in Tasmania. In: Shepherd SA, Tegner MJ, Guzman del Proo SA (eds) Abalone of the world; biology, fisheries and culture. Fishing news books, Oxford, pp 318-341

Naylor JR, Andrew NL, Kim SW (2006) Demographic variation in the New Zealand abalone *Haliotis iris*. *Marine and Freshwater Research* 57: 215-224

Orensanz JM, Jamieson GS (1995) The assessment and management of spatially structured stocks: An overview of the North Pacific symposium on

invertebrate stock assessment and management. *In* proceedings of the North Pacific symposium on invertebrate stock assessment and management. *Canadian Special Publication of Fisheries and Aquatic Sciences* 125: 441-459

Orensanz JM, Hand CM, Parma AM, Valero J, Hilborn R (2004) Precaution in the harvest of Methuselah's clams - the difficulty of getting timely feedback from slow-paced dynamics. *Canadian Journal of Fisheries and Aquatic Science* 61: 1355-1372

Orensanz JM, Parma AM, Jerez G, Barahona N, Montecinos M, Elias I (2005) What are the key elements for the sustainability of 'S-fisheries'? Insights from South America. *Bulletin of Marine Science* 76: 527-556

Palsboll PJ, Berube M, Allendorf FW (2007) Identification of management units using population genetic data. *Trends in Ecology and Evolution* 22: 11-16

Palumbi SR (2003) Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* 13: S146-S158

Perry RI, Zhang ZY, Harbo R (2002) Development of the green sea urchin (*Strongylocentrotus droebachiensis*) fishery in British Columbia, Canada - back from the brink using a precautionary framework. *Fisheries Research* 55: 253-266

Preece PAG, Mayfield S, Saunders TM (2004) Biology of and feasibility fishing for roe's abalone (*Haliotis roei*). Report to the abalone industry association of South Australia. SARDI Aquatic Sciences, RD04/0024, Adelaide

Prince JD (1991) A new technique for tagging abalone. *Australian Journal of Marine and Freshwater Research* 42: 101-106

Prince J (2005) Combating the tyranny of scale for Haliotids: Micro-management for microstocks. *Bulletin of Marine Science* 76: 557-577

Prince JD, Hilborn R (2003) The development of industry based sustainability surveys for the Californian sea urchin fishery advisory committee. Californian sea urchin fishery advisory committee, Los Alamitos

Prince JD, Peeters H, Gorfine H, Day RW (2008) The novel use of harvest policies and rapid assessment to manage spatially complex abalone resources (genus *Haliotis*). *Fisheries Research* 94(3): 330-338

Prince JD, Sellers TL, Ford WB, Talbot SR (1987) Experimental-evidence for limited dispersal of Haliotid larvae (genus *Haliotis*, mollusca, gastropoda). *Journal of Experimental Marine Biology and Ecology* 106: 243-263

Prince JD, Sellers TL, Ford WB, Talbot SR (1988a) Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca, Gastropoda). *Journal of Experimental Marine Biology and Ecology* 122: 91-104

Prince JD, Sellers TL, Ford WB, Talbot SR (1988b) Recruitment, growth, mortality and population-structure in a southern Australian population of *Haliotis rubra* (Mollusca, Gastropoda). Marine Biology 100: 75-82

Prince JD, Shepherd SA (1992) Australian abalone fisheries and their management. . In: Shepherd SA, Tegner MJ, Guzman del Proo SA (eds) Abalone of the world; biology, fisheries and culture. Fishing news books, Oxford

Punt AE (2003) Extending production models to include process error in the population dynamics. *Canadian Journal of Fisheries and Aquatic Science* 60: 1217-1228

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Raimondi PT, Forde SE, Delph LF, Lively CM (2000) Processes structuring communities: Evidence for trait-mediated indirect effects through induced polymorphisms. *Oikos* 91: 353-361

Robles C, Robb J (1993) Varied carnivore effects and the prevalence of intertidal algal turfs. *Journal of Experimental Marine Biology and Ecology* 166: 65-91

Saunders T, Mayfield S (2008) Predicting biological variation using a simple morphometric marker in the sedentary marine invertebrate *Haliotis rubra*. *Marine Ecology Progress Series* 366: 75-89

Saunders T, Mayfield S, Hogg A (2008) A simple, cost-effective, morphometric marker for characterising abalone populations at multiple spatial scales. *Marine and Freshwater Research* 59: 32-40

Saunders T, Mayfield S, Hogg A (2009) Using a simple morphometric marker to identify fine-scale management units for abalone fisheries. *ICES Journal of Marine Science* 66: 305-314

Schnute JT, Richards LJ (1990) A unified approach to the analysis of fish growth, maturity, and survivorship data. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 24-40

Shepherd SA (1973) Studies on Southern Australian abalone (genus *Haliotis*) I. Ecology of five sympatric species. *Australian Journal of Marine and Freshwater Research* 24: 217-257

Shepherd SA, and Steinberg PD (1992) Food preferences of three Australian abalone species with a review of the algal food of abalone. In: Shepherd SA, Tegner MJ, Guzman del Proo SA (eds) Abalone of the world: Biology, fisheries and culture. Blackwell Scientific Publications Ltd. Oxford, pp 169-181

Shepherd SA, Baker JL, Johnson DW (1995) Yield-per-recruit and egg-per-recruit analyses of the Omani abalone, *Haliotis mariae*. *Marine and Freshwater Research* 46: 663-668

Shepherd SA, Brown LD (1993) What is an abalone stock - implications for the role of refugia in conservation. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2001-2009

Shepherd SA, Cannon J (1988) Studies on Southern Australian abalone (genus *Haliotis*) X. Food and feeding in juveniles. *Journal of the Malacological Society of Australia* 9: 21-26

Shepherd SA, del Proo SAG, Turrubiates J, Belmar J, Baker JL, Sluczanowski PR (1991) Growth, size at sexual maturity, and egg-per-recruit analysis of the abalone *Haliotis fulgens* in Baja-California. *Veliger* 34: 324-330

Shepherd SA, Godoy C, Clarke SM (1992b) Studies on Southern Australian abalone (genus *Haliotis*) XV. Fecundity of *H. laevigata. Journal of the Malacological Society of Australia* 13: 115-121

Shepherd SA, Hearn WS (1983) Studies on Southern Australian abalone (genus *Haliotis*) IV. Growth of *Haliotis laevigata* and *Haliotis rubra*. *Australian Journal of Marine and Freshwater Research* 34: 461-475

Shepherd SA, Laws HM (1974) Studies on Southern Australian abalone (genus *Haliotis*). II. Reproduction of five species. *Australian Journal of Marine and Freshwater Research* 24: 217-257

Shepherd SA, Lowe D, Partington D (1992a) Studies on southern Australian abalone (genus *Haliotis*). XIII. Larval dispersal and recruitment. *Journal of Experimental Marine Biology and Ecology* 164: 247-260

Slatkin M (1985) Gene flow in natural-populations. *Annual Review of Ecology and Systematics* 16: 393-430

Smith SJ, Rago P (2004) Biological reference points for sea scallops (*Placopecten magellanicus*): The benefits and costs of being nearly sessile. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1338-1354

Sponaugle S, Cowen RK, Shanks A, Morgan SG, Leis JM, Pineda JS, Boehlert GW, Kingsford MJ, Lindeman KC, Grimes C, Munro JL (2002) Predicting self-recruitment in marine populations: Biophysical correlates and mechanisms. *Bulletin of Marine Science* 70: 341-375

Steffani CN, Branch GM (2003) Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: Responses to wave exposure. *Marine Ecology Progress Series* 246: 197-209

Stephens SA, Broekhuizen N, Macdiarmid AB, Lundquist CJ, McLeod L, Haskew R (2006) Modelling transport of larval New Zealand abalone (*Haliotis iris*) along an open coast. *Marine and Freshwater Research* 57: 519-532

Strathmann RR, Hughes TR, Kuris AM, Lindeman KC, Morgan SG, Pandolfi JM, Warner RR (2002) Evolution of local recruitment and its consequences for marine populations. *Bulletin of Marine Science* 70: 377-396

Swain DP, Foote CJ (1999) Stocks and chameleons: The use of phenotypic variation in stock identification. *Fisheries Research* 43: 113-128

Swain DP, Hutchings JA, Foote CJ (2005) Environmental and genetic influences on stock identification characters. In: Cadrin SX, Friedland KD, Waldmann JR (eds) Stock identification methods applications in fishery science. Elsevier Academic Press, London, pp 45-85

Swearer SE, Shima JS, Hellberg ME, Thorrold SR, Jones GP, Robertson DR, Morgan SG, Selkoe KA, Ruiz GM, Warner RR (2002) Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science* 70: 251-271

Tarbath D, Mundy C, Haddon M (2003) Tasmanian abalone fishery 2002. TAFI, Taroona, Tasmania

Tarbath DB (2003) Seasonal variation in size at sexual maturity of the blacklip abalone *Haliotis rubra*. TAFI, Taroona, Tasmania

Taylor BL, Dizon AE (1999) First policy then science: Why a management unit based solely on genetic criteria cannot work. *Molecular Ecology* 8: S11-S16

Taylor MS, Hellberg ME (2003) Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. *Science* 299: 107-109

Tegner MJ (1993) Southern California abalones - can stocks be rebuilt using marine harvest refugia. *Canadian Journal of Fisheries and Aquatic Sciences* 50: 2010-2018

Tegner MJ, Basch LV, Dayton PK (1996) Near extinction of an exploited marine invertebrate. *Trends in Ecology and Evolution* 11: 278-280

Tegner MJ, Butler RA (1985) Drift-tube study of the dispersal potential of green abalone (*Haliotis fulgens*) larvae in the Southern-California bight - implications for recovery of depleted populations. *Marine Ecology Progress Series* 26: 73-84

Temby N, Miller K, Mundy C (2007) Evidence of genetic subdivision among populations of blacklip abalone (*Haliotis rubra* leach) in Tasmania. *Marine and Freshwater Research* 58: 733-742

Thorpe RS (1975) Quantitative handling of characters useful in snake systematics with particular reference to intraspecific variation in the ringed snake *Natrix natrix* (l*). Biological Journal of the Linnean Society* 7: 27-43

Tissot BN (1988) Morphological variation along intertidal gradients in a population of black abalone *Haliotis cracherodii* Leach 1814. *Journal of Experimental Marine Biology and Ecology* 117: 71-90

Trussell GC (1996) Phenotypic plasticity in an intertidal snail: The role of a common crab predator. *Evolution* 50: 448-454

Tyrer B (1995) Management arrangements for blacklip abalone (*Haliotis rubra*) fishdown exercises in the Southern Zone abalone fishery. Background and discussion paper for the abalone fishery management committee.

Wells FE, Keesing JK (1989) Reproduction and feeding in the abalone *Haliotis roei* (Gray). *Australian Journal of Marine and Freshwater Research* 40: 187-197

Wells FE, Mulvay P (1995) Good and bad fishing areas for *Haliotis laevigata*: A comparison of population parameters. *Marine and Freshwater Research* 46: 591-598

Wilen JE (2004) Spatial management in fisheries. *Marine Resources and Economics* 19: 7-19

Withler RE, Campbell A, Li SR, Brouwer D, Supernault KJ, Miller KM (2003) Implications of high levels of genetic diversity and weak population structure for the rebuilding of northern abalone in British Columbia, Canada. *Journal of Shellfish Research* 22: 839-847

Worthington D, Andrew NL (1995) Small-scale variation in demography and its implications for an alternative size limit in the fishery for blacklip abalone (*Haliotis rubra*) in New South Wales, Australia. *Canadian Special Publication of Fisheries and Aquatic Sciences* 125: 341-348

Worthington DG, Andrew NL (1997) Does covariation between growth and reproduction compromise the use of an alternative size limit for the blacklip abalone, *Haliotis rubra*, in NSW, Australia? *Fisheries Research* 32: 223-231

Worthington DG, Andrew NL, Hamer G (1995a) Covariation between growth and morphology suggests alternative size limits for the blacklip abalone, *Haliotis rubra*, in New South Wales, Australia. *Fisheries Bulletin* 93: 551-561

Worthington DG, Doherty PJ, Fowler AJ (1995b) Variation in the relationship between otolith weight and age - implications for the estimation of age of 2 tropical damselfish (*Pomacentrus moluccensis* and *P wardi*). *Canadian Journal of Fisheries and Aquatic Sciences* 52: 233-242

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