ASPECTS OF THE BIOLOGY AND ECOLOGY OF THE SOUTH AFRICAN ABALONE *HALIOTIS MIDAE* LINNAEUS, 1758 (MOLLUSCA: GASTROPODA) ALONG THE EASTERN CAPE AND CISKEI COAST.

THESIS
Submitted in Fulfilment of the
Requirements for the Degree of
Master of Science
of Rhodes University

by

AIDAN DAVID WOOD

January 1993

Frontispiece: The South African abalone *Haliotis midae* Linnaeus, 1758.

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ACKNOWLEDGEMENTS

To my supervisor, Dr. Colin Buxton for his support, encouragement and insight throughout the study, I am deeply indebted. Without the support and cooperation of the many people who helped with the diving work in this study, none of this would have been possible, and I am extremely grateful to Dr. Colin Buxton, Bruce Mann, Angus Paterson, Pete Britz, Tim Andrew, Dr. Rob Tilney, Prof. Tom Hecht, Marc Griffiths, Mark Dixon, Larry Oellerman, Peter Thorpe, Anton Pretorius, Andre Bok, Kevin Heasman and Paul Stevens for their assistance. A special thanks to Prof. Pete Cook, Neville Sweijd, Colleen Parkins and Paul Hanekom from U.C.T. and Angus Mackenzie from Sea Fisheries Research Institute (SFRI) for their help in the tagging operation at Great Fish Point, to Gerry van Niekerk of Atlas Sea Farms in Port Elizabeth for providing transport to and diving assistance at Bird Island, and to Chris Heineken of Atlas Sea Farms in Saldanha Bay for additional assistance at Bird Island.

Dr. Sarah Radloff, Larry Oellerman and Kevin Heasman are thanked for their assistance with the statistical analyses, and I am grateful to Linda Coetzee for her patience in helping me get to grips with Word Perfect.

I further wish to thank the following people for their input during this project: Rob Tarr at SFRI for his advice on tagging and transecting methods. Angus Mackenzie for supplying the original data from tagged Bird Island animals. Margaret Crampton and Eve Cambray for the continuous and enthusiastic supply of abalone literature. Bill Wesson for revealing his secret caches of perlemoen at the Mgwalana wreck site (among others). Greg Foster for his assistance in histological staining techniques. Dr. Colin Buxton, Angus Paterson, Bruce Mann, Judy Lang, Marc Griffiths, Dr. Rob Tilney, Neville Sweijd and Craig Clayden for constructive advice on methods and results.

The Foundation for Research and Development are thanked for bursaries in 1991 and 1992. The Ciskei Directorate for Agriculture, Forestry and Rural Development are thanked for supplying the incentive and financial backing for this project and for ensuring the supply of abalone and off road vehicle permits.

A final special thank-you to Sandy Abreu for her support and her realization and understanding that field trips were necessary, and to my parents for having faith in me and supporting me in the realization of my goals.

ABSTRACT

The South African abalone *Haliotis midae* Linnaeus, 1758, is an important commercial, recreational and aquaculture mollusc species. It is the largest of the six haliotid species found in South African waters and has the second largest distributional range aside from *Haliotis spadicea* which is widely exploited by rock and surf anglers as bait.

Analysis of population structure at Great Fish Point revealed that *H. midae* exhibited a high degree of microhabitat specificity, and that while dietary habits played a role in habitat selection, it was ultimately the activities of predators which confined size classes to particular niches and restricted all animals to nocturnal activities. Large (> 100 mm SL) exposed animals relied on shell thickness and adhesion to combat predators, while small (> 45 mm SL) sub-boulder animals and medium sized (50 - 95 mm SL) animals relied on their cryptic microhabitats and the protective spine canopies of co-resident urchins (*Parechinus angulosus*) for daytime protection. Populations of *H. midae* were discontinuously distributed along the coast, occupying small isolated reefs which offered a suitable array of microhabitats and a good food supply. They mostly inhabited shallow intertidal and subtidal reefs, but were occasionally encountered on deeper subtidal reefs at 4 - 5 meters.

Mean length- and width-at-age were determined from growth rings composed of alternate conchiolin (dark) and aragonite (white) bands in the internal nacreous shell layer. Growth was described by the Special Von Bertalanffy growth equation:

$$L_t(\text{mm}) = 176.998918\ (1 - e^{-0.242419[t + 0.495494]})$$

$$W_t(\text{mm}) = 159.705689\ (1 - e^{-0.195439[t + 0.421164]})$$

The ageing technique used was validated for animals from Great Fish Point and Mgwalana using independent tag-return data. The same data provided evidence that growth rates varied between animals from Great Fish Point and Bird Island. The growth data also showed that *H. midae* exhibited a high degree of individual variation in growth rate. Males and females exhibited similar growth rates.

Exposed large animals showed a preference for red seaweeds, in particular *Plocamium corallorhiza* and *Hypnea spicifera*, while small sub-boulder cryptic animals included larger proportions of brown (*Ralfsia expansa*) and green (*Ulva* spp.) algae in their diets. Exposed individuals also exhibited a higher degree of selectivity towards prey items, but in general, stomach contents reflected the most abundant seaweed types. Both drift and attached algal species were utilized by *H. midae* which was a nocturnal feeder. Pigments from red algae were incorporated into the shell layers giving the shells a pink or brick red colour.

Haliotis midae is a dioecious broadcast spawner. Gonad Bulk Indices in combination with detailed histological examination of gonads showed that individuals were iteroparous, asynchronous spawners and that the breeding season extended from March through to October, although the peak spawning activity was between April and June. Males and females can spawn partially, totally or not at all, with atresia of residual gametes occurring after spawning. There is no resting stage, and gametogenesis is initiated directly after spawning. The structure of the ovary and testis and the process of gametogenesis is typical of haliotid species. A 1:1 sex ratio was observed from all populations studied. Sexual maturity was first attained in the 40 - 59 mm SL size class, although evidence for the smallest size at first spawning was recorded at 54.6 mm SL for females and 69 mm SL for males. Sizes at 50 % sexual maturity were 72.5 mm SL (52.8 mm SW) at Great Fish Point, 72.5 mm SL (57.4 mm SW) at Mgwalana, 73.7 mm SL (51.2 mm SW) at Cape Recife, and 73.5 mm SL (53.8 mm SW) at Kelly's Beach. *Haliotis midae* was typically highly fecund, although a high degree of variation resulting in poor relationships between fecundity/shell length and gonad weight/shell length. The relationship between fecundity and gonad weight was linear.

In the Eastern Cape, *H. midae* possessed a faster growth rate, smaller size at sexual maturity, smaller maximum size and lower longevity when compared to conspecifics in Western Cape waters. A smaller minimum legal size of 93 mm SW is proposed for Eastern Cape animals and it is suggested that the closed season be moved to the peak spawning period between April and June. The benefit of a closed season during the spawning period is questioned, and the feasibility of closed areas as a management option for *H. midae* in the Eastern Cape is discussed.

CHAPTER 1 GENERAL INTRODUCTION

The phylum Mollusca is one of approximately 20 major divisions of the Animal Kingdom (Cox 1962). The molluscs we know as abalone (perlemoen) are dioecious, prosobranch archaeogastropods belonging to the family Haliotidae, the largest genus being *Haliotis* (Cotton 1959), comprising over 90 described species worldwide (Sloan & Breen 1988). The genus has been divided into 15 subgenera with *Haliotis midae* Linne, 1758 being recognized as the type species of the subgenus *Euhaliotis* (Cotton *op. cit.*; Lindberg 1992), and possibly the genotype for *Haliotis* (Sloan & Breen *op. cit.*). The genus is distributed from subarctic to antarctic waters, but is most commonly found inhabiting intertidal and subtidal reefs in temperate and tropical localities (Boolootian *et al.* 1962; Peck & Culley 1990). The northern or pinto abalone *Haliotis kamtschatkana* has the northernmost distribution, being found at Sitka Island, Alaska approximately 58^0N (Sloan & Breen *op. cit*). The literature does not reveal the species with the southern-most distribution, however, it would have to be one of the southern Australian species, *viz: Haliotis laevigata, Haliotis rubra, Haliotis scalaris, Haliotis cyclobates, Haliotis roei* or *Haliotis coccoradiata* (see Lindberg *op. cit.*). Haliotids were mentioned as early as ca. 347 B.C. by Aristotle (Olley & Thrower 1977) who referred to them as *Agria lepas*, the wild limpets, while others called them *Thalattion us*, the marine or sea ears, a name which bears resemblance to a common name used by the English and Greeks and to a limited extent locally for abalone, *viz:* "venus ears". There are as many as two dozen common names in over 15 languages which may be encountered in the literature concerned with abalones.

Throughout their distribution, haliotids are exploited commercially and recreationally for the food value of the muscular foot and the decorative nature of the shell (Sinclair 1963; Pritchard 1982; Wright 1982). A characteristic of most abalone fisheries is the history of high catches followed by declines (Mottet 1978; Harrison 1986; Sloan & Breen 1988; Tegner 1989; Hecht & Britz 1992; Tarr 1992). It is this aspect of fisheries which has prompted the investigation of abalone ecology and biology over the last 30 years, with much of the knowledge gained being applied not only to management but to culture as well (Shepherd *et al.* 1992). Aspects of reproduction have been widely studied and are reviewed by Boolootian *et. al.*(1962), Poore (1973) and Shepherd & Laws (1974). Wells & Keesing (1989) summarised the research concerned with the general ecology, reproduction, growth, mortality and feeding biology of Australian species, while the relationship between recruitment and mortality were surveyed for a commercial species in South Australia by Shepherd (1990). The induction of settlement and metamorphosis of larvae and their dietary and habitat requirements were described by Barlow (1990), Moss & Tong (1992), Slattery (1992) and Searcy-Bernal *et al.* (1992), while growth and development of the larval stages were described by Murayama (1935), Oba (1964) and Yano & Ogawa (1977). The feeding biology and digestion of several species has been investigated by Sakai (1962a), Leighton (1966), McLean (1970), Poore (1972a) and Tutschulte & Connell (1988a). Age and growth are together probably the single most important aspect in fisheries biology and understandably there is a wealth of information on the topic, e.g. Sakai (1962b), Leighton & Boolootian (1963), Forster (1967), Leighton (1971), Poore (1972c), Shepherd & Hearn (1983), Clavier & Richard (1986), Prince *et al.* (1988), Shepherd (1988) and Keesing & Wells (1989). Movement has been studied by Poore (1972b), Ault & DeMartini (1987) and Shepherd & Godoy (1989) while predation and the escape responses of abalone to various predators were considered by Pilson & Taylor (1961), Parsons & Macmillan (1979), Hines & Pearse (1982) and Shepherd & Turner (1985). Population structure was described for various species by Hayashi (1980b), Brown (1991), Schiel & Breen (1991) and Peck & Culley (1990) who also considered genetic variation in relation to mating and gene flow amongst and between populations. A potential use for abalone in polyculture systems has been investigated by Tenore (1976), where abalone could browse on seaweeds which are used in the system to remove nutrients generated by culture organisms such as bivalves. As a result, polyculture systems could be maintained free of waste accumulation. Due to increased fishing pressures on abalone stocks around the world, seeding of hatchery-reared juveniles into wild populations which was pioneered by the Japanese (Shaw 1982) has become an appealing approach to resource enhancement. Investigations into the feasabiltiy of such ventures have been performed by Cochard & Flassch (1981) for *Haliotis tuberculata*, Tegner & Butler (1985a; 1989) for *Haliotis rufescens*, and Breen (1986) and Emmet & Jamieson (1988) for *Haliotis kamtschatkana*.

With respect to research in South Africa, Muller (1984; 1986) comprehensively covered aspects of the ecology, biology and taxonomy of the siffie *Haliotis spadicea*. Newman, in a detailed investigation of *H. midae* on the West coast published on its movements (1966), reproduction (1967b), growth (1968) and distribution and productivity (1969). Newman (1967a) also reviewed the status of abalone research in South Africa. Subsequent to this Barkai & Griffiths (1986; 1987) investigated the dietary habits as well as the consumption, absorption efficiency, respiration and excretion of *H. midae*. The potential of the species as a culture animal prompted Genade *et al.* (1988) to investigate spawning, larval development and early growth under controlled conditions. A general overview of the biology and fishery of *H. midae* was published by Tarr (1987), while the history and future of the fishery in South Africa was comprehensively reviewed by Tarr (1992).

Southern Africa boasts six *Haliotis* species (Figure 1.1). A visual key and description appears in Muller (1986) and is based on the original descriptions of Barnard (1963) which outline the specific differences in external shell shape and colour, number of shell whorls, and ridges.

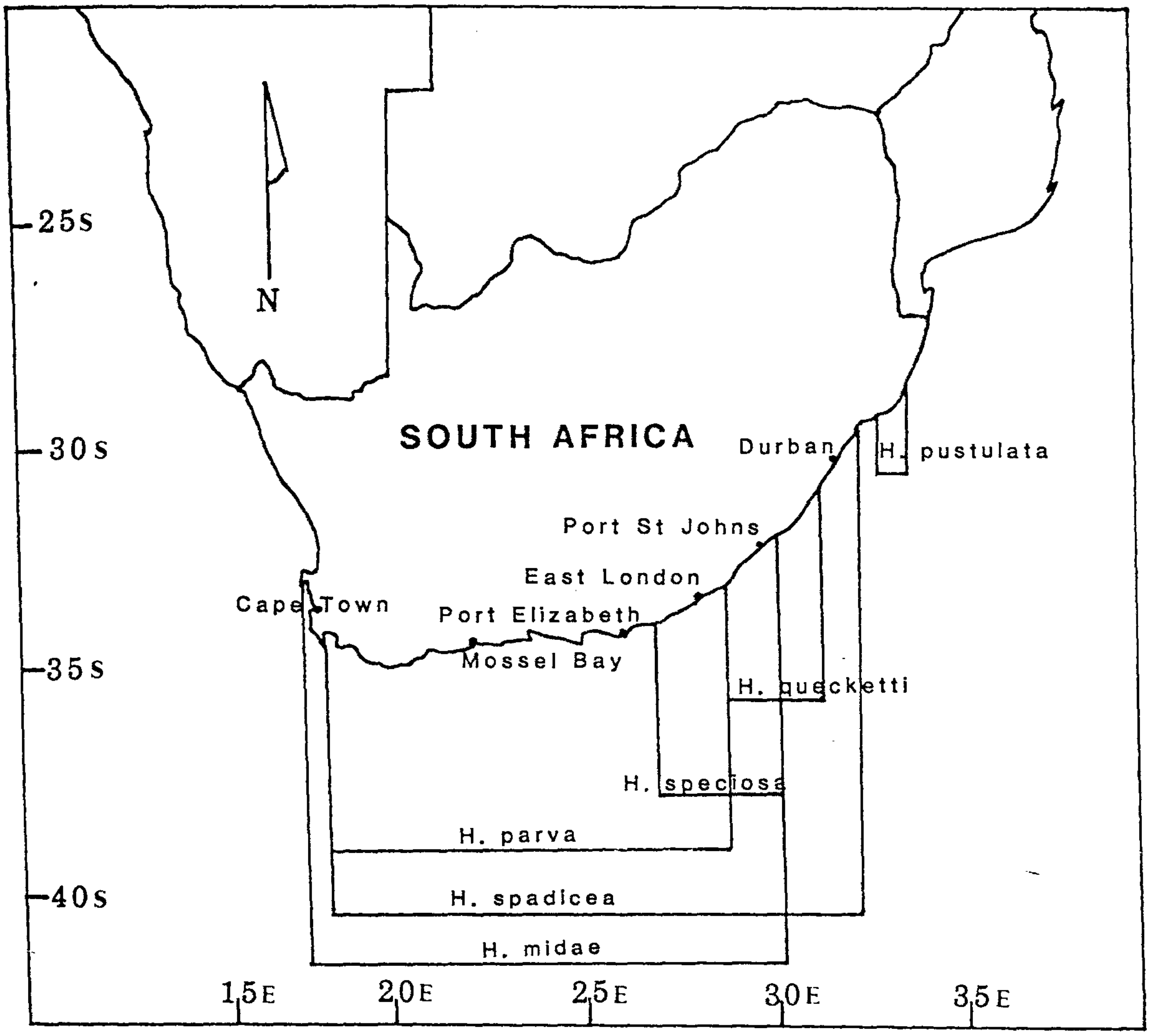

Figure 1.1 The distribution of *Haliotis* spp. in Southern Africa (after Muller 1986).

Haliotis midae is the largest of the six species, with a wide distributional range, from St Helena Bay to just north of Port St Johns in the Transkei, exceeded only by *H. spadicea*. Only the Californian red abalone *Haliotis rufescens* and perhaps the Japanese "awabi" *Haliotis gigantea* are larger than *H. midae* which attains a maximum size of 230 mm standard length (SL) at an age of approximately 30 years (Newman 1968). Cox (1962) noted that larger species of *Haliotis* are found in the cooler currents along the shores of the continents where brown seaweeds predominate. This holds true for the Californian red abalone *Haliotis rufescens* and appears to be the case for the South African perlemoen *H. midae*. It is by far the most abundant of our abalone species and is most commonly found in the intertidal zone and down to about 10 m depth although there are records of it extending its range to depths of 35 m in places (Barkai & Griffiths 1986). As a result of its abundance, *H. midae* is the target of commercial and recreational fisheries along much of its range. It is most abundant between St Helena Bay and Cape Agulhas (Barkai & Griffiths *op. cit.*) which is where the present fishery from Cape Columbine to Quoin Point is located (Tarr 1992; see Figure 2.1). A commercial Total Allowable Catch (TAC) of 600 tonnes whole weight/year is divided amongst five companies which fish in seven zones in the Southern Cape annually (Anonymous 1991). A small commercial venture (TAC of 3 tonnes whole weight/year divided between two concessionaires) has recently been revived at Hamburg in the Ciskei. Current legislation dictates that recreationals are restricted to 4 animals/man/day, while both recreationals and commercials are subject to a minimum size of 11.4 cm shell width and a closed season from the 1st August to the 31st October each year.

The tendency for abalone such as *H. midae* to be sedentary and restricted to a particular reef, their discontinuous distribution along the east coast, their preference for a shallow water habitat, the non-cryptic nature of larger legal-sized animals, relatively high mortality of sub-legal sized animals from damage incurred from removal, unpredictable recruitment, slow growth rates and abundance of natural predators, makes them particularly susceptible to over exploitation (Mottet 1978; Sainsbury 1982; Breen 1986; Tegner & Butler 1989). This therefore necessitates correct management and conservation measures. The bulk of Newman's research (1966-1969) as well as the feeding study by Barkai & Griffiths (1986) were performed in South-Western and Western Cape waters. Newman (1969) noted that the differences in temperature over the geographical range of *H. midae* could influence the maximum size, growth rate and size at maturity. For this reason he postulated that *H. midae* in the Eastern Cape differed from its conspecifics further west in that;

(1) they had a faster growth rate,
(2) they matured at a smaller size,
(3) and they achieved a smaller maximum size.

In March 1991, the Ciskei Directorate of Agriculture, Forestry and Rural Development approached the Department of Ichthyology and Fisheries Science at Rhodes University to carry out an investigation on the feasibility of a perlemoen fishery along their coast. The main aim of this study was therefore to study aspects of the biology and ecology of *H. midae* in the Eastern Cape. The study sites are described in Chapter 2, and an investigation of population structure in relation to microhabitat type and availability, food availability, and predation pressures is described in Chapter 3. Aspects of age and growth, feeding biology and reproductive biology are presented in Chapters 4, 5 and 6 respectively. Chapter 7 incorporates a summary and considerations for management.

CHAPTER 2 STUDY SITES

2.1 Introduction

The intertidal and shallow subtidal rocky shore, which is the preferred habitat of *H. midae* in the Eastern Cape, is recognized as being one of the most stressful for plants and animals (Branch & Branch 1981). The South African coastline exhibits a marked temperature gradient from west to east which in turn has a marked effect on the distribution and composition of intertidal fauna and flora (Newman 1969). The distribution of marine animals and plants of intertidal populations can be grouped into the following biotic zones (after Stephenson 1944 and Day 1974):

(1) The East Coast - mainly comprising the subtropical population of Natal, but extending to Port St Johns or the Bashee River in the Transkei. The abundance of many tropical Indo-west-Pacific species together with a few temperate forms from the Cape Province as well as a few endemic species ensures a very high diversity.

(2) The South Coast - extends from the Transkei to Cape Agulhas, although the composite species are most commonly encountered between Cape Agulhas and Algoa Bay. The subtropical Indian Ocean species are replaced by a warm-temperate fauna and flora comprising a high degree of endemic forms as well as a component shared with the East coast on one hand and the West coast on the other. Some cosmopolitan forms are in evidence as well.

(3) The West Coast - extends from Cape Agulhas to Walvis Bay, but is well developed from about Kommetjie northwards where it ultimately overlaps with the tropical West African biota. Made up of a cold-temperate water fauna well supplied with endemic forms mixed with species whose main distribution lies farther east. Species richness and diversity are both lower than for the warm temperate and tropical zones.

(4) A certain number of species are encountered around the whole of the South African coastline, and are thus common in all three zones described above.

Major changes in biota define the boundaries of the above zones, but many species are not easily compartmentalised and there is a high degree of overlap of species between regions. Various boundaries have been drawn to delimit the Eastern Cape region. For the purpose of this project I have used the confines proposed by Lubke (1988) from Cape St Francis to Kei Mouth (Figure 2.1) which is situated in the heart of the South Coast zone. As a direct affect of the rise and fall of tides, plants and animals in the intertidal zone are distributed according to their ability to withstand the variable and often harsh physical conditions resulting from a combination of exposure time to air and exposure to wave action.

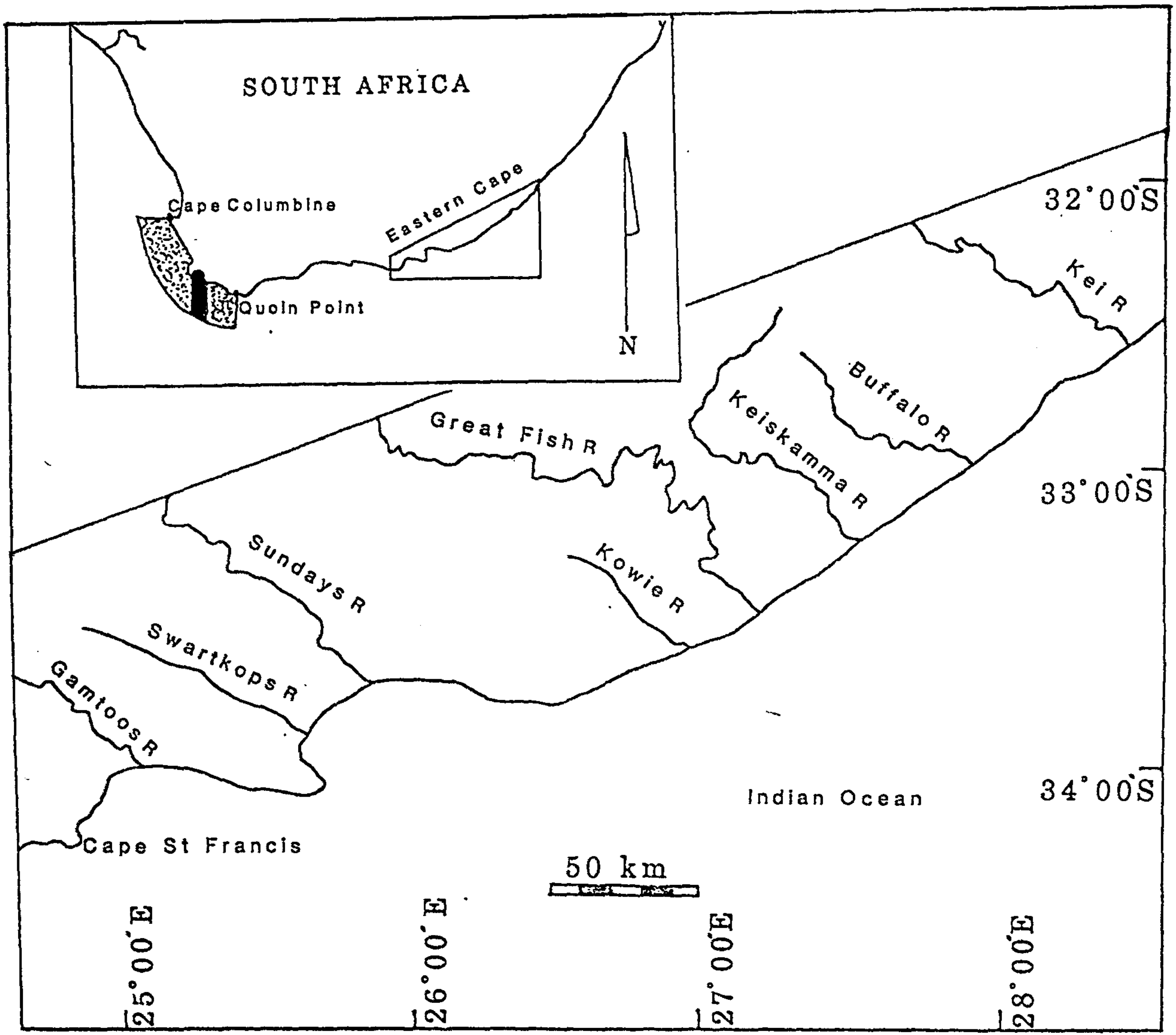

Figure 2.1 The eastern Cape coastal region between Cape St Francis and Kei Mouth (after Lubke 1988). The speckled region between Cape Columbine and Quoin Point is the area where *H. midae* is commercially exploited; the shaded region (False Bay) is closed to fishing (after Tarr 1992).

Five distinct zones are recognized on rocky shores, *viz.* the Littorina, Upper Balanoid. Lower Balanoid, Cochlear or Argenvillei and Infratidal zones (Branch & Branch 1981). These five zones are occupied by different species (with a degree of overlap) in the various biotic regions along the coast. Indicator species have been described for the three regions and are summarised in Day (1974) and Branch & Branch (*op. cit*). The pattern of zonation for the Eastern Cape mostly resembles that of the Southern Cape (Lubke 1988). Table 2.1 lists the more common species in the five zones as described by Branch & Branch (*op. cit.*), Beckley (1988), Seagrief (1988), and from personal observations.

Haliotis midae is found subtidally, although some medium sized individuals may venture up into

Table 2.1 **Key species along a rocky-shore transect in the Eastern Cape. The Cochlear and Infratidal zones are combined due to the great degree of overlap in species composition, especially with respect to seaweeds. (M - Mean; LW - Low Water; HW - High water; S - Spring Tide; N - Neap Tide). After Branch & Branch (1981), Beckley (1988) and Seagrief (1988).**

Zone	Faunal Composition	Floral Composition
Littorina - submerged periodically between MHWN and MHWS.	*Littorina knysnaensis*	*Porphyra capensis*
	L. africana	*Bostrychia mixta*
	Cyclograpsus punctatus	*Enteromorpha sp.*
Upper Balanoid - submerged from the period between MLWN and MHWN and at MHWS.	*Chthamalus dentatus*	*Porphyra capensis*
	Tetraclita serrata	*Caulacanthus ustulatus*
	Octomeris angulosa	*Iyegaria stellata*
	Patella granularis	*Enteromorpha sp.*
	P. oculus	*Hildenbrandtia rosea*
	Oxystele variegata	*Ralfsia expansa*
	O. sinensis	*Bostrychia mixta*
	Actinia equina	*Gelidium pristoides*
	Acanthochiton garnoti	*Gigartina paxillata*
	Chiton tulipa	*Ulva spp.*
Lower Balanoid - exposed at MLWN and MLWS.	*Patella longicosta*	*Codium lucasii capense*
	Pseudactinia flagellifera	*Hypnea spicifera*
	Parechinus angulosus	*H. rosea*
	Patiriella exigua	*Laurencia flexuosa*
	Amphiura capensis	*Gelidium pristoides*
	Plagusia chabrus	*G. amansii*
	Burnupena pubescens	*Ralfsia expansa*
	Oxystele sinensis	*Hildenbrandtia rosea*
	O. tigrina	*H. pachythallos*
	O. variegata	*Bryopsis spp.*
	Gibbula rosea	*Lithothamnion sp.*
	Balanus algicola	*Chaetangium erinaceum*
	Octomeris angulosa	*Codium platylobium*
	Patella oculus	*C. fragile capense*
	P. granularis	*Corallina spp.*
	Perna perna	
	Dinoplax gigas	
	Gunnarea capensis	
	Pomatoleios kraussii	
	Siphonaria capensis	
	S. oculus	

Table 2.1/...

Table 2.1 continued.

Zone	Faunal Composition	Floral Composition
Cochlear - exposed only at MLWS.	*Bunodactis reynaudi*	*Caulerpa filiformis*
Infratidal - submerged at all times.	*Actinia equina*	*C. holmesiana*
	Pyura stolonifera	*Hypnea spicifera*
	Patella cochlear	*H. rosea*
	P. longicosta	*Plocamium corallorhiza*
	P. tabularis	*P. suhrii*
	P. miniata	*Ralfsia expansa*
	P. argenvillei	*Lithothamnion sp.*
	Perna perna	*Lithophyllum sp.*
	Dinoplax gigas	*Bryopsis spp.*
	Gunnarea capensis	*Amphiroa ephedraea*
	Oxystele sinensis	*Arthrocardia sp.*
	O. tigrina	*Cheilosporum cultratum*
	O. variegata	*Corallina sp.*
	Burnupena cincta	*Callithamnion stuposum*
	Thais spp.	*Halimeda cuneata*
	Marthasterias glacialis	*Gracilaria beckeri*
	Patiria granifera	*Ecklonia biruncinata*
	Pseudonereis variegata	*Stypopodium zonale*
	Austromegabalanus cylindricus	*Larencia flexuosa*
	Striostria margaritacea	*L. natalensis*
	Haliotis midae	*L. glomerata*
	H. spadicea	*Chondrococcus hornemannii*
	H. parva	*C. tripinnata*
	Parechinus angulosus	*Dictyota naevosa*
	Plagusia chabrus	*D. dichotoma*
	Turbo sarmaticus	*Dictyopterus longifolia*
	T. cidaris	*Gelidium amansii*
	Comanthus wahlbergi	*G. cartilagineum*
	Ophiothrix trigrochis	*Sargassum heterophyllum*
	Hymeniacedon perlevis	*S. longifolium*
	Haliclona sp.	*Spyridea cupressina*
	Roweia frauenfeldi frauenfeldi	*Aeodes orbitosa*
	R. stephensoni	*Botryocarpa prolifera*
	Orchoporella buskii	*Calliblepharis fimbriata*
	Chaperia sp.	*Pterosiphonia cloiophylla*
	Octopus vulgaris	*Champia compressa*
	Chorisochismus dentex	*Codium platylobium*
	Patiriella exigua	*C. fragile capense.*
	Neostichopos grammatus	*Gelidium versicolor*
		Plocamium cornutum

the cochlear and lower balanoid zones to occupy available crevices. Perlemoen smaller than 40 mm shell length (SL) are cryptic, hiding beneath boulders. Medium sized animals may occupy crevices or beneath boulder spaces but may also appear on exposed surfaces. Larger animals may be found in crevices or on exposed surfaces but animals > 135 mm SL are exclusively encountered in the open (see Chapter 3). Indicator species for *H. midae* on East Cape reefs are *Pyura stolonifera, Gunnarea capensis, Parechinus angulosus, Dinoplax gigas, Patella cochlear, Patella oculus, Turbo sarmaticus, Plocamium corallorhiza, Hypnea spicifera, Sargassum heterophyllum, Lithothamnion* sp. and *Ecklonia biruncinata.* The brown mussel *Perna perna* which is abundant in the intertidal rocky shore of the East Cape was absent from all sample sites except for a few at Cape Recife. This could be as a result of the high incidence of colonies of the polychaete worm *Gunnarea capensis* which now occupies most of the area usually colonised by mussels.

2.2 Study sites

2.2.1 Cape Recife (Figure 2.2)

Cape Recife (34^{o} 1' 44" S, 25^{o} 42' 28" E) is a Nature Reserve situated on the rocky headland on the south-western end of Algoa Bay. The sample site was on the protected side of the headland and was sheltered from the westerly and south-westerly winds which dominate the Port Elizabeth area. Wave-cut platforms predominate in the nearshore zone and give way to a sheltered, shallow zone of 30 - 50 cm comprising rocky ridges and boulders (Figure 2.3). Cape Recife is a popular site for the local people and tourists who use the area for recreational fishing and diving. Dense beds of *Laurencia glomerata* and *Laurencia natalensis* are evident together with the chiton *Dinoplax gigas* and the urchin *Parechinus angulosus*. Very few juvenile *H. midae* are found beneath the boulders and almost no adults are present. This zone is particularly accessible at low tides (both spring and neap) and is protected from the high tide swell except in times of very large seas. These factors facilitate easy exploitation from even the most novice divers, and the paucity of marine fauna in this area bears testament to this. Beyond this zone, approximately 80 meters offshore, is prime adult perlemoen habitat. The water depth varies from about 80 cm at spring low tide to 2 - 2.5 meters at spring high. Large pinnacles covered with red bait (*Pyura stolonifera*) predominate and the sea floor is covered by large (50 - 100 cm diameter) boulders. Large numbers of adult perlemoen are found attached to open rock faces or sheltering in crevices and under overhangs. The seaweeds *P. corallorhiza* and *H. spicifera* dominate this region along with *D. gigas, P. angulosus, Marthasterias glacialis, Bunodactis reynaudi, T. sarmaticus* and *Plagusia chabrus*. A few individuals of *H. spadicea* were evident

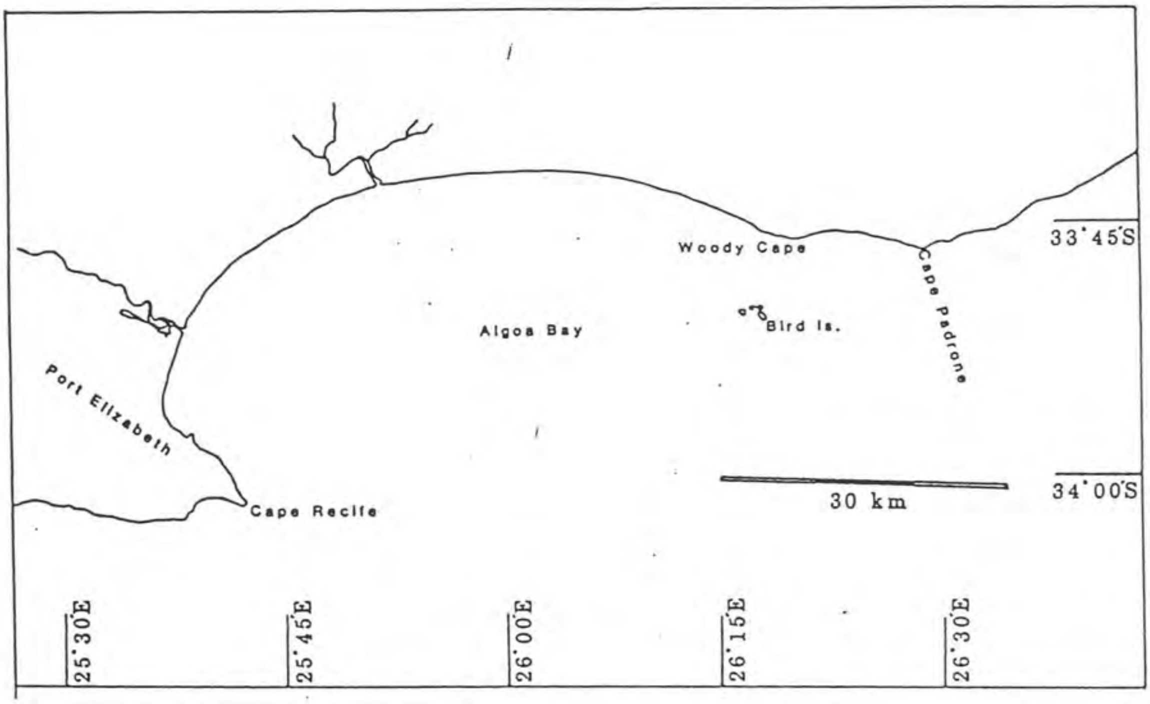

Figure 2.2 The Algoa Bay area showing the location of Cape Recife and Bird Island.

Figure 2.3 The site at Cape Recife showing the wave-cut platforms (W), the sheltered, shallow boulder zone (B) and the deep subtidal zone (S).

in crevices by themselves, but they were scarce. The tides in this area are semi diurnal with a mean spring tide range of 1.54 +- 0.14 meters, and a mean neap tide range of 0.58 +- 0.21 meters. This site could be worked at all times except when large swells, resulting from storms or strong westerly winds, were running. Throughout the sampling period (May 1991 - July 1992) there was never any difficulty with regard to sand deposition which is common during the winter months in this region (Muller 1984).

2.2.2 Kelly's Beach (Figure 2.4)

Situated near Port Alfred, Kelly's Beach (33^0 36' 21" S, 26^0 53' 52" E) was sampled from May -July 1992 during peak gonad activity to obtain information on sex ratios and maturity (see Chapter 6). The area comprises a small bay known as Sharks Bay (Figure 2.5) which contains medium sized boulders (50 -80 cm diameter) and a dense mat of seaweed dominated by *P. corallorhiza, H. spicifera, Laurencia flexuosa, Calliblepharis fimbriata, Gelidium amansii, Chondrococcus hornemannii, Botryocarpa prolifera, Codium platylobium* and *Ulva* spp. Few large perlemoen were found on these boulders and moderate numbers of juveniles were found beneath them along with *P. angulosus, D. gigas, P. oculus, Patella longicosta, Asterina exigua, Ophiothrix trigrochis, Roweia frauenfeldi frauenfeldi, Neostichopos grammatus, Burnupena pubescens, Thais capensis, Oxystele* spp. and *P. chabrus*. To the left of the bay is a series of large, red bait covered pinnacles arranged perpendicular to the shore and parallel to one another. These would be periodically exposed at spring low tide, but were submerged for the remainder of the tidal cycle. An abundance of overhangs and crevices provided ideal habitat for *H. midae* amongst an abundance of encrusting corallines and sponges. Crevices were shared with *Oxystele sinensis, P. angulosus, P chabrus, M. glacialis* and *T. sarmaticus*, while open rock faces were characterised by *P. cochlear, P. oculus*, and various *Siphonaria* species. Collecting in Sharks Bay could be done at almost any time except during stormy sea conditions, while the pinnacles could only be sampled at spring low or during neap tides if the sea was exceptionally calm. The reef where perlemoen are found at Kelly's Beach was not very extensive as they do not appear to extend onto the reef to the right of Sharks Bay. This fact coupled with the high incidence of recreational exploitation mainly from local people has adversely affected this population. Legal sized animals are rare except in the most turbulent waters which are avoided by most divers.

2.2.3 Great Fish Point (Figure 2.4)

Approximately 5 kilometres south-west of Fish River mouth is the Great Fish Point (33^0 31' 11" S, 27^0 6' 58" E). While this small headland affords some protection from the south-westerly

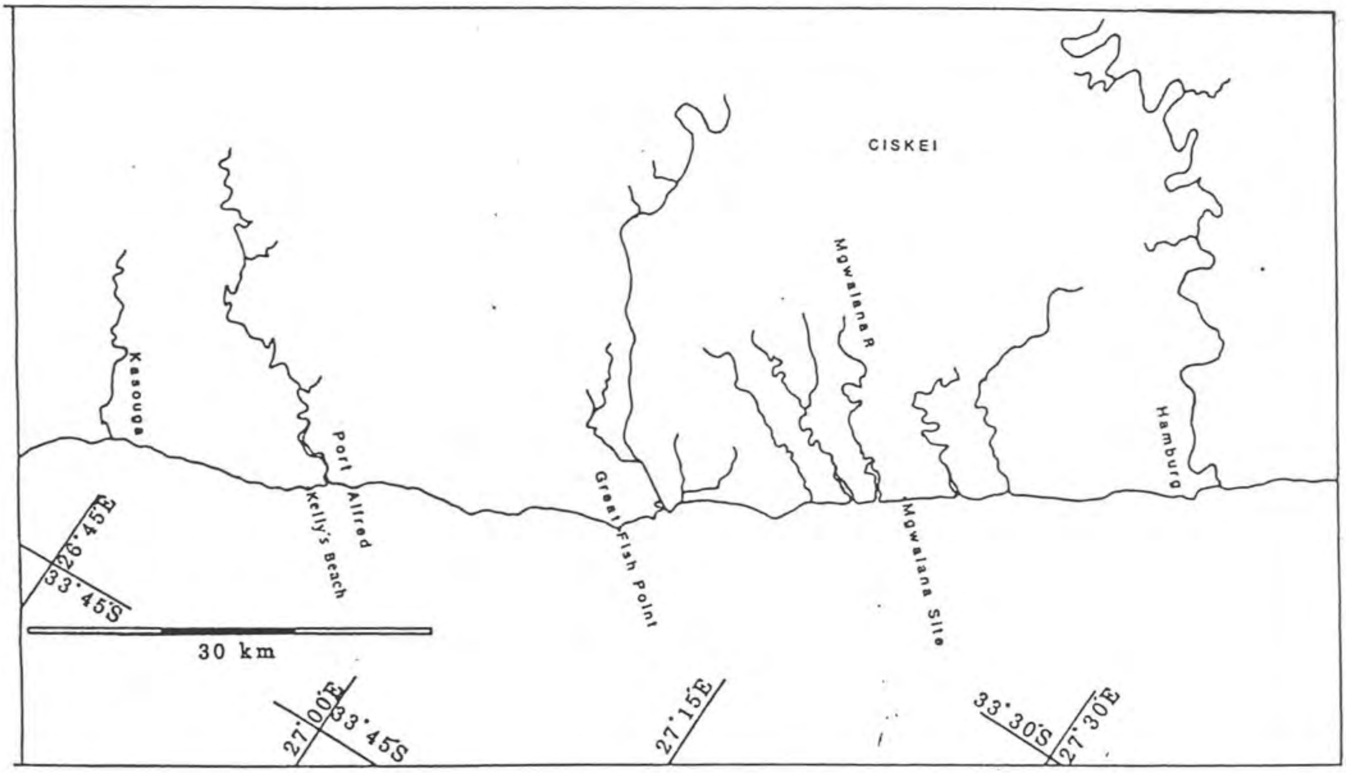

Figure 2.4 Location of the study sites at Kelly's Beach, Great Fish Point, and Mgwalana.

Figure 2.5 Kelly's Beach near Port Alfred showing Sharks Bay (SB), and the large red-bait covered pinnacles and ridges (P).

winds, the sampling site is exposed to the strong north-easterlies which blow frequently throughout the year. A series of ridges run parallel to each other and at an oblique angle to the shore (Figure 2.6). Beyond these ridges are several small pinnacles with a few larger isolated pinnacles in deeper water. Between the ridges are a series of gullies which are filled with small to medium sized boulders (20 - 45 cm in diameter). The substratum in deeper water around the pinnacles comprises large flat rocks (1 meter or more across) and large boulders (80 - 120 cm diameter). This site was prone to sand inundation during winter, with the bulk of sand moving into the gullies and shallow intertidal zone.

The gullies were inundated with water except at spring low tide, and at spring high depth approached 1 meter. The presence of small boulders made this an ideal habitat for small perlemoen which occurred cryptically with a multitude of encrusting sponges, *Lithothamnion* sp, *P. angulosus, O. trigrochis, Patiriella exigua, Actinia equina, D. gigas, R. f. frauenfeldi* and *N. grammatus.* The boulders themselves are coated with *Ralfsia expansa, Hildenbrandtia* spp., *Bryopsis* spp. *Codium lucasii capense, Peyssonnelia* sp., *Gelidium pristoides, Corallina* spp. and *Arthrocardia* sp. Dense mats of *Caulerpa filiformis* characterized the sandy patches (this was also evident in deeper water) and large colonies of *G. capensis* were prevalent as well.

The tips of the parallel ridges and pinnacles may be exposed at low tides, but their large surface area and abundance of crevices provided ideal attachment sites for medium sized and large perlemoen. The pinnacles themselves were covered by seaweeds such as *H. spicifera, P. corallorhiza, G. amansii, Codium* spp., *Corallina* spp., *Ulva* spp., *Amphiroa ephedraea* and *R. expansa.* The urchin *P. angulosus* was abundant together with *T. sarmaticus, P. chabrus, Oxystele* spp. *M. glacialis, P. cochlear, P. oculus, Siphonaria* spp. and *Octopus granulatus.* The barnacles *Tetraclita serrata* and *Octomeris angulosa* covered the exposed tips of reef wherever there was space.

Red bait covered the pinnacles in deeper water, and a few fronds of *E. biruncinata* had found purchase amongst these filter feeders. Some small perlemoen still seek refuge amongst the red bait pods or in small crevices and overhangs of the pinnacles. These pinnacles were submerged for most of the time except at spring low tide for a few hours. The deeper water (60 - 380 cm) was essentially adult perlemoen habitat. Large boulders and flat rocks provided the ideal surface for attachment of large animals, with very few juveniles being observed beneath the rocks. Some areas were almost devoid of any life except for a coating of *Lithothamnion* sp. giving the entire region a pinkish tinge. Few limpets were present, but mostly *P. chabrus, O. granulatus, M. glacialis, P. angulosa* and a variety of sponges and bryozoans shared this domain with *H. midae.* The dominant seaweeds were *H. spicifera, Hypnea rosea, P. corallorhiza, Halimeda cuneata, C.*

filiformis (in sandy areas), *Duthiophycus setchellii*, *Corallina* spp., *A. ephedraea*, *L. flexuosa*, *G. amansii*, *Spyridea cupressina*, *C. fimbriata* and *C. hornemannii*. Despite its protected position, this site could only be worked a couple of hours prior to low tide and for the first few hours of an incoming tide. The overall shallowness of the reef enhanced the surge and made diving difficult once the tides started pushing or if there was a large swell running.

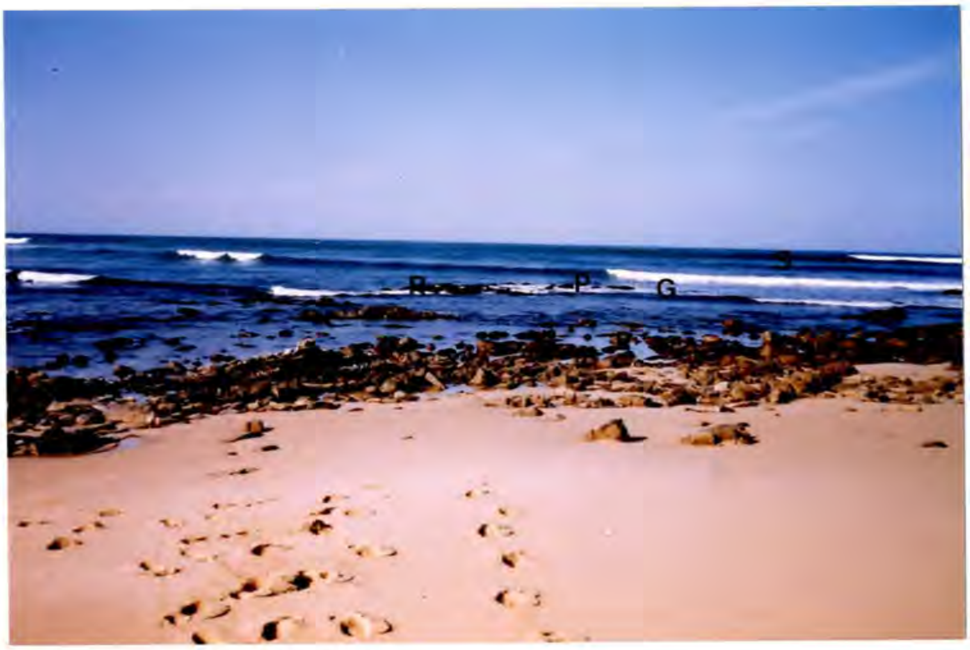

Figure 2.6 Great Fish Point, illustrating the ridges (R), small pinnacles (P), gullies (G) and deeper subtidal regions (S).

2.2.4 Mgwalana (Figure 2.4)

This site lies approximately 5 kilometres north east of the Mgwalana estuary in the Ciskei (33^{0} 24' 19" S, 27^{0} 17' 10" E). The reef was located at the site of an old wrecked trawler which ran aground, and is a landmark along the Fish River hiking trail. The site was very exposed and was buffeted by the prevailing east and west winds. The low relief nature of the reef also meant that it was exposed for a very short time at low water (Figure 2.7), and under normal sea conditions one could work in the perlemoen habitat for approximately an hour either side of low tide. The entire reef becomes submerged at high tide, and when stormy seas prevailed access onto the reef even at spring low tide was hazardous. A series of ridges project out perpendicular to the beach. They ran parallel to each other and were separated by gullies with sand covered bottoms. Subtidally at depths ranging from 40 - 150 cm there were numerous submerged ridges and pinnacles (Figure 2.8).

The sandy gullies had few boulders, none of which were inhabited by perlemoen. Dense mats of *C. filiformis, Enteromorpha* sp. and *Halimeda cuneata* characterized these areas as did aggregations of the Cape oyster *Crassostrea margaritacea.* Intertidal ridges were mostly covered by colonies of *G. capensis.* There were, however, dense sheets of *Chthamalus dentatus* higher up the shore while *O. angulosa, T. serrata, Siphonaria* sp. and *Patella* spp., along with seaweeds such as *Ulva* spp., *R. expansa, Porphyra capensis* and *Gracilaria beckeri* were present lower down. Subtidally the pinnacles were encased with *P. stolonifera* and the east coast kelp *E. biruncinata.* Another brown seaweed, *S. heterophyllum* was fairly abundant, with the rhodophytes *P. corallorhiza, H. rosea* and *H. spicifera* being well represented. Large perlemoen were concentrated on open rock faces, normally near the bases of subtidal pinnacles. Medium sized animals were found amongst red bait pods and in most available crevices. Small perlemoen were found in crevices and amongst the dense mats of kelp fronds in regions which were less exposed to wave action at low tide and where encrusting algae such as *R. expansa, Hildenbrandtia* spp. and *Lithothamnion* sp. were found. The perlemoen shared their habitat with *P. chabrus, T. sarmaticus, D. gigas, Oxystele* spp., *P. angulosus, O. granulatus, A. equina, B. reynaudi* and a host of bryozoans and encrusting sponges. The Mgwalana site was prone to sand deposition in the winter months, although the sandy gullies received the deposits while the ridges and pinnacles were unaffected.

Daily temperatures could not be measured at the sites themselves, and readings were obtained from the Port Elizabeth Municipality who take daily readings at Humewood beach. These were taken as an indication of annual temperature fluctuations at Cape Recife which was located only a few kilometres away. For the other three sites, daily readings taken at the marine laboratory of the Department of Ichthyology and Fisheries Science in Port Alfred were used as an indication of water temperatures on this section of coast. Mean annual surface temperatures appear in Figure 6.46 and 6.47 in Chapter 6 for Cape Recife and Port Alfred respectively. At all sites, wind induced upwellings occur in summer and early autumn resulting in sudden drops in water temperature. The coldest temperatures were recorded during a sampling trip in December 1991 when the temperature dropped to 11.2^{0} C at Great Fish Point and Mgwalana. Strong north-easterly winds combined with the spring and summer rains which cause the Keiskamma and Great Fish Rivers to come down in flood resulted in the prevalence of dirty water during these months. While the mean water temperature was colder in winter, the conditions for working were usually better, with cleaner water and less powerful winds prevailing.

Figure 2.7 The reef at Mgwalana at low spring tide. At high tide, very little of the reef remains visible.

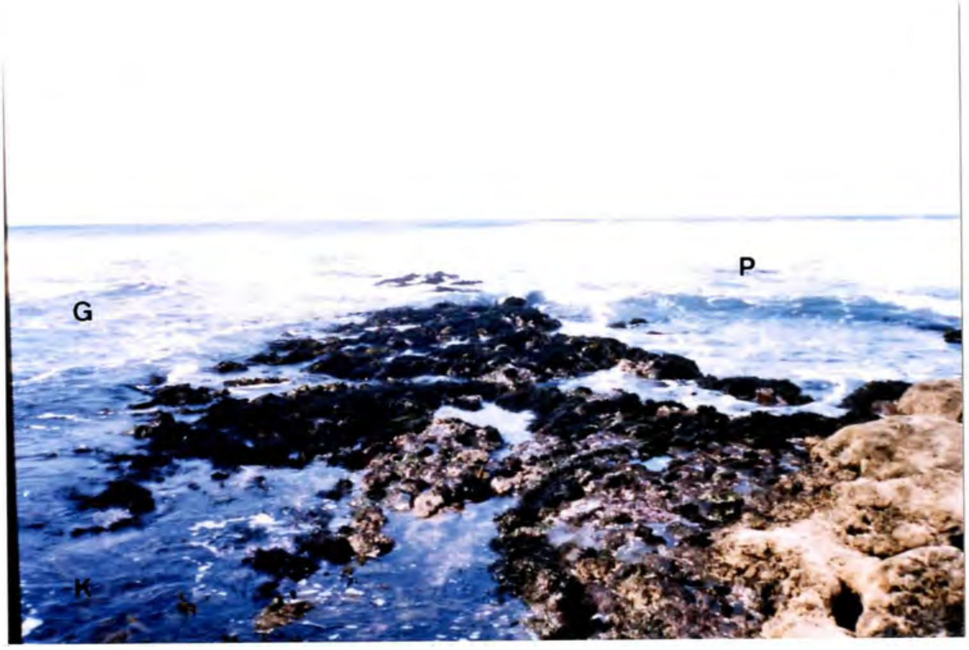

Figure 2.8 A close up of one of the ridges at Mgwalana at spring low tide illustrating the subtidal pinnacles (P), gullies with sand inundated subtrates (G), and dense kelp (*E. biruncinata*) beds (K) which are ideal juvenile *H. midae* refuge areas.

CHAPTER 3 POPULATION STRUCTURE AND HABITAT REQUIREMENTS

3.1 Introduction

The majority of abalone species are found in the shallow sublittoral areas of temperate and tropical seas (Hayashi 1980b). In addition to the preferred depth and temperature regimes, the general habitat requirements for abalone include a good supply of food, good water circulation to remove wastes and sediments, and the correct substrate for attachment and protection from predators (Tegner & Butler 1989). It is perhaps this last consideration which is the most important determining factor with respect to population structure. Juvenile and medium sized animals cannot rely on shell thickness for protection and so must rely on their habitat being inaccessible to predators. Conversely, the thick-shelled large animals are free from certain predators and can occupy more exposed sites. As a result, abalone of specific sizes live in very distinct microhabitats, with intermediate sized animals being found in areas common to both juveniles and large individuals (Shepherd 1973b; Tegner & Butler *op. cit.*). Fundamental to the management of natural stocks is an identification and understanding of the habitat requirements of newly settled larvae and juveniles (Shepherd & Turner 1985), as their ability to select the correct substrate is crucial to their subsequent survival. These specific habitat requirements for abalone of different sizes could be a major reason for the discontinuous distribution observed for haliotid species (e.g. Forster 1962; Newman 1969; Shepherd *op. cit.*). The other considerations of habitat suitability for *H. midae* are more than adequately fulfilled by the site at Great Fish Point. Food is in abundant supply, with ninety-three algal species being identified (see Chapter 5), the reef is extensive and diverse in terms of relief, and is situated in the rough water of the inshore surf zone which ensures adequate water movement even at extreme low spring tides.

Studies of population structures which make use of length-frequencies have been used to establish the health of a stock in relation to other stocks subject to fishing pressures (Schiel & Breen 1991). Care must be taken in interpreting such data, however, as there are a number of other feasible explanations for observed size-frequency distributions other than that of fishing mortality, *viz*:

(1) Differential growth rates among geographic regions resulting in lower maximum sizes where growth rates are faster and *vice versa*. Variation in growth can be very localized and dependant on habitat and food quality (Tegner 1989), quantity and availability (Breen 1980).

(2) Size distributions could reflect differential recruitment patterns, i.e. poor recruitment for a few years as a result of unsuccessful spawning or larval deaths could result in the absence of

prominent cohorts for that period and could be misinterpreted at a later stage as resulting from overfishing.

(3) Natural mortality resulting from bad weather, adverse water temperatures, high levels of predation or red tides (e.g. Horstman *et al.* 1991) could be higher in some regions, thereby causing discrepancies in size classes between sites.

Observed distributions could be explained by any one or all of the above factors, but only extensive sampling to give a long time series of data and experimentation (Schiel & Breen 1991) enables one to determine the cause of the observed pattern (e.g. Hayashi 1980b).

The phenomenon of recruitment variability is a central problem when trying to understand the dynamics of exploited abalone populations (Shepherd & Godoy 1989). With respect to this, determination of population densities and standing stock levels have important implications in the field of fisheries biology when present levels have to be used to predict future population densities resulting from potential recruitment (Peck & Culley 1990). Sustained productivity in wild stocks on which fisheries are dependant is largely dependant on the natural recruitment of juveniles (Prince *et al.* 1987; Brown 1991). Incidences of recruitment overfishing which have resulted in the subsequent collapse of abalone fisheries have been documented (e.g. Breen & Adkins 1980b; Breen 1986; Sluczanowski 1984). Extensive or restricted larval dispersal will determine whether or not an adult stock is dependant on larvae from a local or distant origin for recruitment. From a management perspective, biological, geographical and hydrological influences would all need to be assessed in order to determine a stock-recruitment relationship for local populations (Day & Leorke 1986; Brown *op. cit.*).

The aims of this study were to identify the various habitats occupied by perlemoen and to assess the population structure within those habitats. Based on the species composition of fauna and flora within each habitat along with the reef structure the observed patterns of distribution of *H. midae* were explained by taking feeding habits, movement and predator/prey interactions into account. Absolute densities could not be worked out for each habitat, and no attempt was made to estimate probable recruitment levels based on the parent stock size. However, relative densities of cryptic and exposed perlemoen within and between habitat types were examined.

3.2 Materials and Methods

This part of the study was confined to the population at the Great Fish Point site.

3.2.1 Habitat types

Five potential habitats for *H. midae* were identified based upon the degree of water movement, water depth, types of seaweeds and their abundance and the topography of the reef (Figure 3.1). The five regions were called shallow intertidal, exposed pinnacles, shallow gullies, subtidal *Caulerpa* beds, and deep subtidal. The estimates for abundance of algae were taken from the quadrat samples used for the dietary study (see Chapter 5) as well as additional quadrats of 0.25 m^2 each in the regions not sampled during the feeding study. The shallow intertidal and exposed pinnacles together with shallow gullies were the areas concerned in the dietary study where 23 and 27 quadrats had been sampled respectively. An additional 15 and 10 quadrats were sampled in the *Caulerpa* beds and deep subtidal regions respectively, where the five most abundant seaweeds, by visual estimation of relative percentage cover, were recorded. Measures of faunal densities apart from *H. midae* were not determined quantitatively and animals which share the various habitats with *H. midae* were identified from visual observations throughout the period of this project.

3.2.2 Population structure

The five habitat types were sampled for perlemoen using ten meter linear transects. Weighted polypropylene lines were used in all the habitats except for the exposed pinnacles where strong wave action dictated the use of heavy galvanized steel chain. Transecting was performed over two days with a total of 35 being completed (Table 3.1). Fewer transects were completed on the second day owing to strong south-westerly winds which had prevailed the previous day and night and which were persistent still gusting the following day. The resultant increase in the swell allowed only limited access to the deep water and exposed pinnacles.

Table 3.1 A summary of the transects performed at Great Fish Point on the 24th and 25th of November 1992.

Habitat type	Number of 10 m transects	
	24/11/92	25/11/92
Shallow intertidal	4	4
Exposed pinnacles	6	1
Shallow gullies	2	-
Subtidal *Caulerpa* beds	6	-
Deep subtidal	10	2
Totals	28	7

Figure 3.1 The site at Great Fish Point illustrating the five potential habitats for *H. midae*, *viz*: shallow intertidal (I), exposed pinnacles (P), shallow gullies (G), *Caulerpa* beds (C), and deep subtidal (S).

Due to the paucity of perlemoen recorded in the *Caulerpa* beds on the first day this habitat was not transected on the second day. One less diver on the second day also precluded the transecting of the shallow gullies again. Divers using SCUBA gear performed the transecting in all the areas except the shallow intertidal where snorkelling gear sufficed in the prevailing calmer conditions. A meter wide corridor down one side of the transect line was searched for exposed (open rock face) and cryptic (overhangs, crevices or beneath boulders) perlemoen which were measured to the nearest 5 mm and recorded on an underwater slate. The line was moved randomly to other sites within the same habitat upon completion of each transect. Transects from the two days were pooled for each habitat type and analyzed using size frequency plots.

3.3 Results

3.3.1 Habitat description

Shallow intertidal

This area was submerged at all times with the exception of a few large rocks and the *G. capensis* colonies which were exposed at low spring tides. The depth ranged from about 15 cm at low tide to 80 cm at high tides but varied considerably when stormy weather and strong seas prevailed. The weather also influenced the degree of water movement, which was normally calm at low water and increased as the tide started to push, until at high tide, there was a considerable amount of surge along the bottom.

The substratum was dominated by small boulders of approximately 15 - 25 cm in diameter which were securely embedded in a sandy bottom. Interspersed among these boulders were large flat shelves of rock deeply seated in the sand, and large rugged rocks some of which were smothered by *Gunnarea* colonies. There were patches of sand devoid of any hard substratum over which transects were not performed. The pink encrusting coralline alga *Lithothamnion* dominated the underside of boulders but was absent from topside surfaces which were dominated by the chlorphytes *Ulva* spp., *Caulerpa racemosa, Codium fragile capense* and *Codium stephensiae*, the soft encrusting phaeophyte *Ralfsia expansa* and the rhodophytes *G. pristoides, Corallina* sp., *Arthrocardia carinata, P. corallorhiza* and *L. natalensis*. The sand covered areas were carpeted with *C. filiformis* and patches of *Codium platylobium*. Drift seaweeds were common at the sand boulder interface and in the water column. The dominant faunal life occurred beneath the boulders and in sheltered crevices and overhangs of the larger rocks and comprised *P. angulosus, O. trigrochis, P. exigua, D. gigas, N. grammatus, R. f. frauenfeldi, A. equina, M. glacialis* and *G. rosea*.

Exposed pinnacles

The tops of these pinnacles were exposed at most low tides, but were periodically inundated by waves at this time. They were covered at high tides and depth varied from exposed to 50 cm at high water. Even at low tide, the constant breaking of waves ensured considerable water motion. At all other times when the pinnacles were covered the surge was very strong.

The pinnacles comprised large areas of open rock face with an abundance of overhangs, holes and crevices, while small to medium sized boulders (25 - 45 cm in diameter) were scattered at their base. Unlike the intertidal region, *Lithothamnion* was found beneath the boulders and on exposed surfaces where it was obscured by other branching macroalgal species. The topsides of boulders were clear except for *Lithothamnion, R. expansa* and areas which appear to have been grazed bare, most likely by the urchin *P. angulosus* and the alikreukel *T. sarmaticus* both of which abounded in the cryptic areas of this habitat. Other macroalgae which were common included *H. spicifera, P. corallorhiza, G. amansii, Corallina sp., A. ephedraea* and *Ulva* spp. The exposed sites of the reef at low tides were sprinkled with the barnacles *T. serrata* and *O. angulosa* and several *Siphonaria* limpet species, with large numbers of the winkles *Oxystele* spp. being found in all cryptic niches. Two potential predators of *H. midae*, namely *P. chabrus* and *M. glacialis* were encountered in the crevices, caves and boulder regions.

Shallow gullies

Situated in close proximity to the exposed pinnacles, gullies were the deeper regions which separated the pinnacle ridges from one another. Depth varied from approximately 45 cm at low tide to close to a meter at high tide. They were, therefore submerged at all times and water movement was moderate except at high water when the bottom surge became stronger.

Few small boulders were found, most measure between 45 and 60 cm in diameter and were embedded in a sand substratum over bedrock. In relation to the pinnacle regions, there were fewer cryptic niches available to organisms, and open rock faces prevailed. A great variety of seaweeds were found in this region, e.g. *H. spicifera, H. rosea, P. corallorhiza, G. amansii, H. cuneata, Duthiophycus setchellii, Corallina sp. A. ephedraea, L. flexuosa* and *C. hornemannii.* The same potential predators found in the exposed pinnacle habitat were encountered here together with *O. vulgaris* and the predatory dog whelk *Thais capensis*. The shallow gullies were cohabited by a host of other animals, the most abundant of which were *N. grammatus, B. reynaudi, D. gigas, Chiton tulipa, T. sarmaticus, P. angulosus, Oxystele* spp. and a mixture of bryozoans and encrusting sponges.

Subtidal *Caulerpa* beds

Depth in this habitat which was submerged at all times varied from about 40 cm at low water to 120 cm at high spring tides. Movement of water was constant with the force behind it being dependant on the tidal stage and the prevailing sea conditions.

Large submerged ridges with open but roughly contoured rock faces were patchily spaced throughout the region as were a few medium sized boulders. Large areas of the sea bed were covered with very small boulders (2 cm to 10 cm in diameter). The remainder of the region comprised patches of sand carpeted with *C. filiformis*, which was also the most abundant alga in this habitat. The ridges comprised many crevices and holes many of which were home to *O. vulgaris*. Pink encrusting corallines cover the ridges and medium boulders, but the small boulders were virtually denuded of life. Other floral species included *Ulva* spp., *H. spicifera, H. rosea, P. corallorhiza, Corallina* sp. *A. ephedraea, Bryopsis* sp. and *Sarcocornia capensis*. The urchin *P. angulosus*, rock crab *P. chabrus*, chitons *D. gigas* and *C. tulipa*, winkles *Oxystele* spp. and anemones *A. equina* and *B. reynaudi* were the fauna commonly encountered in the *Caulerpa* bed habitat.

Deep subtidal

As the name suggests this was the deepest habitat sampled with depth ranging from 2.3 meters at low tide to about 3.8 meters at high spring tide. The surge was always quite considerable and could become very rough when a large swell was running.

Large flat rocks covered the bottom which provided large areas of smooth open faces relatively free from seaweed growth. Small rocks and larger boulders were interspersed with sand amongst the flat rocky substratum. Encrustation by *Lithothamnion* is extensive and sometimes total on a few rocks. Red seaweeds such as *H. spicifera, H. rosea, G. amansii, P. corallorhiza, S. cupressina, C. fimbriata, Botryocarpa prolifera* and *C. hornemannii* were the most dominant types. Encrusting sponges and bryozoans shared this habitat along with large specimens of *P. oculus*. *Plagusia chabrus, O. vulgaris, M. glacialis, P. angulosus, T. sarmaticus, T. capensis* and *D. gigas* also co-inhabited this region with *H. midae*.

3.3.2 Population structure

Shallow intertidal

There was a complete absence of exposed perlemoen from the 120 animals measured in the 80 m^2 area covered in this habitat (Figure 3.2). The largest individual was estimated at 110 mm shell length with the smallest one measuring only 5 mm in length. The majority of animals encountered were between 20 and 40 mm long, and no perlemoen between 80 and 100 mm shell length were recorded.

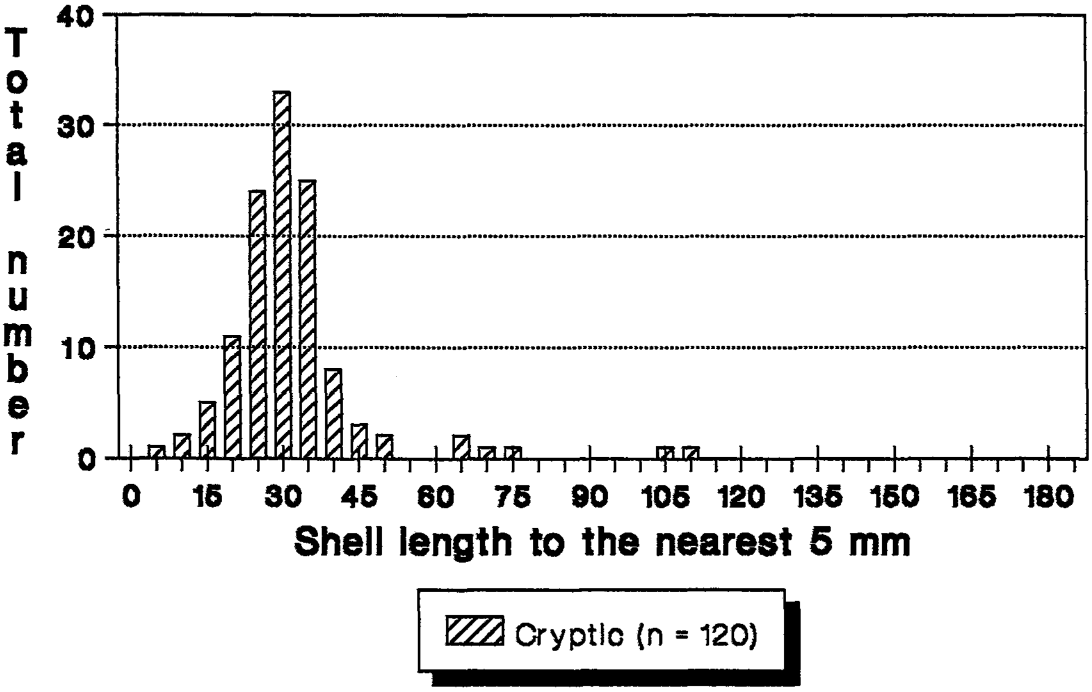

Figure 3.2 Size distribution of *H. midae* sampled by visual assessment in the shallow intertidal habitat at Great Fish Point in November 1992.

Exposed pinnacles

The greatest range of perlemoen sizes was encountered in this habitat (Figure 3.3). A total area of 70 m^2 was transected and 114 exposed and 248 cryptic animals were recorded. All sizes below 50 mm in length were cryptic while some of the larger animals measuring as much as 120 and 130 mm were also found in crevices. The smallest size found in this habitat was 5 mm. The largest individuals of 135 and 140 mm were found exclusively in exposed positions.

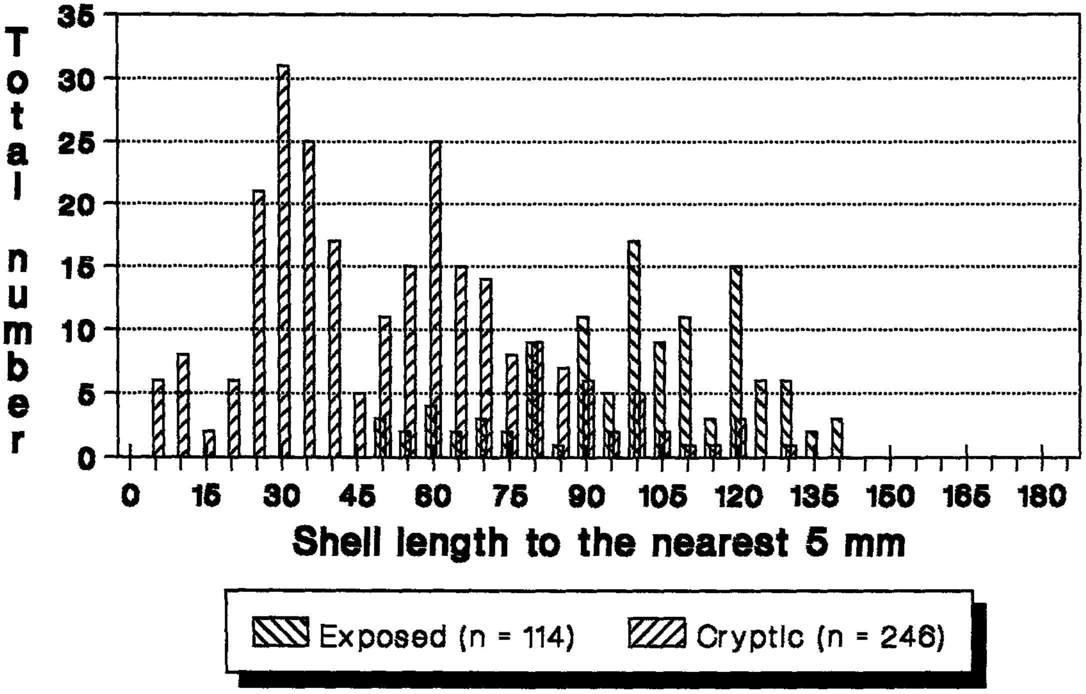

Figure 3.3 Size distribution of *H. midae* sampled by visual assessment in the exposed pinnacle habitat at Great Fish Point in November 1992.

Shallow gullies

Forty perlemoen comprising 13 cryptic and 27 exposed animals were recorded in the 20 m^2 area sampled (Figure 3.4) ranging in size from 35 mm to 140 mm shell length. Between 40 and 80 mm there appeared to an overlap in microhabitat utilization. All animals > 80 mm were encountered on exposed rock faces while those < 40 mm were cryptic.

Subtidal *Caulerpa* beds

This habitat was found to be unsuitable to the perlemoen *H. midae* as only 3 animals were encountered in 6 transects covering an area of 60 m^2 on the first day. Two cryptic and one exposed individual measuring 40, 50 and 140 mm respectively were sampled.

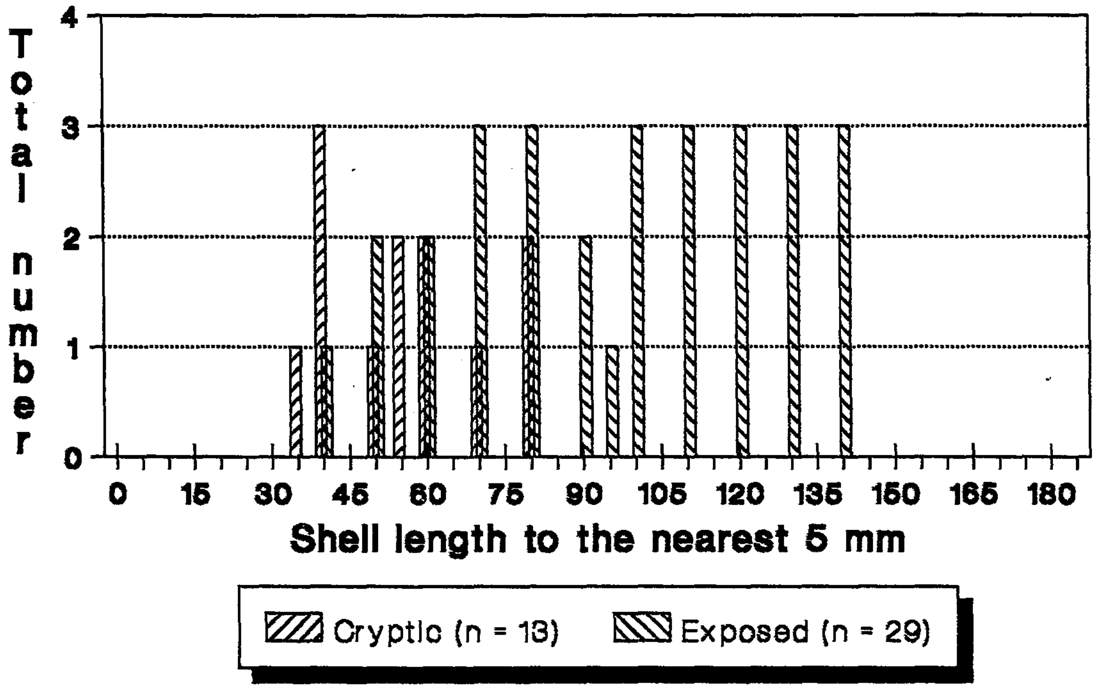

Figure 3.4 Size distribution of *H. midae* sampled by visual assessment in the shallow gully habitat at Great Fish Point in November 1992.

Deep subtidal

Relatively few cryptic perlemoen were measured in this habitat, only 26 compared with the 69 exposed individuals counted from 12 transects covering 120 m^2 (Figure 3.5). The overlap of sizes utilizing both niches was between 80 and 120 mm shell length. All perlemoen smaller than 80 mm were cryptic and those larger than 120 mm were exposed. The smallest individuals found cryptically were 20 mm while a few around 160 mm and a large animal estimated close to 180 mm were measured in the open.

A total of 618 perlemoen were measured from the 35 transects covering a total area of 350 m^2. Considering all habitat types combined (Figure 3.6) it was clear that animals smaller than 45 mm and larger than 130 mm were exclusively cryptic and exposed respectively.
Between these two extremes there was a certain degree of overlap, although perlemoen up to 75 mm were predominantly cryptic, while those larger than 95 mm were more common in the open. Similar numbers of cryptic and exposed animals were found between 75 mm and 95 mm. This appeared to be the size range at which the transition from being predominantly cryptic to being predominantly exposed took place.

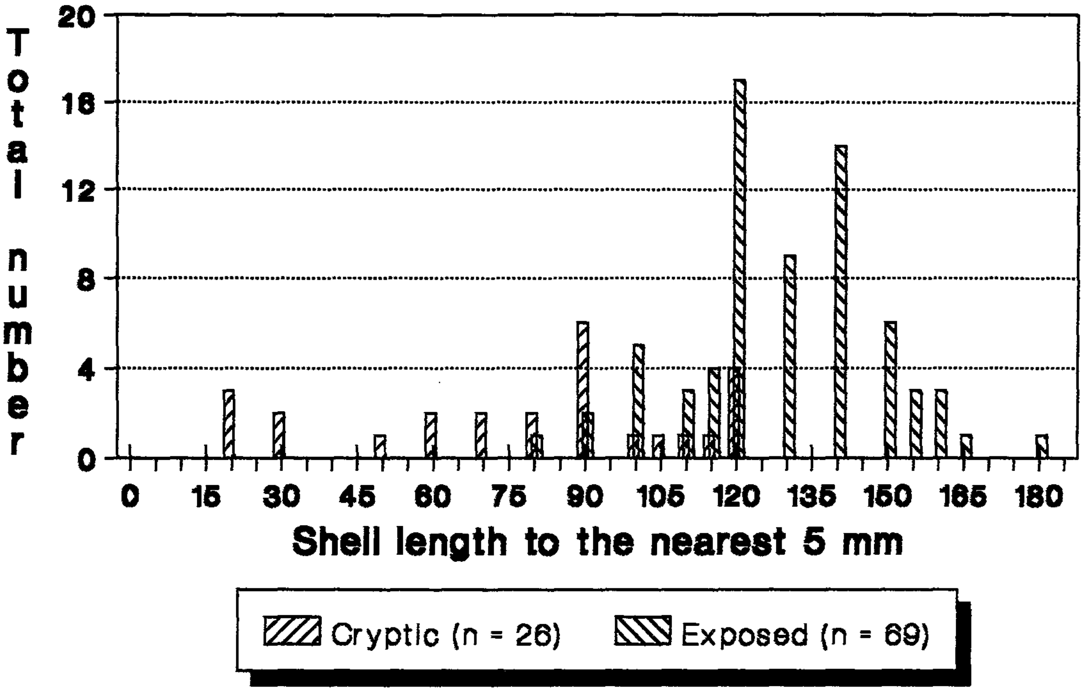

Figure 3.5 Size distribution of *H. midae* sampled by visual assessment in the deep subtidal habitat at Great Fish Point in November 1992.

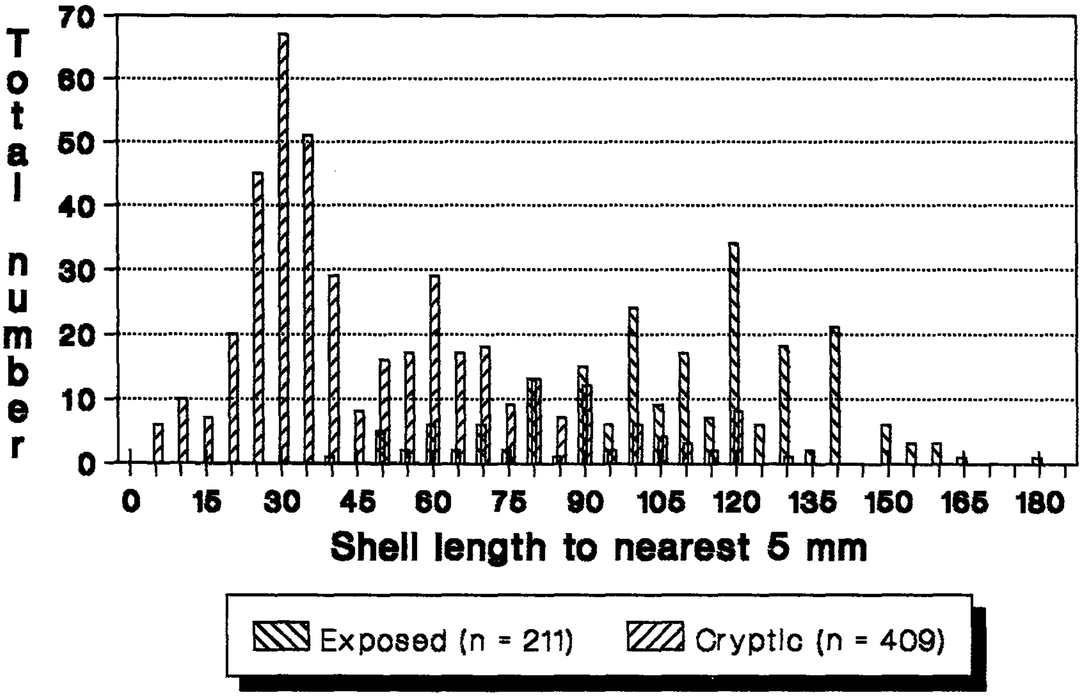

Figure 3.6 Size distribution of *H. midae* sampled by visual assessment in all habitats at Great Fish Point in November 1992.

Figure 3.7 shows the result of a transect performed in the shallow gully habitat. The same transect was sampled twice, first as described in the methodology with perlemoen being measured *in situ*, after which the same diver cleared the 10 m^2 area and measured the animals ashore. The discrepancy between the two counts in terms of size numbers was considerable, providing a slightly different picture of the size. This demonstrates that while the method used was relatively quick allowing the maximum number of transects possible to be performed in the short time available, cleared transects should ultimately be performed for greater accuracy and are a definite prerequisite for estimates of absolute densities or standing stock. Prince & Ford (1985) and McShane & Smith (1988) stated that searching was an inaccurate method of measuring abundance of abalone, and searching is diver dependant often resulting in underestimates of smaller cryptic (< 20mm) abalone. It would seem that removal sampling along transects by competent divers is the only sure method of obtaining accurate data on abundance and population structure.

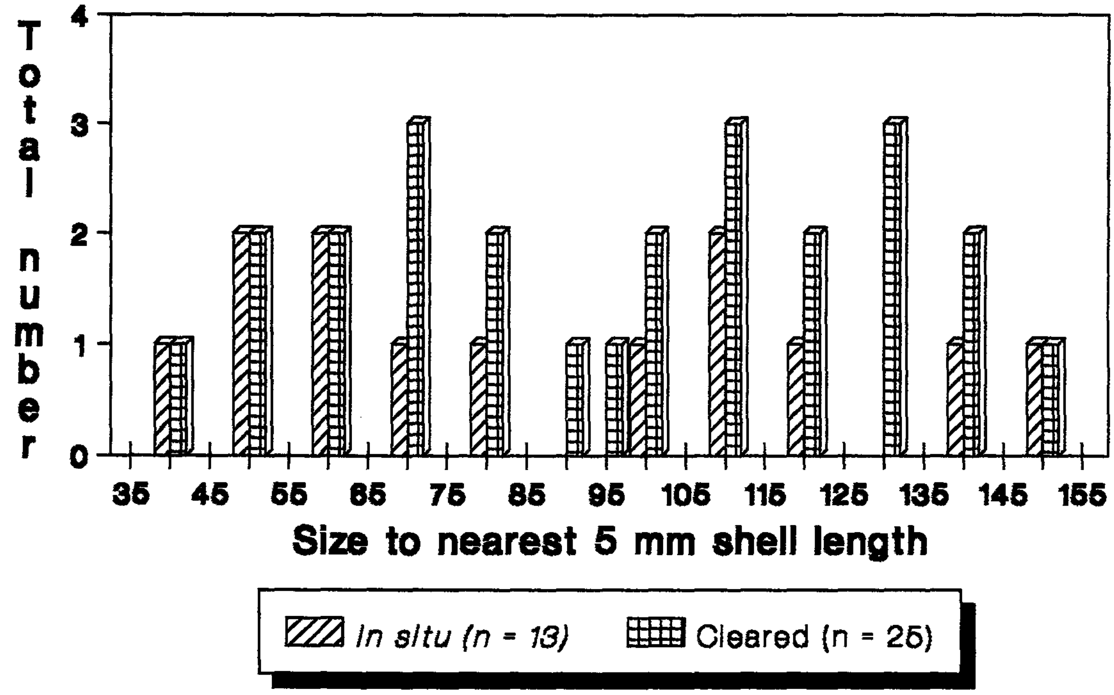

Figure 3.7 A comparison between visual assessment and clearance of a 10 m^2 transect in the shallow gully habitat at Great Fish Point in November 1992.

The relative densities of *H. midae* within the various habitat types is presented in Table 3.2. The dominance of cryptic or exposed animals was dependant on the habitat and changed markedly between habitats as the substrate in deeper water provided more open space for adults and fewer

fewer boulders and crevices for sheltering smaller individuals.

Table 3.2 Relative densities of exposed and cryptic *H. midae* determined from linear transects in five habitat types at Great Fish Point on the 24th and 25th November 1992.

Habitat type	Densities (number of animals / m^2)		
	Cryptic	Exposed	Total
Shallow intertidal	1.5	-	1.5
Exposed pinnacles	3.51	1.63	5.14
Shallow gullies	0.65	1.35	2.0
Subtidal *Caulerpa* beds	0.033	0.017	0.05
Deep subtidal	0.21	0.58	0.79

3.4 Discussion

In the shallow intertidal area the only cryptic niche available was beneath boulders, whereas in the other four habitat types cryptic niches were found beneath boulders, in holes, caves or crevices. The difficulty encountered in working in the surf zone advocated that all cryptic habitats be grouped as one to facilitate easier recording underwater by divers. With a few exceptions, however, visual observations from all sample sites throughout the duration of this study showed that small animals (0 - 45 mm) were most commonly found under boulders. Medium sized animals (50 - 90) were cave and crevice dwellers while large individuals (> 100 mm) were found in exposed areas of the reef. It was also observed that while medium sized animals were sometimes found beneath boulders, and large animals in crevices, no small individuals were ever encountered anywhere except beneath rocks. For the remainder of this discussion the terms small, medium sized and large will correspond to the above mentioned size classes.

The lack of perlemoen in the *Caulerpa* beds could be explained by a combination of several factors relating to substratum, food and predators, *viz*:

(1) Although *Lithothamnion* was abundant, and provided potentially large settlement areas for larvae, there were few boulders which could have provided suitable concealment for the small animals. Crevices were abundant, but are not the preferred habitat of the smaller size classes. Smaller boulders were also prone to being periodically turned over by wave action and would therefore not be suitable refuges for small animals (e.g. Sinclair 1963).

(2) The few juveniles which may have found refuge would have been subjected to extreme predation pressures from the many crabs and octopus in the area.

(3) The small areas of available open rock face were rugged and as such do not provide the smooth planar surfaces which adult perlemoen require for attachment (Sinclair *op. cit.*; Tegner & Butler 1989).

(4) Crevices and holes which are ideal for medium sized animals were plentiful amongst the rugged rocks, however, the absence of suitable niches for small and large animals precluded them from being present as well.

The shallow intertidal region provided an ideal habitat for small animals which were afforded shelter beneath the many medium and large sized boulders whose undersurfaces were covered by *Lithothamnion.* Crustose coralline algae such as *Lithothamnion* provide the cue for settlement in abalone and other marine invertebrates such as the chiton *Tonicella lineata* (Barnes & Gonor 1973), the sea stars *Stichaster australis* and *Coscinasterias calamaria* (Barker 1977) and *Patella cochlear* (Branch 1975). In addition, this crustose algae acts as a substratum for diatoms and bacteria which form the basic diet of sub-5 mm abalone. Although some medium sized animals were found along the transects, they were few and only a single large animal (105 mm) was encountered. Although medium sized perlemoen were found cryptically in the other habitats they were almost exclusively occupying holes or crevices. The few crevices which were present on the larger rocks were exposed at low tides, and while *H. spadicea* which occupies exposed crevices are able to cope with the threat of desiccation for short periods of time (Muller 1984), this would not appear to be true for *H. midae* as none were observed to occupy these exposed positions. Large open rock faces were not common and were mostly covered by sand which precluded them from being inhabited by *H. midae*. Algae such as *H. spicifera, H. rosea* and *P. corallorhiza* were not abundant in this shallow habitat, and as they featured prominently in the diets of larger animals (see Chapter 5), their scarcity could in part explain the absence of the larger size classes of *H. midae.*

The diversity of sizes of *H. midae* in the exposed pinnacle habitat was attributed to the vast array of available microhabitats. Boulders were available for sheltering small animals, crevices and holes for harbouring medium sized animals and smooth open rock faces for larger individuals. The availability of space for all sizes also accounted for the greatest densities of exposed and cryptic animals out of all the habitats. Many surfaces contained *Lithothamnion* and were available as settlement sites, and the preferred food types of small animals *R. expansa* and *Corallina sp.*

could account for the high incidence of the small size classes. Drift algae was always present, and the high energy wave action ensured that attached algae were constantly fragmented. The preferred algal prey items of the larger animals were dominant in the attached form in this habitat as well. Urchins were plentiful but bare areas on rock surfaces which are an indication of their extensive grazing activity were virtually absent. It would appear that the rich supply of encrusting and branching macroalgae was sufficient to supply both *H. midae* and *P. angulosus* in this habitat. The alikreukel was also abundant, and there appeared to be a sufficient supply of its favoured food, *Corallina* sp. (Lombard 1977), to support them and the small *H. midae* as well.

In the gully region exposed animals were dominant. The predominance of large open surfaces as opposed to cryptic niches made this habitat better suited to the larger emergent perlemoen. Available cryptic niches were occupied by medium sized animals but the smaller animals were noticeably absent. This was attributed to the lack of appropriate settlement surfaces and the paucity of boulders in this habitat.

The deep subtidal area was even less hospitable to the small and medium sized animals. The large rocks had few crevices or overhangs to shelter medium sized animals and boulders were few and scattered. *Lithothamnion* was abundant, and larval settlement did take place because small animals were found under most of the available boulders. The general lack of suitable cryptic niches for juveniles and medium sized animals meant that animals either migrated from the area soon after settling or that mortality due to predation was high in theses smaller size classes. As a result this prime adult habitat was not overcrowded, and densities were low. One transect produced only a single emergent 165 mm SL animal and diver observations indicated that large perlemoen did not occupy all available surfaces, but instead were encountered in small isolated groups. The deep water supported the largest animals encountered, including a specimen of 180 mm SL. The abundance of red algae was well suited to the dietary preference of larger animals, and drift algae was always present.

The study showed, that with a small degree of overlap, small and large perlemoen live in very distinct microhabitats. The observed change in habitat from beneath rocks and boulders for small animals, to cryptic habitats such as caves and crevices for medium sizes and finally to exposed rock faces for large animals appeared to be a result of changes in diet with size and/or escapement from the pressures of predation (e.g. Sloan & Breen 1988). Generally speaking most animals are under the greatest threat of predation when they are small and so those which grow quickly are less likely to die (Day & Leorke 1986). Sedentary organisms such as abalone which are slow growing have instead evolved mechanisms of avoidance such as the adoption of a cryptic habitat during the crucial early years (Shepherd 1973b; Cooper *et al.* 1976). The dietary study in Chapter 5 supported these observations, showing that there was a change over in food eaten once animals had outgrown the sub-boulder stages. However, medium and large sized animals had the same feeding habits, most likely as a result of the large degree of niche overlap. So although both feeding and predation restraints may confine the smaller sizes to their sub-boulder existence, with predation probably being the more important of the two, it is strictly predation pressures which restrict medium sized animals to their predominantly crevice microhabitat.

Predators such as octopus and crabs were rarely encountered in the shallow boulder habitat, but overturned boulders were quickly set upon by roving blacktail *Diplodus sargus capensis* and zebra *Diplodus cervinus hottentotus*, two common inshore sparid fishes which have been recorded as predators of *H. spadicea* (Muller 1984), and which were quick to accept offerings of small *H. midae*. The sea star *M. glacialis* and the dog whelk *Thais capensis* were present in this region and were a threat to the sub-boulder juveniles. To avoid predation, small animals restrict foraging movements on the surface of boulders to the nighttime, when most of these predators were inactive.

The presence of *H. midae* wherever urchins were found indicated that the abalone were dependant on the urchins for survival. This has been observed for other haliotid species, and it has been determined that urchins benefit abalone in a number of ways. The method adopted by urchins when they feed ensures that patches of coralline algae such as the encrusting *Lithothamnion sp.* are maintained free from overgrowth (Breitburg 1984). In addition to a number of other cues such as mucous trails of conspecifics (Momma 1973; Seki & Kan-no 1981a), larval abalone are induced to settle on such patches of encrusting corallines (Saito 1981; McShane & Smith 1988) which also act as a source of nutrition by supplying benthic diatoms and bacteria to recently metamorphosized animals (Shepherd 1973b; Morse & Morse 1984; Shepherd & Turner 1985).

To avoid predators which are capable of accessing sub-boulder spaces, young of the year *H. midae* along with small urchins occupy the spaces beneath the spine canopies of adult urchins which shared the boulder microhabitat during the day (Figure 3.8). This phenomenon is common to juvenile perlemoen around the world (Tegner & Butler 1989) as a means of predator avoidance during the day, although Day (unpublished data, in Tegner & Butler *op. cit.*) found that urchins were avoided by juvenile *H. rufescens* on reefs near Santa Barbara California, and Breen (1980) reported that juvenile northern abalone *H. kamtschatkana* were found on smooth bedrock or boulders in deep water away from urchins. As small abalone grow and move onto a diet of macroalgae (see Chapter 5), they become more dependant on drift algae which may accumulate at the sand/rock interface in the boulder habitat occupied by juveniles (Tegner & Butler *op. cit.*), or which may become ensnared in the spines of urchins thereby making them more accessible. Urchins are still used for protection by medium sized crevice dwelling abalone. These animals are too large to hide beneath the spine canopy and are instead surrounded by several urchins when they are at rest during the day. Minimal protection is afforded at night when both *H. midae* and *P. angulosus* are active away from their daytime cryptic habitats, but now the nocturnal inactivity of most predators provides the safety canopy for both species.

Figure 3.8 Two juvenile *H. midae* (J) beneath a boulder in the shallow intertidal habitat together with adult and juvenile urchins (U) and the encrusting coralline alga *Lithothamnion* sp. (L).

Predators such as the dog whelk, octopus, crabs and starfish were numerous in the pinnacle, gully and deep water habitats. Medium sized *H. midae* are no longer prone to predation by crabs, as they are difficult to dislodge. They have also been frequently observed sharing crevices with crabs, and shells from medium sized animals were not found with the rough chipped edges which indicates predation by crabs. The threat from whelks and octopus was real though as they are capable of drilling through shell, while digestive juices from sea stars may weaken the shell or any exposed body parts. Octopus caves or holes were easily identified by the pile of shells left outside the lair. When approached the octopus used these shells attached to their suckers as shields to seal off the entrances to their lairs (personal observation). It was noted that large crevices and ledges generally housed few perlemoen, urchins or alikreukels, presumably because they could still be accessed by predators. All available cryptic niches were occupied in many areas which accounted for the exposed medium sized animals in sites which were overcrowded. Large areas of *Lithothamnion* in the deeper water most likely induces high settlement rates, but the paucity of suitable juvenile refuges must result in high post larval mortalities. Large animals were almost exclusively emergent and by virtue of a very thick shell have little to fear from predators apart from man.

Abalone are capable of slow movement and most workers concur that it is minimal and confined to feeding activities (Stephenson 1924; Ino 1952; Cox 1962; Sinclair 1963; Shepherd 1975; Mottet 1978; Shepherd & Godoy 1989). Some studies have, however, contradictory findings which indicate that certain abalone species are capable of undertaking extensive migratory journeys (e.g. Newman 1966; Koike *et al.* 1972). This study has shown that in order to survive on a daily basis even limited movement is an asset. Small *H. midae* from the intertidal area have to migrate to more suitable habitats when they outgrow their protective boulder niche, and the same applies to medium sized animals which undergo the transition from cryptic to exposed. Once exposed, the large perlemoen move very little as the presence of a scar or homesite on the rock surface beneath them suggests. Migration between microhabitats is a common occurrence in abalone. The ormer *H. tuberculata* settles in shallow water and moves to deeper localities with age (Peck & Culley 1990). Movement in *H. laevigata* varied according to the availability of suitable microhabitats, with cryptic animals moving about when crevices were not available until suitable shelter could be found. Conversely, the presence of medium-sized *H. midae* in emergent positions seems to suggest that they do not move away from their immediate environment when all available cryptic spaces are occupied by conspecifics, urchins and alikreukels.

A high degree of microhabitat specificity was demonstrated by five sympatric species of southern Australian abalone which occupied the same habitat but which exhibited very little microhabitat overlap (Shepherd 1973b).

This study showed that *Haliotis midae* of various sizes had definite requirements with regard to habitat. While size may have dictated the array of microhabitats available to them, it was ultimately predators which confined them to the microhabitat in which they were found. Food availability may have played a minor role, perhaps more so during the transitional phase from the boulder stage to the caves and crevice stages, but it was more likely that once confined to a certain microhabitat type they were restricted by the activity of their predators to nocturnal feeding excursions, when they fed on algae in their immediate environment, favouring those which were most abundant. Larvae metamorphosized and settled on suitable substratums and then migrated to crevices and finally exposed rock faces as they grew, a situation which occurred for *H. midae* in the South-Western Cape as well (Newman 1968). The most productive areas of the reef were the sites which provided enough microhabitats for all size classes such as was found on the exposed pinnacles.

CHAPTER 4 AGE AND GROWTH

4.1 Introduction

Mathematical models used in the formulation of management strategies rely heavily on the accurate determination of age and growth data to provide a basic framework for the assessment of the status of exploited stocks (Ricker 1975), for proposing regulatory measures (Butterworth *et al.* 1989) and which will ensure sustainable utilization of those stocks (Poore 1972c). In fisheries management growth rates are important for yield-per-recruit and egg-per-recruit models, and they provide information on the time lag between spawning and reproductive recruitment (Day & Fleming 1992). Growth rate is also a vitally important consideration for mariculture as costs are drastically reduced by fast growth (Day & Fleming *op. cit*). It is no surprise then that growth and age determination are the most extensively studied aspects of haliotid biology (Sainsbury 1982).

Growth starts immediately after fertilisation, and although the topic of larval development has not been dealt with in this study, there has been considerable work done on the subject. As early as 1886 and 1889, Bouton (in Muller 1984) recorded some rather fragmented data, mainly due to the difficulty experienced in inducing artificial fertilisation, on the development of haliotids. Murayama (1935) managed to induce spawning in *Haliotis gigantea* and described in detail the developmental stages and metamorphosis of reared larvae. Once techniques for inducing spawning in captive abalone became available, further studies of abalone propagation and larval development became possible, e.g. Ino (1952) and Oba (1964). Once the development of early stages had been studied and described, the effects of various environmental parameters on growth could be determined, e.g. the effect of temperature on larval development rate and juvenile growth rate and survival (Leighton 1972; 1974). More recently, studies have investigated the induction of settlement and metamorphosis of larvae due to various chemical cues arising from crustose algae, mucous trails of conspecifics and food types (Seki & Kan-no 1981a,b; Barlow 1990; Searcy-Bernal *et al.* 1992), and post-settlement survival (Slattery 1992).

Determination of age and growth rates in abalone after settlement has received the most attention, and there are a variety of methods available to the biologist which are dependant on circumstances and the intended study species. Before these methods are evaluated it is first necessary to describe the formation and structure of the haliotid shell:

The mantle, or pallium, which is the epithelial covering of the visceral hump and mantle skirt is the tissue directly responsible for the secretion and deposition of the prosobranch gastropod shell. The shell is composed of an organic base, conchiolin, which may or may not be impregnated with organic salts of calcium, in particular calcium carbonate. It has been determined that the deposition of calcium salts is a physiochemical event which occurs extracelluarly (Fretter & Graham 1962). The organic matrix of conchiolin appears to be a complex of substances but is composed largely of protein which may vary from one individual to the next. Primary growth normally takes place at the free edge or pallial edge of the mantle skirt where new rings of conchiolin impregnated with calcium carbonate are laid down. The calcareous material is in the crystalline form of prisms of calcite (Wilbur 1964) lying normal to the shell surface. This layer of shell is known as the prismatic layer (Figure 4.1). Secondary growth involves the deposition of additional calcareous matter to thicken and strengthen the prismatic layer. Plates of calcium carbonate crystals known as aragonite which are orientated parallel to the shell surface are deposited with bands of conchiolin (Fretter & Graham *op. cit*). This arrangement is known as nacre or mother-of-pearl in the lower prosobranchs and this internal shell layer is known as the nacreous layer (Figure 4.1). The successive alternate layers of plates of white aragonite and dark conchiolin in the nacreous layer result in banding patterns (Wilbur *op. cit.*; Poore 1972c; Day & Fleming 1992). The shell is covered externally by a thin layer of conchiolin which is not impregnated with mineral material. This protein sheet is called the epidermis or periostracum (Figure 4.1). As is typical of prosobranchs from warmer seas (Fretter & Graham *op. cit.*), the periostracal layer is very thin and delicate and is often eroded away in larger animals exposing the inner prismatic and nacreous layers.

4.1.1 Ageing techniques

Length-at-age data

Growth marks on whole shells and in longitudinal shell sections.

Growth parameters may be estimated in several species of abalone in which marks visible on the surface of whole shells represent changes in calcification. However, it is important to determine whether the marks occur regularly and at the same time each year so that increments between them consistently represent one year of growth (Day & Fleming 1992). Forster (1967) found this method to be unreliable for *H. tuberculata* because of the large amount of variation in the timing of the formation of the growth marks. A single mark was sometimes formed after a year, but there were sometimes two or no marks after a years growth as well. Extra growth marks resulting from disturbances such as tagging were visible at times and were difficult to distinguish from annual marks. Sakai (1960) sectioned shells of *H. discus hannai* and found that marks visible on whole shell surfaces were associated with discontinuities in the nacreous layer while the extra disturbance marks were strictly external. He determined that marks corresponded to periods of gonad maturation and spawning, but stressed that the timing of growth marks varied and were sometimes not visible at all. Poore (1972c) found definitive growth marks on shells > 40 mm for *H. australis* and > 20 mm in *H. virginea*. As was the case for *H. discus hannai*, marks were associated with interruptions in the boundary between the outer prismatic and inner nacreous layers in sectioned shells. The marks observed for *H. australis* were identified as being annual and formed in late autumn or early winter. No validation of growth marks was obtained for *H. virginea*, but incremental measurements suggested considerable variation in growth rate through the year (Poore *op. cit.*). As a result of size-selective sampling or mortality, the mean sizes at previous ages estimated from growth marks on older animals may be biased if the growth marks are not representative of the sizes of younger abalone at that time (Day & Fleming 1992) - an occurrence known as 'Lee's phenomenon' (see Ricker 1969). Growth marks on whole shells and in sectioned shells of large animals can be used to determine age to provide length-at-age data for all sizes as long as the age when the first mark was laid down is known. Growth marks were not visible on whole shells of *H. midae* and no interruptions were observed between the prismatic and nacreous layers in longitudinal shell sections in this study.

Banding patterns in the nacreous layer

Alternate dark (conchiolin) and white (aragonite) bands in the nacreous layer, have been used by various workers to age abalone, and have been recognized as being one of the most powerful tools available for estimating growth (Shepherd & Breen 1992). By grinding down the tip of the whorl Munoz-Lopez (1976) determined that dark conchiolin layers were laid down in winter months and white aragonite layers in summer for three species of Californian abalone. He assumed that these layers were annual and related numbers of layers to shell lengths for *Haliotis corrugata*, but neglected to verify this with independent ageing data. Similar light and dark bands were visible in sections through the spire of *H. gigantea* (Hayashi 1955), and subsequently after independent growth trials Inoue & Oba (1980) suggested that they were annual. Rings have also been identified and verified by independent growth studies in *H. tuberculata* (Forster 1967; Hayashi 1980b), *H. discus discus* (Kojima *et al.* 1977), *H. diversicolor diversicolor* and *H. diversicolor aquatilis* (Kim & Cheung in Schiel & Breen 1991). Prince *et al.* (1988) related numbers of bands to shell size for *H. rubra*, and found that three minor rings were laid down in the first 16 months, and a major ring after 20 months. Subsequent to this, rings are deposited on an approximate annual basis. Independent length-frequency and tag return data were used to verify the ages at which rings were deposited. Cross sections of *H. iris* shells exhibit obvious rings, however, verification by independent tag return data (Schiel & Breen 1991) showed that rings were neither annual or semi-annual and stressed the need for further validation. There are no further records of the use of growth rings in the nacreous layer other abalone species. The accuracy of this technique for older animals which do not grow appreciably is doubtful however as there is a masking of the rings which become compressed up against the prismatic layer in larger shells.

The use of external growth marks or internal growth-increment patterns have both been extensively used to age many other commercially important molluscs, e.g. the blue mussel *Mytilus edulis* (Richardson *et al.* 1990), the surf clam *Spisula solidissima* (Ropes & Shepherd 1988), the ocean quahog *Arctica islandica* (Ropes 1988), the northern quahog or hard clam *Mercenaria mercenaria* (Arnold *et al.* 1991), the Atlantic deep scallop *Placopecten magellanicus* (Ropes & Jearld 1987) and the horse mussel *Modiolus modiolus* (Anwar *et al.* 1990). Unlike abalone, the internal banding patterns are often visible in both the prismatic and nacreous shell layers (Anwar *et al. op. cit.*; Richardson *et al. op. cit.*), although most studies have shown that the internal nacreous layer provides the best results. The formation of growth patterns are not always periodic, however, certain repeating structural features do exhibit a periodicity of formation and the frequency of deposition may vary from sub-daily to annual (Ropes & Jearld *op. cit.*; Arnold *et al. op. cit.*).

Length-frequency data

The identification and isolation of cohorts or size classes from length-frequency data is the most commonly used method for obtaining length-at-age data (Clavier & Richard 1986; Day & Fleming 1992). A simple inspection of modes known as the Peterson method is the crudest but often most reliable method (Macdonald & Pitcher 1979). Length-frequency analyses are best suited to animals which have a very short, well defined spawning season (Shepherd & Hearn 1983; Keesing & Wells 1989), as it prevents false interpretation of merged cohorts resulting from spawnings close together and highly variable juvenile growth rates (Leighton 1974; Shepherd 1988). Sexes may also grow at different rates forming two overlapping cohorts, and two strong recruitments in a year may result in two separate cohorts. Apart from the Peterson method, there are several computer programmes available which can be used to analyze such data and provide maximum likelihood estimates of the mean lengths of the component cohorts (e.g. MacDonald

& Pitcher 1979; Schnute & Fournier 1980; Erzini 1990; Fournier *et al.* 1990). Ideally a long time series of data from a population with a restricted spawning season, a short pelagic larval phase and rapid post-settlement growth is required (Newman 1968; Poore 1972c; MacDonald 1987), although graphical and computerized methods are available for analyzing single distributions as well (Erzini *op. cit.*).

Length-increment data

This may be accumulated using both internal and external growth increment patterns, cohorts from length-frequency histograms or from tagging studies. Biased results from increment patterns due to Lee's phenomenon and the long time series needed for the analysis of increments between year classes all but rule out these two possibilities (Day & Fleming 1992). Tagging studies on the other hand have been recognised by many workers as the most reliable method for abalone growth studies, and have been used extensively (e.g. Leighton & Boolootian 1963; Forster 1967; Newman 1968; Poore 1972c; Wright 1975; Sainsbury 1982; Shepherd & Hearn 1983; Ault 1985; Shepherd 1988; Sloan & Breen 1988; Keesing & Wells 1989; Tegner *et al.* 1989).

In this study the growth parameters for *H. midae* from two sites on the east coast were determined and compared with existing information on the growth rate and maximum size of *H. midae* (Newman 1968).

4.2 Materials and Methods

4.2.1 Size-at-age determination

The lack of growth marks both externally on whole shells and internally between the prismatic and nacreous layers in longitudinal sections precluded the use of this technique in growth studies. Furthermore, it was decided that length-frequency data would not be feasible for a number of reasons, *viz:*

(1) *Haliotis midae* has a protracted spawning season (see Chapter 6).

(2) The period of this study did not allow for a long time series of data.

(3) Although potentially suitable larval settlement areas were abundant (see Chapter 3), no recently metamorphosized animals or juveniles smaller than 11 mm could be found in any great numbers.

Preliminary investigations showed that incremental layers were visible in the nacreous layer in the region of the shell whorl. A total of 225 animals obtained from the Great Fish Point and

Mgwalana sites during the month of August 1992 were used for analysis. All shells were collected on the same day and ranged in size from 12 to 172 mm length. The immediate area around the whorl was removed, embedded in resin, sectioned on a single diamond blade saw to a thickness between 0.1 and 1 mm and mounted on a glass slide with DPX mountant. Sections were viewed under a stereo dissecting microscope using reflected or transmitted light for thick and thin sections respectively. Shells which exhibited severe abrasion of the periostracum and prismatic layers, which sometimes exposed the underlying nacreous layer, were excluded from the analysis. Shells which were infested with the boring polychaete *Polydora hoplura* were also excluded from the analysis, because the layers of nacre were obliterated by the boreholes, and extra layers were deposited around the holes for support (e.g. Prince *et al.* 1988). Day & Fleming (1992) have also warned against the use of infested shells because growth rate may be retarded thereby leading to erroneous results. The sections were counted three times by one reader at three day intervals, and sections whose ring counts were different on any of these occasions were rejected. Of the original 225 shells, 183 were eventually included in the study.

Preliminary growth trials performed by Erasmus (1992) at the University of Cape Town showed that two sets of rings were laid down in the nacreous layer annually. A single set comprises 1 dark conchiolin and 1 white aragonite layer, i.e. the shells in Figures 4.1, 4.2, 4.3 and 4.4 would be in their 1st, 2nd, 4th and 5th years of growth respectively. The number of rings were related to individual shell lengths and widths to determine mean lengths- and widths-at-age. Mean sizes-at-age were found not to differ significantly between males an females (Table 4.1) and all data was pooled for the estimation of growth parameters.

Length and width data was modelled using PC-Yield Version 2.2 (Punt 1992) to determine the best fit curve for the data. The Special Von Bertalanffy growth model was fitted by iteration to the data using the absolute error submodel. Growth was described by the following equation:

$$\mathbf{L_{(t)} = L_{\infty} [1 - e^{-K (t - to)}]}$$

where; $L_{(t)}$ is the length at age t, L_{∞} is the theoretical maximum length, K is Brody's growth coefficient i.e. the proportional rate at which L approaches L_{∞}, t is age, and t_0 is the theoretical age when length is zero.

4.2.2 Mark-recapture study

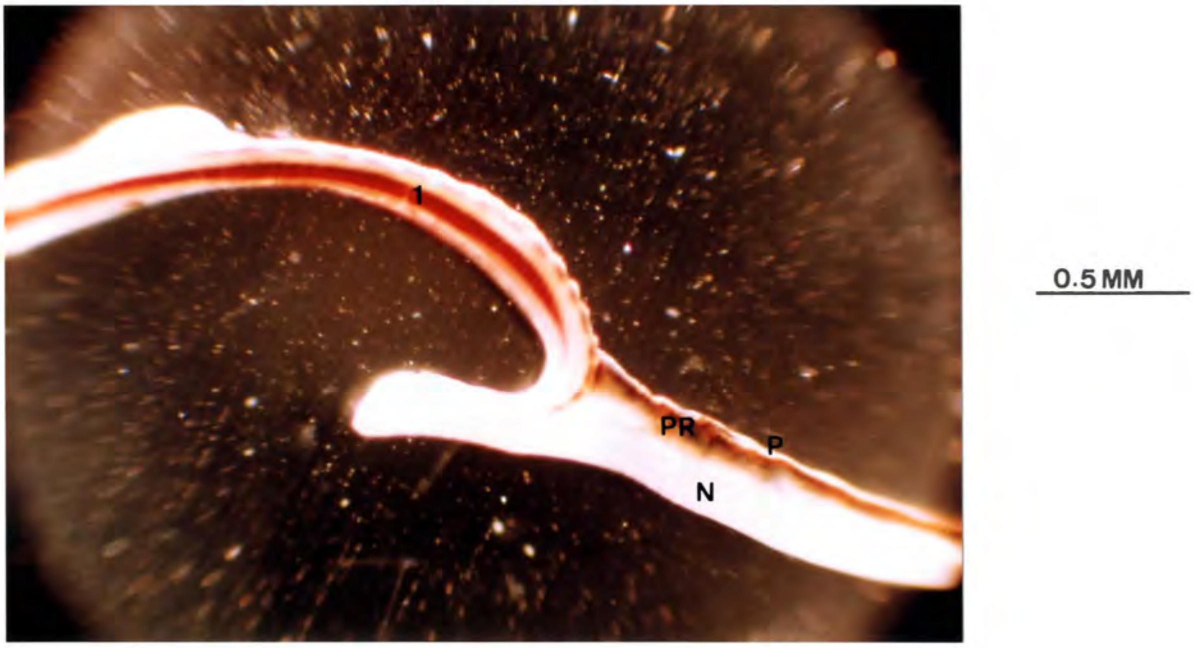

Figure 4.1 Cross-section through a shell of *H. midae* (18 mm Sl; 11.8 mm SW) from Great Fish Point illustrating the thin periostracum (P), outer prismatic layer (PR) and inner nacreous layer (N). With one-and-a-half sets of rings in the nacreous layer, this animal was in its 1st year of growth.

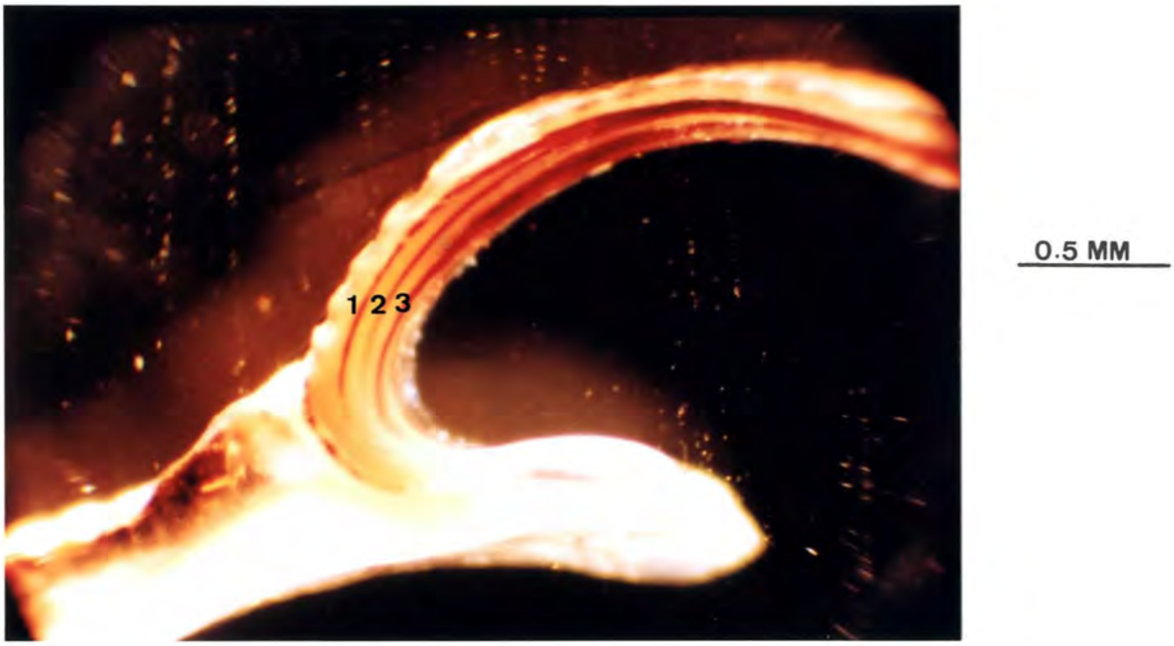

Figure 4.2 Cross-section through a shell of *H. midae* (21.4 mm SL; 13.7 mm SW) from Mgwalana with three sets of rings in the nacreous layer indicating that this animal was in its 2nd year of growth.

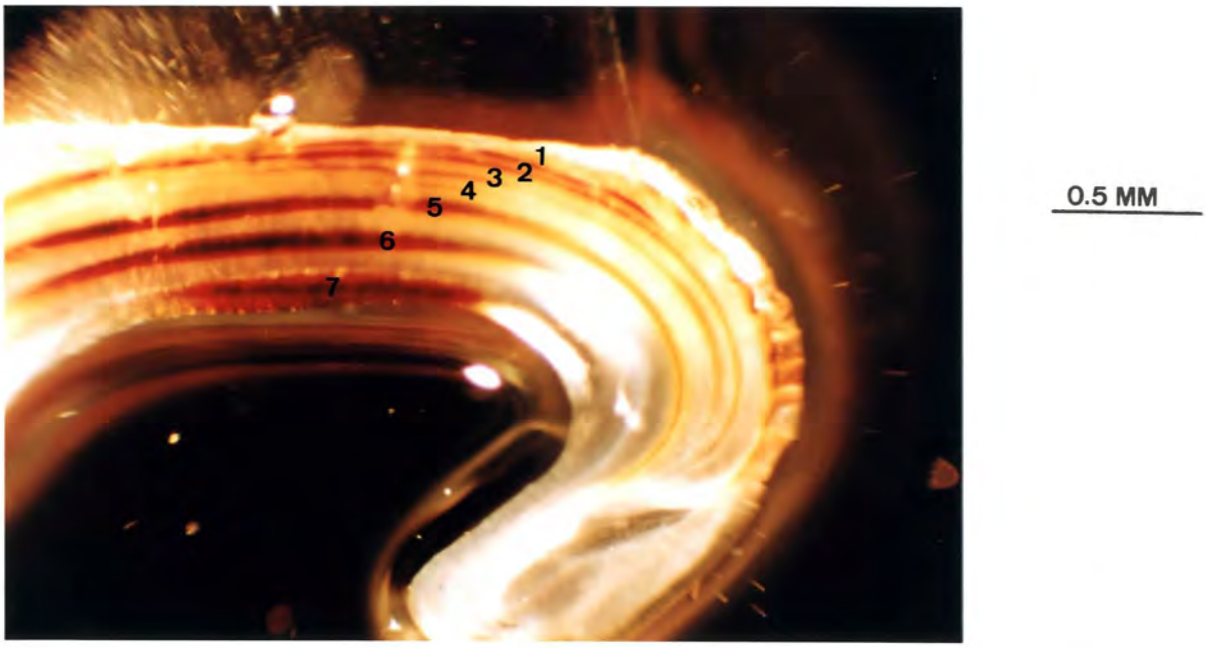

Figure 4.3 Cross-section through a shell of *H. midae* (101 mm SL; 80 mm SW) from Mgwalana with seven sets of rings in the nacreous layer, indicating that this animal was in its 4th year of growth.

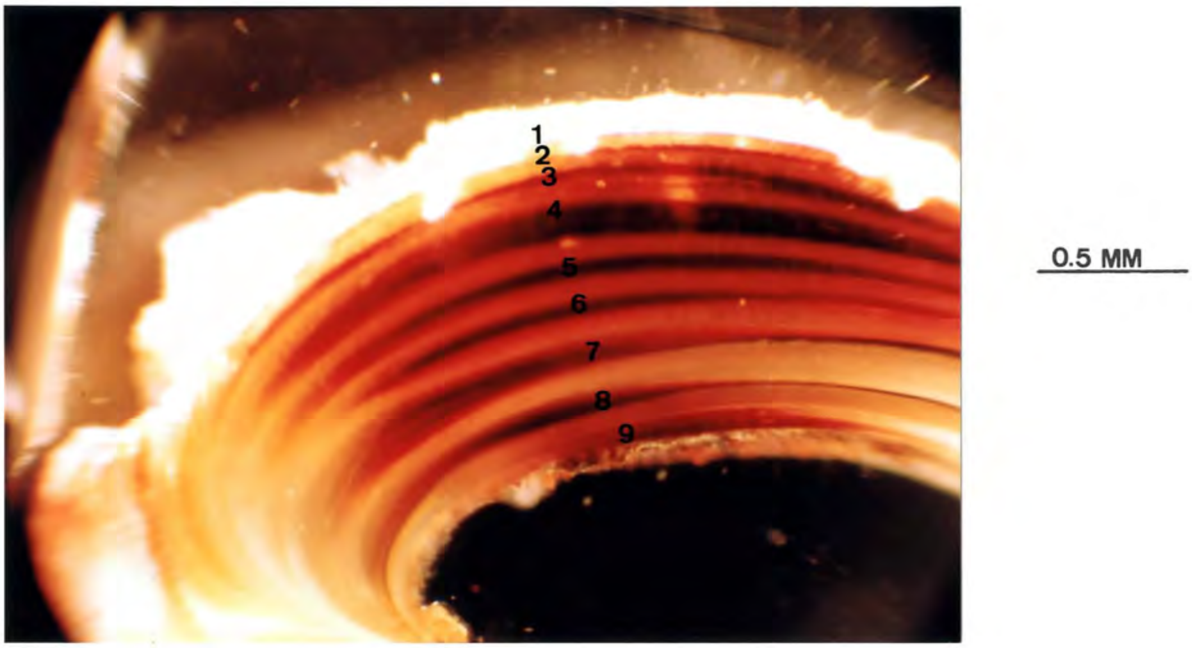

Figure 4.4 Cross-section through the shell of *H. midae* (120.2 mm SL; 93.7 mm SW) from Great Fish Point with nine sets of rings in the nacreous layer, indicating that this animal was in its 5th year of growth.

Table 4.1 Scheffe's Analysis of Variance at the 95 % confidence interval for the observed mean lengths- and widths-at-age of male and female *H. midae* sampled from Great Fish Point and Mgwalana in August 1992.

Age	Source of variation	Sum of squares	d.f.	F-ratio	Sig. level
2	Between groups	32.66667	1	0.301	0.6182
	Within groups	434.66667	4		
	Total corrected	467.33333	5		
3	Between groups	169.6321	1	1.549	0.2352
	Within groups	1423.4973	13		
	Total corrected	1593.1293	14		
4	Between groups	120.40033	1	1.661	0.2199
	Within groups	942.16900	13		
	Total corrected	1062.5693	14		
5	Between groups	50.59205	1	1.256	0.2813
	Within groups	563.98545	14		
	Total corrected	614.57750	15		
6	Between groups	0.01361	1	0.000	0.9877
	Within groups	529.47556	10		
	Total corrected	529.48917	11		
7	Between groups	51.21212	1	1.153	0.3109
	Within groups	399.77333	9		
	Total corrected	450.98545	10		

Beamish & McFarlane (1983) stressed the importance of age validation, stating that the use of inaccurate ages could cause serious errors in the management and understanding of exploited populations. Because estimates of age are fundamental to an understanding of the biology of a species and the dynamics of populations, it is essential that all age classes be validated by mark-recapture studies or the use of known-age animals. The belief that east coast perlemoen have different growth parameters to South-Western and Western Cape animals, precluded the use of known-age animals from Newmans' study (1968). Instead, a mark-recapture study was initiated in September 1991 at the Great Fish Point site. Tagging studies involve several assumptions, *viz*:

(1) The process must not affect growth. Additional external growth marks can appear on shells which correspond to the time of tagging (Forster 1967; Poore 1972c), and exposure to heat during the operation can also have adverse affects (e.g. Shepherd & Hearn 1983). For this reason it is recommended (Sainsbury 1982; Mcshane *et al.* 1988) that tagging take place *in situ* (e.g. Wright 1975).

(2) The presence of the tag must not influence growth. Positioning of tags in the respiratory pores (Newman 1968; Poore *op. cit*; Prince *et al.*1988; Prince 1991) or threading wire or

spaghetti tags through several pores (McShane *et al. op. cit.*; Muller 1984) are likely to interfere with normal processes, while grooves filed on the shell margin (e.g. Tutschulte & Connell 1988b) would have the same effect. Tag loss from abrasion and fish 'predation' is greater for tags such as floy and spaghetti tags which protrude. Labels glued to the outside of the shell (e.g. Forster 1967; Prince *et al.* 1988) are the least intrusive and are less likely to be scraped off or mistaken for food.

(3) Tagged and recaptured animals must be a random subset of the population to prevent biased results (Hearn 1986 in Day & Fleming 1992) due to differential growth, mortality and visibility (i.e. cryptic or emergent).

(4) Periods between tagging and recapture should be whole years to account for seasonal variation in growth if standard growth equations are to be fitted (e.g. Shepherd & Hearn 1983).

All of the above aspects were considered and accounted for during the tagging study, except number (4), because returns were not being used for actual ageing studies, but for validation only.

Highly variable recapture rates of between 1 and 20 % for other studies necessitate the tagging of as many animals as possible to ensure adequate numbers of returns (Leighton & Boolootian 1963). A total of 244 perlemoen were tagged over two days ranging in size from 63.5 mm to 145.6 mm shell length (Figure 4.5). Perlemoen larger than 145 mm were rare at the site and the tagging method precluded the use of smaller individuals. Animals were collected from different parts of the reef and placed in a tidal rock pool to combat dehydration. The area of the shell close to the whorl was scrubbed clean, a small amount of Prattley putty pressed onto the surface and a numbered copper disc pushed down into the putty. Shell length and width were measured using vernier callipers. The putty sets underwater and due to its toxic nature which inhibits settlement and fouling by epibiota (Rob Tarr, Sea Fisheries Research Institute [SFRI], personal communication) the copper discs can remain visible to divers for periods in excess of five years (personal observation; Figure 4.6). Tagged animals were returned to the water immediately and held in position by SCUBA divers until they adhered to the substrate. Mortality resulting from this method was very low, with only 12 (4.92%) dead animals being found in the twelve months following tagging. Monthly attempts to recover individuals proceeded after two-and-a-half months, in December 1991, and continued until November 1992. Further attempts were made to recover perlemoen from Bird Island (see Figure 2.2 - Chapter 2) which had been tagged in a similar manner in August of 1986 and 1987 by SFRI personnel (Angus MacKenzie, SFRI, personal communication).

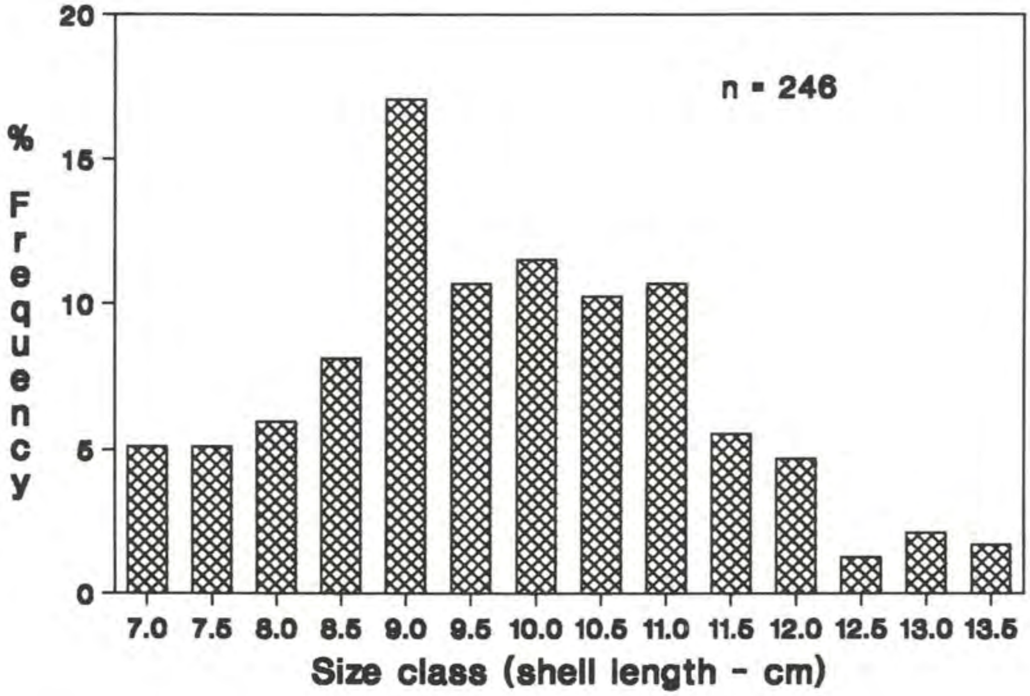

Figure 4.5 Size distribution of *H. midae* tagged at Great Fish Point on the 25th and 26th of September 1991.

Figure 4.6 Tagged *H. midae*, recaptured on the 16th June 1992 at Great Fish Point, which illustrate the position of the tags and their visibility despite extensive growth of other epibiota on the shells.

Shepherd & Hearn (1983) adapted the Von Bertalanffy growth equation to give:

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

where; L_1 was the measured length at release, Δt was the period of freedom in years from marking to final recapture, and ΔL the growth increment over this period. The other parameters are the same as previously described for the Von Bertalanffy growth equation. By calculating increments from this equation and estimating new lengths for comparison against actual observed increments and sizes of recaptured individuals, the validity of the ageing technique employed in this study could be ascertained. Width measurements and increments were similarly calculated by substituting W for L in the above equation.

4.2.3 Morphometric relationships

During the sampling period from April 1991 to September 1992 a wealth of data was accumulated which was used for morphometric analyses. Shell length and width, as well as total mass, shucked mass and shell mass were determined. Relationships of the following relative growth parameters were made for *H. midae* from the sites at Bird Island, Cape Recife, Great Fish Point and Mgwalana, and then for all sites combined:

shell length / shell width
shell length / total mass
shell length / shucked mass
shell length / shell weight
shell width / total mass
shell width / shucked mass
shell width / shell weight

Data for males and females from all sites was pooled.

4.3 Results

4.3.1 Sizes-at-age

The growth curves for lengths and widths at age for *H. midae* appear in Figures 4.7 and 4.8 respectively. Ten age classes were identified with a maximum size of 172.0 mm shell length and 156.0 mm shell width being recorded. Growth was described by the Special Von Bertalanffy model as follows:

1) for length at age: $\mathbf{L_t(mm) = 176.998918\ (1 - e^{-0.242419\,[\,t\,+\,0.495494\,]})}$

2) for width at age: $\mathbf{W_t(mm) = 159.705689\ (1 - e^{-0.195439\,[\,t\,+\,0.421164\,]})}$

Table 4.2 illustrates the goodness of fit of the model to the data with the similarity between the observed and calculated values being highly significant ($\chi^2 = 0.0019$, $0.05 < P < 0.975$ for length; $\chi^2 = 0.00005$, $0.05 < P < 0.99$ for width).

Table 4.2 Observed mean length- and width-at-age and calculated mean length- and width-at-age (from the Von Bertalanffy growth equation) for *H. midae* sampled at Great Fish Point and Mgwalana during August 1992.

Age (years)	Observed length (mm)	SD	Calculated length (mm)	Observed width (mm)	SD	Calculated width (mm)
1	22.47	6.06	20.03	13.76	2.83	12.62
2	47.71	12.08	53.82	32.86	10.14	38.73
3	81.91	20.27	80.34	62.53	17.27	60.21
4	100.96	15.04	101.15	76.95	12.76	77.87
5	117.70	16.60	117.48	92.20	13.72	92.40
6	133.62	13.48	130.29	108.65	12.41	104.35
7	139.18	7.96	140.35	112.80	7.96	114.17
8	146.27	15.12	148.23	121.64	12.15	122.26
9	153.64	15.12	154.42	130.98	12.59	128.91
10	159.88	14.37	159.29	133.83	12.84	134.37

4.3.2 Tag returns

Twenty-nine perlemoen constituting a recapture rate of 11.89 % were recovered from Great Fish Point (Table 4.3). Fewer animals were found as the period after tagging increased and on some trips no tagged animals could be found. This could be due to a number of reasons (Newman 1966):

(1) Tagging mortality - this was unlikely as only 12 (4.92 %) dead animals with tagged shells were found.

(2) Tag loss - this is difficult to ascertain, but no shells were found with only putty and no tag. Two tags on their own have, however, have been found on the sea bed at Bird Island approximately 5 years after they were fitted and illustrates that tag loss is probably very low.

(3) Limited search intensity - anywhere between 2 to 7 divers utilizing SCUBA were used on occasions to search for tagged perlemoen over a wide area. Each diver could search for a period of up to one-and-a-half hours, and familiarity with the area suggested that we covered it well

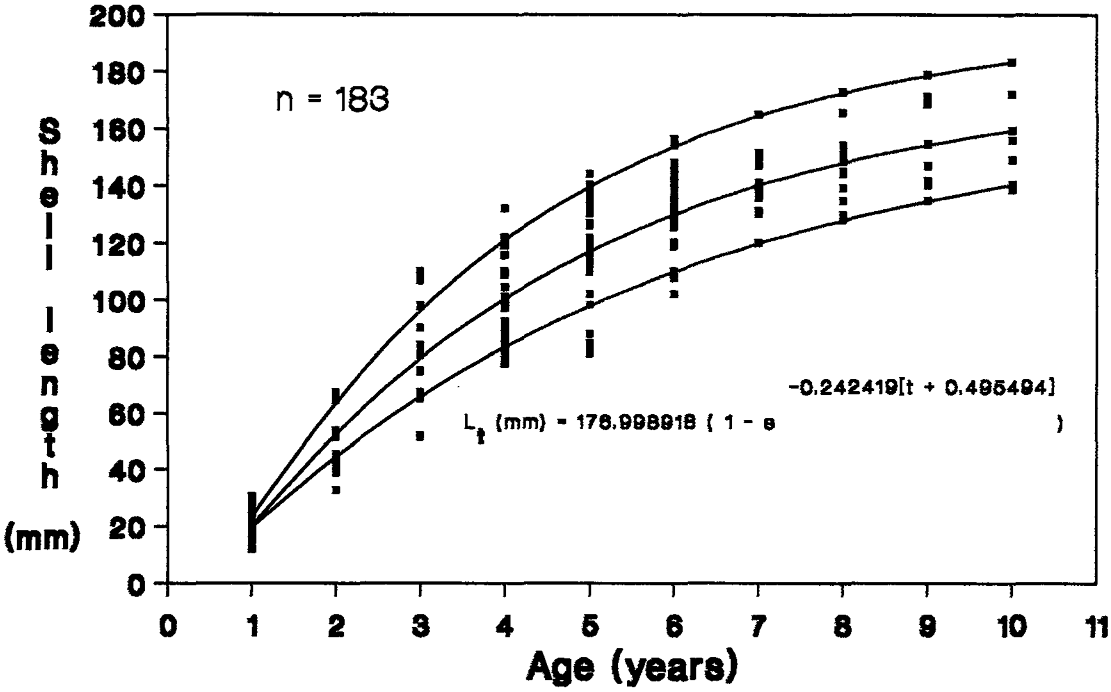

Figure 4.7 Mean length-at-age with 95% confidence limits for *H. midae* sampled at Great Fish Point during August 1992.

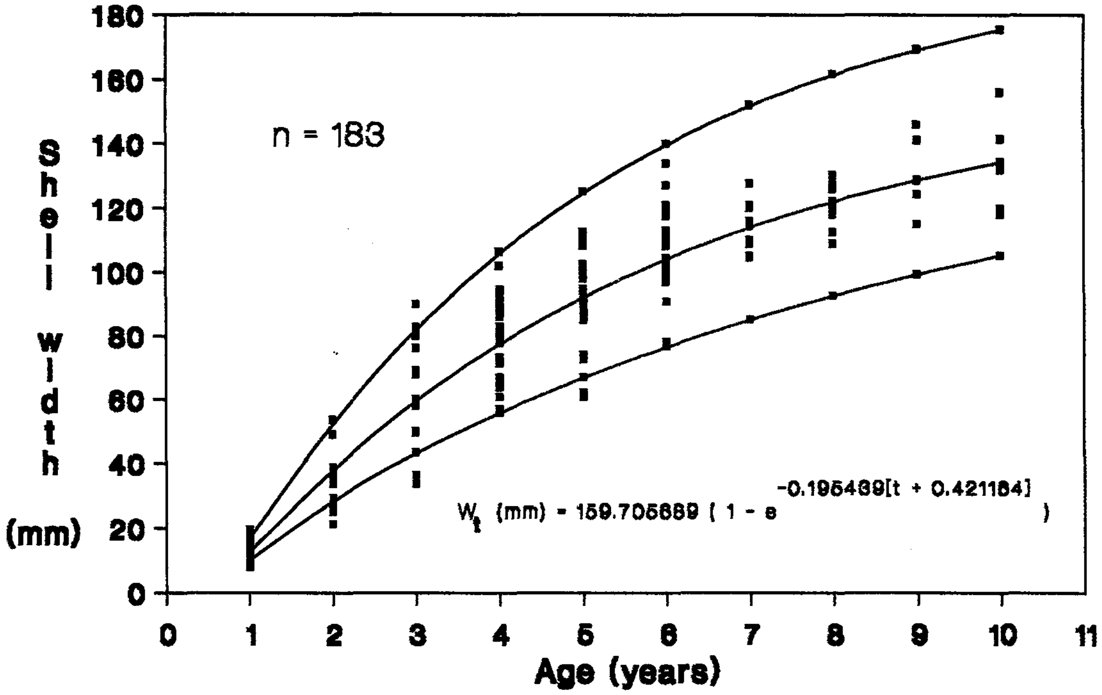

Figure 4.8 Mean width-at-age with 95% confidence limits for *H. midae* sampled at Great Fish Point during August 1992.

Table 4.3 A summary of recaptured *Haliotis midae* from Great Fish Point and Bird Island.

Tag number	Date tagged	Length (mm)	Width (mm)	Recaptured	Days free	Length (mm)	Width (mm)	Increment (L- mm)	Increment (W - mm)
Fish River Point									
G043	25/09/91	81.3	63.8	10/12/91	76	85.9	66.8	4.6	3.0
G056	25/09/91	90.5	70.6	10/12/91	76	94.0	75.0	3.5	4.4
G079	25/09/91	109.5	83.0	10/12/91	76	109.6	84.4	0.1	1.4
G111	25/09/91	94.2	68.1	10/12/91	76	97.8	74.9	3.6	6.8
G136	25/09/91	108.3	86.5	10/12/91	76	109.3	87.3	1.0	0.8
G176	26/09/91	97.1	71.9	10/12/91	75	100.6	77.0	3.5	5.1
G177	26/09/91	99.9	74.1	10/12/91	75	101.6	77.6	1.7	3.5
G184	26/09/91	99.4	69.6	10/12/91	75	101.2	73.0	1.8	3.4
G193	26/09/91	94.6	66.7	10/12/91	75	97.1	70.6	2.5	3.9
G007	25/09/91	76.5	59.1	26/03/92	183	91.9	71.4	15.4	12.3
G012	25/09/91	112.9	85.0	26/03/92	183	124.9	95.0	12.0	10.0
G033	25/09/91	79.1	65.0	26/03/92	183	92.9	71.0	13.8	6.0
G035	25/09/91	137.0	104.2	26/03/92	183	140.9	111.4	3.9	7.2
G052	25/09/91	94.7	71.7	26/03/92	183	109.9	82.9	15.2	11.2
G069	25/09/91	101.6	83.0	26/03/92	183	111.9	91.4	10.3	8.4
G080	25/09/91	117.2	87.6	26/03/92	183	121.0	99.9	3.8	12.3
G084	25/09/91	112.1	90.6	26/03/91	183	117.4	93.7	5.3	3.1
G180	26/09/91	120.3	95.5	26/03/92	182	124.0	98.9	3.7	3.4
G214	26/09/91	73.8	53.3	26/03/92	182	85.1	64.4	11.3	11.1
G015	25/09/91	85.2	63.5	16/06/92	265	95.9	72.4	10.7	8.9
G051	25/09/91	109.0	83.3	16/06/92	265	116.2	90.1	7.2	6.8
G071	25/09/91	105.0	78.0	16/06/92	265	113.0	84.7	8.0	6.7
G078	25/09/91	118.1	93.7	16/06/92	265	122.9	95.1	4.8	1.4
G146	25/09/91	115.3	89.6	16/06/92	265	119.2	91.4	3.9	1.8
G158	25/09/91	100.3	79.0	16/06/92	265	116.9	95.3	16.6	16.3
G173	26/09/91	106.7	80.4	16/06/92	264	117.1	89.6	10.4	9.2

Table 4.3/...

Table 4.3 continued.

Tag number	Date tagged	Length (mm)	Width (mm)	Recaptured	Days free	Length (mm)	Width (mm)	Increment (L– mm)	Increment (W - mm)
G060	25/09/91	74.1	51.8	12/07/92	292	98.4	72.8	24.3	21.0
G055	25/09/91	145.6	117.7	18/08/92	329	147.1	123.0	1.5	5.3
G011	25/09/91	112.8	91.4	13/10/92	384	123.5	101.2	10.7	9.8
Bird Island									
B774	24/08/86	96.7		06/10/91	1872	129.1		32.4	
B776	24/08/86	97.2		06/10/91	1872	141.2		44.0	
B802	25/08/86	100.3		06/10/91	1871	136.2		35.9	
B837	25/08/86	115.6		19/01/92	1976	131.5		15.9	
B488	25/08/86	95.3		19/01/92	1976	122.0		26.1	
B786	24/08/86	113.3		19/01/92	1977	135.4		22.1	
B745	24/08/86	80.9		19/01/92	1977	130.0		49.1	
B847	24/08/86	83.5		19/01/92	1977	137.3		53.8	
B765	24/08/86	94.3		19/01/92	1977	120.5		26.2	
B963	27/08/86	78.3		19/01/92	1974	131.4		53.1	
C424	21/08/87	63.3		19/01/92	1614	113.5		50.2	

during the searches.

(4) Movement away from the experimental area. This seems the most likely explanation at the Great Fish Point site. Abalone are capable of moving (see Lissmann 1945) sometimes covering large distances (Newman 1966). It has also been stated that marked animals generally disperse out of the area in which they were returned after tagging (Day & Leorke 1986) probably as a result of the physical disturbance of being handled (Sinclair 1963; Ault & DeMartini 1987; Shepherd & Godoy 1989). Despite collecting nine animals after two-and-a-half months (Table 4.3) from the *Caulerpa* beds to which they had been returned, this area was later discovered to be unsuitable in terms of microhabitat requirements for small and medium sized animals (see Chapter 3). Due to a combination of handling and being replaced in inhospitable terrain, all tagged animals appeared to have moved away from the *Caulerpa* beds approximately 4 months after being placed there. All subsequent returns were found as far as 30 meters from the return site and it is possible that they could have moved even farther afield.

Expected length and width increments have been calculated for all returns and the observed and calculated sizes compared for each return period (Table 4.4). The observed and expected lengths and widths for the returns from Great Fish Point were not significantly different (ANOVA, $P > 0.05$). The differences between observed and calculated sizes from Bird Island returns, however, were significant (ANOVA, $P < 0.05$). The tag return data validated the age estimates obtained from Great Fish Point and Mgwalana animals, however, the difference between the observed and expected sizes for Bird Island animals suggests that the same growth parameters were not valid and could not be applied to them. The discrepancy between the observed sizes which were smaller than the estimated sizes for recaptured Bird Island animals suggested a slower growth rate for these animals when compared to animals from the other two sites. Subsequent ring counts from the nacreous layers of the Bird Island recaptures showed that animals equal in size to ones from Great Fish Point or Mgwalana were older by one to two years. This confirmed that the recaptured animals from Bird Island exhibited a slower growth rate.

The above finding suggested that growth was variable between habitats, and this was augmented by the differences in morphometric relationships which have been calculated for all sites. Table 4.5 summarizes the regression equations all of which provide significant fits to the data ($P > 0.05$). The morphological growth relationships for *H. midae* from Cape Recife are illustrated in Figures 4.9 - 4.15. Growth was not isometric and all the relationships were described by power ($Y = aX^b$) and exponential ($Y = e^{(a + bX)}$) functions.

Table 4.4 Calculated length and width increments and calculated and expected lengths and widths of recaptured *Haliotis midae* from Great Fish Point and Bird Island.

Tag Number	Δt (years)	ΔL (mm)	ΔW (mm)	Observed L (mm)	Calculated L (mm)	Observed W (mm)	Calculated W (mm)
Great Fish Point							
G043	0.21	4.74	3.85	85.9	86.04	66.8	67.65
G056	0.21	4.29	3.58	94.0	94.79	75.0	74.18
G079	0.21	3.35	3.07	109.6	112.84	84.4	86.07
G111	0.21	4.11	3.67	97.8	98.30	74.9	71.78
G136	0.21	3.41	2.94	109.3	111.71	87.3	89.43
G176	0.21	3.96	3.52	100.6	101.06	77.0	75.42
G177	0.21	3.82	3.43	101.6	103.72	77.6	77.53
G184	0.21	3.85	3.61	101.2	103.25	73.0	73.21
G193	0.21	4.08	3.73	97.1	98.68	70.6	70.43
G007	0.5	11.47	9.37	91.9	87.97	71.4	68.47
G012	0.5	7.32	6.96	124.9	120.22	95.0	91.96
G033	0.5	11.18	8.82	92.9	90.28	71.0	73.82
G035	0.5	4.57	5.17	140.9	141.57	111.4	109.37
G052	0.5	9.40	8.19	109.9	104.10	82.9	79.89
G069	0.5	8.61	7.14	111.9	110.21	91.4	90.14
G080	0.5	6.83	6.71	121.0	124.03	99.9	94.31
G084	0.5	7.41	6.43	117.4	119.51	93.7	97.03
G180	0.5	6.47	5.98	124.0	126.77	98.9	101.48
G214	0.5	11.78	9.91	85.1	85.58	64.4	63.21
G015	0.75	15.25	13.11	95.9	100.45	72.4	76.61
G051	0.75	11.30	10.41	116.2	120.3	90.1	93.71
G071	0.75	11.97	11.13	113.0	116.97	84.7	89.13
G078	0.75	9.79	8.99	122.9	127.89	95.1	102.69
G146	0.75	10.25	9.55	119.2	125.55	91.4	99.51
G158	0.75	12.74	11.00	116.9	113.04	95.3	90.00

Table 4.4/...

Table 4.4 continued.

Tag Number	Δt (years)	ΔL (mm)	ΔW (mm)	Observed L (mm)	Calculated L (mm)	Observed W (mm)	Calculated W (mm)
G173	0.75	11.68	10.81	117.1	118.38	89.6	91.21
060	0.83	18.75	16.16	98.4	92.85	72.8	67.96
G055	0.92	6.28	6.91	147.1	151.87	123.0	124.61
G011	1.04	14.3	12.56	123.5	127.1	101.2	103.96
Bird Island							
C424	4.42	74.75		113.50	138.05		
B774	5.125	57.11		129.10	153.81*		
B776	5.125	56.76		141.24	153.96*		
B802	5.125	54.56		136.20	154.86*		
B837	5.42	44.89		131.50	160.49*		
B488	5.42	59.74		122.00	155.04*		
B786	5.42	46.58		135.40	159.87*		
B745	5.42	70.26		130.00	151.16*		
B847	5.42	68.37		137.30	151.87*		
B765	5.42	60.47		120.50	154.76*		
B963	5.42	72.17		131.40	150.47*		

* - difference between observed and calculated is significant ($P < 0.05$).

Table 4.5 Summary of all regression equations for the morphometric growth relationships of *Haliotis midae* from Great Fish Point, Mgwalana, Cape Recife, Bird Island and for all sites combined.

Relationship	Site	Regression equation	r^2	n
Shell width vs Shell length	Great Fish Point	$SW = 0.446306 \times SL^{1.11889}$	0.9967	553
	Mgwalana	$SW = 0.39355 \times SL^{1.15015}$	0.9696	299
	Cape Recife	$SW = 0.381224 \times SL^{1.15138}$	0.975	153
	Bird Island	$SW = 0.414933 \times SL^{1.13396}$	0.9862	46
	Combined	$SW = 0.433755 \times SL^{1.12642}$	0.9942	1051
Whole weight vs Shell length	Great Fish Point	$WW = 0.000149 \times SL^{3.00994}$	0.9967	553
	Mgwalana	$WW = e^{(2.076501 + 0.0295098SL)}$	0.9606	299
	Cape Recife	$WW = 0.000127 \times SL^{3.0397}$	0.9706	153
	Bird Island	$WW = 0.000117 \times SL^{3.03487}$	0.9813	46
	Combined	$WW = 0.000139 \times SL^{3.03042}$	0.9948	1051
Shucked weight vs Shell length	Great Fish Point	$ST = 0.000183 \times SL^{2.84692}$	0.99	553
	Mgwalana	$ST = 0.000098 \times SL^{2.99355}$	0.9493	299
	Cape Recife	$ST = 0.000268 \times SL^{2.75731}$	0.9526	153
	Bird Island	$ST = 0.000136 \times SL^{2.87007}$	0.9645	46
	Combined	$ST = 0.000170 \times SL^{2.86506}$	0.9847	1051
Shell weight vs Shell length	Great Fish Point	$SG = 0.000009 \times SL^{3.40522}$	0.9943	553
	Mgwalana	$SG = e^{(0.882733 + 0.0325539SL)}$	0.9414	299
	Cape Recife	$SG = 0.000009 \times SL^{3.4275}$	0.9682	153
	Bird Island	$SG = 0.000021 \times SL^{3.23451}$	0.9794	46
	Combined	$SG = 0.000008 \times SL^{3.43745}$	0.989	1051
Whole weight vs Shell width	Great Fish Point	$WW = 0.001212 \times SW^{2.70677}$	0.9931	553
	Mgwalana	$WW = 0.000868 \times SW^{2.78762}$	0.9585	299
	Cape Recife	$WW = 0.001854 \times SW^{2.60987}$	0.9728	153
	Bird Island	$WW = 0.001376 \times SW^{2.6518}$	0.9768	46

Table 4.5/...

Table 4.5 continued.

Relationship	Site	Regression equation	r^2	n
	Combined	$WW = 0.001180 \times SW^{2.7138}$	0.9902	1051
Shucked weight vs Shell width	Great Fish Point	$ST = 0.001465 \times SW^{2.53833}$	0.9895	553
	Mgwalana	$ST = 0.001415 \times SW^{2.55177}$	0.9411	299
	Cape Recife	$ST = 0.003181 \times SW^{2.35825}$	0.9474	153
	Bird Island	$ST = e^{(2.106220 + 0.0280541SW)}$	0.9622	46
	Combined	$ST = 0.001476 \times SW^{2.53531}$	0.984	1051
Shell weight vs Shell width	Great Fish Point	$SG = 0.000115 \times SW^{3.03929}$	0.9949	553
	Mgwalana	$SG = e(1.415622 + 0.0347128SW)$	0.9445	299
	Cape Recife	$SG = 0.000174 \times SW^{2.95385}$	0.9777	153
	Bird Island	$SG = 0.000279 \times SW^{2.83631}$	0.9819	46
	Combined	$SG = 0.000114 \times SW^{3.04635}$	0.9913	1051

SL - Shell length
WW - Whole weight
SW - Shell width
ST - Shucked weight
SG - Shell weight

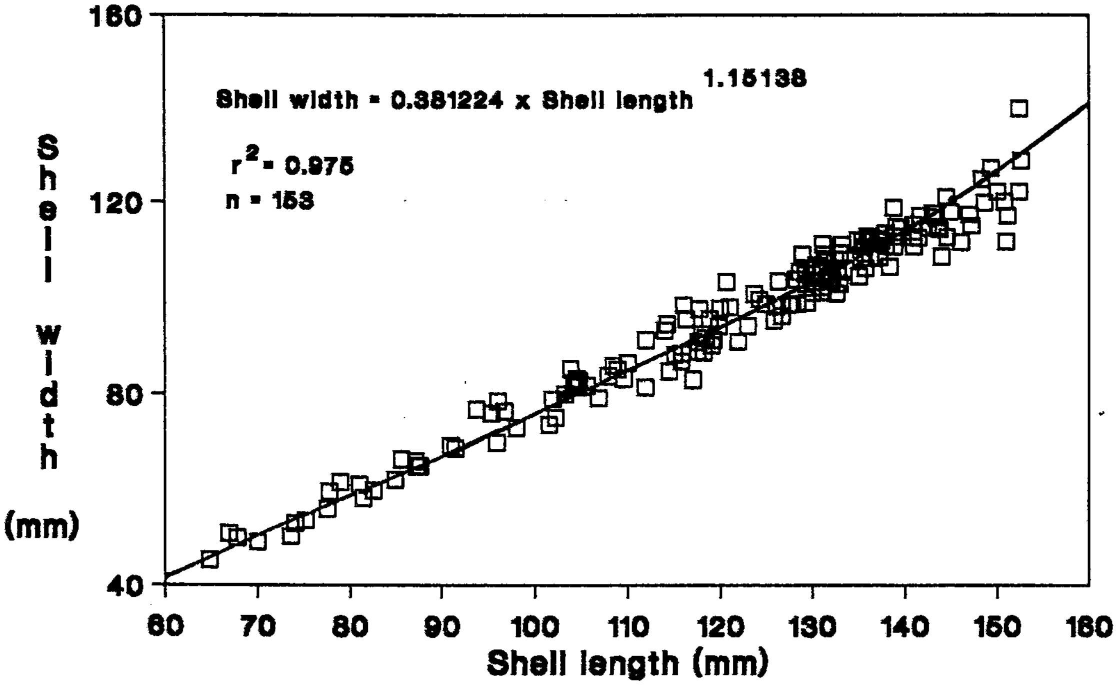

Figure 4.9 The relationship between shell width and shell length for *H. midae* sampled at Cape Recife from May 1991 to July 1992.

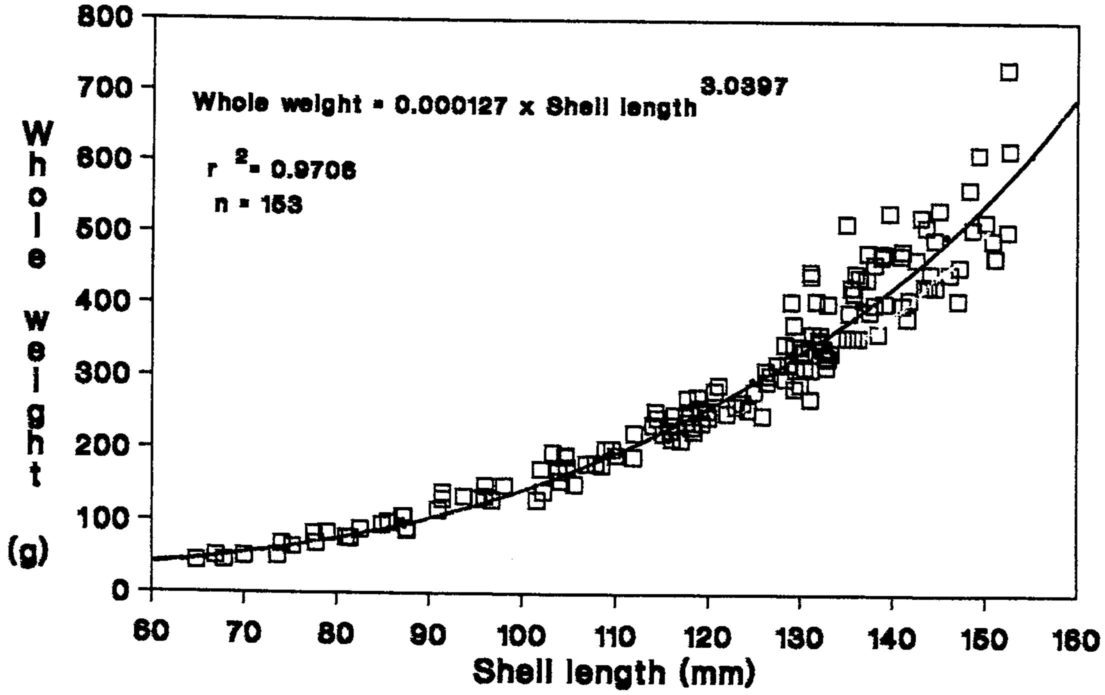

Figure 4.10 The relationship between whole weight and shell length for *H. midae* sampled at Cape Recife from May 1991 to July 1992.

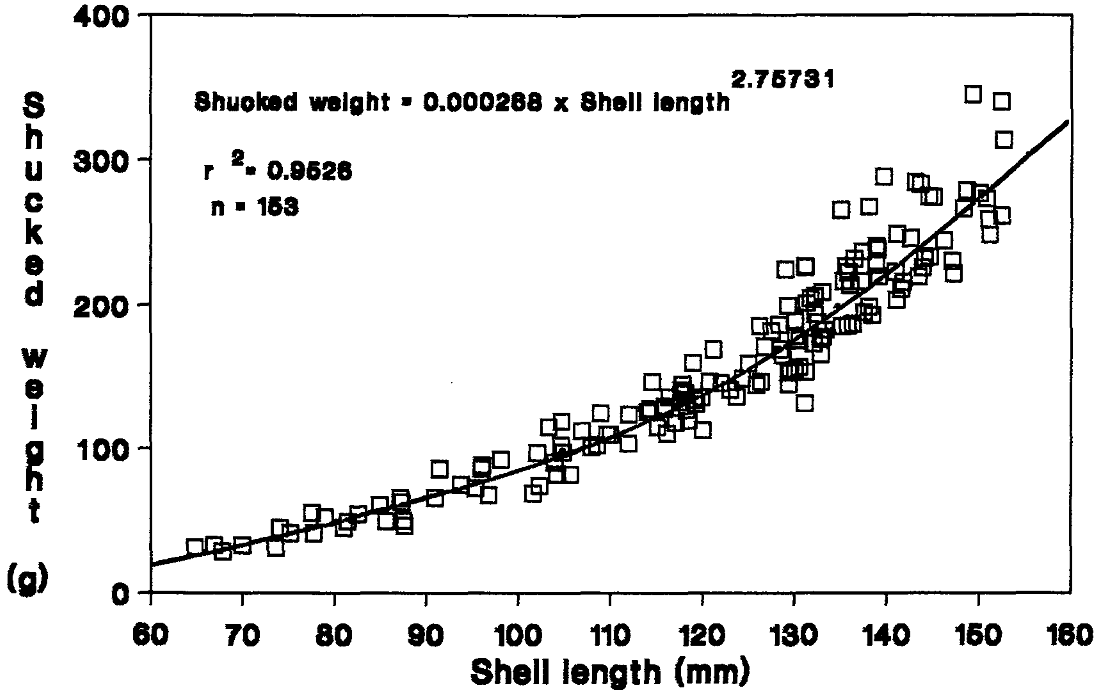

Figure 4.11 The relationship between shucked weight and shell length for *H. midae* sampled at Cape Recife from May 1991 to July 1992.

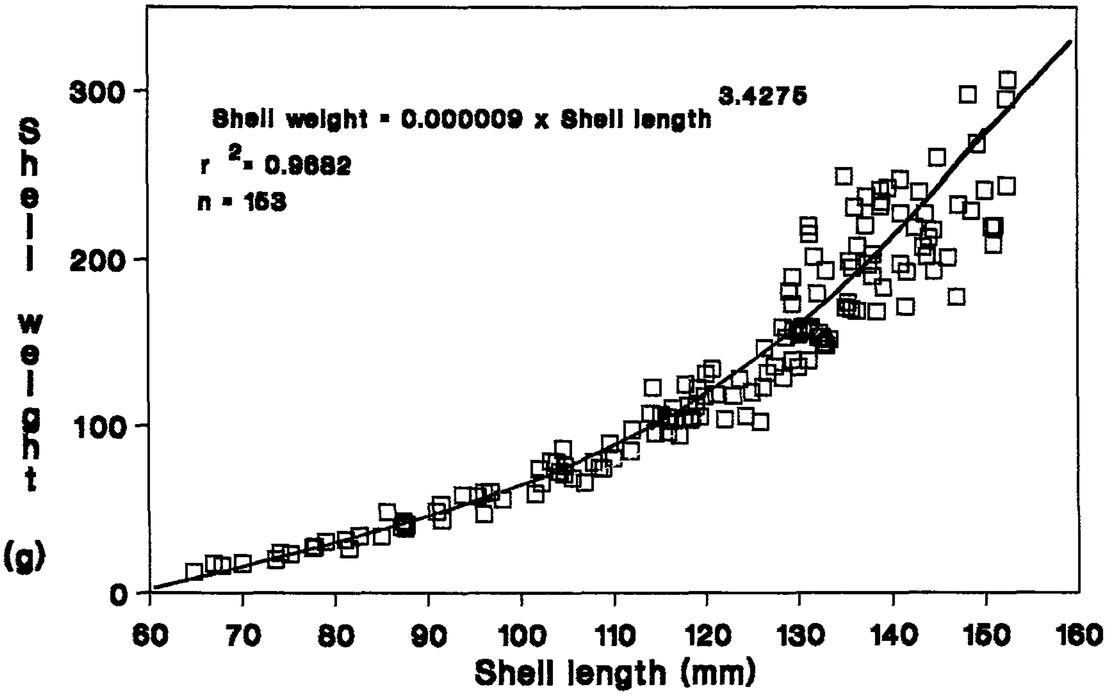

Figure 4.12 The relationship between shell weight and shell length for *H. midae* sampled at Cape Recife from May 1991 to July 1992.

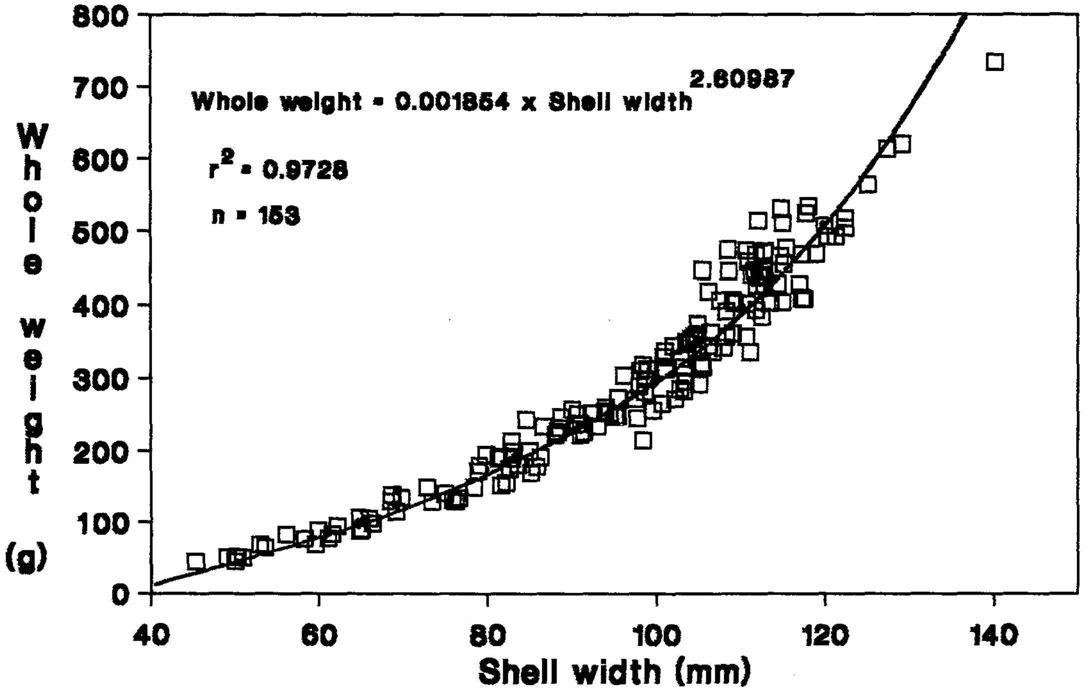

Figure 4.13 The relationship between whole weight and shell width for *H. midae* sampled at Cape Recife from May 1991 to July 1992.

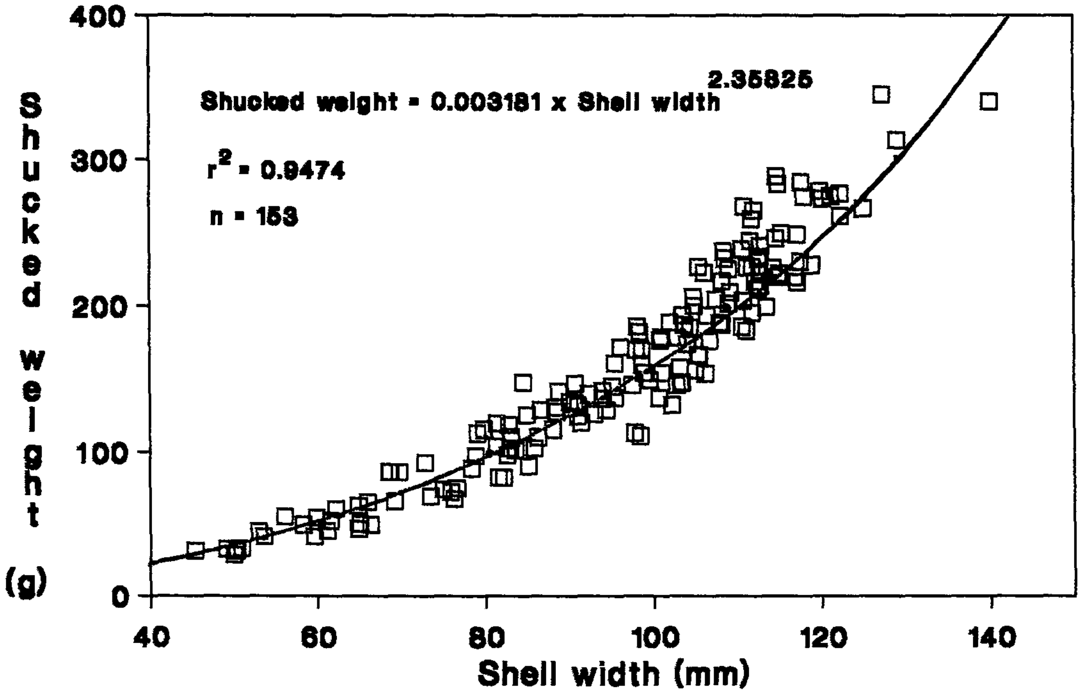

Figure 4.14 The relationship between shucked weight and shell width for *H. midae* sampled at Cape Recife from May 1991 to July 1992.

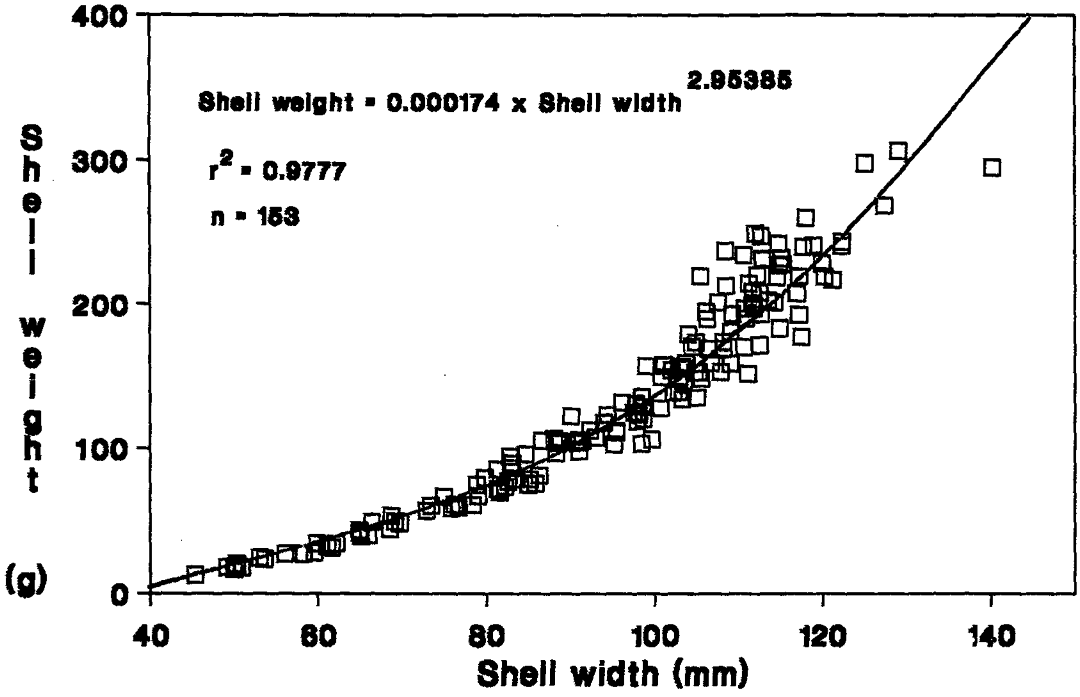

Figure 4.15 The relationship between shell weight and shell width for *H. midae* sampled at Cape Recife from May 1991 to July 1992.

4.4 Discussion

The growth of *H. midae* was typical of that in other members of the genus *Haliotis* and was well described by the Von Bertalanffy growth model. Annual increments were as much as 34 mm SLin the first few years of growth, but began to decline in large sexually mature animals. Decreases in annual growth increments after sexual maturity are well documented for haliotids (Forster 1967) and are caused by the partitioning of energy between growth and gamete production (Shepherd & Hearn 1983).

Studies of growth parameters for many haliotid species in the field have been extensive (Day & Fleming 1992). The majority of growth studies have made use of the Von Bertalanffy growth model, which adequately describes growth over a broad size range for most haliotids (Sainsbury 1982; Sloan & Breen 1988).

A comparison between studies of haliotid growth given in Table 4.6 shows that growth rates differ significantly between species. This is not an unusual phenomenon (Sainsbury 1982) however, and intra-specific variation is also evident (Kojima *et al.* 1977; Mottet 1978). Newman's (1968) growth parameters for *H. midae* in the Western Cape are different from those obtained in this study (Table 4.6). The suspected faster growth rates and smaller maximum sizes of the East Coast animals have thus been confirmed in this study. It was also apparent that longevity was considerably less (10 as opposed to 30 years) in the temperate Eastern Cape waters. The present minimum legal size of 114 mm shell width was attained at an age of 6.83 years as opposed to 12.33 years for Western Cape animals. Using the values obtained in Chapter 6, the sizes at 50 % sexual maturity were 52.83 mm, 57.46 mm, 51.20 mm and 53.83 mm shell width for Great Fish Point, Mgwalana, Cape Recife and Kelly's Beach respectively, which correspond to ages of 2.64, 2.92, 2.57 and 2.68 years respectively. This was in contrast to the 7.06 years needed for *H. midae* to reach its size at 50% maturity of 80 mm shell width in the Western Cape (ages for Western Cape animals were calculated from Figure 12 in Newman 1968).

The tag returns from Bird Island and some unpublished data from a tagging project at Roman Bay in the south-western Cape (Neville Sweijd, Department of Zoology, University of Cape Town, personal communication) suggest that growth varied on a localized scale in both regions and highlighted the need for a more detailed study. The small sizes at 50 % sexual maturity for animals from all four sample sites in this study were all attained during the third year of growth, and were an indication that growth patterns along this section of coast were very similar. Each situation, however, is likely to be unique. For example, Shepherd & Laws (1974) found that populations of *H. rubra* and *H. laevigata* which matured at a smaller size had slower growth rates, and Poore (1972c) attributed the smaller maximum size of *H. iris* at one site to a slower growth rate as well. To further complicate matters, Sainsbury (1982) found that sizes at maturity were the same for two populations of *H. iris* despite a lower growth rate at one site. Of interest is that the growth rate of 0.06 for *H. midae* in the South-Western Cape (Newman 1968) is the second slowest rate next to a value of 0.02 for *H. discus discus* (Kojima *et al.* 1977). However, the corresponding L_∞ value for *H. d. discus* in the above study was 744 mm shell length, with parameters having been determined from increments in length from external growth checks. Although L_∞ is only a theoretical value, a value of 744 mm is improbable for a species whose theoretical maximum lengths from other studies ranged from 167 to 319 mm shell length. It would seem likely therefore that *H. midae* in the cool South-Western Cape waters has in fact the lowest growth rate of all abalone studied. Apparently the cold waters around Sitka Island in Alaska (58°N) do not hinder growth in *H. kamtschatkana* (Sloan & Breen 1988).

When comparing growth parameters it should be remembered that different techniques such as tagging, length frequencies or ring counts often provide different K and L_∞ values (Keesing & Wells 1989). Variation is even apparent when a single technique is used, for example tag returns over a short time period tend to underestimate K and overestimate L_∞, and growth parameters

Table 4.6 Von Bertalanffy growth parameters for various haliotid species.

Species	Author	Parameters K	 L_∞ (mm)
H. australis	Poore (1972c)	0.32	87
H. corrugata	Tutschulte & Connell (1988b)	0.09-0.11	169-202
	Guzman del Proo (1992)	0.15-0.98	119-210
H. discus discus	Kojima (1976) and Kojima *et al.* (1977)	0.22-0.27	167-188
H. discus hannai	Sakai (1962b)	0.07-0.24	134-369
H. diversicolor aquatilis	Kim & Chung (1985 in Day & Fleming 1992)	0.21	78
H. d. diversicolor	"	0.18	89
H. fulgens	Tutschulte & Connell (1988b)	0.09-0.10	179-205
	Guzman del Proo (1992)	0.34-0.39	126-189
	Shepherd *et al.* (1991)	0.38	183
	Morales & Ortiz (1989)	0.28-0.44	177
H. gigantea	Ino (1952) and Kurogane *et al.* (1974)	0.35-0.41	205-221
H. iris	Poore (1972c)	0.31	146
	Sainsbury (1982)	0.16-0.17	130-132
	Schiel & Breen (1991)	0.11-0.31	130-153
H. kamtschatkana	Quayle (1971)	0.20-0.32	124-137
	Schnute & Fournier (1980)	0.22	133
	Fournier & Breen (1983)	0.20-0.25	92-108
	Breen (1986)	0.16-0.51	95-124
	Sloan & Breen (1988)	0.16-0.50	95-137
H. laevigata	Shepherd & Hearn (1983)	0.41-0.59	115-148
H. midae	Newman (1968)	0.059	193.3*
	This study	0.195	159.71*
		0.242	176.99
H. roei	Keesing & Wells (1989)	0.25-0.79	79-87
H. rubra	Harrison & Grant (1971)	0.22-0.24	160-175
	Shepherd & Hearn (1983)	0.32-0.41	139-144
	McShane *et al.* (1988)	0.27-0.35	117-133
	Prince *et al.* (1988)	0.29	140
	Prince (1989 in Day & Fleming 1992)	0.47	155
	Tegner *et al.* (1989)	0.27	201
	Tegner *et al.* (1992)	0.22-0.27	192-200
H. tuberculata	Forster (1967)	0.27-0.40	99-119
	Hayashi (1980b)	0.33-0.45	98-115
	Clavier & Richard (1985)	0.37	108
H. virginea	Poore (1972c)	0.32-0.45	62-64

*** - parameters based on shell width.**

are distorted unless the size range tagged is representative of animals in the population (Shepherd & Hearn (1983).

Sources of variation in intra-specific growth patterns are many and have been attributed to depth, gender, habitat or locality, individual variation and seasons. Locality is important as it incorporates the effects of food supply (Breen 1980; Shepherd & Hearn 1983), exposure to wave action (Breen & Adkins 1979) and local temperature regimes (Newman 1969; Leighton 1974). Newman (1968) determined that growth was seasonal for *H. midae* and appeared to be associated with spawning. Seasonality was not addressed in this study, but if growth was associated with spawning in the Eastern Cape, the protracted breeding season (Chapter 6) would result in variable seasonal growth patterns within populations. Leighton & Boolootian (1963) found that while food was the primary factor limiting growth rate in *H. cracherodii* seasonal variation accompanied the gonad maturation and sexual cycle. The maximum growth which takes place in summer for *H. discus hannai* (Sakai 1962b) was attributed to high water temperatures, however, minimal growth in winter was not attributed to decreased temperatures but instead to the maturation of gonads. A distinct edge of new growth at the anterior portion of the shell in spring led Poore (1972c) to believe that *H. iris* and *H. australis* exhibited a seasonal growth pattern with rapid growth occurring during spring months and slow growth in late autumn and early winter.

While other aspects such as dietary differences may play a role, temperature difference is probably the primary factor causing the discrepancies in growth rates between different regions, such as the South-Western and Eastern Cape (Newman 1969). Similar temperature regimes have also been invoked as the reason for similar growth patterns in two populations of northern abalone separated by 563 kilometres (Quayle 1971). Laboratory experiments have shown that there were temperature optima for abalone growth under non food-limited conditions (Leighton 1974; Paul & Paul 1981). At the same time, however, growth could be inhibited or slowed at low temperatures (Sakai 1962b). Assuming that food is not limiting in the Eastern or South-Western Cape, the colder Benguela waters may be inhibiting growth in *H. midae* in the South-Western Cape. Discrepancies in growth characteristics of *H. rubra* and *H. laevigata* at different locations (Shepherd & Hearn 1983; Keesing & Wells 1989) have been attributed to a combination of factors, *viz:* differing temperature regimes, food availability and different periods of reproductive activity. Similarly, it would be advisable to invoke a combination of effects such as diet, locality and temperature differences to explain the observed growth differences in *H. midae*.

The individual lengths- and widths- at-age comprising the various size classes of the growth curves suggest that *H. midae* in the Eastern Cape exhibits extreme individual variation. Variation in habitat has often been suggested as the reason for variation in growth rate (Sloan & Breen 1988), and Breen & Adkins (1979) developed an hypothesis to explain differences in population structure in *H. kamtschatkana* at different localities, which stated that abalone in protected or semi-exposed locations with high-quality food grew faster and attained a larger maximum size than those in exposed places with low-quality food. Transplant experiments from exposed habitats with low quality food such as *Pterygophora* forests to nearby *Macrocystis* forests which are more protected resulted in increased growth in *H. kamtschatkana* (Fournier & Breen 1983). In contrast Hayashi (1980b) found that *H. tuberculata* grew faster and attained a larger size in an exposed situation than in a more protected sublittoral habitat. By virtue of their shallow surf zone habitat in the Eastern Cape, *H. midae* could be considered as occupying an exposed habitat, and while some conspecifics in the Western Cape are found in shallow water, their habitat is mostly subtidal amongst *E. maxima* kelp forests, and could be considered protected. Although *H. midae* in the Western Cape attains a larger maximum size, their growth rate is slower than the exposed East Cape animals.

Growth rate variation on a localized scale where temperature regimes do not vary to any great extent, is more likely to be as a result of a combination of factors relating to habitat type such as degree of exposure to wave action, which could further be related to microhabitat availability i.e. two medium sized animals, one cryptic and one exposed, would be subject to different degrees of exposure which could potentially affect growth. For example, the exposed animal may require more energy to counteract the effects of wave action in order to maintain its position while the cryptic animal is more protected and can channel more energy into growth. Food availability, both quantity and quality, are factors which differed between habitats and could therefore have resulted in the observed individual variation in size. Animals from Cape Recife, Mgwalana and Great Fish Point exhibit very similar breeding patterns (see Chapter 6) and while it is feasible that the reproductive cycle influences growth, it is unlikely that it could be invoked as the cause for inter-habitat variation in this case.

It is important to note that the growth parameters of K and L_∞ are means of distributions of these parameters for individuals (Wright 1975; Sainsbury 1980) and so it is feasible for the L_∞ value to be exceeded by animals in populations where variability in growth rate is high (Shepherd & Hearn 1983). Depending on circumstance, individuals of the same size may grow at different rates and individuals may also grow at different rates at different times (Wright *op. cit.*). This may well explain the observed distribution or variance in each age class, and as a result the exact age of a particular perlemoen cannot be determined to any degree of certainty from its size alone.

In dioecious molluscs, females tend to be more numerous especially in larger size classes (Fretter & Graham 1962), and while this may imply that differential gender growth is common, it is rare in abalone, although it has been documented for *H. laevigata* (Shepherd & Hearn 1983). Although differential mortality was first thought to adequately explain the skewed sex ratio, annual growth increments from tagging studies showed that females of the species actually grew 25 % faster and achieved a larger size. The only other mention of differential growth between sexes was for laboratory conditioned *H. rufescens* (Ault 1985) in which females apparently grew faster. This study has shown that males and females have similar growth rates and that *H. midae* has equal sex ratios at all sites (see Chapter 6). Biased sex ratios towards females have been reported for *H. lamellosa* (Bolognari 1953), *H. scalaris* (Shepherd & Laws 1974) and *H. rufescens* (Giorgi & DeMartini 1977), while males appeared to dominate samples of *H. rubra* (Shepherd & Laws *op. cit.*), *H. roei* (Poore 1973) and *H. pustulata* (Pearse 1978). However, none of these studies invoke differential growth as being the cause for the skewed ratios. The implication for management of faster growth in either sex is that the faster growing sex will be recruited to the fishery earlier and be subject to greater fishing mortality resulting in a change to the natural sex ratio and a possible long-term deleterious effect on recruitment to the fishery (Shepherd & Hearn 1983; Ault *op. cit.*).

Present management strategies and legislation regarding *H. midae* are based upon parameters obtained from studies on south-western and western Cape animals. The minimum legal size is set at a safe level above the size at 50 % maturity so as to afford a degree of protection to the spawner stock by enabling animals to reproduce for a number of years before being recruited to the fishery. This is a common strategy in fisheries management, but based upon the findings of this study it is clear that the present option of a blanket restriction upon all perlemoen based upon the growth parameters of south-western and western Cape animals is inadequate. The full implications for management of *H. midae* on the east Cape coast are discussed in Chapter 7.

CHAPTER 5 FEEDING

5.1 Introduction

Adult and sub-adult abalone are herbivorous and feed by trapping drift seaweeds under their muscular foot (Wells & Keesing 1989). Although abalone also forage or graze on attached plants, it is a rare occurrence (Cox 1962). It would appear as if *H. midae* exhibits both feeding patterns, as Newman (1968) observed them grazing fronds of the kelp *E. maxima* while Branch & Branch (1981) noted that *H. midae* also fed by trapping frond tips under their feet. Trap-feeding is described as being an energetically economical method of feeding when compared to active grazing (Tarr 1989). Adults of *H. kamtschatkana* were shown to prefer diatoms when in captivity although several species of algae were also acceptable food items (Paul *et al.* 1977). Newly settled juveniles are also known to graze diatoms from the rock surface for the first few months of development (Tomita & Tazawa 1971; Tarr 1987; Shaw 1991), and some work has shown that abalone also ingest hydrozoans, copepods, small gastropods, compound ascidians, bryozoans, forameniferans and sponges (Ueda & Okada 1940; Leighton & Boolootian 1963; Shepherd 1973b). Abalone have long radulae with rows of numerous teeth which are used to break up algae into small pieces (McLean 1970).

Dietary composition and feeding habits have been described for most exploited abalone species, but there is a poor understanding of the factors which may affect the choice of a particular diet. Three factors have, however, been proposed (Shepherd & Steinberg 1992), *viz:*

(1) Chemoreception and the presence of chemical metabolites which can be either feeding deterrents or feeding incitants (e.g. Sakata & Ina 1992).

(2) Algal morphology or toughness.

(3) Nutritive value.

Shepherd & Steinberg (*op. cit.*) also propose that the great degree of variation in feeding habits by abalone worldwide could reflect a variation in the digestive ability with respect to certain seaweed types, particularly brown seaweeds. Feeding preference experiments performed on 11 algivorous invertebrates by Leighton (1966) showed that the degree of toughness could not solely explain differential algal consumption, and that the use of chemical perception was a more likely explanation. Recent work by Taniguchi *et al.* (1991; 1992) demonstrated the presence of a chemical (phlorotannins) defense mechanism in some laminarious algae which acted as a feeding deterrent against marine herbivores, including the Japanese abalone *H. discus hannai.*

Some of the earliest works on abalone feeding biology were performed on *H. tuberculata* by Stephenson (1924) and Crofts (1929) who described feeding methodology and algal preference respectively, although Crofts (*op. cit.*) neglected to qualify or quantify the diet. The first authoritative works on dietary composition were by Ueda & Okada (1940) on two Japanese abalone *H. kamtschatkana* and *H. gigantea*, and Sakai (1962a) who described algal preferences and feeding in relation to growth and gonad maturation in a third species, *H. discus hannai*. Subsequent dietary studies have described the changes in food preferences during the first few years of life. Tomita & Tazawa (1971) showed that newly settled abalone changed from a predominantly diatomaceous diet to one comprising macroalgae as they grew, and Tutschulte & Connell (1988a) and Shepherd (1973b) demonstrated that feeding behaviour changed with size and differed amongst sympatric species with juveniles of most species moving around to graze attached algae at night while adults remained stationary on home sites to capture drift algae.

While descriptions of dietary composition have demonstrated that floral abundance at a site has a major controlling effect on the diet of abalone (Tunbridge 1967), selection of food types is not common, having been reported for *H. australis* at one site in New Zealand (Poore 1972a) and *H. midae* in the Western Cape (Barkai & Griffiths 1986). The availability of attached and drift algae together with the degree of water movement will dictate the feeding habits of abalone at any one site (Shepherd 1973b), e.g. the absence of drift seaweeds would require that resident abalone adopt a predominantly grazing feeding behaviour. However, in areas denuded of attached seaweed abalone have been known to starve rather than move or utilize available drift components (Macginitie & Macginitie 1966). Environmental influences on dietary composition, such as temperature, have been investigated for *H. midae* at Marcus Island and Mas Bay in the Western Cape (Barkai & Griffiths *op. cit.*), and for *H. tuberculata* during controlled experiments where low temperatures were found to severely limit feeding (Peck 1989).

Pigmentation of the ostracal shell layers in *H. rufescens* were found to reflect its diet in nature (Leighton 1961). The implications were that colour sequences in shells could potentially be used as indicators of floral succession in the habitats of the respective animals. However, the feasibility of this was limited unless the feeding habits of the resident abalone could be determined, i.e. whether they were consuming the macroalgae in their immediate vicinity or food which had been carried to them from distant origins by currents (Olsen 1968).

There is a paucity of information regarding feeding in *H. midae* other than from the Western Cape and Bird Island (Barkai & Griffiths 1986; Tarr 1989). This study was initiated to investigate the dietary composition and algal preferences in Eastern Cape perlemoen which occupied exposed and cryptic habitats. The seasonality of feeding in the exposed animals was conducted as well, and the timing and method of feeding was also assessed in both exposed and cryptic individuals.

5.2 Materials and Methods

This aspect of the study was confined to the Great Fish Point site. Cryptic animals were all collected from the sub-boulder microhabitat in the shallow intertidal zone described in Chapter 3. Exposed animals were collected from the pinnacles and shallow gully regions also referred to in Chapter 3 and comprised both large crevice dwellers and animals occupying open rock faces. With regard to seasons, the following months were chosen to represent particular seasons; October 1991 - Spring, January 1992 - Summer, April 1992 - Autumn and July 1992 - Winter. Most other haliotids (Wells & Keesing 1989; Muller 1984) are nocturnal feeders, and algae are still present and recognisable in the crop and stomach for up to twelve hours after ingestion. After 24 hours, however, only a fraction of food remains and digestion is well advanced (Shepherd 1973b). Based upon these facts, collection of animals took place between 08h00 and 09h30 at which time the stomach contents indicated what was ingested the previous night and minimized diurnal differences in stomach fullness (e.g. Wells & Keesing *op. cit.*).

Forty exposed animals from the pinnacle and gully regions were collected each season by two divers using snorkelling gear. The animals ranged in size from 80 - 150 mm SL.

Sixty cryptic individuals were collected during a spring low tide in July 1992. At this time, the boulder micro-habitat in the intertidal zone at the site was shallow (15 - 30 cm deep) which made for easier collection. All moveable boulders were upended, and because small abalone are negatively phototropic, small animals could be collected as they moved to avoid the sunlight. Most animals were between 11 and 30 mm SL, although a few above 30 mm were sampled as well.

5.2.1 Food availability

In November 1992 the floral composition at the Great Fish Point site was analyzed using 0.25 m^2 quadrats. Twenty-seven quadrats were randomly thrown in the pinnacle and gully areas, and a further 23 in the shallow boulder habitat which sheltered the cryptic animals. The approximate percentage cover of the five most abundant attached algal species were visually estimated for each quadrat and recorded underwater. An estimate of percentage abundance of available flora was calculated from the pooled quadrat results in each habitat, and related to abundance of seaweeds in the diet. The regions sampled for this part of the study were subjected to considerable wave action throughout the tidal cycle, and as a result drift seaweeds could not be quantified using quadrats. Drift and attached algal species were, however, collected throughout the study and identified to species level (Seagrief 1967; 1988; Simons 1976; Branch & Branch

1981), in order to assess overall floral composition at the site.

5.2.2 Stomach content analysis

The digestive system of *H. midae* was typical of the genus *Haliotis* and is illustrated in Figure 5.1. Once ingested, food enters the buccal region where a generous supply of mucus is added before it is carried down the oesophagus by powerful ciliary currents and into the large, thin-walled muscular crop which opens into a small stomach. From the stomach, the intestine extends anteriorly then posteriorly and finally anteriorly again to the rectum and anus (McLean 1970). Whole gut contents were considered to be food present in the crop and stomach, hereafter referred to as stomach contents. The methods used were similar to those of Poore (1972a) and Shepherd (1973b). The entire visceral mass from each individual was stored in 10% formalin for two to three weeks, after which a horizontal cut was made at the spiral caecum (Figure 5.1) to expose the crop and entrance to the stomach (Figures 5.2 and 5.3). The contents were removed by thumb pressure exerted along the length of the stomach, and any remaining material was flushed into a petri dish using distilled water and a syringe. Stomach contents were allocated points according to the fullness of the crop and stomach from 0 (empty) to 10 (full). Algal fragments were spread onto a calibrated petri dish or graduated slide and examined under a stereo dissecting microscope. Identification to species level was performed wherever possible, however, if digestion was well advanced or the algal fragments too small they were placed in one of several larger taxonomic groupings. The stomachs' fullness points were then allocated to the various algal species according to the relative area they covered in the petri dish. Various species of abalone have been found to exhibit seasonal trends in feeding (e.g. Shepherd 1973b; Wells & Keesing 1989) and diet has been known to change with age (Shepherd & Cannon 1988). Assuming that this too could be the case for *H. midae*, points values were totalled for each algal species for whole seasons and for 10 mm length size classes, expressed as a percentage of the total points, and compared statistically.

Various methods of stomach contents analysis and their application were critically discussed by Hyslop (1980). Numerical and volumetric methods were impracticle for dealing with food items such as macroalgae which do not occur in discrete units or known volumes, while gravimetric methods were time consuming and tedious for small animals and some larger individuals where minute quantities of algae were involved. Furthermore, Parker (1963) remarked that material stored in formalin experienced an overall increase in weight thereby resulting in errors. Occurrence methods, while providing little indication of the relative amount of each food item

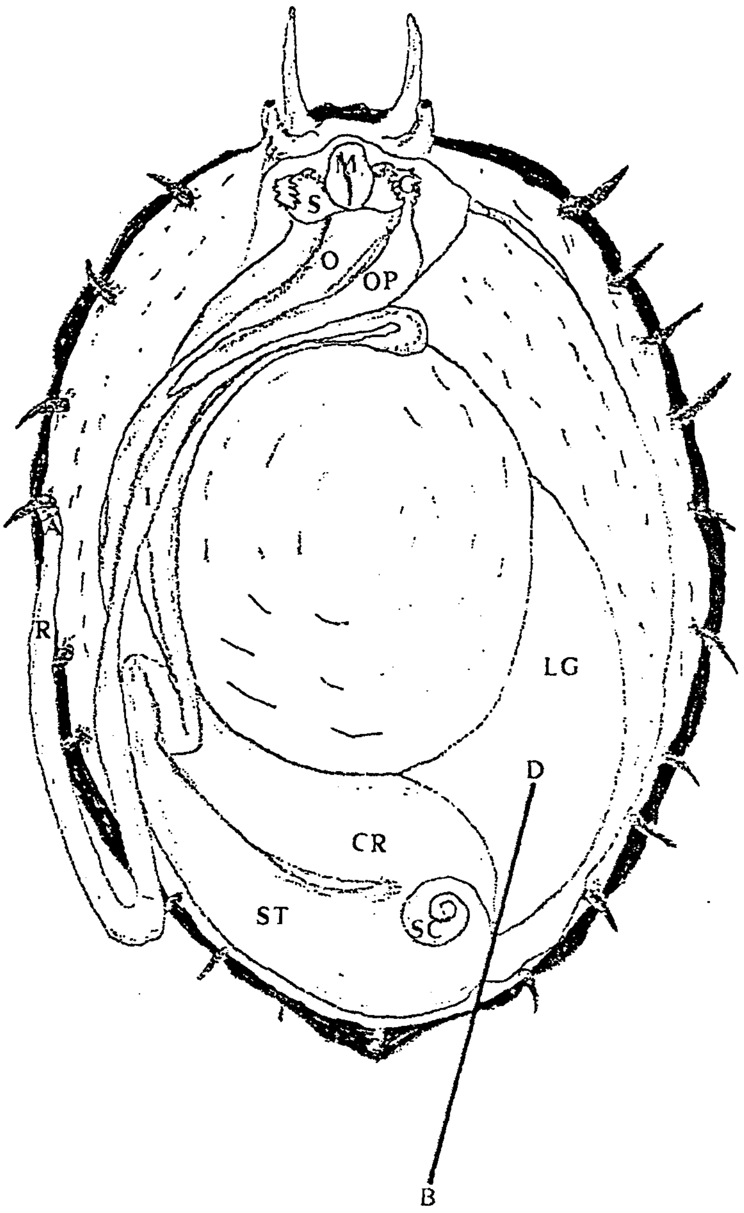

Figure 5.1 **The digestive system of *H. midae*, illustrating the anus (A), crop (CR), salivary gland (G), intestine (I), conical appendage (LG) comprising gonad enclosing the hepatic gland or liver, mouth (M), oesophagus (O), oesophageal pouch (OP), rectum (R), Buccal pouch (S), spiral caecum (SC) and stomach (ST). The line BD was the section cut to expose the crop and entrance to the stomach.**

present in the stomach, do provide a good idea of the overall food spectrum, and can be used to demonstrate seasonal changes in dietary composition (Frost 1977). The points system used in this study has been severely criticized (e.g. Hynes 1950) because of its subjectivity, but this aspect can be reduced by using a calibrated dish or graduated slide as an aid towards determining points allocation. The use of the relative assessment or points method to allocate importance has the advantage of being simple and rapid to apply (Hyslop *op. cit.*) and as a result data from a

Figure 5.3 A horizontal incision at the spiral caecum exposes the crop (C) and the entrance to the stomach (St).

Figure 5.4 The elongate stomach (St) of *H. midae* which leads on from the crop.

large number of stomachs could be recovered rapidly to provide the most informative result (e.g. Shepherd 1973b; Muller 1984).

5.3 Results

5.3.1 Algal composition

Table 5.1 summarises the floral composition at the Great Fish Point site in the exposed and cryptic habitats and indicates the abundance of attached algal species determined from the quadrat samples. Ninety-five species of seaweed were identified from the site, 56 (58.95%) of

Table 5.1 Species composition of macroalgae, abundance of the dominant attached species, and percentage abundance of algal species and other matter in the stomach samples of *H. midae* from Great Fish Point.

	Species	Percentage abundance			
		Attached flora		Stomach samples	
		Exposed habitat	Cryptic habitat	Exposed	Cryptic
DIVISION: CHLOROPHYTA				*1.03*	*6.60*
Order: Ulvales	*Enteromorpha compressa*				
	E. intestinalis				
	Enteromorpha spp.			*0.30*	*0.09*
	Ulva fasciata				
	U. insignis				
	U. rigida				
	U. uncialis				
	Ulva spp.	*2.49*	*12.40*	*1.86*	*0.59*
Order: Cladophorales	*Chaetomorpha crassa*				
	C. natalensis			*0.01*	
	Cladophora rugulosa				
	C. contexta			*0.37*	*1.37*
	Rhizoclonium sp.				
Order: Caulerpales	*Caulerpa filiformis*	*7.66*	*8.01*	*0.12*	
	C. holmesiana			*0.03*	*0.09*
	C. racemosa		*8.01*		
	Codium duthieae			*0.03*	
	C. fragile capense		*4.65*		
	C. lucasii capense		*2.33*	*0.21*	
	C. papenfussii			*0.01*	
	C. platylobium		*4.65*		
	C. stephensiae		*4.91*		
	Codium sp.			*0.09*	*0.98*
	Bryopsis caespitosa				*0.01*
	B. flanaganii				
	B. setacea				
	Bryopsis sp.			*0.39*	
	Halimeda cuneata				
DIVISION: PHAEOPHYTA				*0.34*	*1.60*
Order: Ralfsiales	*Ralfsia expansa*	*1.07*	*9.30*	*1.89*	*6.84*
Order: Dictyotales	*Dictyopterus dichotoma*		*1.03*		
	Dictyota naevosa				
	Stypopodium zonale			*0.31*	

Table 5.1/...

Table 5.1 continued.

	Species	Percentage abundance			
		Attached flora		Stomach samples	
		Exposed habitat	Cryptic habitat	Exposed	Cryptic
	Zonaria subarticulata			0.07	
Order: Sphacelariales	*Splachnidium rugosum*				
Order: Dictyosiphonales	*Endarachne binghamiae*				
	Iyengaria stellata		1.55		
Order: Laminariales	*Ecklonia biruncinata*	0.53			
Order: Fucales	*Sargassum heterophyllum*			0.11	
	S. longifolium				
DIVISION: RHODOPHYTA				14.75	1.46
Order: Bangiales	*Porphyra capensis*				
Order: Nemalionales	*Chaetangium erinaceum*				
	C. ovale				
	Galaxaura diesingiana			0.01	
	Gelidium amansii	3.57		0.88	
	G. micropterum				
	G. pristoides		5.43		
	G. cartilagineum				
	G. versicolor				
Order: Cryptonemiales	*Amphiroa ephedraea*	0.79			
	Arthrocardia carinata	0.71	3.36		
	A. flabellata			0.19	
	Cheilosporum cultratum				
	C. proliferum				
	Corallina sp.	1.07	20.93	0.01	1.19
	Duthiophycus setchellii				
	Lithophyllum sp.				
	Lithothamnion sp.	9.27			
	Chondrococcus hornemannii	1.60		0.03	
	C. tripinnatus				
	Aeodes orbitosa				
	Pachymenia cornea				
	Hildenbrandtia rosea				
	H. pachythallos				

Table 5.1/...

Table 5.1 continued.

	Species	Percentage abundance Attached flora Exposed habitat	 Cryptic habitat	 Stomach samples Exposed	 Cryptic
Order: Gigartinales	*Gracilaria beckeri*	*4.10*		*0.06*	
	G. verrucosa				
	Plocamium beckeri			*0.02*	
	P. corallorhiza	*21.75*	*5.94*	*22.03*	*0.66*
	P. cornutum			*0.01*	
	P. suhrrii			*0.93*	
	Sarcodia capensis				
	Cailiblepharis fimbriata	*1.42*	*0.26*	*1.22*	
	Hypnea rosea	*8.38*	*0.52*	*4.37*	*0.68*
	H. spicifera	*26.20*	*2.84*	*43.21*	*0.19*
	H. viridis				
	Gymnogongrus glomeratus				
	Iridaea capensis				
	Gigartina paxillata				
Order: Rhodymeniales	*Champia compressa*			*0.04*	
Order: Ceramiales	*Ceramium capense*			*0.13*	
	Spyridia cupressina	*3.39*		*1.04*	
	Callithamnion stuposum			*1.57*	*2.69*
	Botryocarpa prolifera			*0.15*	
	Acrosorium acrospermum				
	Martensia elegans				
	Polysiphonia incompta				
	Tayloriella tenebrosa				
	Pterosiphonia cloiophylla			0.69	
	Bostrychia mixta				
	Placophora binderi				
	Polyzonia elegans			*0.60*	
	Acanthophora orientalis				
	Laurencia flexuosa	*2.25*	*0.52*	*0.58*	
	L. glomerata		*1.55*	*0.49*	
	L. natalensis		*1.81*		
	L. pumila				
OTHERS	Debris				*56.27*
	Grit				*17.27*
	Thallus				*0.26*

which were red algae. Green algae constituted 28 (29.47%) of the total, while brown seaweeds comprised only 11 (11.58%) of the species. In the exposed regions red seaweeds (Rhodophyta) were dominant, comprising 13 of the 17 most abundant species, with *H. spicifera, H. rosea, P. corallorhiza* and *Lithothamnion* sp. being the most prominent. Only two species of green algae (Chlorophyta), *viz: Ulva* spp. and *C. filiformis*, featured as abundant in the exposed habitat, the latter being found in dense beds in sand inundated areas. The few brown seaweeds (Phaeophyta) present were not prominent and only two of the species, *viz: R. expansa* and *E. biruncinata* were recorded as abundant. Brown seaweeds were the least abundant floral types in the cryptic habitat as well, however, *R. expansa* was more prevalent than in the exposed habitat. Rhodophytes constituted most species from the quadrat samples, and although *H. spicifera* and *P. corallorhiza* were again featured, the cryptic region supported higher densities of *G. pristoides* and the branching corallines, *A. carinata* and *Corallina* sp. The most notable difference between the habitats, however, was that the green algae comprised the largest component of the quadrat samples in the shallow cryptic habitat, with *Ulva* spp. and *C. filiformis* being recorded as dominant together with *C. racemosa* and several *Codium* species.

Twenty-four species of algae were identified as drift components in the pinnacle and gully habitats (Table 5.2), with *H. spicifera, H. rosea, P. corallorhiza, G. amansii, C. fimbriata* and *C. filiformis* being encountered most frequently. Situated in the high energy surf zone, the surge kept the drift component moving around in the water column, with only large pieces settling on bottom. Twenty-three species of seaweed were identified drifting in the shallow cryptic habitat (Table 5.2), eighteen of which had also been encountered in the exposed region. Pieces were mostly floating on the surface or moving about in the water column, while smaller fragments were often found trapped under the boulders which characterised the habitat. *Chondrococcus hornemannii, C. fimbriata, C. filiformis, G. beckeri, H. spicifera, Ulva* spp. and *P. corallorhiza* were the main species comprising the drift component.

5.3.2 Stomach contents

5.3.2.1 Diet of exposed *H. midae*

No statistical difference was found to exist in dietary composition between size classes for exposed and cryptic animals (Table 5.3) or between seasons for the exposed individuals. All data for exposed *H. midae* was pooled for analysis, and size classes were pooled for the cryptic aspect of the study.

All exposed animals were larger than 80 mm SL. Most stomach contents could be identified to

Table 5.2 Composition of drift algal species from exposed and cryptic areas of the Great Fish Point reef.

Common to both habitats	Exposed habitat only	Cryptic habitat only
Ulva spp.	*Enteromorpha sp.*	*Caulerpa racemosa*
Caulerpa filiformis	*Caulerpa holmesiana*	*Codium fragile capense*
Iyengaria stellata	*Spyridia cupressina*	*Codium platylobium*
Ecklonia biruncinata	*Chondrococcus tripinnatus*	*Porphyra capensis*
Chondrococcus hornemannii	*Champia compressa*	*Laurencia natalensis*
Amphiroa ephedraea	*Polyzonia elegans*	
Corallina sp.		
Sarcodia capensis		
Gracilaria beckeri		
Calliblepharis fimbriata		
Gelidium amansii		
Gelidium pristoides		
Plocamium corallorhiza		
Hypnea rosea		
Hypnea spicifera		
Botryocarpa prolifera		
Laurencia flexuosa		
Laurencia glomerata		

Table 5.3 Results of the Scheffe one-way ANOVA at the 95% confidence level for differences in dietary composition between size classes and seasons for exposed and cryptic *H. midae*.

Source of variation	Sum of squares	d.f.	F-ratio	Significance level
Size classes				
Between groups	81.914	25	0.021	1.0000*
Within groups	83128.218	531		
Total (corrected)	83210.132	556		
Seasons				
Between groups	25.9635	3	0.141	0.9355*
Within groups	9597.9282	156		
Total (corrected)	9623.8917	159		

*** - No statistical difference ($P > 0.05$).**

species level, however, some could only be grouped into genera, and material which was at an advanced stage of digestion had to be placed into one of the three main macro-algal divisions (see Table 5.1). Thirty-seven species of algae were identified from the stomachs, 22 of which were red, 11 green and 4 which belonged to the Phaeophyta. As few as two algal species were found in some stomachs, while some animals had eaten as many as eleven different species. All algal matter in the diet which could be identified to species level had been identified as part of the floral component at the site. It could not be determined whether the stomach contents identified only to the genus or division level originated from the exposed habitat or not. Seventeen of the drift algae component were identified as dietary constituents, while seven species of drift seaweed were not consumed. Nine species of algae which were not observed as drift species in the habitat were found in the diet. The use of a logarithmic selectivity index (Berg 1979) provided a good indication of the relationship between dietary composition and algal availability. Calculated by dividing the log of the % food item in the stomach by the % abundance of attached algae, a positive value indicated selection for the prey item and a value less than zero suggested avoidance (Barkai & Griffiths 1986). Seven species were selected for (Figure 5.4) among which *H. spicifera, H. rosea, P. corallorhiza, R. expansa* and *C. fimbriata* were all important components of the diet. *Haliotis midae* avoided *C. filiformis, G. amansii, G. beckeri, C. hornemannii, Corallina* sp. and *L. flexuosa.* Four species of algae, three of which were corallines, were recorded as abundant from the quadrat samples, but were not ingested, these were *E. biruncinata, A. ephedreae, A. carinata* and *Lithothamnion* sp.

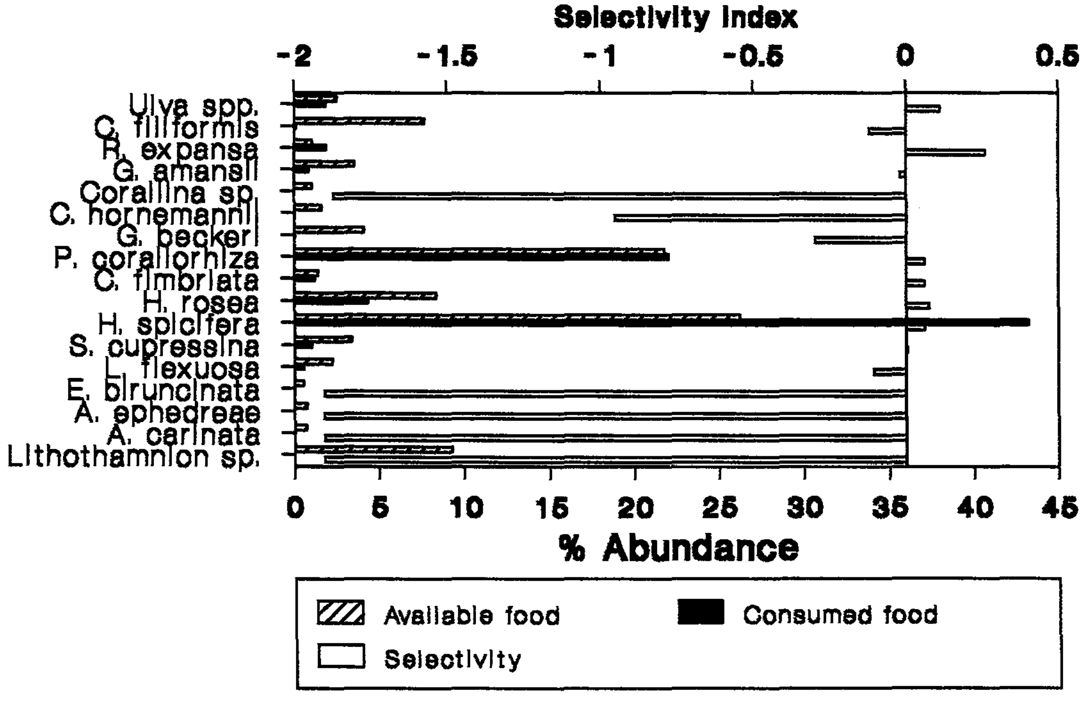

Figure 5.4 Feeding selectivity index for adult *H. midae* sampled from Great Fish Point for the period October 1991 to July 1992.

5.3.2.2 Diet of cryptic *H. midae*

The majority of the cryptic animals (52 out of 60) measured less than 30 mm SL. Stomachs of animals this size were very small and the contents difficult to identify. Twelve species of algae were, however, identified from the stomach contents (Table 5.1). Debris refers to a homogeneous ooze which comprised digested algal matter belonging to any one or all three of the seaweed divisions. Some digested matter was identifiable as either green, brown or red seaweed and placed in the respective division. Grit could have been fine sand, bits of shell or pieces of encrusting coralline algae such as *Lithothamnion* sp., and pieces of thallus were fragments of seaweed which had lost all pigmentation and as such were unrecognisable as a specific type.

Six seaweed species identified in the diet were not part of the drift component, and eighteen of the twenty-three drift species were not found in the diet of small cryptic *H. midae*. There did not appear to be a significant relationship between the abundant attached algae and those species ingested as only six out of the twenty attached species recorded from the quadrats were identified in stomach contents. Figure 5.5 illustrates the results of the log selectivity index calculations, and showed that only two of the six species were selected for, *viz: R. expansa* and *Corallina* sp., while the other four species *P. corallorhiza, H. rosea, H. spicifera* and *Ulva* spp. were ingested only in relatively small quantities. As many as 14 species recorded as abundant in the quadrats were not recorded in the diet.

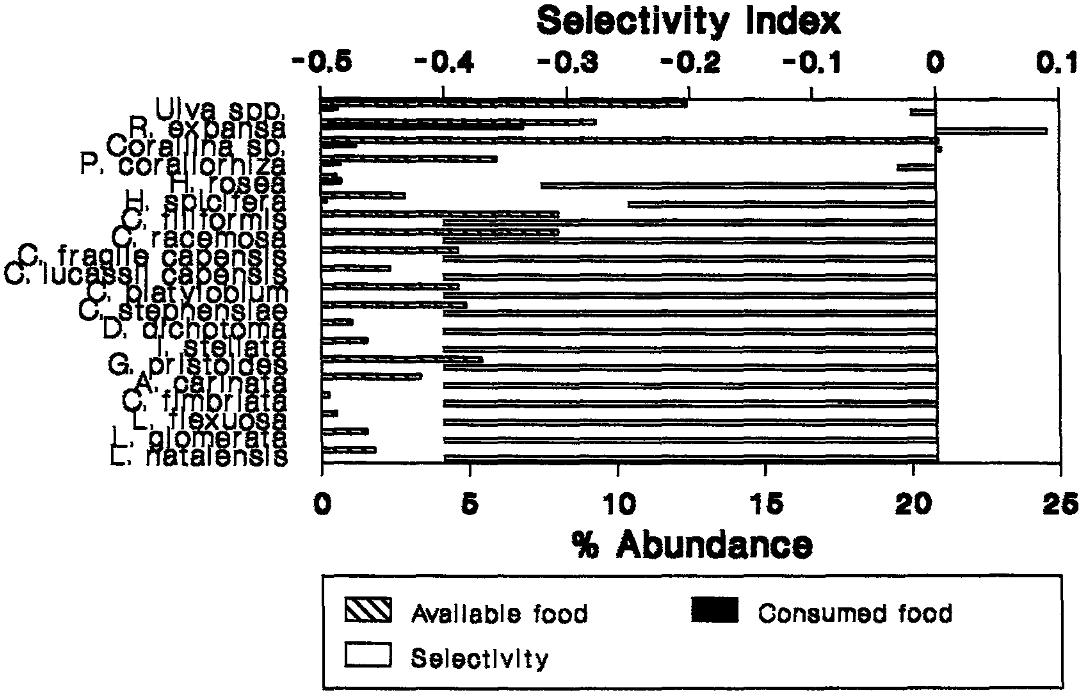

Figure 5.5 Feeding selectivity index for juvenile *H. midae* sampled from Great Fish Point in July 1992.

5.4 Discussion

Haliotis midae is an herbivorous gastropod, with a preference for red algae although a wide variety of seaweeds were eaten in habitats which were rich in algal species. Cryptic animals, however, consumed more green and brown algae than exposed individuals, although the inability to further identify the 'debris' in the gut may have resulted in obscuring the true dietary composition of the cryptic animals. Attached chlorophytes, and the phaeophyte *R. expansa*, were more abundant in the cryptic boulder habitat inhabited by young *H. midae* than in the deeper subtidal pinnacle and gully regions. There was no doubt that the rhodophytes *H. spicifera, H. rosea* and *P. corallorhiza* were the preferred diet of the larger exposed animals although they did show a high degree of selectivity for *Ulva* spp. which were not abundant in the habitat. *Ralfsia expansa* was selected by cryptic animals and supplemented largely by coralline species. The small size classes were not considered by Barkai & Griffiths (1986), but they showed that larger animals had a preference for, and selected, the kelp *E. maxima* and supplemented it largely with *P. corallorhiza* and *H. spicifera* while also demonstrating a strong selectivity for *Ulva* spp. Newman (1969) remarked briefly on the diet of *H. midae* on the east coast saying that *H. spicifera* and *P. corallorhiza* were commonly eaten, although this was not quantified. With the possible exception of shell fragments in the stomachs of cryptics, no animal matter was found in the stomachs of *H. midae*, although this phenomenon has been recorded for several other species. *Haliotis gigantea* and *H. kamtschatkana* ingested hydrozoans and copepods (Ueda & Okada 1940), *H. cracherodii* consumed foraminifera, bryozoans, shell fragments and sponge spicules (Leighton & Boolootian 1963) while *H. spadicea* (Muller 1984) also fed on numerous different non-algal prey.

It would therefore seem that while *H. midae* selected from the available seaweeds in its immediate environment, the more abundant species were generally eaten more frequently. Selection only occurred for the most abundant seaweeds (with the exception of *Ulva* spp. in the exposed habitat) while avoidance of a number of algae, both abundant and scarce seemed to take place. A similar scenario was described for *H. laevigata* (Shepherd 1973b) which was highly selective towards red algae, but also rejected fragments of the red alga *Posidonia australis* even though it was the most abundant drift species at the site. The paua, *H. iris,* appeared to browse randomly on any seaweeds it came into contact with, but also showed a degree of discrimination which was described more as a rejection of certain species than an active seeking out of preferred types (Tunbridge 1967), although this difference was not quantifiable.

While food selection is only possible if a surplus of food is available (Poore 1972a), the role of selectivity is difficult to assess even when food is abundant, because the degree of opportunism will be determined by the degree to which the animal utilises drift algae. Stomach contents alone provide unreliable clues to the feeding habits of algivorous animals in general (Leighton 1966), and in order to answer the question of whether or not selectivity of local flora features significantly in the dietary habits of *H. midae* the preference for specific floral types found at the site would have to have been determined first under experimental conditions. Dietary selection has been demonstrated experimentally for the Californian species *H. corrugata, H. fulgens, H. rufescens* (Leighton *op. cit.*; 1971), and *H. cracherodii* (Leighton & Boolootian 1963), two New Zealand species *H. iris* and *H. australis* (Poore *op. cit.*) and *H. discus hannai* from Japan (Sakai 1962a). Floral composition which differs markedly from place to place has been known to have a major influence on the diet of abalone (Poore *op. cit.*). It can therefore be expected that a feeding study at Cape Recife, Kelly's Beach or Mgwalana would reveal a dietary composition different to that exhibited by the Great Fish Point population based upon the respective sites' floral compositions with respect to both species richness and diversity, e.g. *E. biruncinata* is abundant at the Mgwalana site, and many of the larger emergent animals have been observed with fronds of this kelp clamped beneath the muscular foot.

Other feeding studies around the world have similarly shown that abalone generally have a preference for either red or brown macroalgae, and that this preference changes with respect to its abundance at any one site. Rhodophyta form the principal dietary component in *H. laevigata, H. roei, H. ruber, H. cyclobates, H. scalaris* (Shepherd 1973b), *H. iris, H. australis* (Poore 1972a), and *H. discus hannai* (Tomita & Tazawa 1971). Muller (1984) also found that *H. spadicea* preferred red algae, but that they would eat brown algae such as *E. maxima* and *Dictyota* sp. when the preferred diet was scarce. Phaeophyta were the favoured food items of *H. tuberculata* (Stephenson 1924), *H. gigantea, H. kamtschatkana, H. discus hannai* (Ueda & Okada 1940; Sakai 1962a), *H. rufescens* (Olsen 1968), *H. cracherodii* (Leighton & Boolootian 1963), *H. corrugata, H. fulgens* (Leighton 1966; Tutschulte & Connell 1988a), and *H. sorenseni* (Tegner 1989).

Algal phlorotannins, more specifically phloroglucinol oligomers and polymers, were identified as effective feeding deterrents against marine herbivores (Taniguchi *et al.* 1991; 1992). These toxic chemicals were isolated from several laminarious brown algae, *viz: Ecklonia stolonifera, E. cava, E. kurome* and *Eisenia bicyclis*, and shown to inhibit feeding in the ezo abalone *H. discus hannai*. These four algae were all perennials, and negative results for the presence of toxins were obtained for all annual species tested. The extent to which these toxins are found in other brown seaweeds may be slight, however, as the above summary indicates that brown seaweeds are important dietary constituents of many abalone species. *Haliotis midae* has been documented feeding on the brown algae *E. maxima* and *Sargassum* spp. in the Western Cape (Barkai & Griffiths 1986), and so it may be safe to assume that the brown algal species which were avoided *H. midae* at Great Fish Point were rejected for reasons other than the presence of toxic phlorotannins.

There were no references to green algae forming the bulk of the diet or being exclusively preferred by any species studied thus far. Montgomery & Gerking (1980) found that on the basis of chemical composition, green algae appeared superior to brown and red algae as potential foods. However, Percival & McDowell 1967 in Muller 1984) pointed out that for various reasons, the extracellular carbohydrates of red seaweeds were more susceptible to digestion than those of green and brown algae. Although the higher abundance and availability of red algae at Great Fish Point was most likely the major factor influencing dietary composition, the low incidence of green algae in gut contents may also be a reflection of the difficulty it provides to the digestive system of haliotids which is severely lacking in enzymes capable of degrading linked polymers such as cellulase (McLean 1970).

Poore (1972a) stated that several other factors besides floral composition may influence the choice made by abalone, these were calorific value, palatability and availability of the plant i.e. was it prone to being broken up by waves to become part of the drift component or did stronger attachment and a sturdier structure make it available only to active grazers. Algae such as *H. spicifera, H. rosea* and *P. corallorhiza* were easily detached from their stronghold, while species such as *R. expansa, Ulva* spp., many of the smaller *Codium* species and the majority of the coralline algae (encrusting and branching) were rare in the drift. Experimental work has also shown that many brown algae were more efficiently assimilated by, and promoted faster growth in *H. discus hannai* than certain red algae (Ino 1952; Sakai 1962a), while Leighton & Boolootian (1963) found that brown algae and a single species of red seaweed were the most effective weight producers in *H. cracherodii*. Poore (*op. cit*), however, found the converse was true for *H. iris*, which thrived on a diet of the red alga *Hymenocladia lanceolata*.

Recently settled haliotid juveniles feed on benthic diatoms and other benthic biota such as micro-algae and bacteria which thrive on the crustose coralline red algae functioning as a nursery substrate for newly metamorphosized juveniles (Ino 1952; Morse & Morse 1984; Garland *et al.* 1985; Sloan & Breen 1988). Epiphytic benthic diatoms have also been identified as the most important food source for young juveniles in culture systems (Ebert & Houk 1984). None of these micro-organisms were encountered in the guts of small *H. midae*, however, and one must assume that if they were consumed, it was by recently settled individuals and juveniles less than 10 mm shell length. Sand grains and diatoms dominated the diet of *H. discus hannai* juveniles early on in their first year (Tomita & Tazawa 1971) but had disappeared from the diets of 1 and 2 year olds to be replaced by macroalgae, with stomach contents in older animals sometimes being dominated by a single species of seaweed. Experiments on the food preferences of adult *H. kamtschatkana* (Paul *et al.* 1977) showed that two species of diatoms, *Chaetoceros* spp. and *Navicula* spp., which coated the sides and bottoms of aquaria, were among the preferred food items even in the presence of macroalgae. In the absence of diatoms, however, they fed on seaweeds like other abalone, exhibiting a preference for brown algae.

Unlike *H. spadicea* which was an exclusive nocturnal grazer (Muller 1984), *H. midae* fed by trapping drift algae and grazing attached algae. Animals were observed on several occasions with pieces of drift algae clamped beneath the muscular foot, and many of the species in the diet were identified as drift species. The method of drift algae capture in abalone was described for *H. rufescens* by Cox (1962) as follows: when a fragment of drift alga swept past, the anterior epipodium from both sides of the head region is extended, grasping the frond and pulling it back towards the mouth. Large pieces were passed back under the foot where they could be held for feeding (see also Tarr 1987; 1989).

There is strong evidence for grazing in *H. midae* especially amongst the smaller cryptic animals which lived beneath boulders where algae, with the exception of *Lithothamnion* sp., did not occur. In order to obtain food these animals had to move out onto the boulder surfaces which were covered by *R. expansa*, a flat encrusting alga not encountered in the drift. The only way it could have been included in the diet was for the animals to graze it by rasping it off the rock surface with their radulae. Although it appeared less important in the diet of larger emergent animals, it was still selected and it was concluded that these larger size classes graze as well. Various other species of haliotids have been described as exclusive grazers, e.g *H. roei, H. scalaris* (Shepherd 1973b), *H. australis, H. iris* (Poore 1972a), *H. kamtschatkana* (Paul *et al.* 1977), *H. discus hannai, H. gigantea* (Tomita & Tazawa 1971) and *H. tuberculata* (Forster 1967). With the exception of the last species, whose habitat was not described, the remainder were cave or crevice dwellers and were as a result obliged to move into the open to search for food. This practice has most likely led to the adoption of grazing rather than trapping as a mode of feeding. *Haliotis ruber*, however, is a cave dweller and has been classified both as a grazer and a trapper (Shepherd 1973b). Exclusive trappers whose habitat has been described as open rock face include *H. laevigata, H. iris, H. rufescens* and *H. roei* (Shepherd *op. cit.*; Poore 1972a; Olsen 1968; Wells & Keesing 1989), and *H. corrugata, H. fulgens* and *H. sorenseni* (Tutschulte & Connell 1988a). There are a number of species, such as *H. midae* (Newman 1968), *H. ruber, H. cyclobates* (Shepherd *op. cit.*) and *H. cracherodii* (Olsen *op. cit.*) which are both grazers and trappers and whose habitat may be cave, crevice or open rock faces. There are, however, no cave dwellers which are obligate trappers and no open rock face dwellers which are exclusively grazers. The immediate environment in which abalone find themselves therefore places certain constraints on the acquisition of food, for example, *H. iris* was an active grazer at Taylors Mistake where drift seaweed was virtually absent, while at Kaikoura Reef they were almost exclusively trappers in an area where they received an almost constant supply of drift algae (Poore *op. cit.*). A similar scenario was encountered for *H. roei* at two different sites, where Shepherd (*op. cit.*) found them to be grazers in southern Australia where drift algae were rare, and Wells & Keesing (*op. cit.*) described them as trappers in the Perth area of Western Australia where detached macrophytes were abundant. The differential feeding mechanisms employed by abalone would therefore appear to be the result of a response to differential availability of drift algae. In the case of *H. midae* at Great Fish Point where animals were found under boulders, in crevices, beneath overhangs or on open rock faces, and where attached and drift seaweeds were abundant all year round (personal observation), they acquired food both by grazing and trapping.

The presence of a scar or homesite on the rock surface beneath larger exposed animals was an indication that like other abalone (Sinclair 1963; Poore 1972b), *H. midae* exhibited a homing instinct with minimal movement and a dependence upon drift algae (Sloan & Breen 1988). Studies on *H. corrugata, H. fulgens* and *H. sorenseni* (Tutschulte & Connell 1988a) showed that juveniles moved around to forage at night but adults remained on homesites and relied on drift algae as a food source. Movements by large *H. iris* were deemed to be restricted because the animals returned to the same homesites after feeding a short distance away at night (Tunbridge 1967). However, movement within a species can be highly variable (Mottet 1978) with animals making localized movements when food was scarce (Ault & DeMartini 1987), but remaining stationary when drift algae were abundant (Shepherd 1973b). Sometimes situations could be extreme, with abalone not moving, and starving, when food was scarce (Macginitie & Macginitie 1966).

No nocturnal observations were made on the feeding habits of *H. midae*, but they could be regarded as nocturnal feeders for several reasons, *viz:*

(1) The majority of animals collected between 08h00 and 09h30 had stomachs which were either full or close to full, no empty stomachs were encountered.

(2) Few were observed moving about during daylight hours, and prey items were situated away from the cryptic microhabitat of the smaller size-classes indicating that both movement and feeding were nocturnal activities.

(3) During the day few animals were observed in the feeding position - with the posterior section of the foot clinging to the substratum and the anterior portion of the muscular foot and body raised at an angle [this feeding posture was first recorded and described for *H. rufescens* (Cox 1962), and subsequently for *H. laevigata, H. ruber* (Shepherd 1973b) and *H. midae* (Tarr 1989)].

(4) It was rare to observe an animal with a fragment of seaweed clamped beneath the foot during the day, except during conditions of medium surge or swell when a few individuals were seen with trapped algal fronds.

Barkai & Griffiths (1986) also found the gut of *H. midae* to be fullest in the early morning, but did not mention the time of feeding, however, based on the use of a cyclical feeding model Barkai & Griffiths (1987) determined that feeding occurred in the late afternoon and at night. *Haliotis spadicea* was described as leaving its daytime crevice habitat about one hour after sunset to forage over the substratum, returning before sunrise. However, under certain conditions during rough weather or when water turbidity increased these abalone were also observed feeding during daylight hours (Muller 1984). During exceptionally rough seas, medium and large sized *H. midae* were seen clamped down in crevices and on open rock faces respectively, and none were seen in the feeding posture, presumably because algal drift was swept up into the water column, making it unavailable. Similarly, when conditions were exceptionally calm (see also Shepherd 1973b; Shepherd 1975), the feeding posture was not observed because drift algae was not transported at all. Contrary to observations on *H. midae* at Great Fish Point and for abalone in Southern Australia, laboratory tests on *H. rufescens* (Olsen 1968) demonstrated that more food was consumed with an increasing water current. Environmental factors besides current or surge, such as temperature (Leighton 1966; Barkai & Griffiths 1986), and activities such as spawning (Ino 1952; Sakai 1962a) may, however, also be responsible for observed feeding patterns in abalone.

The significance of nocturnal feeding patterns could be to avoid predators, as the many predators of *H. midae* such as the octopus *O. vulgaris*, the Cape rock crab *P. chabrus* and many reef fishes are inactive at night - this was also proposed by Muller (1984) as the reason for the nocturnal grazing habits of *H. spadicea*, and by Shepherd (1973b) for the nocturnal activity of five Australian species, although one species, *H. ruber*, became active in the late afternoon at times. In Southern Australia, *P. chabrus* is known as the cleft fronted shore crab, but like its South African conspecific, together with other predators of abalone such as senator fish (*Pictilabrus laticlavius*), scaly fins (*Actinochromis victoriae*) and parrot fish (*Pseudolabrus tetricus*), *P. chabrus* was active by day, at dusk and at dawn and inactive at night resting in crevices and caves. The Western Australian abalone *H. roei* was also most active at night between about 18h00 and 04h00 hours when all animals were either in the feeding position or actually feeding on algae (Wells & Keesing 1989).

Sea urchins and abalone are both large invertebrate herbivores which feed nocturnally, and are most often found cohabiting kelp forest communities (Tegner & Levin 1982) or intertidal and subtidal reefs (Shepherd 1973a; personal observation). In addition, both are relatively sedentary, employ the same primary mode of feeding, show similar food preferences, have planktonic larvae and have a number of common predators. These strong ecological similarities have led to the belief that they may well be competitors (Cox 1962; North & Pearse 1970; Tegner & Levin *op. cit.*). Sea urchins are fine-grained grazers, i.e. they graze unselectively and crop close to the substratum which does not allow for the establishment of algal spores, resulting in large areas of bare rock. Abalone are coarse-grained grazers which either catch drift algae or graze algae without cropping closely. "Competitive elimination of a coarse-grained grazer can occur when a fine-grained grazer reduces the resource to such a low level that the other cannot maintain its population" (Shepherd *op. cit.*). The abalone *H. ruber* has been displaced in this way by the black sea urchin *Centrostephanus rodgersii* at two locations in Eastern Victoria, Australia. Red sea urchins *Strongylocentrotus franciscanus* and red abalone *H. rufescens* occupy the same microhabitats in California's kelp forests and competition between them may be important under certain circumstances (Tegner & Levin *op. cit.*). However, in contrast to the above situation between *H. ruber* and *C. rodgersii*, it would seem that in the past *H. rufescens* had the ability to regulate populations of *S. franciscanus* through interference competition when food supplies were adequate. Due to extensive exploitation, however, both species are nowdays maintained well below their carrying capacities and present population levels are instead controlled by predation and environmental factors affecting food supply.

Haliotis midae lives in close association with the sea urchin *P. angulosus*. During the day *P. angulosus* was found under boulders or in caves and crevices with small and medium sized perlemoen while at night they move over the substratum to graze, coming into contact with large emergent *H. midae* occupying open rock faces. Fricke (1979) described *P. angulosus* as an exclusive algal grazer with a preference for *E. maxima* in the False Bay region of the Western Cape. However, more recent work in the Eastern Cape showed *P. angulosus* to be an opportunistic omnivorous nocturnal grazer which is seemingly more of a generalist than *H. midae* (Neville Sweijd, Department of Zoology, University of Cape Town, personal communication). The high densities in which urchins were found at Great Fish Point implied that competition for food and space with *H. midae* could occur. Certain areas of the reef were characterized by large boulders denuded of almost all macroalgae except for the pink encrusting coralline *Lithòthamnion* sp. These 'pink' areas were devoid of *H. midae* but were inhabited by large numbers of urchins. This was strong circumstantial evidence for the competitive exclusion of *H. midae* by urchins due to destruction of available food. However, in the absence of any evidence apart from visual observations, any predictions about the occurrence of competition between these two intertidal cohabiters remains speculative.

The source of pigments in the shells of prosobranch molluscs remains largely unknown, although Comfort (1951) stated that metabolic wastes were the major components of shell pigments. Fretter & Graham (1962) remarked that dietary factors could on occasion affect the colour of the shell by altering the type of pigment (porphyrins or bilins) which was bound to the protein material incorporated in the shell, e.g. the red pigment in the shells of the Californian red abalone *H. rufescens* (Leighton 1961) was identified as a phycoerythrin, a red bilin type pigment of rhodophytes. Red shell colours were indicative of red algal diets in *H. sorenseni, H. rufescens, H. corrugata* and *H. cracherodii,* while a turquoise blue or off white colour was noted for algae other than red varieties (Olsen 1968). Red algae produced a dull red-brown shell colour in adult *H. iris* (Poore 1972a), while juveniles feeding on brown algae exhibited an icy-blue to pale green prismatic layer. Diet seemed to have little influence on shell coloration in *H. australis* or *H. assimilis* (Olsen *op. cit.*). The latter species apparently exhibits a degree of genetic control over the capabilities of individual abalone to incorporate pigments into the various shell layers. The colouring of the shell in *H. midae* from Great Fish Point was a mixture of pink or brick-red and white in most larger animals, while a deep purple was the prominent colour for animals < 30 mm SL (Figure 5.6).

The relationship between shell coloration and diet in abalone could potentially be used to determine trends in floral succession in areas or to trace seasonal variation in abundance of certain algal species provided the animals used are sedentary, live for a decade or more and eat the macroalgae in their immediate vicinity (Leighton 1961; Olsen 1968). Inferences about the dietary composition of abalone could also be based upon shell coloration, e.g. the mottled shell colour of the pinto abalone *H. kamtschatkana*, the flat abalone *H. walallensis* and the threaded abalone *H. assimilis* led Cox (1962) to speculate that their diet contained high levels of coralline and diatomaceous algae. This was later proved to be true for the pinto abalone in laboratory tests by Paul *et al.* (1977). In the case of *H. midae* at Great Fish Point, the red shell colour reflected the predominance of red algae in the diet. Shells from Cape Recife, Kelly's Beach, Bird Island and Mgwalana were all similarly coloured (Figure 5.6). This could be an indication that along the Eastern Cape coast, *H. midae* consumes predominantly red seaweeds as opposed to the kelp *E. maxima* which was its staple diet in Western Cape waters (Barkai & Griffiths 1986).

Figure 5.6 Shells from adult and juvenile *H. midae* from Great Fish Point (F), Mgwalana (M) and Cape Recife (CR) illustrating the similar coloration patterns.

CHAPTER 6 REPRODUCTION

6.1 Introduction

The invertebrate world comprises a diversity of reproductive modes from primitive to highly evolved and which are asexual as well as sexual (Giese 1959). Like many marine invertebrates (e.g. coelenterates, annelids, echinoderms, and molluscs such as lamellibranchs and amphineurans), abalone are dioecious broadcast spawners (Brown 1991) which release their gametes through respiratory pores (Shaw 1991) into the water column. This facilitates external fertilisation (Fretter & Graham 1962; Webber & Giese 1969; Shepherd & Laws 1974; Shepherd 1976) and the development of the ensuing lecithotrophic larval stages (Leighton 1974) which ensure dispersal (Prince *et al.* 1987). In the molluscs, broadcast fertilization is more common in the primitive forms of gastropods (Webber & Giese op. cit.), although it does feature in most of derived forms of chitons and bivalves as well. The duration of the resultant pelagic stages is variable, although the trochophore larvae are usually formed in a matter of hours post-fertilisation. The formation of a larval shell marks the beginning of a transformation into the veliger stage complete with internal organs (Ino 1952). After torsion which results in the positioning of the anus near the head, the larvae spend anywhere from 2 to 14 days in the water column (Oba 1964; Leighton 1974; Glover & Olsen 1985). They are then induced to settle by chemical stimuli from mucous trails of grazing conspecifics (Seki & Kan-no 1981a,b; Barlow 1990; Slattery 1992) or encrusting coralline algae such as *Lithothamnion* spp. (Shepherd 1973b; Morse & Morse 1984; Shaw *op. cit.*), and assume the lives of bottom dwellers. Abalone larvae lack a digestive system which accounts for them being described as lecithotrophic or 'non-feeding' (Manahan & Jaeckle 1992), however, recent evidence has indicated that larvae of *H. rufescens* were capable of 'feeding' by absorbing organic carbon in the form of sugars and amino acids from the surrounding sea water. With the exception of age and growth studies (Sainsbury 1982), reproduction is the most extensively studied aspect of haliotid biology. Since the first detailed study of haliotid reproduction was performed on *H. lamellosa* by Bolognari (1953), there has been a steady flow of publications from all over the world on the topic to the present day. A summary of some of the more noteworthy papers appears in Table 6.1 - studies on South African haliotids are excluded as they are handled separately below.

Newman (1967b) conducted studies concerning gonad structure, sex ratio, sexual maturity, spawning and fecundity in *H. midae*. His studies were, however, limited to populations from the south-western and western Cape, situated at Dassen Island, Sea Point and Stony Point. Subsequently, due the potential of *H. midae* as a culture species, Genade *et al.* (1988) described spawning, development and rearing of the animal under controlled laboratory conditions. Other than the "siffie" *H. spadicea* whose reproductive biology was comprehensively investigated by Muller (1984), reproduction in the other four South African haliotid species has not been studied.

Table 6.1 A review of some studies on the reproductive biology of haliotid species.

Species	Aspects studied	Reference
H. cracherodii & *H. rufescens*.	Spawning seasons related to Gonad Bulk Index (GBI).	Boolootian *et al.* (1962)
H. cracherodii.	Reproductive cycle; gametogenesis; environmental influences.	Webber & Giese (1969)
H. rufescens.	Reproductive cycle; gonad histology & gametogenesis.	Young & DeMartini (1970)
	Reproductive cycle; maturity; maturity; fecundity.	Giorgi & DeMartini (1977)
	Detailed histology; GBI; spawning and cycling.	Ault (1985)
H. iris & *H. australis*.	Gametogenesis; spawning; maturity; fecundity; sex ratios.	Poore (1973)
H. cyclobates, *H. laevigata*, *H. roei*, *H.* *H. rubra* & *H. scalaris*.	Sexual maturity; spawning cycle factors inducing spawning; spawning; sex ratios.	Shepherd & Laws (1974)
H. tuberculata.	Reproductive cycle; gonad indices sex ratio; timing of spawning.	Hayashi (1980a)
H. fulgens, *H. corrugata* & *H. sorenseni*.	Reproductive cycles; sex ratios ratios; fecundity; age at maturity.	Tutschulte & Connell (1981)
H. roei.	Histological reproductive stages GBI; fecundity.	Wells & Keesing (1989)

In order to formulate regulations for an exploited species such as *H. midae*, studies involving aspects of their reproduction are essential. In this chapter a detailed study of *H. midae's* reproductive biology is described from the Eastern Cape, that includes sex ratio, size at sexual maturity, spawning season (timing and duration), gametogenesis, the reproductive cycle and fecundity. The role that environmental parameters play in the initiation and control of spawning are also discussed.

6.2 Materials and Methods

Monthly samples were collected from Great Fish Point at low tide from April 1991 to August 1992 and from Mgwalana from September 1991 to July 1992. No samples were obtained from Great Fish Point in December 1991 due to rough seas and bad visibility, and samples from both sites could not be obtained for February 1992 for similar reasons. Sampling at Cape Recife was performed during May, July, September and November 1991 and May and July 1992. During May, June and July 1992, samples were collected from Kelly's Beach. All samples were collected by free diving, and an attempt was made to get animals from as large an area as well as large a size range as possible, in order to determine the reproductive pattern of the whole population. All animals were shucked and whole weight, shucked weight, shell weight, shell length, shell width and sex were recorded. A variety of methods can be used for determining the reproductive cycle and spawning season of marine invertebrates (Giese 1959), such as observations of spawning both in the field and the lab and assessment of larval densities in the water column, but he recommended that, ideally, one required cytological studies in combination with gonad index values. Both of these aspects along with several others were considered in this study of the reproductive biology of *H. midae*.

6.2.1 Gonad Bulk Index (GBI)

In order to obtain a macroscopic picture of gonad activity and an indication of spawning season and reproductive synchrony within a population, mean monthly GBI's were determined using the modified index of Tutschulte & Connell (1981). The entire visceral mass of each individual was preserved in 10% formalin for three weeks, after which a section was removed from the mid-point of the conical appendage arc length and the linear dimensions of the conical appendage and the digestive gland were measured using vernier callipers (Figure 6.1). Using these measurements, a lower bound estimate of the effective gonad volume (EGV) was calculated as follows:

$$EGV = \frac{AS\,\pi}{96}\left\{8(x+y)^2 - \frac{(x+y+a+b)^3}{(x+y)}\right\}$$

(Symbols are explained in Figure 6.1).

The EGV of each individual was divided by its body weight, which was taken as the drained and blotted weight of the shucked animal, for an estimate of gonad bulk index as follows:

$$GBI = \frac{EGV}{\text{Body Weight}}$$

Two other gonad indices, namely the gonad bulk index (GBI) of Newman (1967b), and the gonad index (GI) used by Boolootian *et al.* (1962) were rejected because Ault (1985) found that they were unable to detect statistically significant changes in mean gonad size throughout the reproductive cycle.

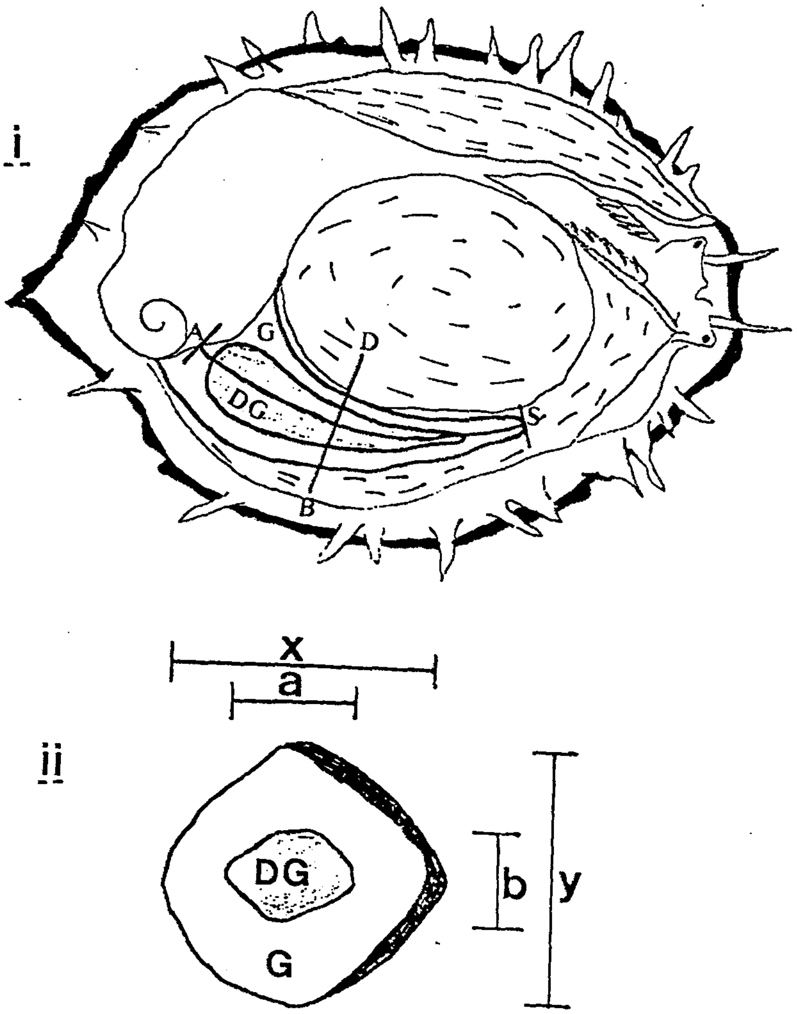

Figure 6.1 i. The position of the section BD halfway along the measured cone length (AS). Part of the gonad (G) has been cut away to reveal the hepatic or digestive gland (DG) within.
ii. The linear dimensions of the digestive gland (a & b) and the entire section (x & y) used for the calculation of a lower bound estimate of the Effective Gonad Volume (EGV).

6.2.2 The Reproductive Cycle

In order to confirm the GBI pattern and for a more accurate assessment of spawning and the reproductive cycle, histological examination of male and female reproductive tissue was performed on a monthly basis. All tissue was fixed in Bouin's solution (Humason 1979) for three days and then stored in 50% ethyl alcohol. The tissue was subsequently dehydrated then embedded in paraplast, sectioned at 7 - 10 microns and stained using Gill's haematoxylin. Preparations were differentiated in acid water, blued in Scott's solution and then counterstained in Eosin Y (Humason *op. cit.*). Tissue preparations were examined and photographed with a Nikon Optiphot compound microscope.

The stages in the reproductive cycle were identified using the criteria described by Wells & Keesing (1989) for *H. roei*. Five stages were identified depending on the type of gametogenic cell types present and their level of development. In addition, the diameter of eggs in which the nucleus was visible were measured for each ovary using an optical micrometer at 63x magnification - all eggs in the field of vision were measured. The percentage volume occupied by mature sperm in each cross-sectional area of testes was also established at 100x magnification. Both egg diameters and percentage mature sperm coverage were expressed as frequency histograms.

6.2.3 Sex Ratios

For a three month period corresponding to peak GBI values in 1991 & 1992, animals which could be sexed macroscopically over as large a size range as possible were collected from all four sample sites. A few of the smaller size classes were examined histologically to determine whether gametes were present in the absence of gonad pigmentation. Although gonad coloration may change during the year, females were always some shade of green, while males ranged from pink to creamy/white (Figure 6.2). They were arranged in 10 mm size classes and a χ^2 test performed to determine whether a 1:1 sex ratio existed for *H. midae*.

6.2.4 Size at Sexual Maturity

The same animals which were used for sex ratio estimates were examined to determine both the size at onset of sexual maturity and the size at 50% sexual maturity. Newman (1967b) used only macroscopic coloration of gonads as an indication of sexual maturity, and while this may suffice for larger individuals smaller animals were examined histologically. The reason for this is that gonadal pigmentation may not necessarily be an indication of the presence of mature gametes, while gametes may also be present in the absence of pigmentation (Giorgi & DeMartini 1977). An individual was classed as being mature if it contained mature gametes (e.g. Shepherd & Laws 1974; Tutschulte & Connell 1981) i.e. males contained spermatozoa and females possessed vitellogenic oocytes.

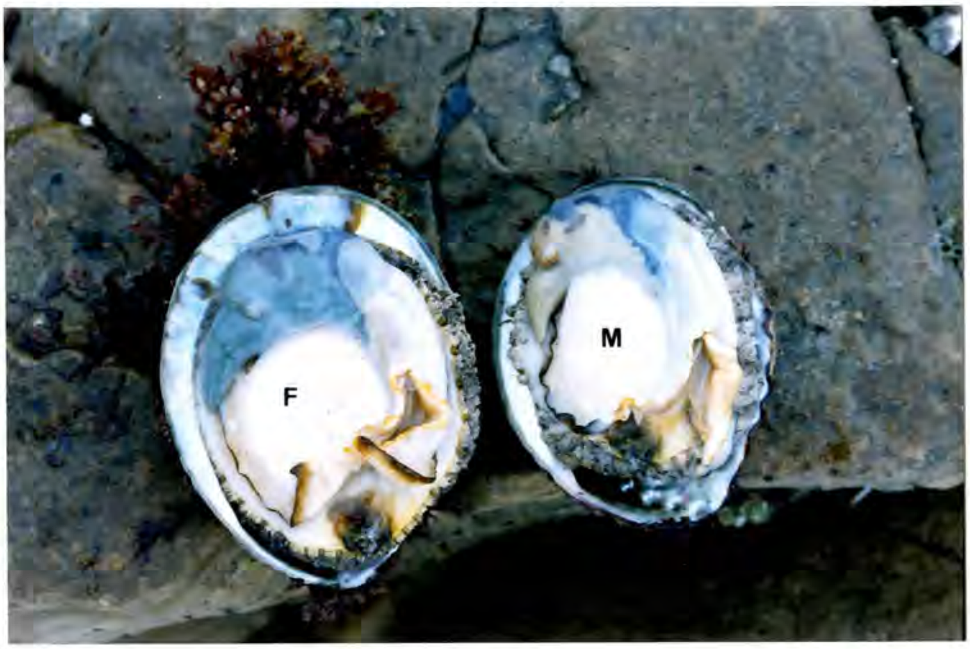

Figure 6.2 Two specimens of *H. midae* from Great Fish Point illustrating the green ovary of a female (F) and the creamy/white testis of a male (M).

6.2.5 Fecundity

The fecundity of *H. midae* was investigated from combined samples at Great Fish Point, Mgwalana and Cape Recife. A total of 96 females over a wide size range were sampled during peak gonad activity in May and June 1992. The ovaries were separated from the rest of the visceral mass after they had been hardened in 10% formalin for a week. The whole gonad mass was recorded and a small piece (0.03 - 0.05 g) excised and stored in 5% formalin. Eggs were separated from the trabeculae with the help of a paint brush and dissecting needle. Counts were made at 15x magnification under a dissecting microscope, using a petri dish with a grid system to ensure accuracy. The total number of eggs in the ovary were then determined as follows:

$$\text{Total number of eggs} = \frac{\text{mass of ovary x number of eggs in fragment}}{\text{mass of fragment}}$$

In ripe ovaries there was a predominance of large mature oocytes, however, there were moderate numbers of smaller oocytes as well (Figure 6.3). In spent ovaries there was a total absence of large oocytes, but the smaller sizes were still present. Based on this, only eggs larger than 100 µm were used in the fecundity counts. Preliminary estimates were made from five females at Great Fish Point collected during the peak GBI phase in May 1991 in order to test for egg density variation in different parts of the ovary. Newman (1967b) described the ovary as "..an extensive organ with a fairly uniform structure". He did, however, recognise the need to test for variation in egg density from different regions of the gonad. Egg counts were made for each of

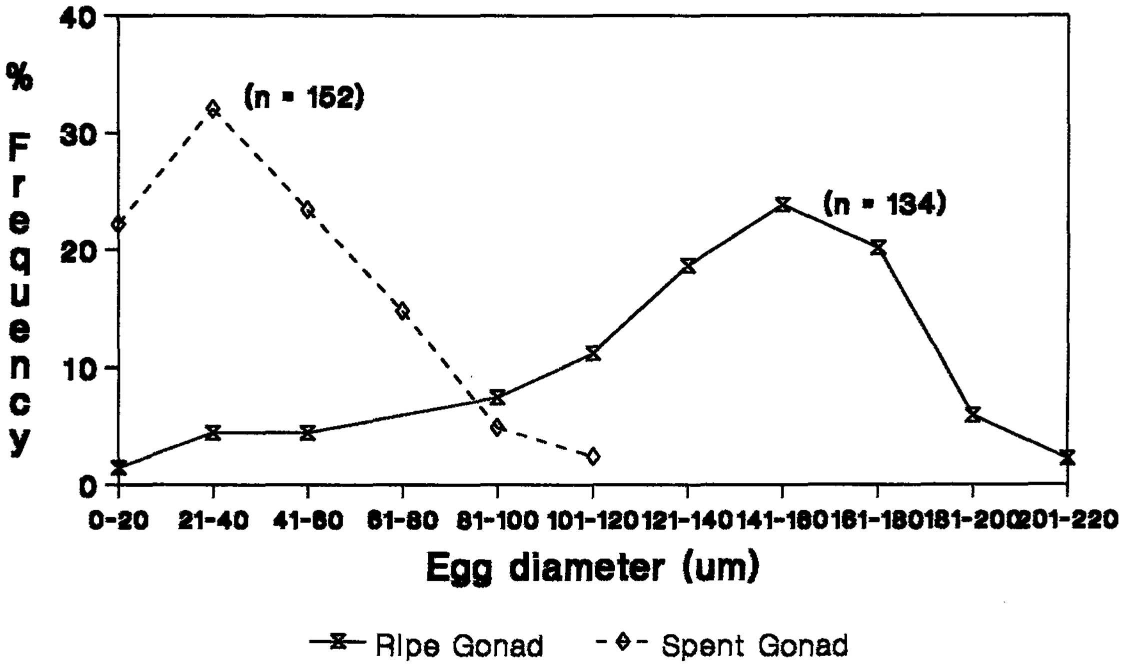

Figure 6.3 Size distribution of oocytes in two ripe and two spent ovaries of *H. midae* from Great Fish Point (May 1992).

the five females from the anterior, middle and posterior parts of the gonad, with each region being counted five times to test for counting error within each sample. Each count was converted to an estimate of number of eggs per gram of ovary. Analysis of variance showed there to be no significant difference between either of the variables (Table 6.2), so one count was made per female from a fragment from the middle portion of the remaining gonads.

Table 6.2 Analysis of variance of eggs per gram from three different areas of the ovary (anterior, middle and posterior) and from five replicate counts per area in five ovaries of *H. midae* collected at Great Fish Point in May 1991.

Source of variation		Shell length (mm)				
		84.3	127.7	130	133.4	143
Between ovary location	SS	67671	2281013	5038453	457333	2187360
	d.f.	2	2	2	2	2
	F-ratio	0.903*	0.970*	1.603*	0.097*	0.786*
Between counts	SS	14873	11694827	9849226	445333	8914293
	d.f.	4	4	4	4	4
	F-ratio	0.993*	2.488*	1.567*	0.047*	1.602*

SS - Sum of squares.
*** - No significant difference (P > 0.05).**

6.3 Results

6.3.1 Gonad Bulk Index

When abalone gonads are in a ripe condition, the EGV and hence the GBI values are at a maximum. When spawning occurs and gametes are voided from the lumen, the gonads collapse thereby decreasing the EGV and GBI. Based upon these assumptions, GBI's were used to track the reproductive activity of *H. midae* populations. They provided an overall idea of the reproductive cycle and hinted at the timing and duration of spawning and recovery, i.e. the degree of synchrony in a population. Care was, however, taken not to assume too much from GBI's as they had several limitations, *viz*:

(1) They provided no indication of the amount of tissue other than gametes in the gonad, and there was no indication of the time at which gametogenesis was initiated after spawning (e.g. Poore 1973; Webber & Giese 1969).

(2) They could not be used as an indicator of the stage of gamete development, particularly in early stages when GBI values were almost identical (e.g. Muller 1984).

(3) Decreases in GBI's did not necessarily indicate spawning, but could instead have been as a result of gamete resorption.

(4) They provided no information on the extent of the spawning event once it had occurred, i.e. whether it was partial or total.

The histological aspect of the study, however, compensated for these limitations.

The GBI's for *H. midae* from the study sites for the duration of the study period are shown in Figures 6.4 (Great Fish Point), 6.5 (Mgwalana) and 6.6 (Cape Recife).

For all three sites peak spawning activity appeared to have taken place in late autumn and early winter 1991 but persisted in parts of the populations until November, with a brief rest period in August and September at Great Fish Point and Mgwalana. A small section of the Great Fish Point population could have spawned between January and February 1992, but no evidence for this was forthcoming from the other two populations. Once again there was a build up to peak condition around April and May 1992 at Great Fish Point and Mgwalana, and the spawning season seemed to be protracted. The population at Cape Recife was still recovering when sampling was terminated in July 1992, with no evidence of spawning. The pattern for all three sites indicated that spawning in *H. midae* was not synchronous as there was no sudden decrease in GBI values but instead a gradual reduction over a 3-4 month period. This assumption was validated below in section 6.3.2.

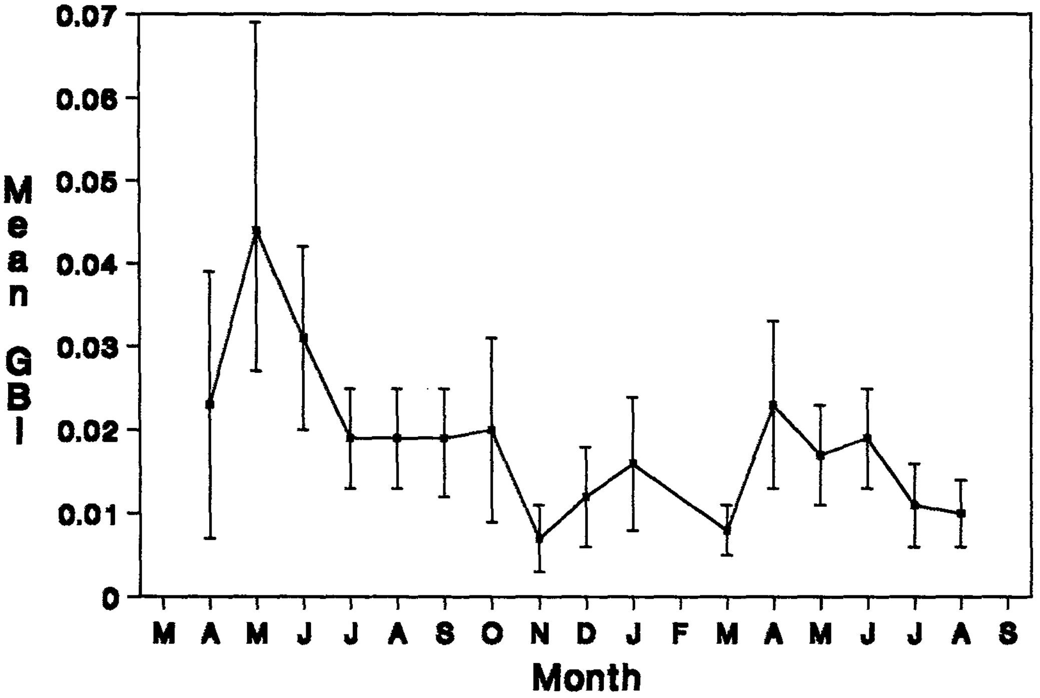

Figure 6.4 The mean monthly GBI's with standard deviations for *H. midae* from Great Fish Point for the period April 1991 to August 1992.

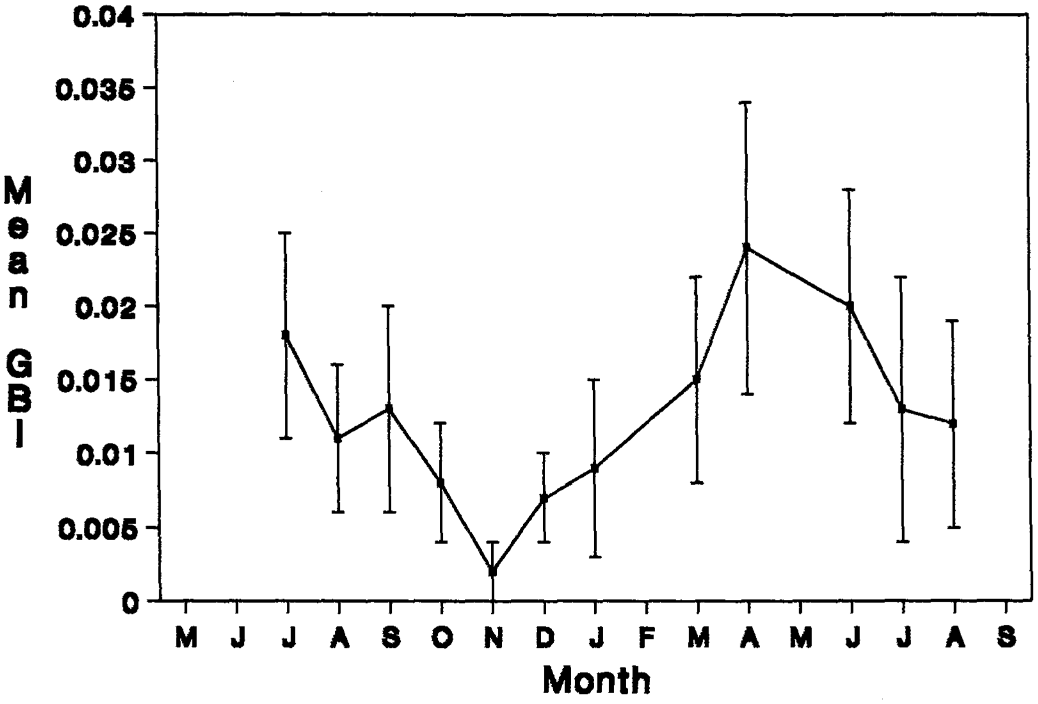

Figure 6.5 The mean monthly GBI's with standard deviations for *H. midae* from Mgwalana for the period July 1991 to August 1992.

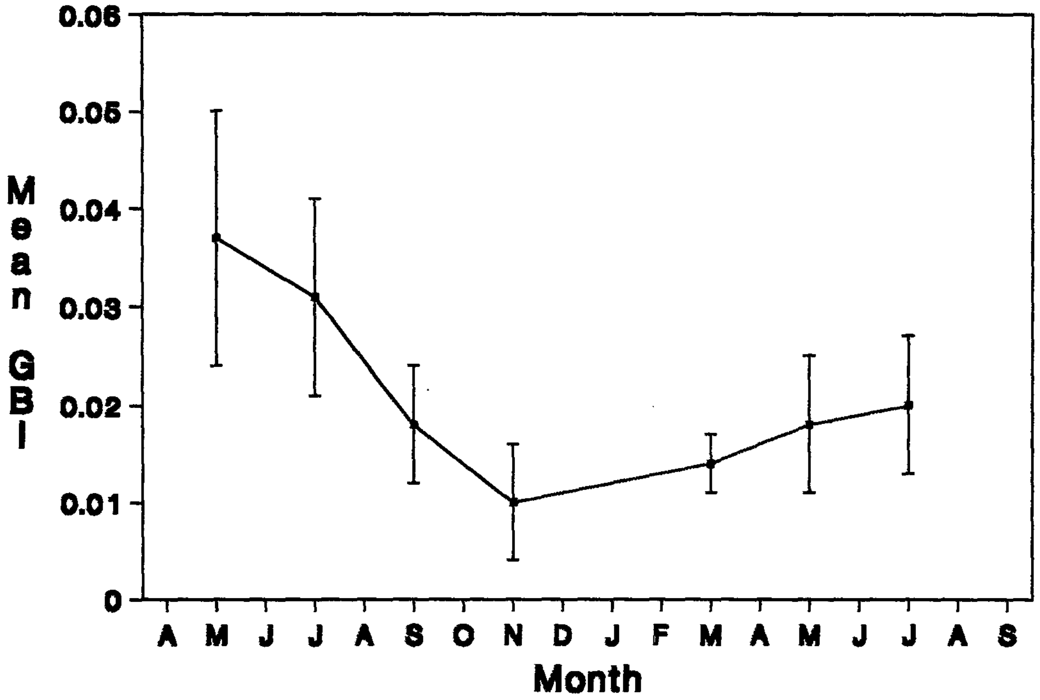

Figure 6.6 Mean monthly GBI's with standard deviations for *H. midae* from Cape Recife for the period May 1991 to July 1992.

6.3.2 Histology of the Reproductive Cycle

Macroscopic description of the ovary

Haliotis midae possessed an extensive superficial gonad (Newman 1967b). The ovary lies spread over the digestive gland and part of the stomach, extending around the horn structure called the conical appendage (Figure 6.1). While the colour of the ovary was generally green, it changed according to its state of development to grey or blue-green (e.g. Shepherd & Laws 1974; Shepherd 1976) to grey or blue-green. Essentially, the ovary consisted of a large lumen bound by germinal epithelium (Newman 1967b) arising from the muscular wall and glandular columnar epithelium which comprised the epidermis. The epidermis was covered by a thin cuticle was lacking from the inner layers between gonad and digestive gland. Electric shock treatment of the gonad in the red abalone *H. rufescens* by Young & DeMartini (1970) led them to believe that contractions of the muscular wall aided in the expulsion of gametes, although Newman (1967b) professed that the gonad walls of *H. midae* were not contractile and that gametes were expelled when the large adductor muscle compressed the visceral mass between the shell and muscular foot.

The lumen of the ovary was packed with trabeculae which consist of connective tissue and muscle fibres in compact arrangement supporting a germinal epithelium. Trabeculae ran parallel to one another (Figure 6.7) and were arranged in a series of polyhedral columns projecting from the outer ovarian wall towards the digestive gland. Some attached to the inner ovarian wall, indicating that they had a supportive role as well as acting as a base for germinal tissue (e.g. Young & DeMartini 1970). Most trabeculae ended freely in the lumen, perhaps to allow for free movement of eggs during spawning (Newman 1967b). Branches of the hepato-genital blood vessels were found in the connective tissue of the inner ovarian wall, and blood sinuses projected into the ovary lumen (Figure 6.8), but were often difficult to see in recovering or ripe gonads due to their being compressed by the egg mass.

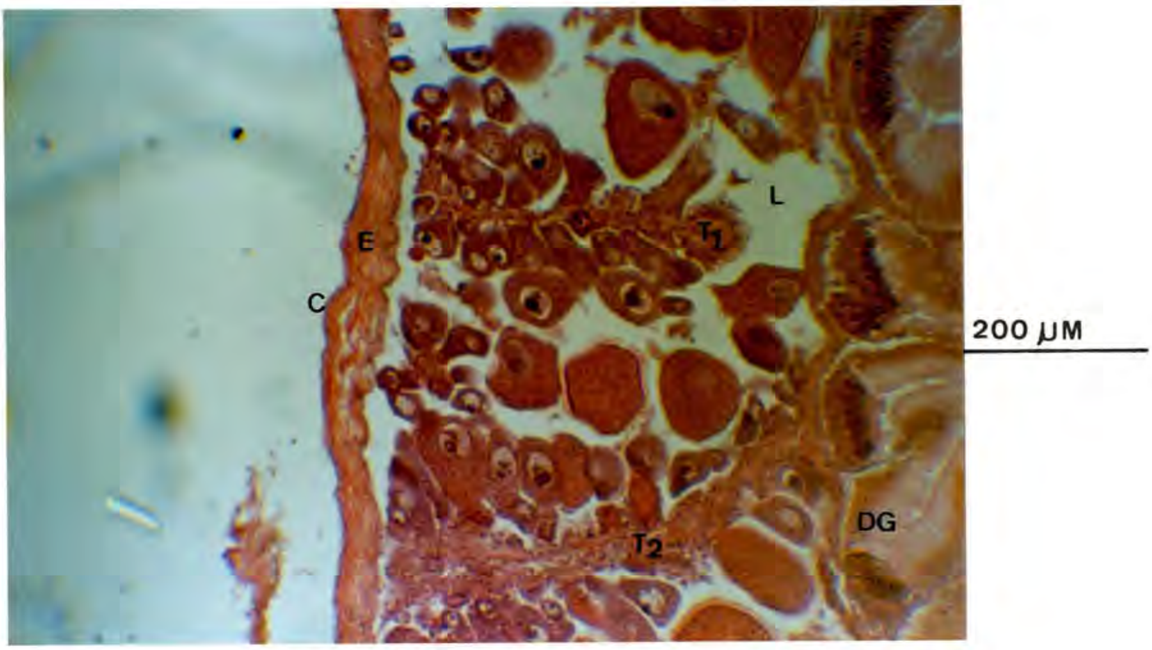

Figure 6.7 **Cross-section through an ovary of *H. midae* illustrating the outer cuticle (C), digestive gland (DG), epidermis (E) comprising a muscular wall and glandular columnar epithelium, gonad lumen (L) and trabeculae, some of which end freely in the lumen (T_1) and others which attach to the inner ovarian wall (T_2).**

Microscopic description of the ovary (Figure 6.9)

Germinal epithelium lined every available surface within the ovary lumen, and in immature individuals was squamous. As the animal matured and oogenesis was initiated, it became cuboidal (e.g. Young & DeMartini 1970). These cuboidal cells were the oogonia and were generally found in dense clusters. They were highly basophilic and less than 14.7 µm in diameter, and gave rise to two distinct types of primary oocytes. The first type were small previtellogenic oocytes, ranging in size from 16 - 46 µm, which were still highly basophilic. Some of the larger

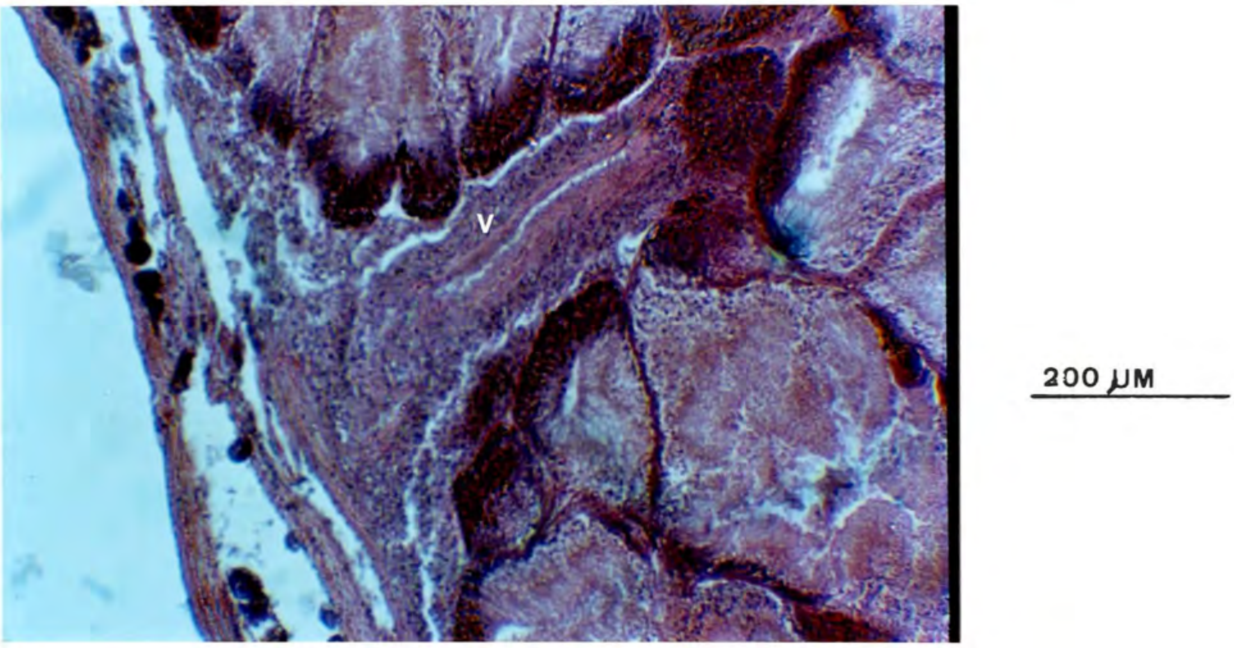

Figure 6.8 Cross-section through an ovary of *H. midae* illustrating a branch of a hepato-genital blood vessel (V) projecting into the gonad lumen.

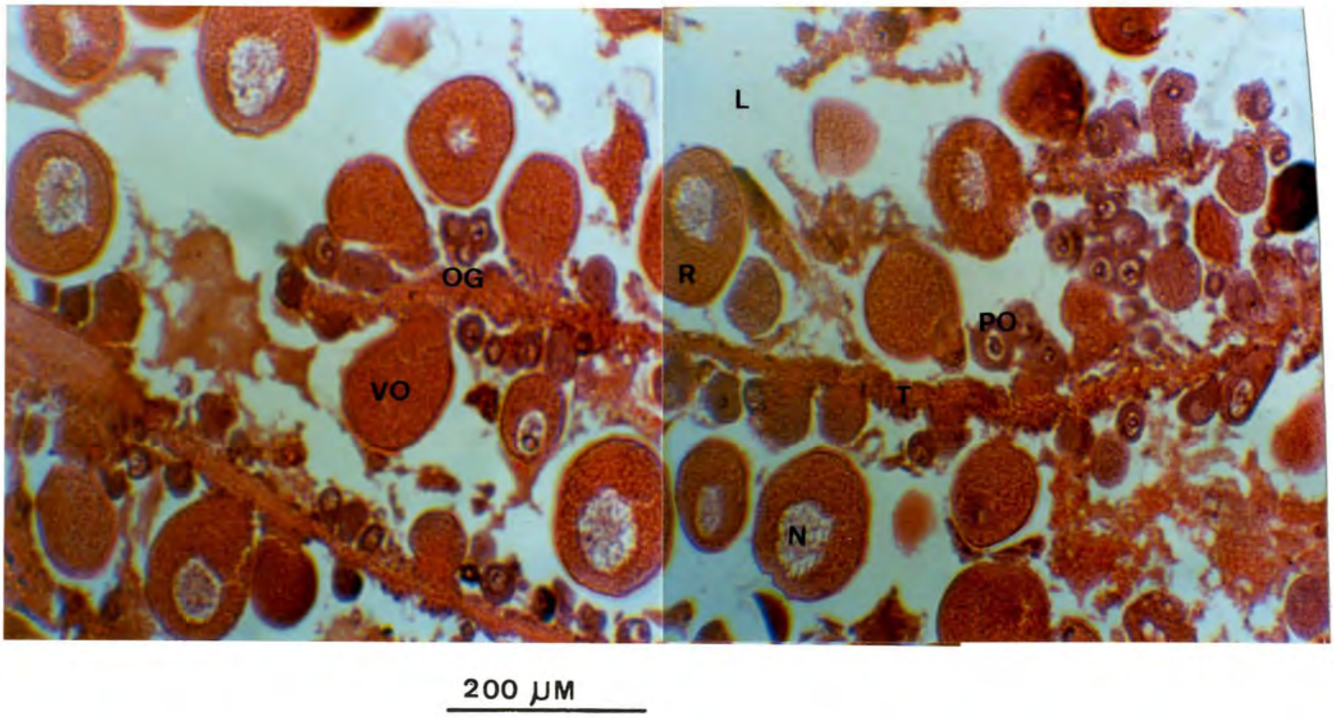

Figure 6.9 Cross-section of *H. midae* ovary illustrating gonad lumen (L), nucleus (N), oogonia (OG), previtellogenic oocytes (PO), ripe eggs or ova (R, trabecula (T), and stalked vitellogenic oocytes (VO).

ones (> 35 µm) were attached to trabeculae by stalks. The second type were larger (50 - 145 µm) and mostly attached by stalks and orientated towards the digestive gland. While the nucleus remained strongly basophilic and gradually migrated to the animal pole opposite the vegetative stalk, the cytoplasm became eosinophilic as vitellogenesis was initiated. During development of the primary oocytes, two eosinophilic membranes were formed around the plasma membrane. In accordance with Young & DeMartini (*op. cit.*) the inner layer was the vitelline membrane and the outer layer the chorion. The final stage of development was the ripe eggs or ova, ranging in size from 150 - 223.5 µm. All were free in the lumen, although the remains of stalks could be seen on recently detached eggs. The nucleus was still present but was obscured in many ova by the evenly distributed yolky mass. In a ripe gonad prior to spawning the eggs were tightly packed and as a result had distorted shapes - bearing this in mind, measurements of ripe eggs may have underestimated true sizes. A thick gelatinous layer formed around the chorion of a mature egg prior to spawning (Figure 6.13).

Macroscopic description of the testis

Externally, the male gonad was arranged in a similar fashion to the ovary around the digestive gland and stomach. While the testis was normally a creamy/white colour, it was also orange or yellow for brief periods depending on the stage of development. The structure of the inner and outer gonadal wall was similar to that of the female. The lumen of the testis was traversed by branching tubules of connective tissue projecting inward from the outer wall (Figure 6.10). As with trabeculae most ended freely in the lumen, but some extended all the way to the inner wall. Lacunae or blood sinuses were present in the tubules (Figure 6.11) and were connected to branches of the hepato-genital blood vessels. The outer surfaces of the connective tissue tubules were surrounded by cuboidal germinal epithelium.

Microscopic description of the Testis (Figure 6.12)

Spermatogonia were produced by the cells of the germinal epithelium and measured approximately 3.14 µm in diameter. From these, smaller primary and secondary spermatocytes were derived which were approximately 1.51 µm in size. Secondary spermatocytes gave rise to highly basophilic spermatids about 0.88 µm in diameter. Spermiogenesis followed and spermatozoa measuring roughly 5.89 µm in length were produced. The tail or flagellum of mature sperm was barely visible even under high magnification and so the above measurement excluded tail length. Essentially, the mature spermatozoon consisted of an anterior eosinophilic acrosome followed by a short clear space and a posterior elongated basophilic nucleus (cf. Young

& DeMartini 1970).

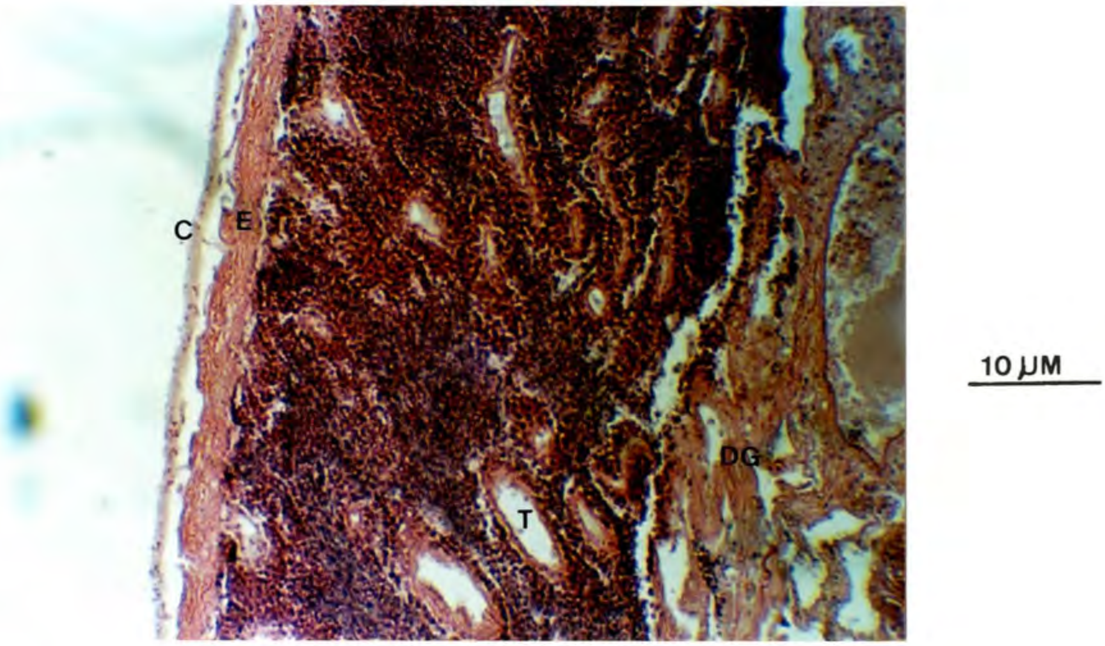

Figure 6.10 Horizontal section through a testis of *H. midae* illustrating the outer cuticle (C), digestive gland (DG), epidermis (E), and tubules (T).

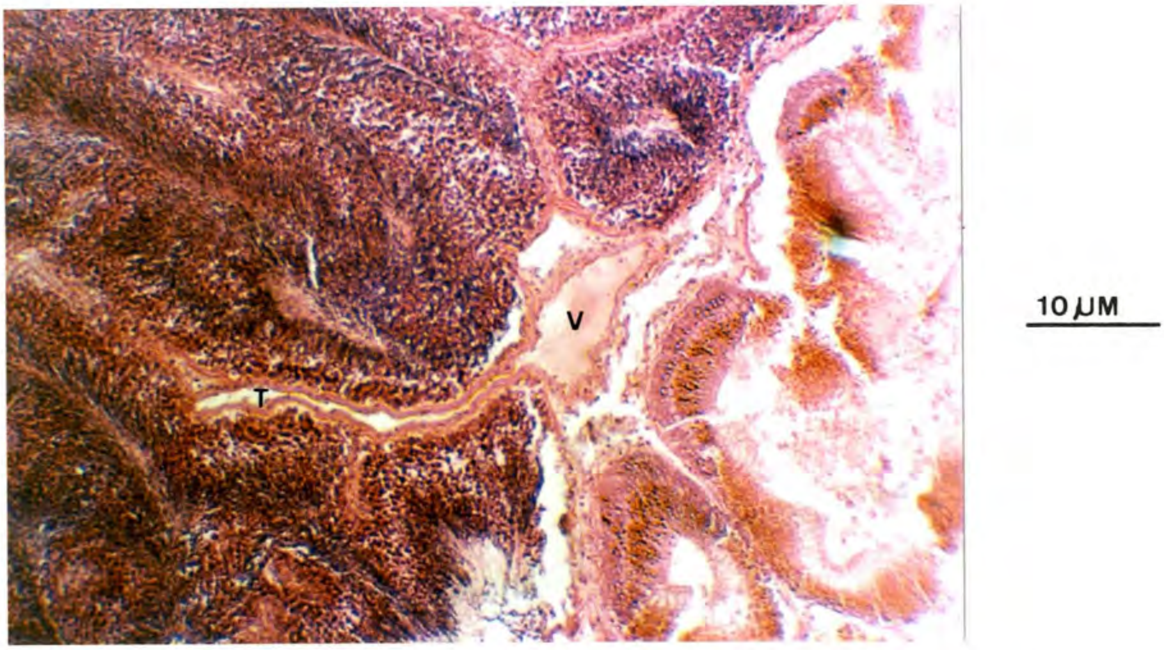

Figure 6.11 Horizontal section through a testis of *H. midae* illustrating a branch of a hepato-genital blood vessel (V) projecting into a tubule (T).

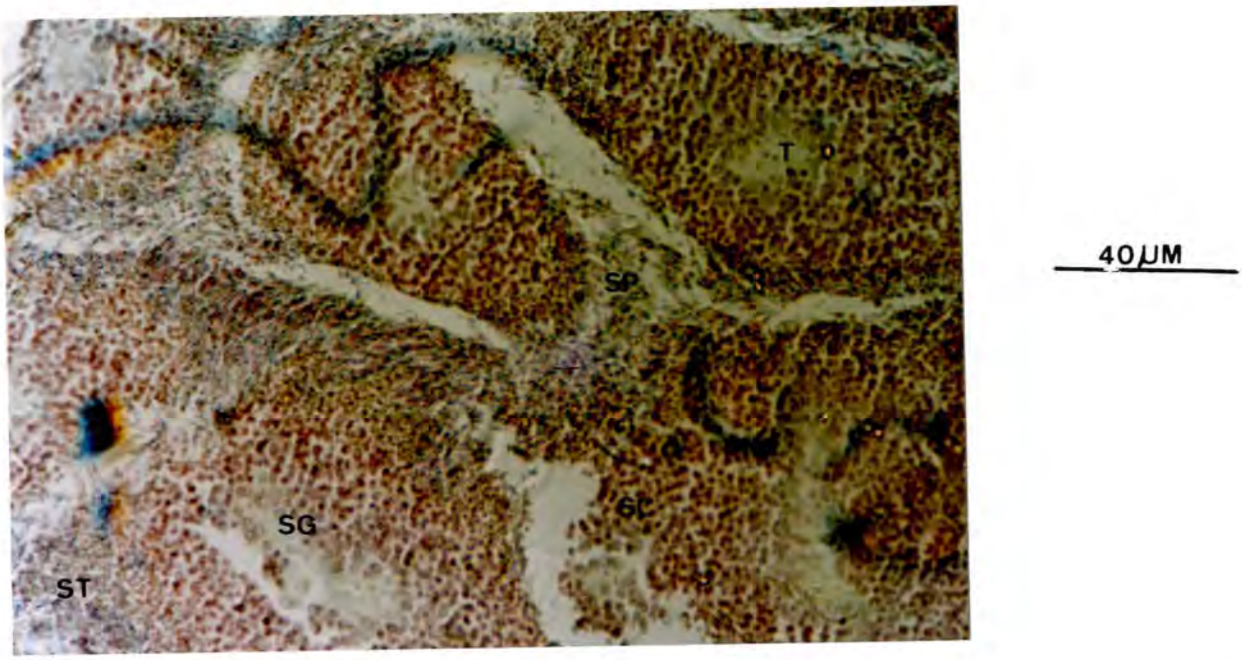

Figure 6.12 Horizontal section of a testis of *H. midae* illustrating primary and secondary spermatocytes (SC), spermatogonia (SG), spermatozoa (SP), spermatids (ST), and connective tissue tubules (T).

Stages of the Reproductive Cycle

The reproductive cycle of *H. midae* was divided into five separate stages. The stages for females are described first:

(1) Ripe (Figure 6.13)

Very large and solid gonad bulk as a result of the lumen being densely packed with mature oocytes. All ripe eggs were free in the lumen and possessed ill defined nuclei obscured by the granular cytoplasm resulting from vitellogenesis. Ripe ova were tightly packed causing distortion and a great array of shapes. The protective gelatinous layer was evident around most ova. There were very few earlier developmental stages such as stalked oocytes or oogonia present.

(2) Partly Spawned (Figure 6.14)

There was still a large gonad volume, however, some areas of the lumen were devoid of eggs and trabeculae were beginning to collapse in these regions. Large numbers of free oocytes were still present, which were still densely packed in certain areas. Although immature oocyte stages were still scarce, oogonia and pre-stalk oocytes were sometimes visible.

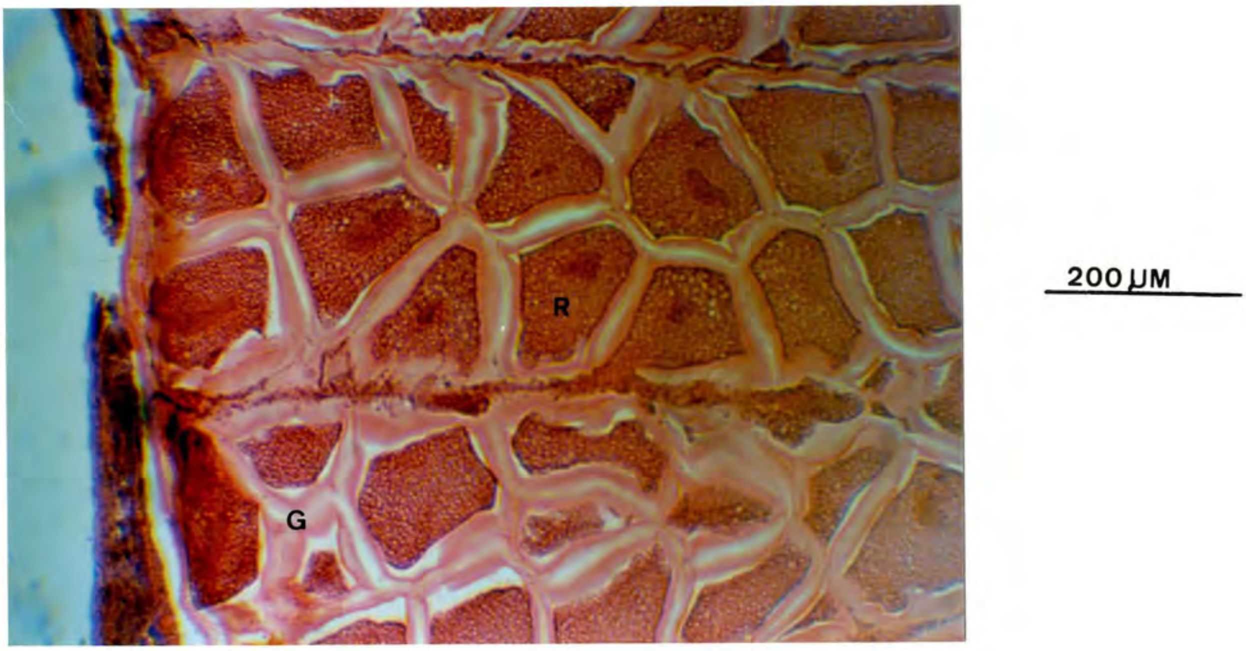

Figure 6.13 Ripe ovary of *H. midae* illustrating the protective gelatinous layer (G) which surrounds the ripe eggs (R) which are tightly packed and distorted.

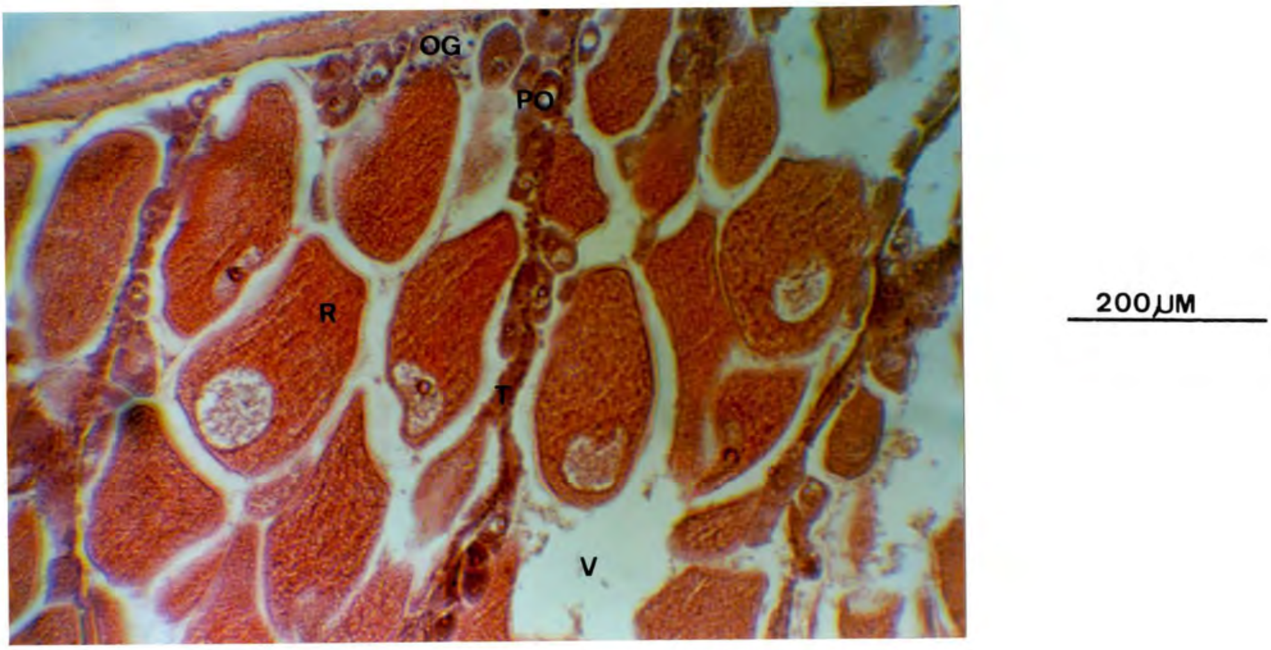

Figure 6.14 Partially spawned ovary of *H. midae* with empty areas where eggs have been voided (V). Numerous ripe eggs (R) are still present, but oogonia (OG) and previtellogenic oocytes (PO) are already gathered on the germinal surfaces of the trabeculae (T).

(3) Fully Spawned or Spent (Figure 6.15)

Gonad volume was small as trabeculae have folded leaving the ovary without support. Some unspawned free oocytes were still present, but were usually atretic. In some areas atresia was fairly advanced and the lumen was filled with a cytoplasmic "soup". Oogonia and early oocytes were present in moderate numbers soon after spawning, indicating the potential for rapid recovery.

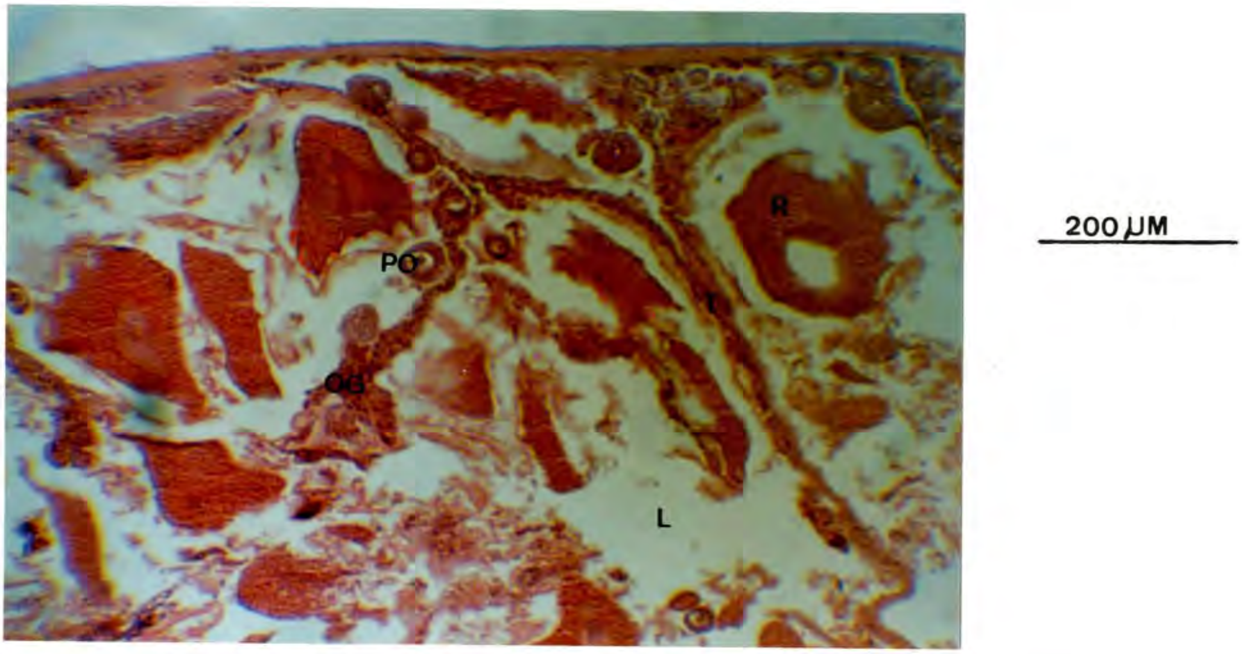

Figure 6.15 Fully spawned or spent ovary of *H. midae* with collapsed trabeculae (T) and an empty lumen (L) except for some oogonia (OG), previtellogenic oocytes (PO), and a few unspawned eggs (R).

(4) Recovery Stage 1 (Figure 6.16)

This stage was also known as the early recovery stage. Atresia of the last few unspawned oocytes was still ongoing in the early stages, and the gonad was still collapsed. All gametogenic stages were present though only a few mature oocytes were visible. The most numerous cells were oogonia on the germinal epithelial lining and previtellogenic oocytes, although there were also moderate numbers of stalked oocytes at various stages of vitellogenesis. Indications were that this stage was short lived, about 2 - 3 weeks, as it was rare in tissue preparations.

Figure 6.16 Recovery stage 1 in an ovary of *H. midae* with atretic oocytes (A), and numerous oogonia (OG), previtellogenic oocytes (PO), and some small stalked vitellogenic oocytes (VO).

(5) Recovery Stage 2 (Figure 6.17)

Active recovery. There was a marked increase in gonad volume and bulk resulting from the rapid growth of stalked primary oocytes and the reformation of trabeculae. Although some ripe ova were present, stalked and newly detached vitellogenic oocytes were the dominant cell type. Moderate numbers of oogonia and early oocytes indicated that oogenesis was still actively occurring. Except when animals were spawning at the peak of their breeding season, most were at this stage of development, but seemed capable of moving rapidly through to the ripe, spawning or spent stages at their time of spawning.

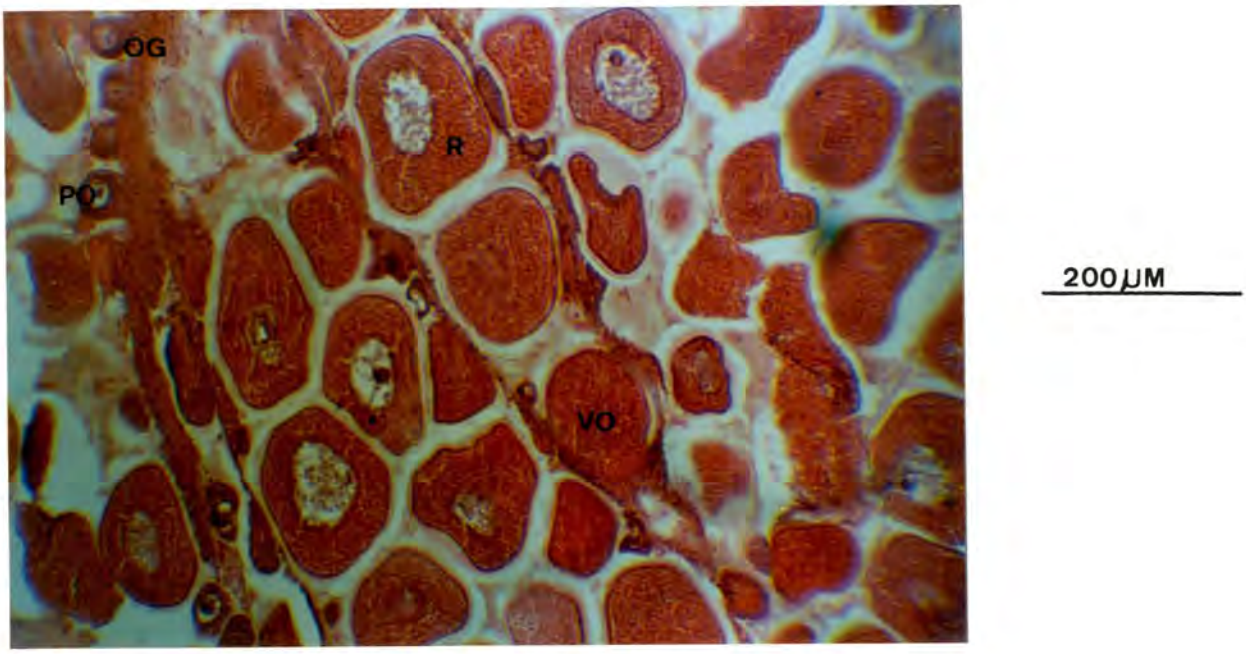

Figure 6.17 Recovery stage 2 in a *H. midae* ovary illustrating the predominance of vitellogenic oocytes (VO) and ripe eggs (R). Also present, but in lower numbers, are oogonia (OG) and previtellogenic oocytes (PO).

The reproductive stages in males were as follows:

(1) Ripe (Figure 6.18)

Large gonad volume densely packed with mature spermatozoa compressing the tubules. Thin layers of spermatids were still present in some regions with few or no spermatocytes and spermatogonia around the tubules.

(2) Partly Spawned (Figure 6.19)

Gonad volume was still effectively large, although there were empty spaces around some tubules where sperm had already been expelled. Other regions still appeared as in the ripe stage except that virtually no spermatids were present. Spermatocytes and spermatogonia were still rare or totally absent, but could have been obscured by the sperm mass.

(3) Fully Spawned or Spent (Figure 6.20)

Gonad volume was drastically reduced as most of the sperm had been voided from the lumen causing the gonad to collapse. Some unspawned spermatozoa were still present but they were mostly atretic. A thin layer of spermatogonia and primary spermatocytes were present around some of the tubules.

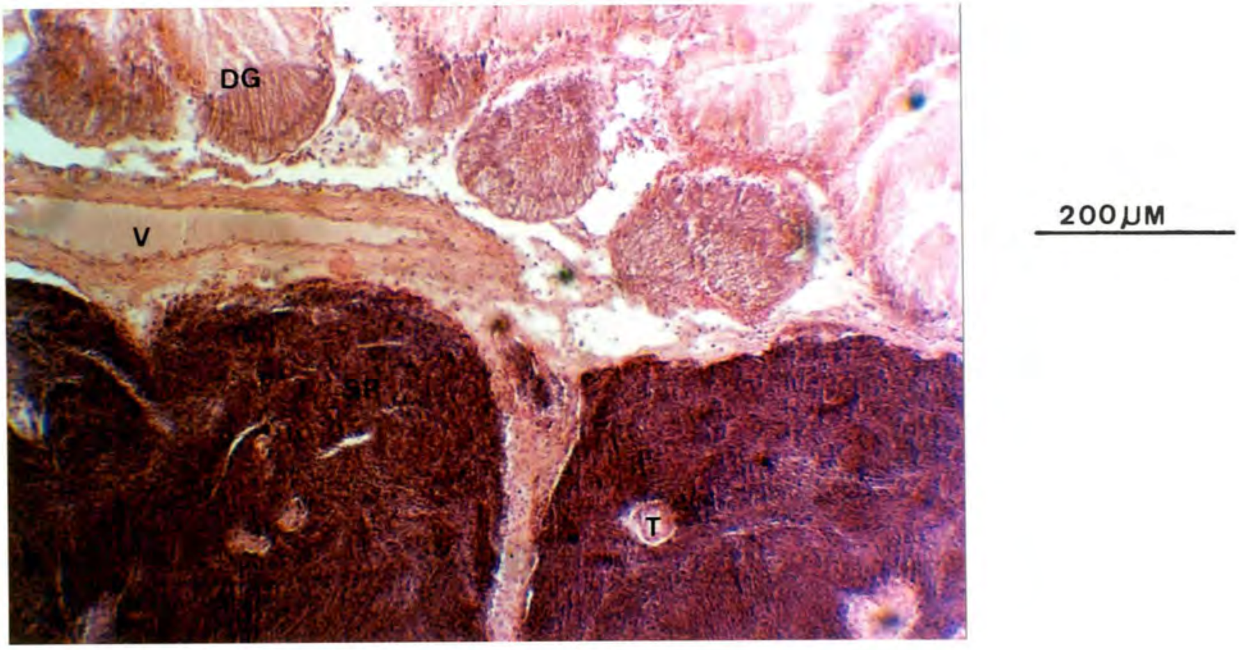

Figure 6.18 Ripe testis of *H. midae* with dense layers of sperm (SP) surrounding the tubules (T) and obscuring all other gametogenic stages. A hepato-genital blood vessel (V) is visible in the area between gonad and digestive gland (DG).

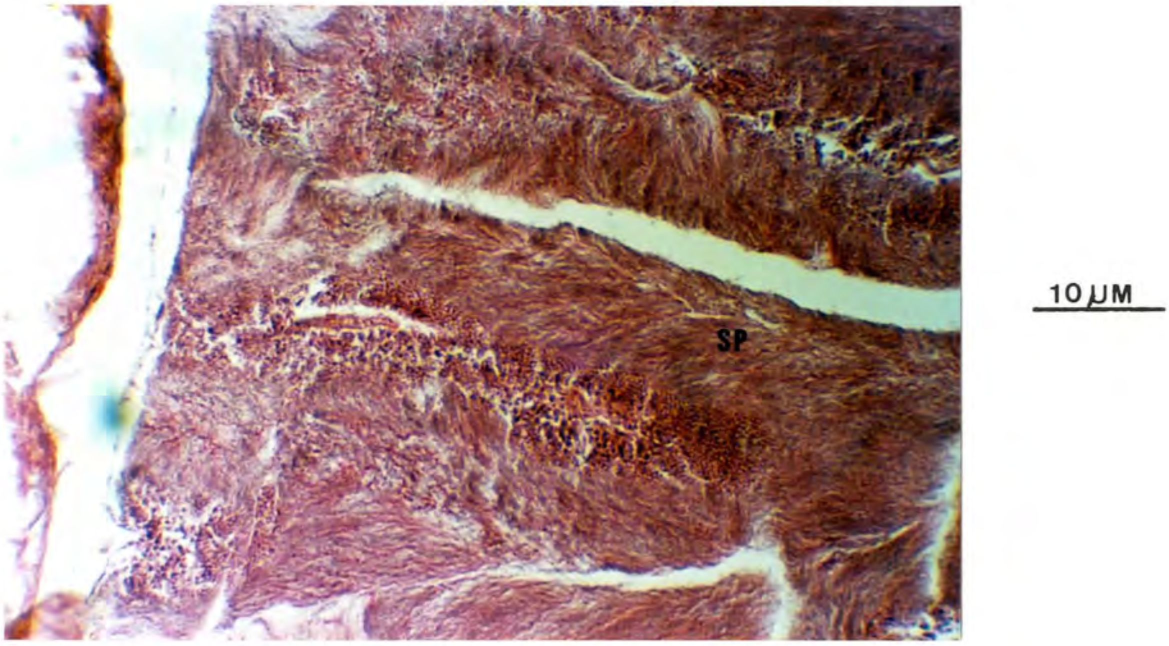

Figure 6.19 Partially spawned testis of *H. midae* with empty areas where sperm (SP) has been expelled and areas where sperm is still densely packed, obscuring other cell stages.

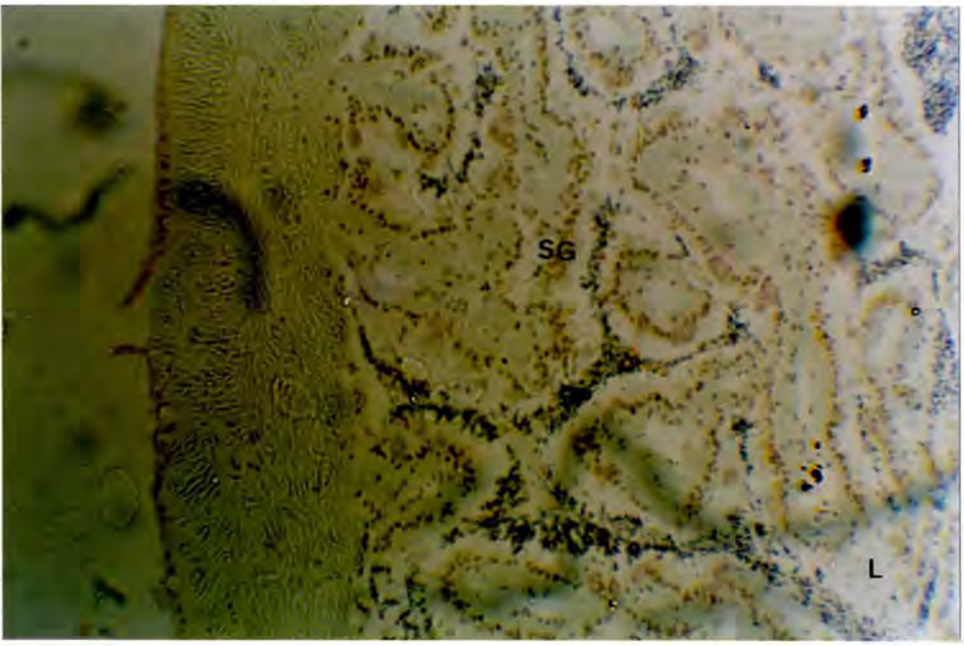

Figure 6.20 **Fully spawned or spent male *H. midae* showing residual layers of sperm (SP) in a largely empty, collapsed lumen (L). Thin layers of spermatogonia (SG) are visible around compressed tubules.**

(4) Recovery Stage 1 (Figure 6.21)

Early recovery. The gonad began to take shape again as dense layers of spermatogonia and spermatocytes accumulated around the germinal tissue surrounding the tubules. There were moderate numbers of spermatids in the lumen and a few thin layers of spermatozoa were visible. This stage was of short duration and seemed proceed directly after the cessation of spawning.

(5) Recovery Stage 2 (Figure 6.22)

Active recovery. All gametogenic stages were well represented in the testis which once again had a large volume and was highly organised. Spermatocytes and spermatids were numerically the most abundant cell types, although substantial quantities of sperm were present in some regions. As was the case for females, this stage was the most common in animals outside their spawning season, at which time the testes would rapidly mature to the ripe stage.

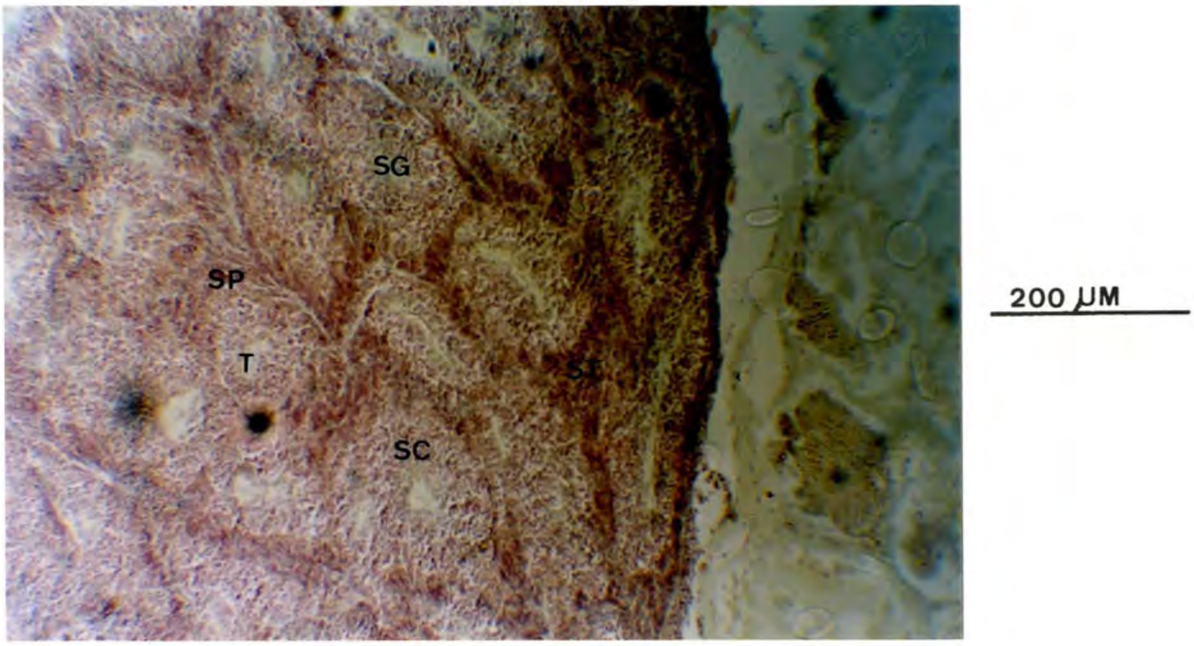

Figure 6.21 Testis of *H. midae* at recovery stage 1 with tubules (T) surrounded by dense layers of spermatogonia (SG) and spermatocytes (SC). Moderate numbers of spermatids (ST) are visible in places, but sperm (SP) is scarce.

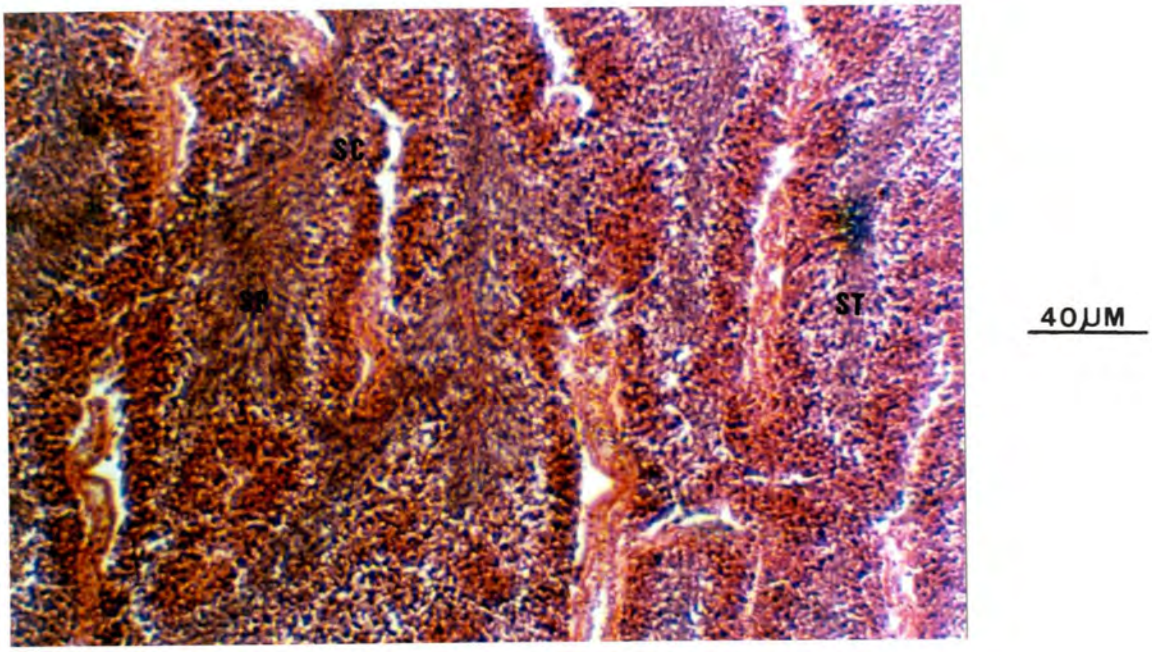

Figure 6.22 Testis of *H. midae* in recovery stage 2 with numerous spermatocytes (SC) and spermatids (ST). Sperm (SP)is prevalent only in some regions.

The quantities of mature sperm and eggs at various stages of development in the gonads of Great Fish Point animals (Figures 6.23 and 6.24) revealed that the reproductive cycle conformed to the pattern inferred from GBI values.

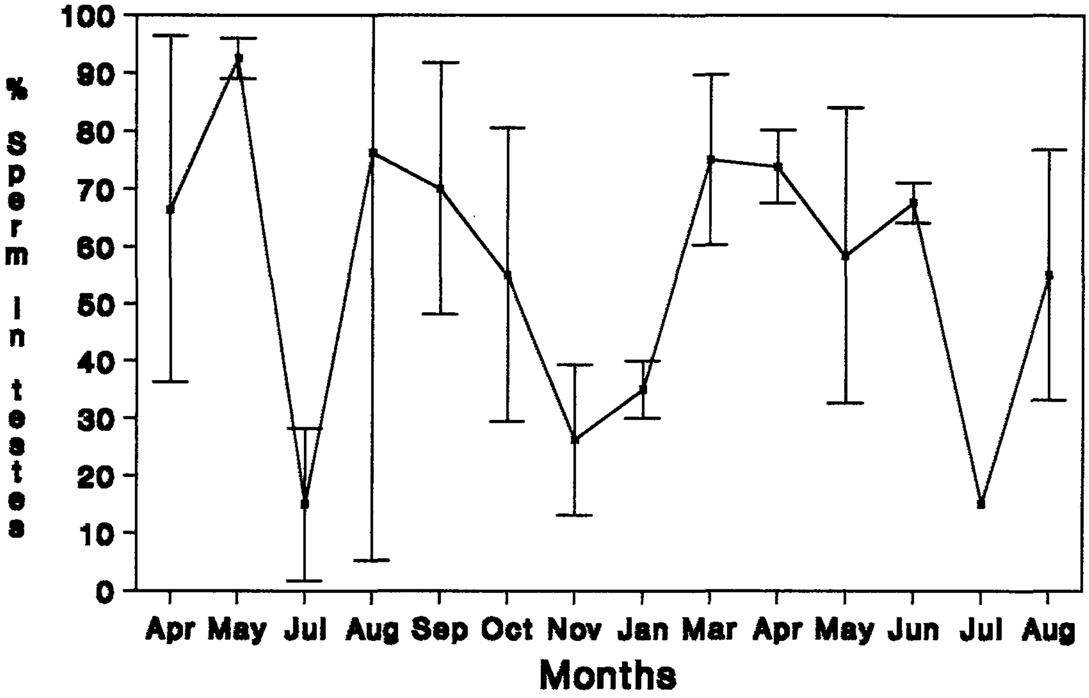

Figure 6.23 Percentage levels of sperm in cross-sectional areas of testes from male *H. midae* sampled at Great Fish Point from April 1991 to August 1992.

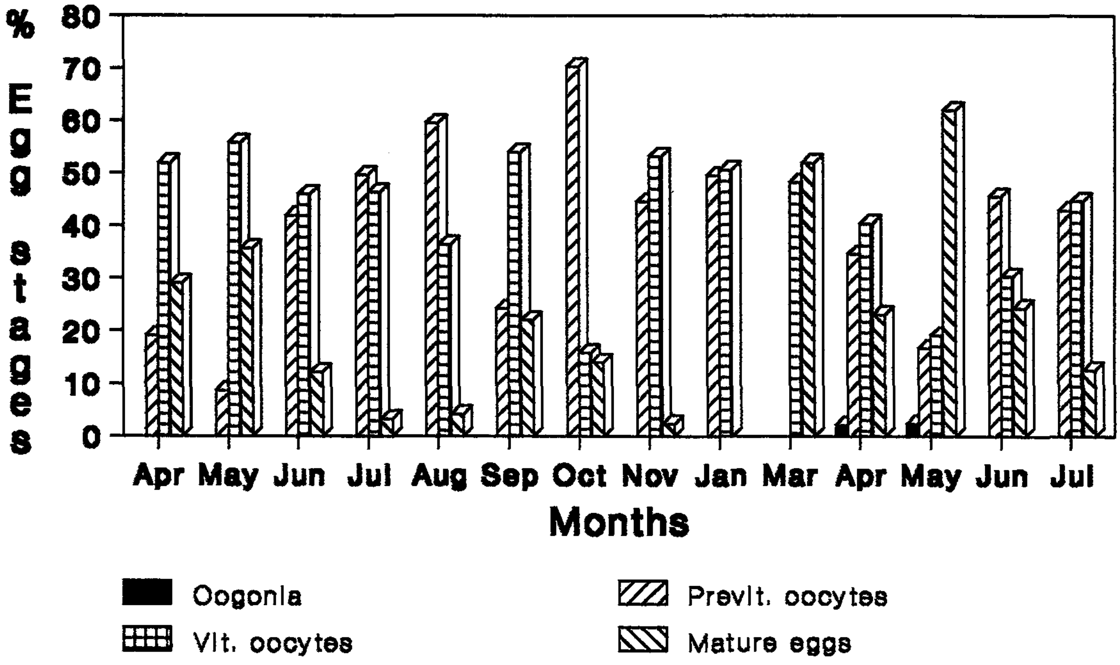

Figure 6.24 Percentage composition of egg stages in the ovaries of female *H. midae* sampled at Great Fish Point from April 1991 to July 1992.

In males, high levels of sperm which steadily decreased until November 1991 confirmed the protracted spawning during late autumn, winter and spring. A steady increase of sperm levels until April 1992 facilitated initiation of spawning in autumn once again. Large numbers of vitellogenic and mature oocytes in April and May 1991 indicated a high percentage of ovaries in the 2nd recovery and ripe stages, and the presence of previtellogenic oocytes confirmed that spawning had occurred, because they typified gonads in the early recovery period soon after the release of gametes. Active recovery and spawning continued until November after which there was a virtual disappearance of mature oocytes indicating the predominance of recovery stages. The cycle was initiated once more early in 1992, peak ripeness was achieved in May, and spawning was still ongoing when sampling was terminated at the end of July.

Quantities of oogonia were not truly represented because their tendency to form dense clusters made counting difficult. Histological preparations, however, showed them to be present in significant numbers, particularly in spent ovaries and those in the 1st stage of recovery (Figure 6.25). The same could be said for spermatogonia which concentrated around the tubules soon after spawning. In both sexes this inferred that gonadal recrudescence was initiated soon after spawning.

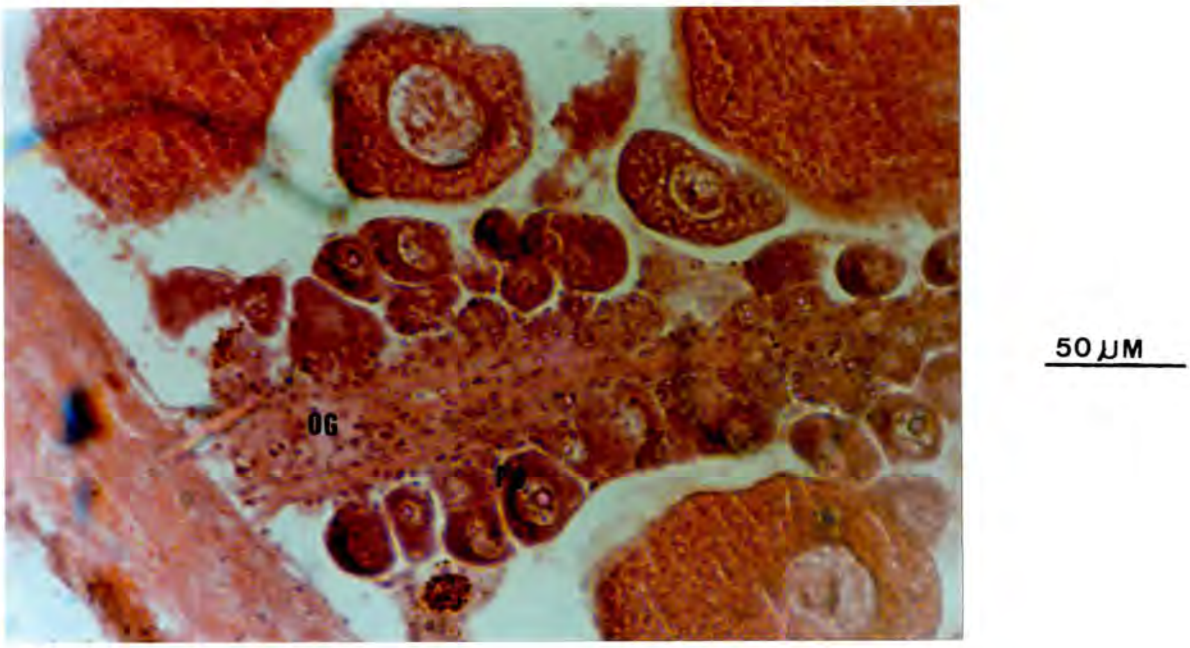

Figure 6.25 Dense aggregations of oogonia (OG) and previtellogenic oocytes (PO) accumulated on the trabecula of a recently spawned female *H. midae*.

By the time sampling was initiated at Mgwalana in October of 1991, it appeared that the spawning period was drawing to a close (Figures 6.26 and 6.27). Levels of mature spermatozoa were on the decline reaching their lowest levels in November 1991. Numbers of mature eggs decreased markedly in the early summer months of 1991 as well. The presence of oogonia and the dominance of previtellogenic oocytes at this time indicated that there were very few ripe gonads and that only a small proportion of the population was still spawning. Based on the high numbers of vitellogenic oocytes and moderate numbers of mature eggs, it appeared if some animals spawned in December 1991. A steady build up of sperm and late stage oocytes followed until peaks were attained in March/April 1992, thereby marking the beginning of the 1992 spawning season. This pattern was similar to the one exhibited by the Great Fish Point population, with a protracted season of spawning which peaked in early winter.

The Cape Recife population was sampled only six times, however, a good idea of their reproductive cycle was obtained (Figures 6.28 and 6.29). As was the case with the other two populations, the winter of 1991 was the peak period. Spawning occurred right through winter until spring with November 1991 being the most inactive month with respect to spawning, but the most active w.r.t. recovery, with oogonia and previtellogenic oocyte levels at their highest. There was no data for the next five months, however, by May 1992 the pattern from the previous year was repeating itself with testes full of sperm and ovaries with high numbers of vitellogenic oocytes and mature eggs. At all three sites, the presence of previtellogenic oocytes in the ovaries almost all year round indicated that gametogenesis occurred throughout the year and not discreetly over a few short months.

Table 6.3 summarizes the reproductive cycle of *H. midae* described from histological examination of gonads throughout the study period at all three sites, and highlights a number of points:

(1) The spawning season in *H. midae* was not synchronous, but protracted with ripe, spawning and spent gonads being found from April to October 1991, in December 1991 and from March to August 1992.

(2) At any one time there existed a number of different reproductive stages in a population, e.g. in April 1991 and 1992 at Great Fish Point, October 1991 and June 1992 at Mgwalana and May 1992 at Cape Recife.

(3) Recovery after spawning, defined by the initiation of gametogenesis, was rapid, with gonads in the first recovery stage being found throughout the spawning period and oogonia and spermatogonia being present in recently spawned gonads.

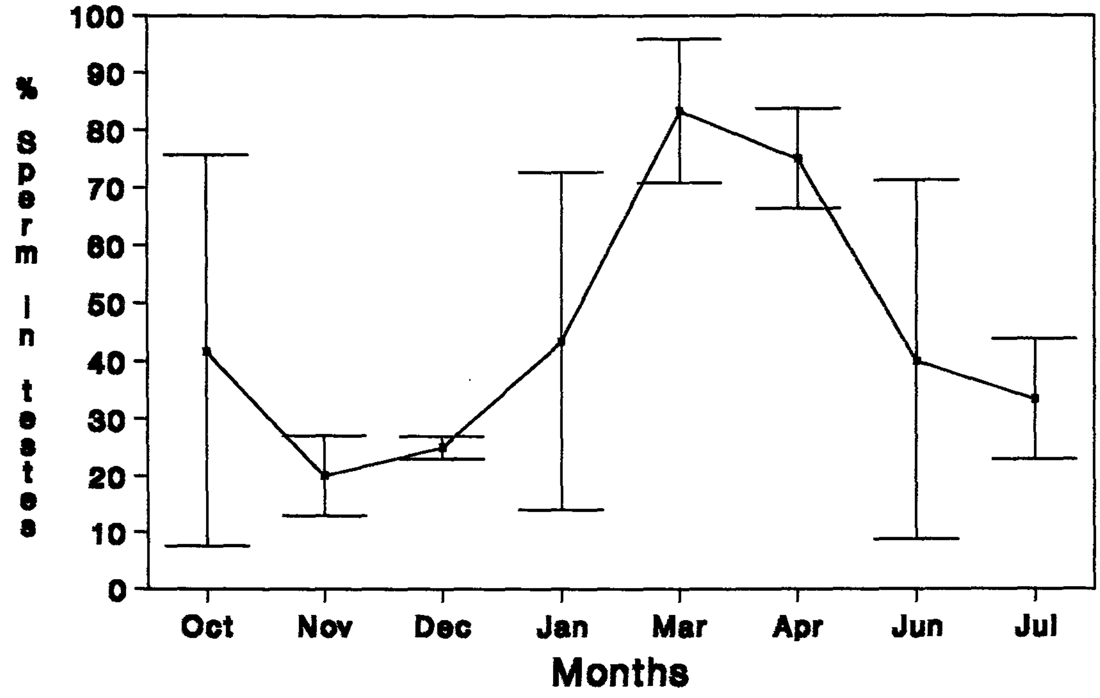

Figure 6.26 Percentage levels of sperm in cross-sectional areas of testes from male *H. midae* sampled at Mgwalana from October 1991 to July 1992.

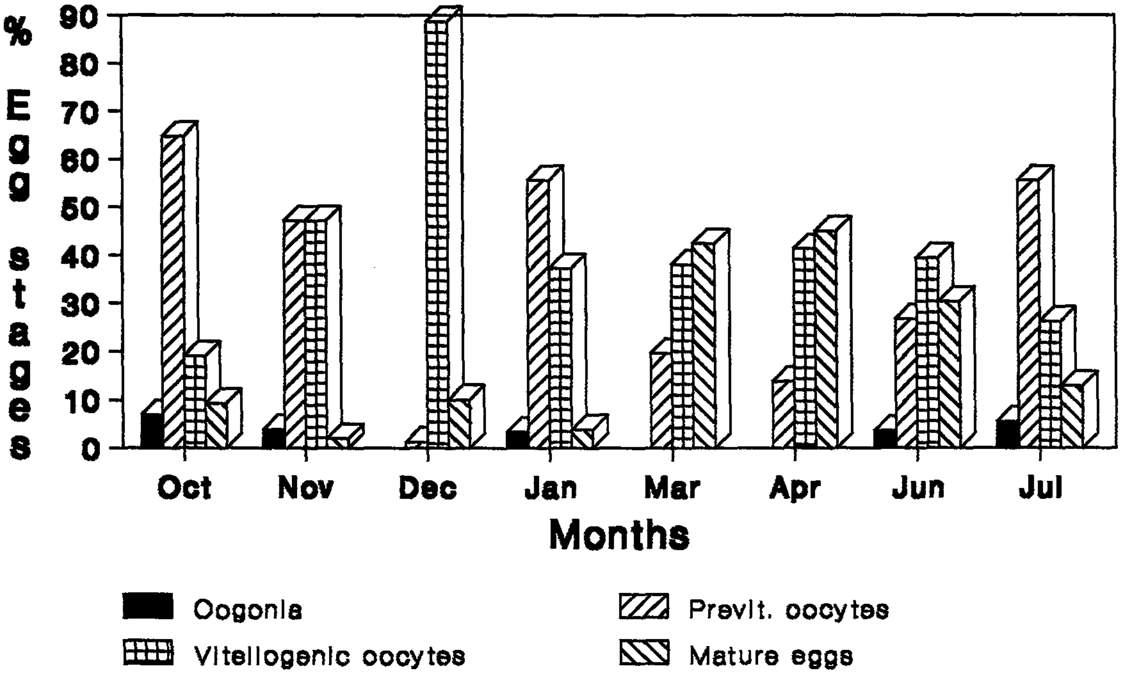

Figure 6.27 Percentage composition of egg stages in the ovaries of female *H. midae* sampled at Mgwalana from October 1991 to July 1992.

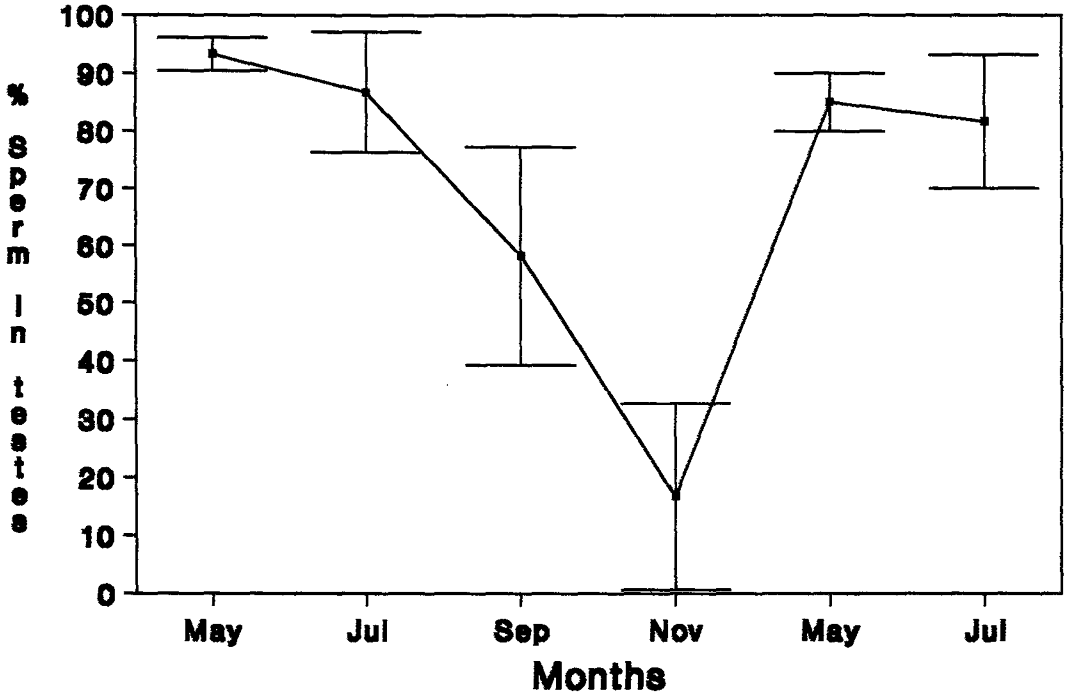

Figure 6.28 Percentage levels of sperm in cross-sectional areas of testes from male *H. midae* sampled at Cape Recife from May 1991 to July 1992.

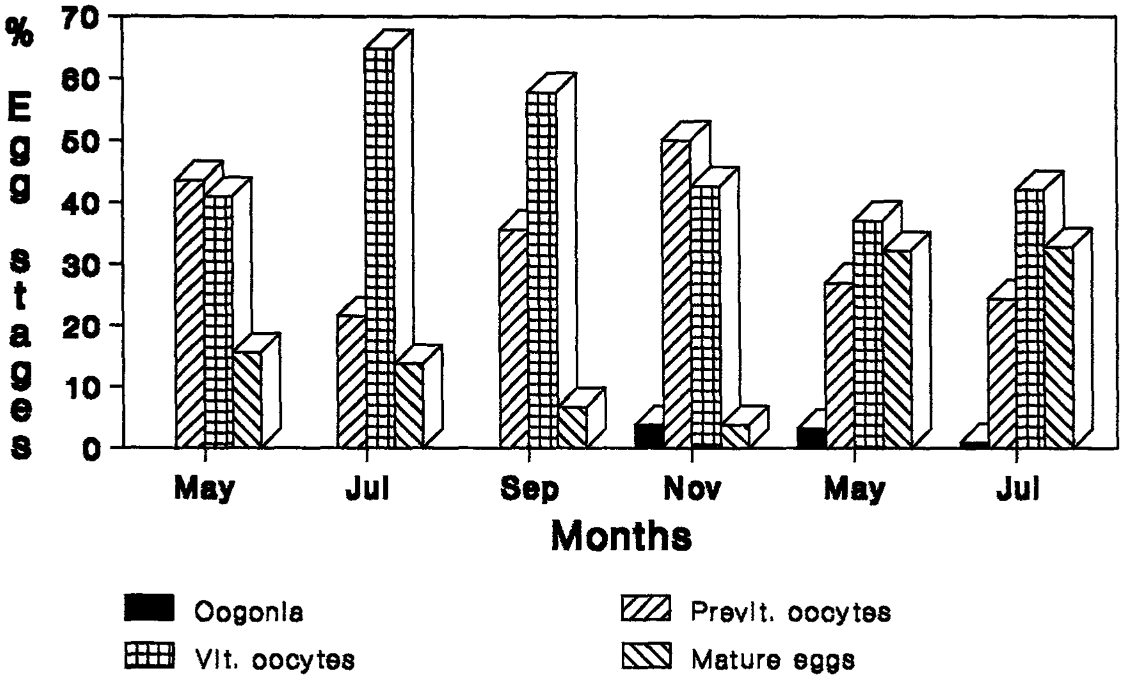

Figure 6.29 Percentage composition of egg stages in the ovaries of female *H. midae* sampled at Cape Recife from May 1991 to July 1992.

Table 6.3 Reproductive stages in pooled male and female *H. midae* at Great Fish Point, Mgwalana and Cape Recife for the period April 1991 to August 1992.

Month	Fish Point				Mgwalana				Cape Recife			
	Males		Females		Males		Females		Males		Females	
	n	Stage	n	Stage	n	Stage	n	Stage	n	Stage	n	Stage
April	1	RS1	3	Sq								
	3	RS2										
	2	R										
	4	Sq										
	1	St										
May	1	R	1	R					3	R	1	Sq
	1	Sq	1	Sq							2	St
June	1	R										
	1	Sq										
July	1	Sq	2	RS1					2	R	2	St
	2	St							1	Sq		
August	1	RS2	1	RS1								
	3	R	2	RS2								
September	2	RS2	1	I					2	RS2	3	RS2
	2	R	3	RS2					1	R		
	1	Sq	1	St								
October	3	RS2	2	RS1	1	RS2	1	RS1				
	1	R	1	RS2	1	R	1	RS2				
					1	St						
November	4	RS2	2	RS2	1	I	2	RS1	2	RS1	2	RS2
					2	RS1	1	RS2	1	RS2		
December					1	Sq	3	R				
					2	St						
January	3	RS2	3	RS2	1	RS1	1	RS1				
					2	RS2	3	RS2				
March	4	RS2	3	R	2	RS2	3	R				
					1	Sq	1	St				
April	3	RS2	1	RS1	2	R	1	R				
	1	Sq	1	R	1	Sq	2	Sq				
	1	Sq										
May	1	RS1	2	R					1	R	1	RS1
	1	RS2							2	Sq	1	R
	1	R									2	Sq
June	1	RS2	1	Sq	1	RS1	2	R				
	1	Sq	2	St	1	RS2	1	St				
					1	Sq						
July	1	RS1	1	RS2	3	RS2	1	RS2	1	R	1	Sq
	1	St	1	St			1	St	2	Sq	1	St
August	2	Sq										
	1	St										

I - Immature; R - Ripe; Sq - Spawning; St - Fully spawned or spent; RS1 - Recovery stage 1; RS2 - Recovery stage 2.

6.3.3 Sex Ratios

All data from the four sites was consistent with a 1:1 sex ratio (Table 6.4). A few small individuals without pigmented gonads were found to possess gametes (Figure 6.30) and this stressed the importance of histological work if accurate determination of sex ratios were to be ascertained.

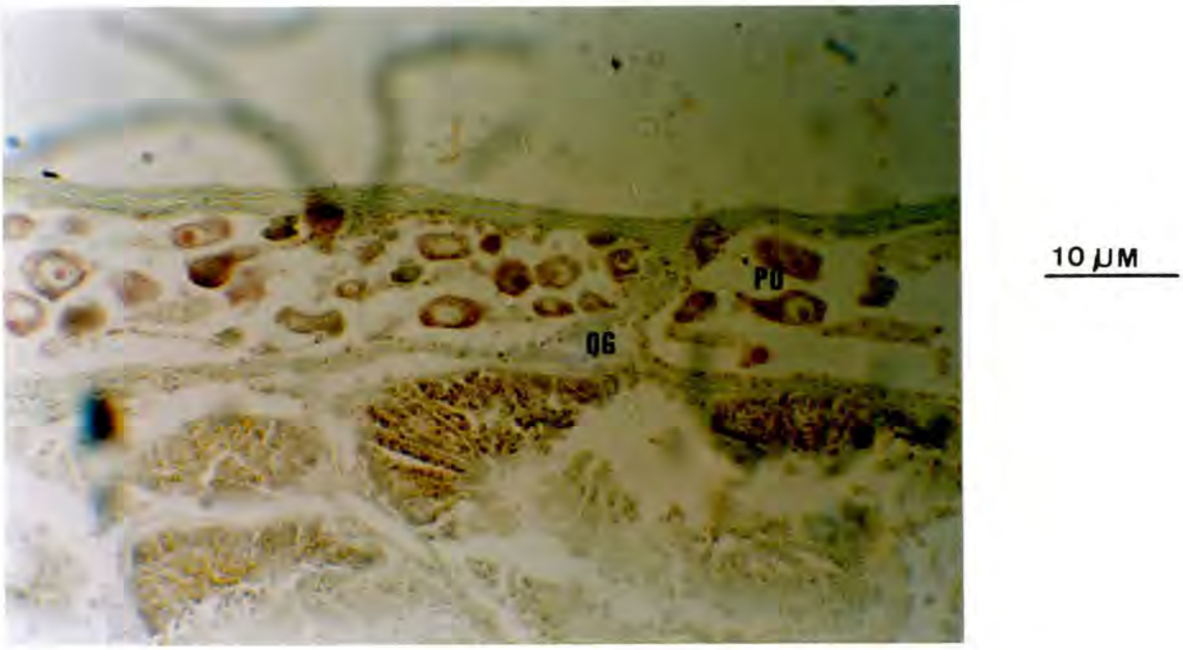

Figure 6.30 Cross-section through the conical appendage of a 46.7 mm SL *H. midae*. Although no pigmentation was macroscopically visible, the oogonia (OG) and previtellogenic oocytes (PO) confirmed that the animal was a female.

6.3.4 Size at Sexual Maturity

Figures 6.31 - 6.34 illustrate the sexual maturity of *H. midae* at differing sizes at Great Fish Point, Mgwalana, Cape Recife and Kelly's Beach Cape Recife respectively. At all four sites, the onset of sexual maturity occurred in the 40 - 59 mm shell length (SL) class and the corresponding 20 - 39 mm shell width (SW) class. All animals in the size classes below this were identified as immature. All gonads which lacked pigmentation were found to be immature (Figure 6.35), while some pigmented gonads were also classed as immature due the absence of mature sperm (Figure 6.36) or vitellogenic oocytes (Figure 6.37). Sizes at 50% sexual maturity were 72.51 mm SL and 52.83 mm SW at Great Fish Point, 72.51 mm SL and 57.46 SW at Mgwalana, 73.77 mm SL and 51.20 mm SW at Cape Recife, and 73.58 mm SL and 53.83 mm SW at Kelly's Beach. At Mgwalana, all animals above 100 mm SL (80 mm SW) were sexually mature, while at the remaining three sites 100% maturity was observed in animals >120 mm SL (100 mm SW). The smallest mature female (54.6 mm SL and 36.9 mm SW) was also the smallest female to have spawned (Figure 6.38). The smallest mature male measured 55.4 mm SL and 36.8 mm SW, however, the smallest male which could be identified as having spawned was only 69 mm in length (Figure 6.39).

Table 6.4 CHI^2 tests of sex ratios for *Haliotis midae* from Great Fish Point, Mgwalana, Cape Recife and Kelly's Beach.

Size Class (SL - mm)	Males	Females	χ^2 Value
		Fish River Point	
40 - 59.9	-	1	1
60 - 79.9	4	4	0
80 - 99.9	16	20	0.444
100 - 119.9	38	44	0.439
120 - 139.9	76	80	0.103
140 - 159.9	37	29	0.969
160 - 179.9	2	2	0
Total	173	180	0.139
		Mgwalana	
60 - 79.9	2	3	0.200
80 - 99.9	6	8	0.286
100 - 119.9	8	8	0
120 - 139.9	35	39	0.216
140 - 159.9	30	25	0.454
Total	81	83	0.024
		Cape Recife	
40 - 59.9	-	1	1
60 - 79.9	8	6	0.285
80 - 99.9	9	10	0.052
100 - 119.9	21	17	0.421
120 - 139.9	27	29	0.071
140 - 159.9	18	16	0.117
Total	83	89	0.209
		Kelly's Beach	
40 - 59.9	1	-	1
60 - 79.9	8	10	0.222
80 - 99.9	18	16	0.117
100 - 119.9	30	24	0.667
120 - 139.9	21	17	0.421
140 - 159.9	7	5	0.333
Total	85	72	1.076

6.3.5 Fecundity

A weak relationship between gonad weight and shell size was evident (Figure 6.40), with larger individuals possessing larger gonads. The high degree of variation, however, was explained by the extended spawning season which made the inclusion of only ripe ovaries for counting unlikely. Females with spent ovaries, exhibiting the characteristic dull green colour, were excluded from any counts, however, the active recovery, ripe and partially spawned stages were impossible to discern macroscopically and the inclusion of ovaries at these different stages of maturity in the sample was the most feasible explanation for the observed pattern.

The linear relationship between gonad weight and fecundity (Figure 6.41) was to be expected,and because gonad weight increased with animal size (Figure 6.40) it was reasonable to assume that fecundity would be directly related to size.

Figure 6.42 illustrates this relationship between fecundity and shell length and indicated that egg production in *H. midae* was not only prolific but highly variable as well. Newman (1967b) also

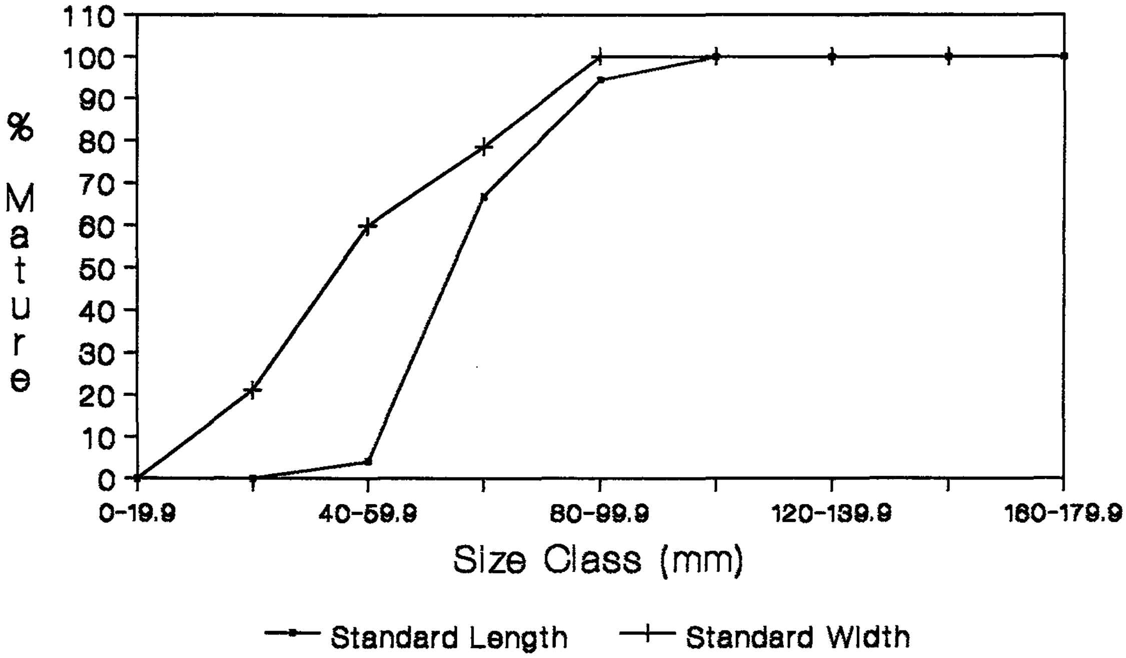

Figure 6.31 Sizes at sexual maturity for *H. midae* at Great Fish Point.

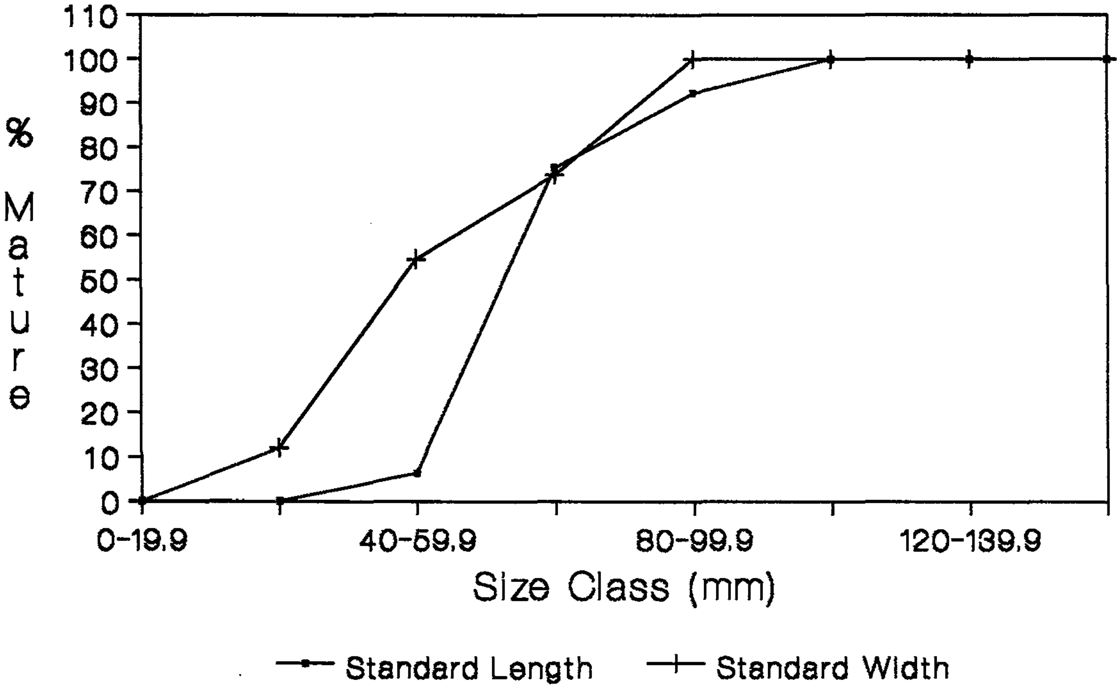

Figure 6.32 Sizes at sexual maturity for *H. midae* at Mgwalana.

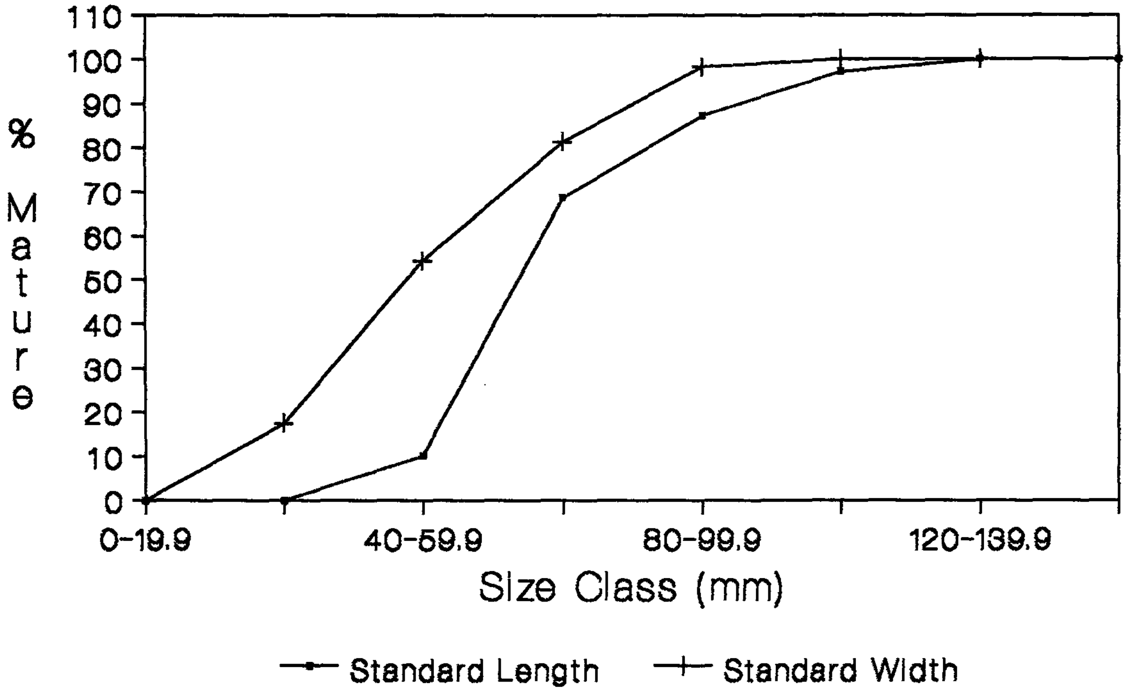

Figure 6.33 **Sizes at sexual maturity for *H. midae* at Cape Recife.**

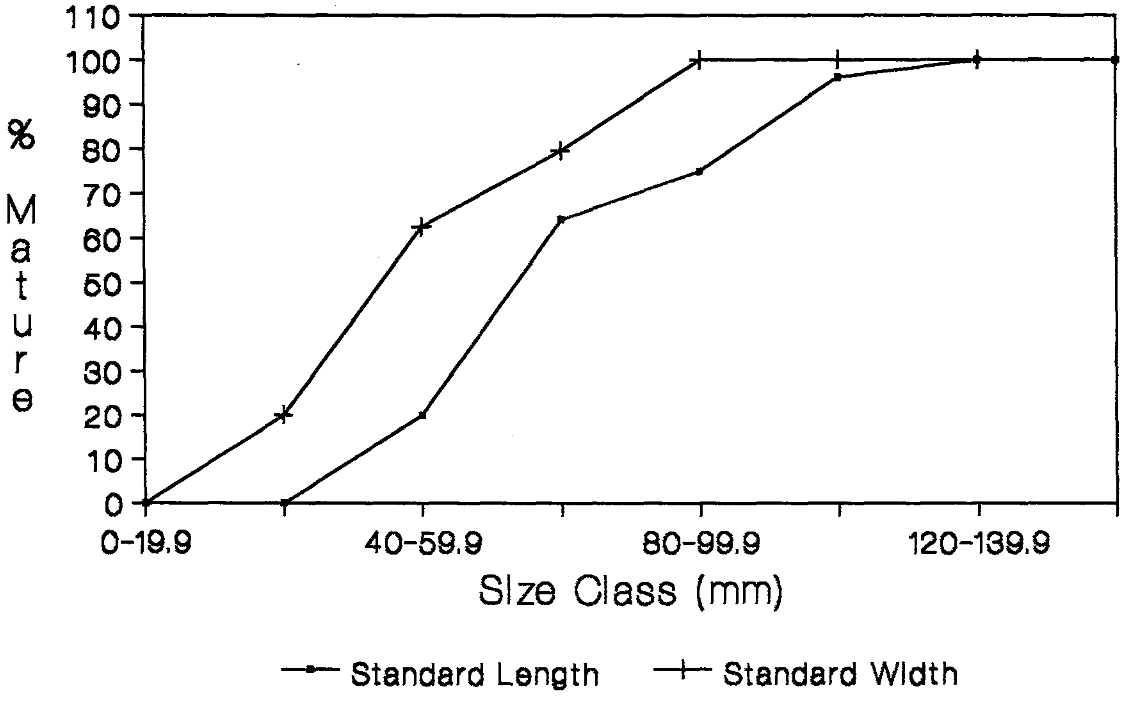

Figure 6.34 **Sizes at sexual maturity for *H. midae* at Kelly's Beach.**

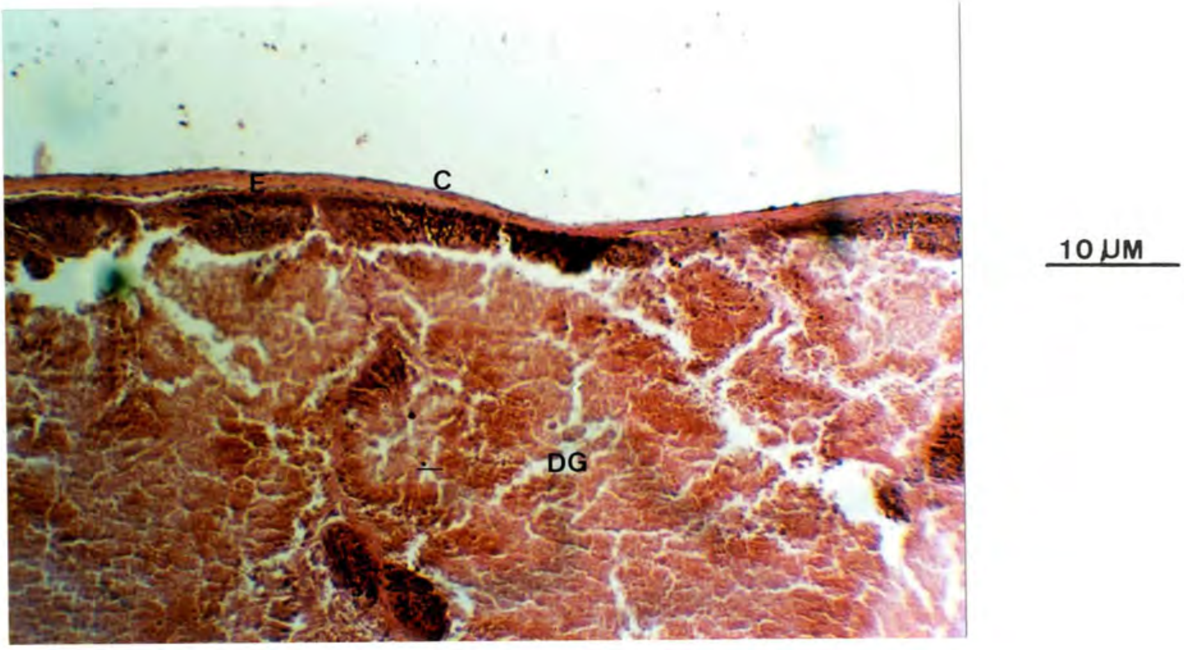

Figure 6.35 An immature *H. midae* (52.1 mm SL) which displayed no pigmentation. A cuticle (C) and epidermis (E) overly the digestive gland (DG) with no sign of germ cells or a gonad lumen.

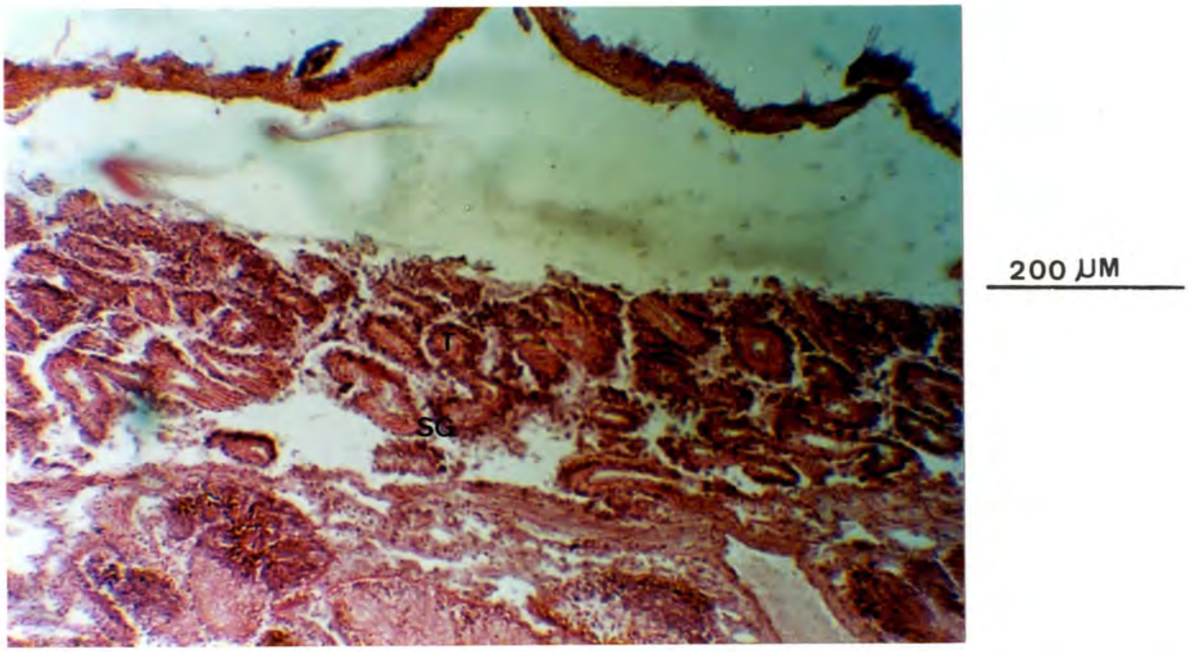

Figure 6.36 The testis of a 53 mm SL *H. midae* with spermatogonia (Sg) around the tubules (T). Although this individual had a pigmented gonad, no mature sperm were visible, classifying it as immature.

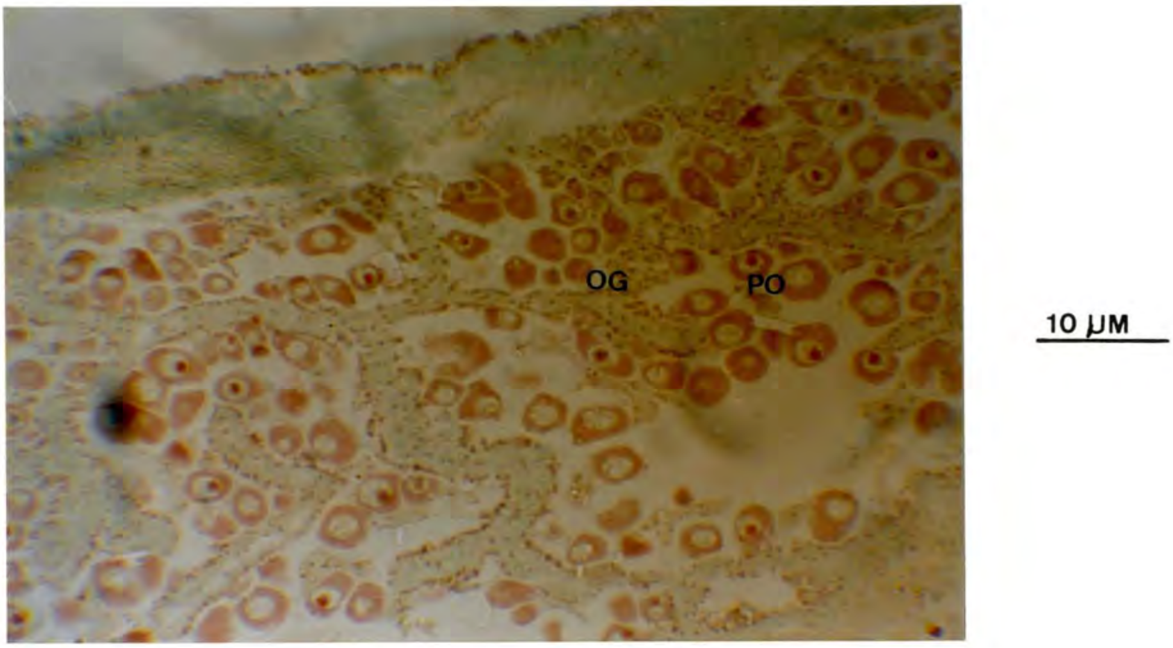

Figure 6.37 This ovary of a 49.2 mm SL female *H. midae* was pigmented and clearly contained oogonia (OG) and previtellogenic oocytes (PO), however, the absence of vitellogenic and mature oocytes classifies this individual as immature.

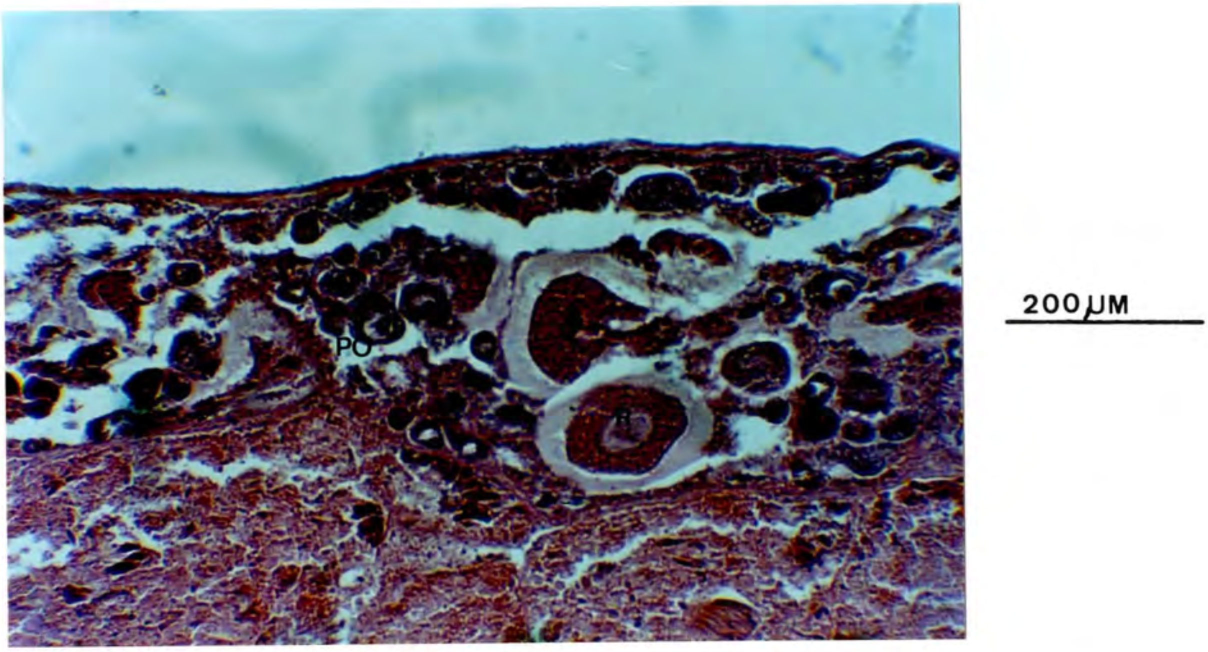

Figure 6.38 The spent ovary of a female *H. midae* measuring just 54.6 mm SL. Residual ripe eggs (R) are visible together with the earlier previtellogenic oocyte (PO) stages. This was the smallest female specimen known to have spawned during the study.

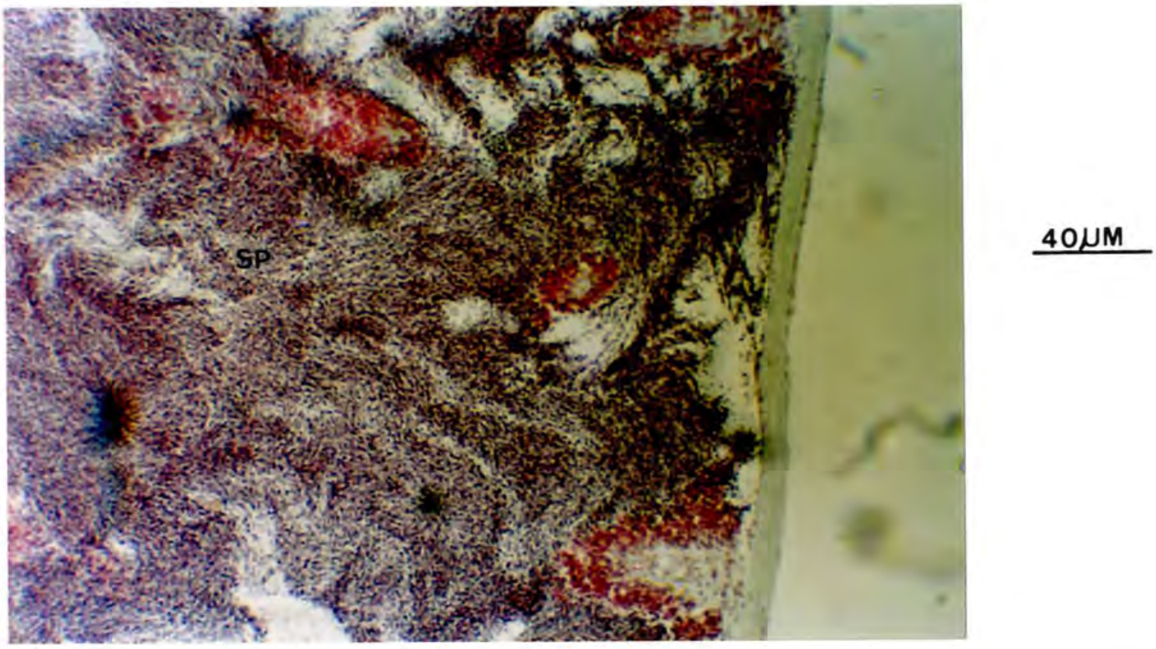

Figure 6.39 The partially spawned testis of a 69 mm SL male *H. midae* still with copious amounts of sperm (SP) in the lumen. This was the smallest male known to have spawned during the study.

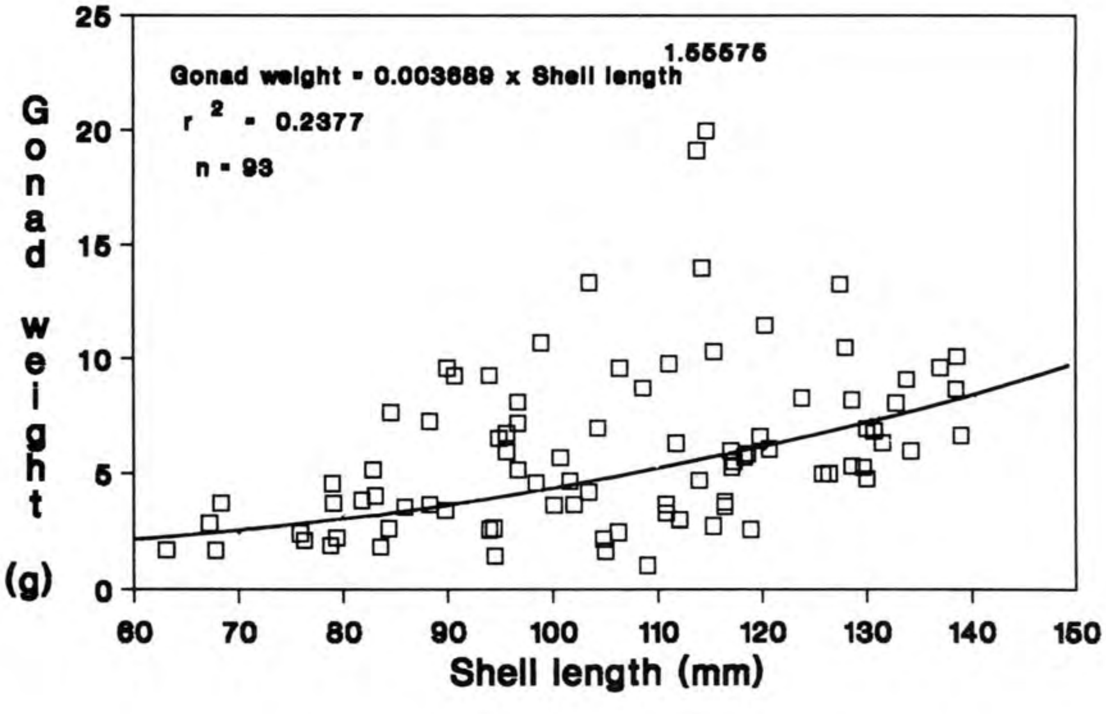

Figure 6.40 The relationship between gonad weight and shell length for *H. midae* sampled at Great Fish Point, Mgwalana and Cape Recife during May and June 1992.

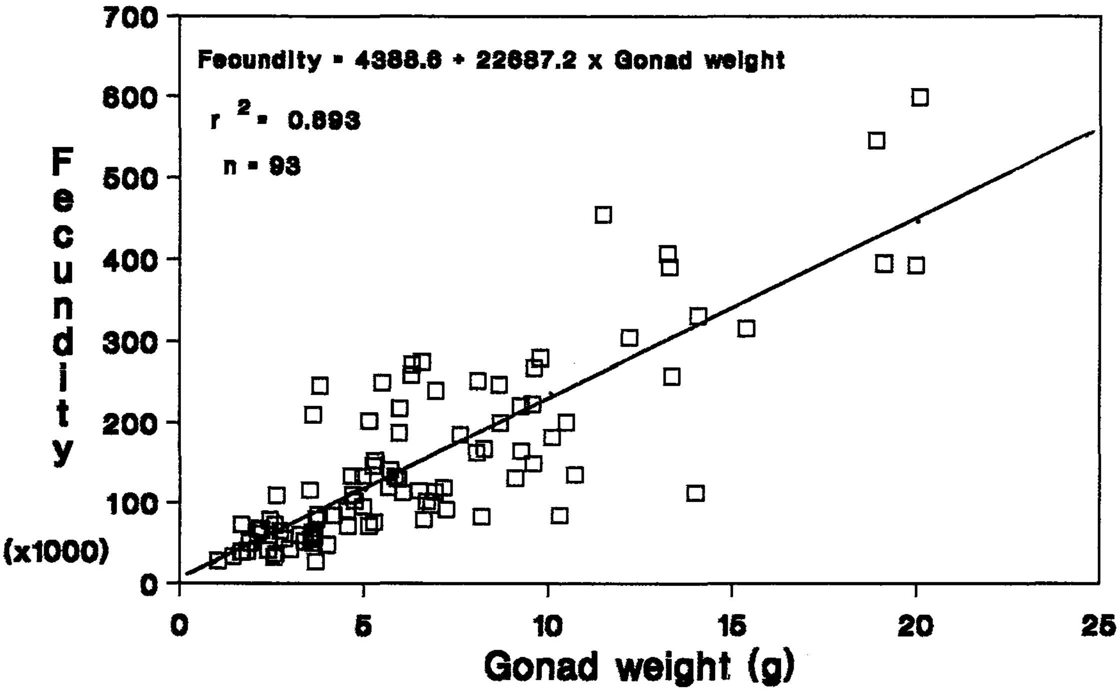

Figure 6.41 The relationship between fecundity and gonad weight for *H. midae* sampled at Great Fish Point, Mgwalana and Cape Recife during May and June 1992.

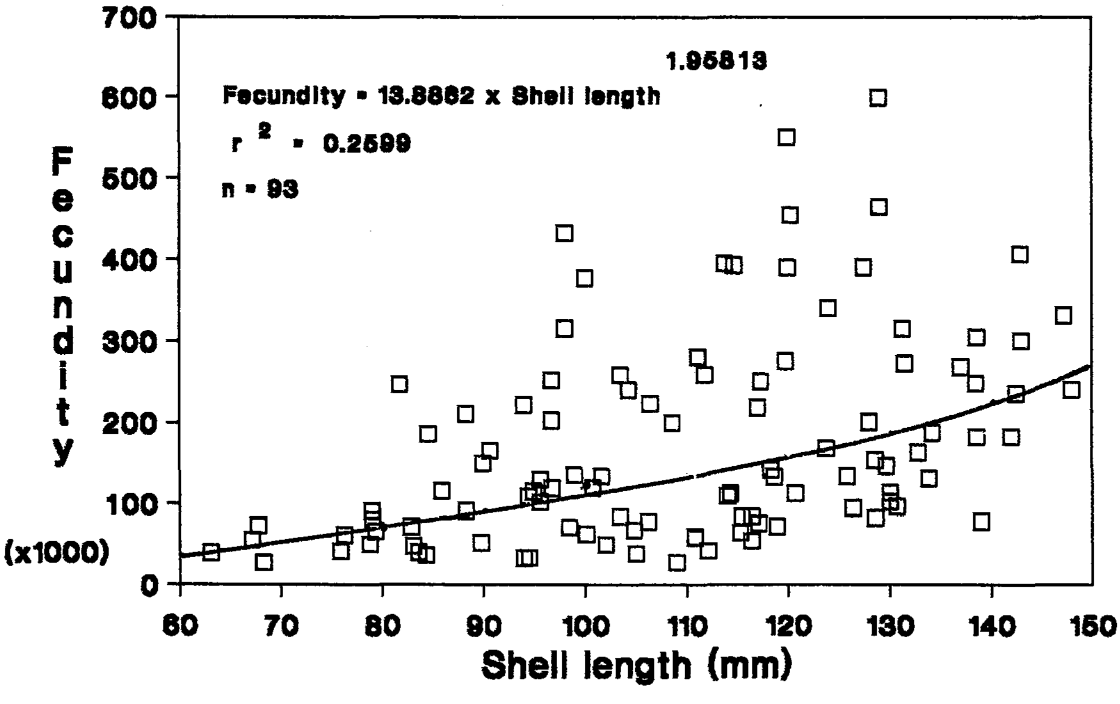

Figure 6.42 The relationship between fecundity and shell length for *H. midae* sampled at Great Fish Point, Mgwalana and Cape Recife during May and June 1992.

found this to be the case for *H. midae* at Stony Point. There were several factors which could have contributed to this phenomenon, *viz:*

(1) A loss of eggs during removal of the ovary from the visceral mass and during fixation.

(2) Partial spawning could have taken place prior to collection.

(3) Atresia of eggs could have occurred, either in conjunction with a partial spawning or without spawning having taken place. Both situations were observed in histological preparations.

As mentioned above, the implications of a protracted spawning season complicated matters and probably led to the observed scatter in Figures 6.40 and 6.42, so that actual fecundity may be best reflected by the upper limit of the data points. It is perhaps important to note that these were only estimates of fecundity or measures of each individuals' potential. There was no way of knowing whether the animals collected would have spawned partially, totally or even at all.

6.4 Discussion

6.4.1 Gonad Bulk Index

The use of GBI's on their own to describe the breeding cycle in any organism can result in erroneous conclusions (Giese 1959). This was highlighted by Boolootian *et. al.* (1962) who noted that spawning occurred all year round in *H. rufescens* because of similar gonad index values throughout the period of study. Subsequent to this, however, a detailed histological study by Giorgi & DeMartini (1977) showed it to be a summer spawner (see Table 6.5 in section 6.4.2). While GBI's can be used to estimate the possible reproductive cycle they cannot pin-point the component processes such as timing of spawning or initiation of gametogenesis. These problems were enhanced in *H. midae* which had a prolonged spawning season. Due to the occurrence of partial spawning, there was often a lack of reduction in gonad volume because of the trabeculae and tubules which retained their structure and which prevented the collapse of the gonad. In temperate marine zones where short spawning seasons are more common, a steep gonad index curve with a single peak provides good evidence of spawning (Wilk *et al.* 1990).

In *H. cracherodii* when GBI values were low there was a distinct increase in the size of the hepatic gland prior to the breeding season (Boolootian *et al.* 1962), and as the gonad increased in size the hepatic gland subsided. Although evidence for or against was lacking it was proposed that the gland stockpiled nutrients essential to gamete development. No such relationship was found for *H. rufescens* in the same study, however, and it would appear that nutrients required for hepatic and gonadal growth were always available.

The actual process of determining the GBI has several inherent problems which made it difficult to ensure absolute accuracy, *viz*:

(1) Male gonads did not seem to harden as well as ovaries in formalin and tended to be softer. This was particularly evident outside of the spawning season when the lumen was not full and the tubules were collapsed. The resultant distortion of the conical appendage sections can lead to faulty measurements.

(2) In both males and females outside their peak breeding season it was difficult to differentiate between gonad and hepatic gland boundaries.

Used in combination with detailed cytological studies, however, the reproductive cycle of *H. midae* was established.

6.4.2 Reproductive Cycles

Strictly speaking, the reproductive cycle encompasses the events from the time of activation, through growth, gametogenesis, spawning, recession of gonadal activity and the duration of the resting period (Giese 1959). Reproductive biology of the genus *Haliotis* has been extensively studied (Table 6.1), and according to their spawning periodicities, species can be broadly grouped into three categories (Boolootian *et al.* 1962; Shepherd & Laws 1974), *viz*:

(1) Summer spawners - the breeding season may extend from the end of spring till early autumn.

(2) Those that spawn in seasons other than summer - also known as winter breeders.

(3) Year-round spawners.

The breeding seasons of haliotid species are summarized in Table 6.5, and highlight the tendency for the same species to have different spawning seasons at different locations. This was most marked in *H. ruber* and led Shepherd & Laws (1974) to emphasize the importance of local environmental conditions in the regulation of reproductive periodicity. Of the 21 species studied twelve were summer spawners, eleven winter breeders and three spawned all year round. In several studies on marine molluscs, summarized by Boolootian *et. al.* (1962), 85% of the animals considered were found to be summer breeders, however, when considering abalone on their own there seemed to be more of an equal distribution of summer and winter breeders. In Table 6.5, four of the summer breeders were classed as winter breeders as well, *viz: H. corrugata, H. cracherodii, H. iris* and *H. discus hannai*, while one winter and one summer spawner were also classed as all year spawners, *viz. H. roei* and *H. rufescens* respectively. These facts enforce the above statement about geographical location having a major influence on the timing of a species' breeding season. There was some doubt, however, as to whether *H. rufescens* did spawn all year round, as Boolootian *et. al.* (1962) based their findings on monthly gonadosomatic indices which alone are not sufficient to define the reproductive cycle, and although Young & DeMartini (1970) used histological techniques, they were vague in describing actual spawning events, mentioning only that "..apparently mature gametes were found in the gonads all year round." Muller (1984) found a shift in the breeding season in *H. spadicea* from two sites only 12 km apart. While Newman (1967b) found some overlap in the spawning season of *H. midae* from three sites, there was sufficient difference in the timing and intensity at each site to support the theory that abalone spawn at different times at different localities. In this study, there appeared to be a large degree of overlap in the breeding season of *H. midae* from Great Fish Point, Mgwalana and Cape Recife. Although based on a short time series of data, the Cape Recife population appeared to have the shortest spawning season, and although the Mgwalana population was only 15 km from Great Fish Point, it had the most extended breeding season from March through to December. Along the south and west Cape coasts, *H. midae* was regarded as a cold water species, but was known to breed both in summer and winter. Certain cold water limpet species have been known to breed exclusively in winter (Branch 1974), and Muller (1984) showed that in the warmer waters of its distribution, the abalone *H. spadicea* spawned in summer. In the temperate Eastern Cape waters, the bulk of the breeding season for *H. midae* was in the winter months and not in summer as originally proposed by Newman (1967b).

Marine invertebrates in polar, temperate and tropical seas each have distinctive breeding season patterns and larval types (Giese 1959), but there is a degree of deviation from the typical pattern for each region. Animals in temperate areas which have pelagic planktotrophic larvae are restricted to shorter breeding seasons because of the dependence of larvae on appropriate plankton for survival (Giese *op. cit.*). Some marine invertebrates such as haliotids have lecithotrophic pelagic larvae, and will be more likely to exhibit prolonged breeding seasons as the larvae are not dependant on the plankton. Molluscan veliger larvae do, however, absorb complex sugars and monosaccharides from the water column, permitting them to make greater use of these dissolved organic materials as a source of nutrition (Welborn & Manahan 1990). An extended breeding season can mean either that individuals are producing several broods a year or that they are breeding asynchronously (Giese 1959). Populations of *H. midae* exhibited a ubiquitous, non-synchronous spawning season, and histological evidence showed that only a portion of the population spawned each month. Furthermore, it would appear that individuals were not serial spawners and released a portion of or all gametes over a short period of time. Evidence for this was provided by the presence of atretic oocytes and sperm in partially spawned ovaries and testes. There was no microscopic evidence of partial spawning followed by gamete retention for release at a later stage. There is the possibility that in a population in which a small proportion spawn at any one time, several broods may be produced by any one animal but not

Table 6.5 A summary of the spawning periodicities of abalone species grouped according to the timing of spawning during the year.

	Species	Reference	Locality		Spring			Summer			Autumn			Winter		
				(N. hemisphere)	M	A	M	J	J	A	S	O	N	D	J	F
				(S. hemisphere)	S	O	N	D	J	F	M	A	M	J	J	A
1	*H. cyclobates*	Shepherd & Laws (1974)	Tipara Reef (S)			...	...	...								
	H. laevigata	Shepherd & Laws (*op. cit.*)	Tipara Reef (S)			...	...	...	...							
			West Island (S)			...	...	...	...							
	H. pustulata	Shepherd & Laws (*op. cit.*)	Gulf of Suez					...	...	...						
	H. corrugata	Quintanella (1966 in Muller 1984)	Baja California				***	***	***	***	***					
	H. cracherodii	Boolootian *et. al.* (1962)	Monterey California					***	***	***	***	***	***			
		Leighton & Boolootian (1963)	Santa Monica			***	***	***	***	***						
	H. fulgens	Tutschulte & Connell (1981)	Santa Catalina Island				***	***	***	***	***					
	H. iris	Poore (1973)	Taylors Mistake (NZ)							...						
	H. rufescens	Carlisle (1962)	Monterey California						***	***	***					
		Cox (1962)	California				***	***	***	***	***					
		Giorgi & DeMartini (1977)	Mendocino California			***	***	***	***							
	H. lamellosa	Bolognari (1953)	Messina Sicily							***	***					
	H. tuberculata	Crofts (1937)	Channel Islands						***	***	***					
		Boolootian *et.al.*(*op. cit.*)	Roscoff France						***	***						
		Hayashi (1980a)	Channel Islands							***	***					
	H. discus hannai	Sakai (1962a)	Miyagi Japan						***	***	***					
	H. spadicea	Muller (1984)	Humewood Beach (SA)		...	...	...									
			Schoenmakerskop (SA)		...	...	...									
			Partridge Point (SA)		...	...	...									
	H. australis	Poore (1973)	Kaikoura (NZ)		..						...	...				
2	*H. ruber*	Shepherd & Laws (*op. cit.*)	West Island (S)			...	...	...			...	...	...			
			Tipara Reef (S)								...	...	...	...	...	
			Jervis Bay (NSW)		...	...	...	...								

Table 6.5 continued.

	Species	Reference	Locality		Spring	Summer	Autumn	Winter
				(N. hemisphere)	M A M	J J A	S O N	D J F
				(S. hemisphere)	S O N	D J F	M A M	J J A
			Tasmania		......			......
	H. discus hannai	Lee (1974)	Southern Korea			*****	********	**
		Rho & Park (1975)	Yeosu Japan		***	****		
	H. gigantea	Ino (1952)	Chiba Japan				*****	***
	H. sieboldii	Ino (*op. cit.*)	Chiba Japan				**	
	H. midae	Newman (1967b)	Stony Point (SA)		....	..	....	
			Sea Point (SA)		....			....
			Dassen Island (SA)		.....		.....	
		This Study	Fish River Point (SA)		.....		......	....
			Mgwalana (SA)		..	..	....	....
			Cape Recife (SA)		....		...	....
	H. iris	Poore (1973)	Kaikoura (NZ)				....	
			Taylors Mistake				..	
	H. cracheroidii	Webber & Giese (1969)	Monterey California		***			**
	H. sorenseni	Tutschulte & Connell (1981)	Santa Catalina Island		*****			***
	H. corrugata	Tutschulte & Connell (*op. cit.*)	Santa Catalina Island		*********	***		***
	H. scalaris	Shepherd *et al.* 1985	West Island (S)			...	......	
	H. roei	Wells & Keesing (1989)	Perth Western Australia		....	..		......
3	*H. roei*	Shepherd & Laws (1974)	West Island (S)		....	... ..	....	......
	H. scalaris	Shepherd & Laws (*op. cit.*)	Tipara Reef (S)		....	....	... ...	.....
	H. rufescens	Boolootian *et. al.* (1962)	Monterey California		*********	********	********	*******
		Young & DeMartini (1970)	Fort Bragg California		*********	********	********	*******

(1 - Summer spawners; 2 - Winter breeders; 3 - Year round breeders; S - southern Australia; SA - South Africa; NZ - New Zealand; NSW - New South Wales; *** - northern hemisphere; ..... - southern hemisphere).**

synchronously. This was unlikely to be the case for *H. midae* because GBI studies and cytology showed that although spawning was protracted there was a peak over a 2 -3 month period followed by less intense spawning from the remaining proportion of the population, with no indication of recovery to a ripe stage within this time frame by any individual. Giorgi & DeMartini (1977) identified three types of spawning patterns for *H. rufescens* which were observed for *H. midae* as well, *viz*:

(1) Type I - total spawning, resulting in total release of gametes and a total collapse of the gonad (Figures 6.15 and 6.20).

(2) Type II - incomplete spawning, where there was only a partial release of gametes and residual gametes became atretic (Figures 6.43 and 6.44).

(3) Type III - nonspawners, which had ripe gonads but did not spawn, and where the whole gonad became atretic (Figures 6.45 and 6.46).

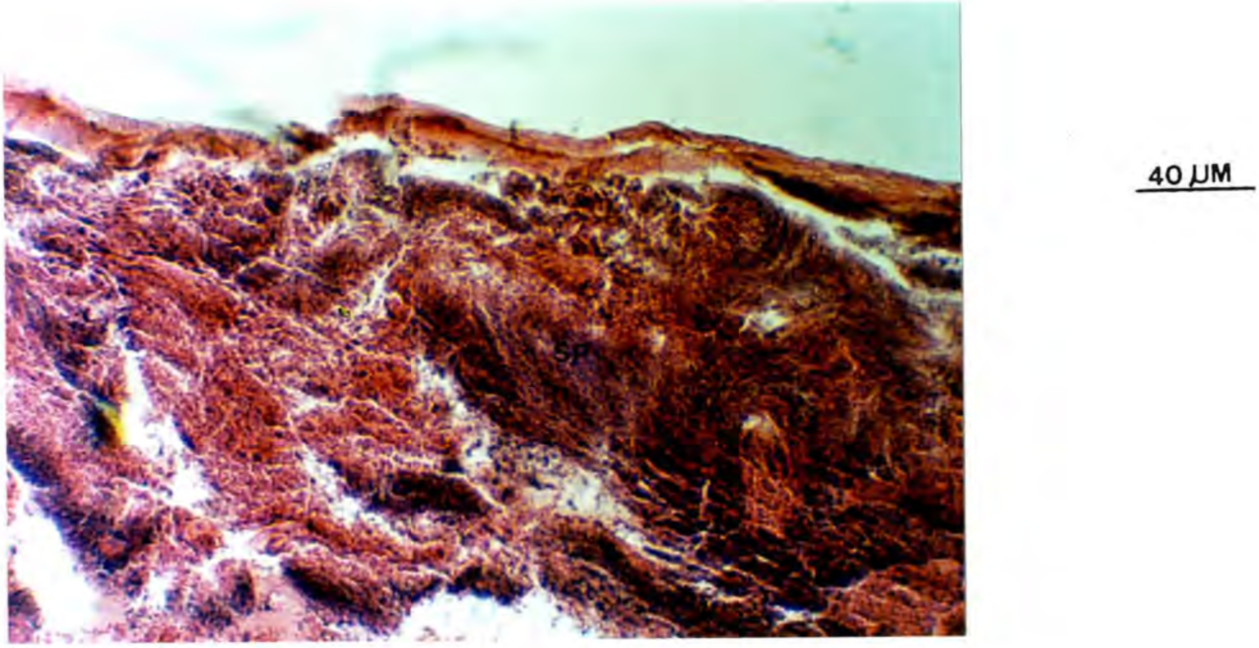

Figure 6.43 **A partially spawned testis of *H. midae* exhibiting atresia (A) of residual sperm (SP).**

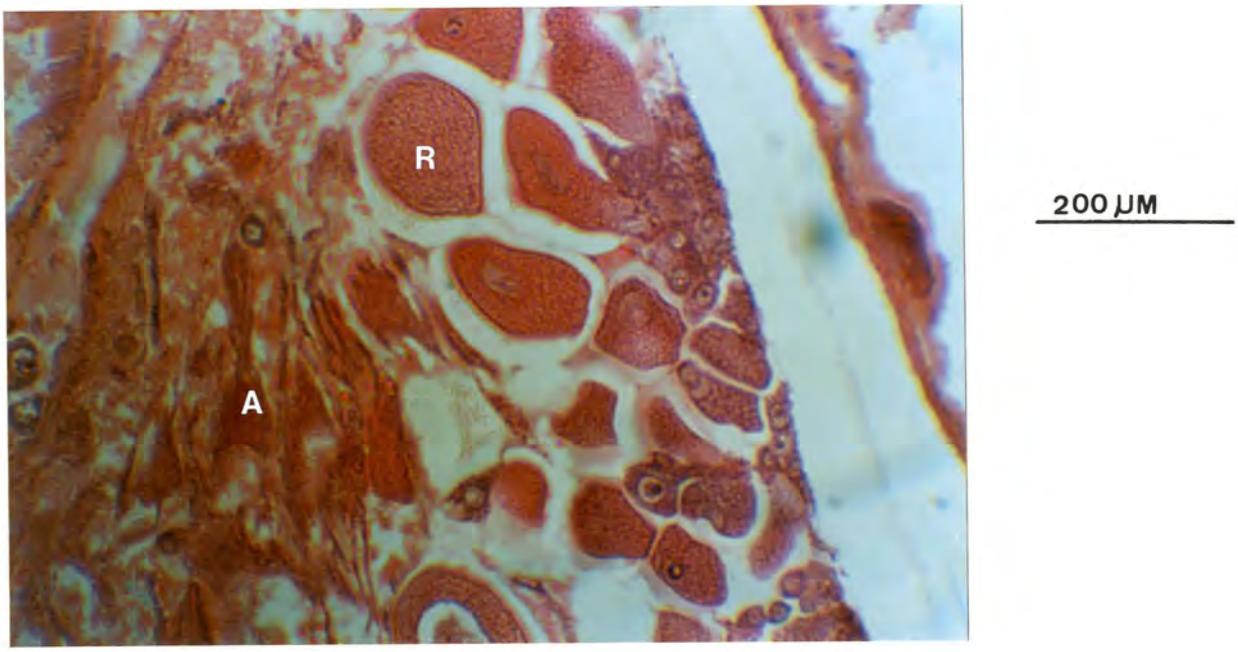

Figure 6.44 A partially spawned ovary of *H. midae* exhibiting atresia (A) of residual ripe eggs (R).

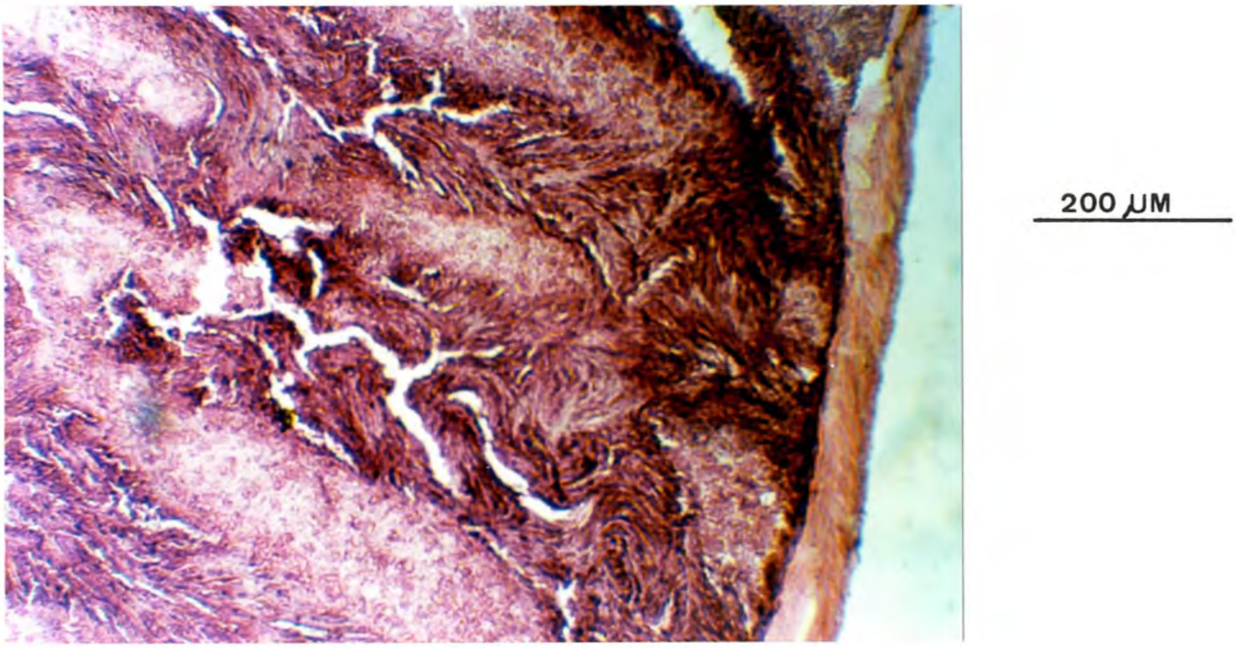

Figure 6.45 A ripe testis of *H. midae* undergoing atresia of all gametogenic material.

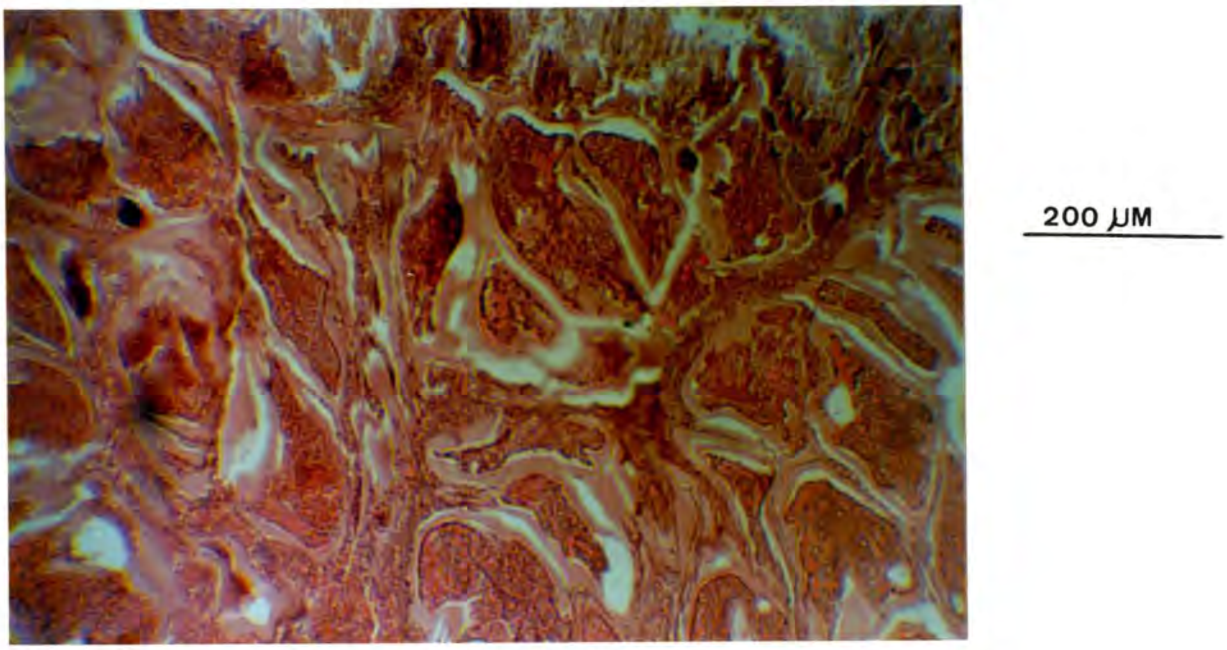

Figure 6.46 A ripe ovary of *H. midae* undergoing atresia of all gametogenic material.

Incomplete spawning was observed for *H. iris* (Poore 1973) and for *H. midae* by Newman (1967b). Degeneration or atresia of unspawned gametes serves to remove them from the gonad lumen, and has been observed in other marine invertebrates such as the sea urchin *Arbacia* punctulata and the bivalve *Macoma balthica* (Harvey 1956 and Caddy 1967 in Giorgi & DeMartini 1977). The presence of a Type III pattern, also described for *H. iris* (Sainsbury 1982), means that once an animal ripens it will not automatically spawn as suggested by Wells & Keesing (1989) for *H. roei*. No matter what pattern is opted for, the tendency in broadcast fertilizers is for their gonads to enter a "resting" stage after spawning in which gametes are absent (Webber & Giese 1969). There was, however, no evidence for this in *H. midae* and gametogenesis was initiated immediately after spawning. In some cases oogonia and spermatogonia were prevalent and actively producing oocytes and spermatocytes in gonads in which atresia of residual gametes was still occurring. Webber & Giese (*op. cit*) found a similar situation in *H. cracherodii*, Giorgi & DeMartini (*op. cit.*) described this for *H. rufescens*, and Shepherd & Laws (1974) identified a similar rapid recovery in *H. cyclobates, H. laevigata, H. roei, H. ruber* and *H. scalaris.*

Aggregative behaviour in abalone during the spawning season has been proposed by Shepherd (1986) for *H. laevigata*, Breen & Adkins (1980a) for *H. kamtschatkana* and by Uno *et al.*(1972 in Shepherd *op. cit.*) for *H. sieboldii*, while Muller (1984) described pairing of *H. spadicea* prior to the breeding season. It was thought that aggregations may be a strategy for maximising contact between sperm and eggs to ensure a high fertilization rate (Shepherd *op. cit.*). No attempt was made in this study to ascertain whether *H. midae* forms spawning aggregations, although in a species which has a protracted and non-synchronous spawning period it may be vital when only a small portion of the population spawn each time.

6.4.3 Sex Ratios

As a rule in dioecious species of molluscs (Fretter & Graham 1964) females tend to be more numerous, a tendency which increases in the older age classes, indicating a higher mortality rate for males. Bolognari (1953) reported a preponderance of females in a sample of 2237 *H. lamellosa*, and in *H. roei* (Branden & Shepherd 1982), *H. rufescens* (Giorgi & DeMartini 1977) and *H. scalaris* (Shepherd & Laws 1974) although males were found to be more numerous below 65 mm SL, females dominated the larger size classes. In contrast, Poore (1973) found a higher number of males in an isolated sample of *H. roei*, Shepherd & Laws (*op. cit*) found males to be more abundant in *H. ruber* and Pearse (1978) reported similar results for *H. pustulata* in the Gulf of Suez. Equal sex ratios have been reported in most other studies, e.g. for *H. tuberculata* (Crofts 1937; Hayashi 1980a), *H. rufescens* (Young & DeMartini 1970), *H. australis*, *H. iris* (Poore *op. cit*), *H. roei*, *H. cyclobates* (Shepherd & Laws *op. cit.*), *H. fulgens*, *H. corrugata*, *H. sorenseni* (Tutschulte & Connell 1981), *H. kamtschatkana* (Sloan & Breen 1988) and *H. midae* Newman (1967b).

Sex ratios can be affected by biased sampling, sex change, differential growth or mortality and by extreme fishing mortality where one sex predominates in size classes above the minimum legal size (Giorgi & DeMartini 1977; Shepherd & Hearn 1983). Hermaphroditism was reported in two specimens of *H. gigantea*, one by Kishinouye (1895 in Murayama 1935) and the other by Murayama (*op. cit.*), and in one specimen of *H. tuberculata* by Girard (1972 in Hayashi 1980a), but not in other haliotid species. Growth rates between males and females have been found to differ for *H. laevigata* in the field (Shepherd & Hearn *op. cit.*) and for *H. rufescens* in the laboratory (Ault 1985). Other than these instances, abalone growth studies have revealed similar growth rates for both sexes. Similarly, growth rates for male and female *H. midae* were not statistically different (see Chapter 4). A single case of higher mortality rates in males has been proposed by Keesing & Wells (1989) for an isolated sample of *H. roei*. Of the four populations sampled in this study, the two at Cape Recife and Kelly's Beach were subject to intensive recreational exploitation but still showed no deviation from an equal sex ratio. The Great Fish Point and Mgwalana populations were subject to very little fishing pressure and also exhibited a 1:1 ratio. It would therefore appear that in the Eastern Cape and in the Western Cape, *H. midae* has an equal sex ratio.

6.4.4 Sexual Maturity

No perlemoen smaller 54 mm SL were sexually mature. All animals below this size were regarded as juveniles. The smallest mature female was 54.6 mm SL and there was evidence of a partial spawning from the cytological examination of its ovary. Although a mature male of 55.4 mm SL was identified, the smallest male to exhibit spawning measured 69 mm SL. Poore (1973) made a similar discovery for *H. iris* and *H. australis* when the minimum size at maturity differed substantially from the size at first spawning. In a comparison between field-conditioned and laboratory conditioned red abalone (Ault 1985), the lab-conditioned animals spawned at a significantly smaller size apparently due to the continuous presence of food. Immature *H. midae* were encountered in animals as large as 120 mm SL. Some of these animals had no gonad material or pigment while others had pigment but lacked sperm or vitellogenic oocytes. The majority of animals in this size range, however, were mature and had the potential to spawn. The presence of ripe, spawning and spent gonads from animals measuring < 100 mm SL confirmed this. All animals larger than 100 mm SL at Great Fish Point and Mgwalana, and > 120 mm SL at Cape Recife and Kelly's Beach were sexually mature over the period of sampling.

In some species of abalone such as *H. fulgens, H. corrugata* and *H. sorenseni* (Tutschulte & Connell 1981) there was a change in growth and survival rates of a particular sex following sexual maturity, which led to a skewing of the 1:1 ratio. In *H. midae*, however, this was not the case as a 1:1 ratio was observed for all size classes above the sizes at sexual maturity.

An important discovery was that the sizes at 50% sexual maturity (51.2 - 57.46 mm SW) were considerably smaller than the 80 mm SW obtained for *H. midae* by Newman (1967b) in the Western Cape. From Chapter 3, these sizes corresponded to the 3rd and 7th years of growth in the respective areas. The size at 50% sexual maturity is an important management consideration as it gives an idea of the size at which animals should be harvested (Muller 1984) while at the same time affording a degree of protection to the spawner stock. The full implications of the smaller maturity sizes are discussed in Chapters 4 and 7. Size at 100% sexual maturity also differed significantly in Western Cape waters, being attained at 105 mm SW which corresponded to an age of 11.3 years (Newman *op. cit*) as opposed to the 80 mm SW and 4.19 years in this study.

6.4.5 Fecundity

Abalone like all broadcast spawners are typically highly fecund, with considerable variability in larger individuals (Sainsbury 1982). For the most accurate estimates of fecundity, sampling immediately prior to spawning would have been desirable, however, due to the asynchronous and protracted breeding season exhibited by *H. midae*, this was not possible. No fecundity estimates for females below 60 mm SL were obtained as gonads were superficial and separation from the hepatic gland proved impractical. Based on the fecundity : length relationship, however, it is apparent that the contribution of eggs from this size class to the overall production in the population would be negligible. Fecundities as low as 100 to 1000 have been recorded in small size classes of *H. iris* by Sainsbury (1982) and were declared negligible as well. Numbers of eggs produced by *H. midae* between 60 - 75 mm SL are higher, but substantial numbers are produced only above 80 mm SL. A decrease in fecundity among larger females was observed by Muller (1984) for *H. spadicea*, and by Giorgi & DeMartini (1977) for *H. rufescens*, and it would appear that senescence of older individuals was the reason for this decline. By virtue of this, the harvesting of the larger members of a stock may be affording a degree of protection to the smaller more fecund members of the population. Commenting on this aspect for *H. midae* is speculative because of the high variability in the counts, however, a decline resulting from senescence is unlikely due to their relatively short lifespan. Table 6.6 provided a summary of some of the fecundity estimates for other haliotid species, and it was evident that *H. midae* was significantly more fecund in the Western Cape where it shared the highest fecundity values with the largest of all haliotid species, *H. rufescens*.

6.4.6 Factors affecting the Reproductive Cycle

Abalone in captivity which are used for aquaculture purposes can be induced to spawn almost at will using a variety of stimuli such as hydrogen peroxide, temperature shock, crowding and sterilized water. The stimuli in nature are, however, poorly understood. Giese (1959) proposed that aspects of the reproductive cycle in marine invertebrates could be influenced in three ways, *viz:*

(1) As the result of a series of endogenous events (circadian rhythms) which accumulate inside the organism.

Table 6.6 Fecundity estimates of various haliotid species reported in the literature.

Species	Reference	Minimum fecundity	SL (mm)	Maximum fecundity	SL (mm)
H. midae	Newman (1967b)	2.50×10^6	109.5*	25.40×10^6	158.0*
	This study	2.73×10^4	68.3	5.99×10^5	129.0
H. spadicea	Muller (1984)	1.50×10^3	38.0	6.00×10^5	65.0
H. iris	Poore (1973)	1.20×10^4	68.0	11.25×10^6	155.0
	Sainsbury (1982)	$10^2 - 10^3$	71.0 - 80.0	1.50×10^6	123.0
H. australis	Poore (*op. cit.*)	4.60×10^4	62.0	2.90×10^6	91.0
H. rufescens	Giorgi & DeMartini (1977)	6.19×10^5	136.0	12.60×10^6	190.5
	Ault (1985a)	1.25×10^5	111.8	25.41×10^6	178.2
H. tuberculata	Hayashi (1980a)	3.80×10^4	49.0	5.10×10^6	115.0
H. roei	Wells & Keesing (1989)	1.63×10^5	35.0	8.60×10^6	122.0

* - Shell width.

SL - Standard length.

(2) As the result of exogenous environmental factors acting on a flexible organism. This is especially applicable to temperate regions where there are distinct annual cycles of light intensity, temperature, nutrients and winds which drive cycles of productivity (Wilk *et al.* 1990).

(3) By a combination of 1 and 2. The possibility of an internal biological clock operating independently is unlikely mainly due to the differences in timing of spawning which are evident in a species which finds itself in two or more different geographic locations. This fact also suggests that exogenous factors instead have the strongest influence on the breeding cycle. Aspects such as photoperiod, tidal shift, temperature change, and temperature shock or quietness after shock (Giese 1959) have been suggested. While these aspects may influence the reproductive cycle throughout the year, the endogenous influence of chemicals (particularly glycogen and certain proteins and lipids) may be important immediately prior to a spawning event.

There is a general consensus in the literature that, in molluscs, temperature is the most important factor (Newman 1967b), acting as a stimulus for spawning as well as gonad maturation (Fretter & Graham 1964). Hayashi (1980a) found that spawning in *H. tuberculata* coincided with maximum water temperatures for the year, however, spawning also varied at different locations where temperatures were similar, and he suggested that other factors such as food supply, population density and structure, current and bottom conditions should be considered as well. Experimental evidence for *H. diversicolor supertexta* (Oba 1964) showed that a decrease in temperature stimulated spawning. *Haliotis midae* spawned twice a year in the south-Western and Western Cape, with rising water temperatures being associated with the summer spawning and declining temperatures prevailing during the autumn event. Newman (*op. cit*) advises caution in interpreting this data, due to the prevalence of variable winds which caused periodic upwelling events which could have had some influence of their own.

Mean monthly sea temperatures from Humewood Beach near Cape Recife showed a decrease from May to June 1991 preceding the peak period of gonad activity for that year, followed by a gradual increase throughout the spawning period (Figure 6.47). A similar drop in temperature again in March 1992 once more preceded the beginning of the breeding cycle in April. However, in contrast to the previous year, a gradual decrease in temperatures accompanied spawning until September. So while it was tempting to invoke a sudden temperature decrease as being the initiator of spawning, it is unlikely because of the duration of the season over many months. The steady increase of temperatures during one season and their decline the following season indicated that temperature was not so influential.

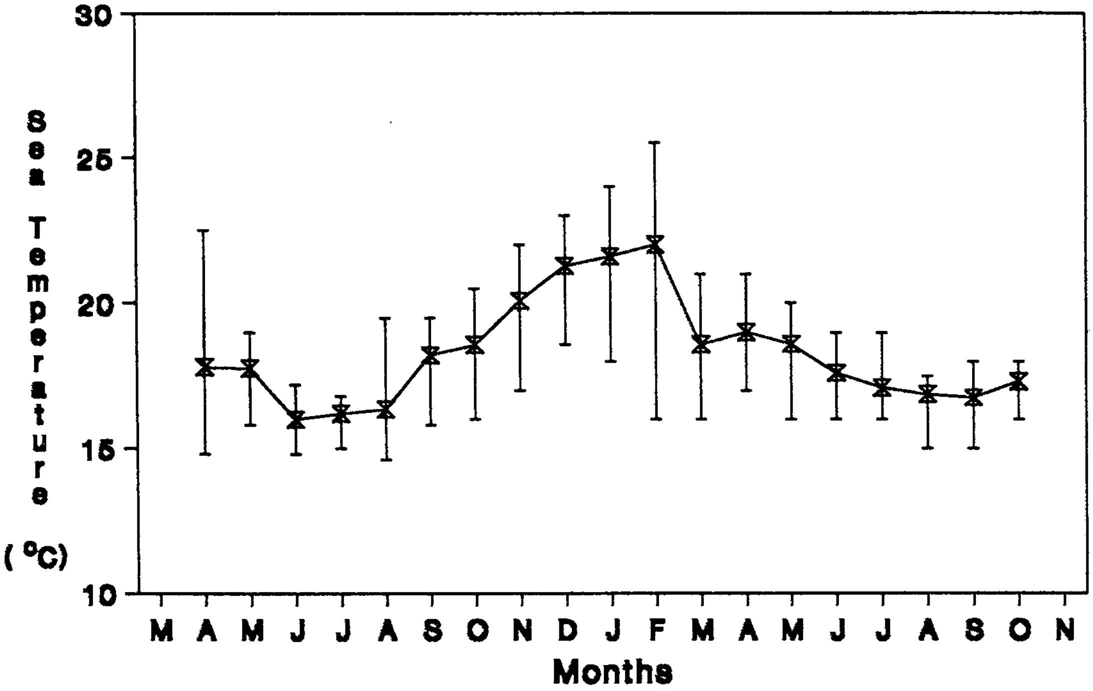

Figure 6.47 Mean monthly sea temperatures for Humewood Beach for the period April 1991 to October 1992.

Temperatures from Port Alfred (Figure 6.48) have been used as a reference for Great Fish Point and Mgwalana. The regime was more erratic than at Humewood Beach, but was similar with the same upward trend during the 1991 spawning season and the decrease the following season. A sharp drop coincided with the onset of spawning in the populations in February of 1992, however, a similar decline in June 1991 only occurred well into the breeding season. The absence of spawning at Great Fish Point and Cape Recife coincided with the highest recorded temperatures during the summer months, but a proportion of the Mgwalana population were still observed to be spawning at this time. Except for an upwelling event recorded at Great Fish Point and Mgwalana in December 1991, there were no records of further upwellings. As a result, the full extent to which temperature had its influence could not be determined, and other factors such as food, tides and photo-period should be considered and investigated in the future.

The effect of water temperature was further complicated in species such as *H. scalaris, H. roei* and *H. rufescens* which were potential all year spawners (Shepherd & Laws 1974; Boolootian *et al.* 1962; Young & DeMartini 1970). Gonad growth, gamete production and the initiation of spawning in other species is controlled by factors other than temperature, such as photoperiod (Webber & Giese 1969) and seasonal changes in food (Boolootian *et. al* 1962). Shepherd & Laws (*op. cit.*) discussed the importance of the supply and availability of food and changes in

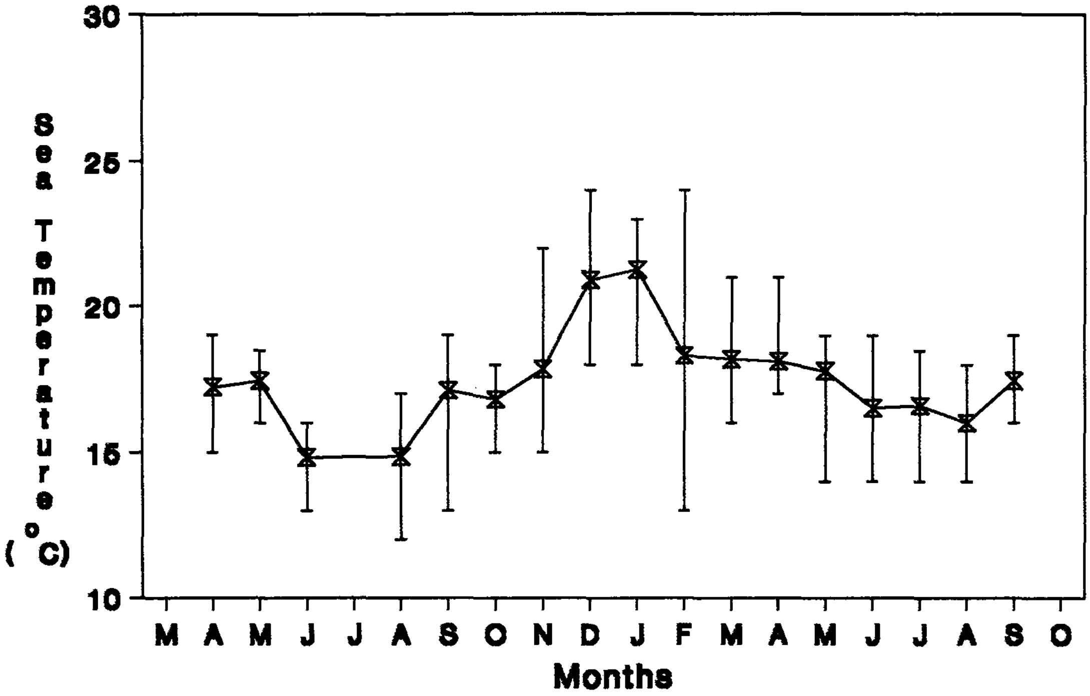

Figure 6.48 Mean monthly sea temperatures for Port Alfred for the period April 1991 to September 1992.

temperature as factors which restricted the spawning periodicities in five sympatric species of abalone which exhibit seasonal differences. They reached no conclusion, however, and stated that the extent to which these differences were endogenous or regulated by seasonal or local environmental factors was problematic.

Once an animal spawns, however, it would appear that the presence of gametes and hormones in the water signals other members who are ready, via receptors linked to the nervous system, to release their gametes as well (Giese 1959) in what has been described as a spawning epidemic (Shepherd 1976).

CHAPTER 7 SUMMARY AND MANAGEMENT CONSIDERATIONS

Like the majority of abalone species (Shepherd 1973b; Peck & Culley 1990), *Haliotis midae* exhibited specific habitat requirements. As a rule, small animals (0 - 45 mm SL) occupied the sub-boulder microhabitat, medium sized animals (50 - 90 mm SL) inhabited other cryptic niches such as caves, crevices and the underside of overhangs, while the larger size classes (> 100 mm SL) were encountered in exposed positions on the flat surfaces of large rocks and pinnacles. This high degree of microhabitat specificity was demonstrated by the virtual absence of *H. midae* from the *Caulerpa* bed habitat at Great Fish Point which did not cater for the requirements of the small and large animals in terms of boulders and exposed, smooth planar surfaces respectively. Changes in microhabitat preference in abalone as they grow can be attributed to a change in diet and/or predation pressures (Sloan & Breen 1988). While the observed change in dietary composition between the small cryptic and larger animals suggested that dietary preferences influenced the move from sub-boulder spaces to more exposed positions, predators ultimately dictated that animals moved to crevice and cave refuges as they outgrew the confines of sub-boulder spaces. The intertidal and shallow subtidal reefs which were home to *H. midae* on the east coast were also host to numerous potential predators which included *Octopus vulgaris, Plagusia chabrus, Thais capensis, Diplodus sargus capensis, Diplodus cervinus hottentotus, Coracinus multifasciatus, Sparadon durbanensis, Myliobatus equila and Pteromylaeus brovinus.* Not only did predators confine the smaller size classes of *H. midae* to specific sheltered niches, but they also restricted them, as well as the larger exposed animals, to predominantly nocturnal activities.

In addition to the protection afforded by the sub-boulder microhabitat, small *H. midae* commonly inhabited the spaces beneath the spine canopies of adult urchins (*Parechinus angulosus*). These urchins were also encountered in crevices and caves where they afforded protection to the resident intermediate sized *H. midae* during daylight hours. Larger exposed individuals relied on their thick shells and strong adhesive force for protection - a strategy which is effective against all predators except man.

While predators appeared to determine the immediate environment in which an individual animal found itself, a larger suite of characters influenced the hospitability of a particular reef to *H. midae*, *viz*:

1. A diversity of suitable and available microhabitats for protection against predators. The absence of suitable niches or the occupation of niches by large numbers of urchins and alikreukels (*Turbo sarmaticus*) may preclude the settlement and establishment of *H. midae*.

2. Sufficient larval settling areas and the presence of the correct settlement cues provided initially by encrusting coralline algae such as *Lithothamnion* sp. (Shepherd & Turner 1985; Shaw 1991) and then in combination with cues from conspecifics such as mucous trails (Seki & Kan-no 1981a,b; Slattery 1992). The encrusting corallines also act as substrates for diatoms and bacteria which fulfil the dietary requirements of recently metamorphosized juveniles.
3. A ready supply of food for juveniles (see above) and adults in the form of attached and/or drift seaweeds.
4. The correct depth and temperature regimes.
5. Good water circulation for the removal of wastes and sediments and transport of drift algae.

Growth of *H. midae* was adequately described by the Von Bertalanffy growth model which has described growth over a broad size range for most haliotids (Sloan & Breen 1988). Growth was typically fast in juveniles and then slowed in larger size classes as the animals became sexually mature (Forster 1967; Shepherd & Hearn 1983). A summary of haliotid growth studies revealed that growth rates differed significantly both inter-specifically (Sainsbury 1982) and intra-specifically (Mottet 1978). Based on tag return data, growth in *H. midae* varied on a localized scale within the Eastern Cape between Great Fish Point and Bird Island, and in the south-western Cape between Roman Bay (N. Sweijd unpublished data) and Stony Point (Newman 1968). The results from this study also indicated that growth differed on a regional scale between the Eastern Cape and the Western Cape with Eastern Cape animals achieving a faster growth rate, a smaller maximum size and a lower longevity. These differences could be attributed to different temperature regimes, dietary differences and gender. Differential growth rates for males and females in abalone are rare (Ault 1985), and there was no indication of it occurring in *H. midae*. Waters in the Western Cape are colder than in the Eastern Cape and growth has been shown to be inhibited in colder temperature regimes (Sakai 1962b; Poore 1972c). In the Western Cape, *H. midae* ate predominantly the brown kelp *Ecklonia maxima* (Barkai & Griffiths 1986) while red seaweeds such as *Plocamium corallorhiza* and *Hypnea spicifera* were the major dietary constituents in Eastern Cape waters, however, in both regions food was not limited and it is doubtful if dietary composition could influence growth to any great extent. Although food was found to influence growth in *H. cracherodii*, major seasonal variations were attributed to gonad maturation and the sexual cycle (Leighton & Boolootian 1963). Since growth also differs between animals with similar dietary profiles in areas with similar temperature regimes, the observed differences in growth patterns for *H. midae* were more likely the result of a combination of all the above factors rather than just one (Shepherd & Hearn 1983; Keesing &

Wells 1989).

Although the smaller maximum size and smaller size at sexual maturity for Eastern Cape animals were attributed to a faster growth rate, some abalone species exhibit smaller maximum sizes and sizes at maturity coupled with slower growth rates (Poore 1972c), while others retain similar sizes at maturity even when growth rates differ (Sainsbury 1982).

It is known that individuals of the same size grow at different rates, and that individuals themselves grow at different rates at different times depending on circumstances prevailing in their immediate environment or microhabitat (Wright 1975). The growth curves for *H. midae* indicated a high degree of individual variation within each age class which meant that the age of an animal could not be determined to any degree of certainty based on size alone.

The present minimum legal size for *H. midae* of 114 mm SW was attained at an age of 6.83 years in the Eastern Cape and after only 12.33 years in the Western Cape.

Floral composition at a site has a major influence on dietary composition (Tunbridge 1967) but feeding patterns of haliotids rarely exhibit selectivity for specific prey items in the field (e.g. Poore 1972a; Barkai & Griffiths 1986), although it has been demonstrated experimentally for several species (Leighton & Boolootian 1963; Sakai 1962a). Feeding behaviour in the field instead depends on food availability (drift and attached algae) and the degree of water movement with respect to transport of drift algae and fragmentation of attached species (Shepherd 1973b). While *H. midae* showed a small degree of selectivity, more so in exposed animals than in cryptic individuals, they generally ate the most abundant seaweeds at the Great Fish Point site. Exposed animals had a preference for red algae, in particular *H. spicifera* and *P. corallorhiza*, while sub-boulder cryptics included a larger proportion of brown (*Ralfsia expansa*) and green (*Ulva* spp.) seaweeds in their diets. Generally, abalone species prefer red (Shepherd 1973b; Poore 1972a; Tomita & Tazawa 1971; Muller 1984) or brown algae (Tutschulte & Connell 1988a; Tegner 1989), but green algae are not major or preferred dietary components (Shepherd & Steinberg 1992). Epiphytic and benthic diatoms, microalgae and bacteria are the primary food source for recently metamorphosized haliotid juveniles (Sloan & Breen 1988; Ebert & Houk 1984), but none were found in *H. midae* although stomachs of juveniles smaller than 11 mm SL were not examined.

Haliotis midae was a nocturnal feeder, utilizing both drift and attached algal species as food sources, a pattern observed for other haliotid species as well (Shepherd 1973b). Other abalone species have been described as exclusive grazers on attached algae (Paul *et al.* 1977; Muller 1984) while others were exclusive drift utilizers (Olsen 1968; Wells & Keesing 1989). It would appear as if a combination of microhabitat utilization and the differential availability of drift algae determined the feeding mechanisms adopted by any one species. The significance of nocturnal feeding excursions was attributed to predation pressures which were extreme during daylight hours (Shepherd 1973b; Muller 1984).

Pigments from seaweeds consumed by abalone are bound to proteins and incorporated in the various shell layers (Leighton 1961; Fretter & Graham 1962). The preferred diet of red algae was reflected in the red shell colour of *H. midae* at Great Fish Point, and similarly coloured shells from animals all along the East Cape coast implied that these animals utilized the rhodophytes as their main food source, unlike *H. midae* in the Western Cape which predominantly consumed *Ecklonia maxima* (Barkai & Griffiths 1986).

Like other haliotids and many primitive molluscs (Shaw 1991; Brown 1991), *H. midae* is a broadcast spawner with lecithotrophic larval stages which are terminated when they are induced to settle by cues from conspecifics or encrusting coralline algae.

Because of the many limitations linked with GBI's (Giese 1959; Webber & Giese 1969; Poore 1973), they were only used to infer probable spawning cycles. Histological evidence confirmed the patterns inferred from mean monthly GBI values, while also being used to describe gonad structure, gametogenesis and the breeding cycle. The spawning season was protracted, extending from March - October (and December at Mgwalana) with the majority of individuals spawning between April and June. The lecithotrophic larval stages facilitate a protracted spawning season because they are not dependant on seasonal planktonic cycles for food, although they are capable of utilizing dissolved organic materials, such as complex sugars, as a source of nutrition (Welborn & Manahan 1990). An extended breeding season implies either that several broods are produced each season or that populations are asynchronous (Giese 1959). Evidence for *H. midae* was that;

a) they were asynchronous, with only a portion of each population spawning each month, and

b) spawning was iteroparous, with no histological evidence of gamete retention, and residual eggs and sperm were reabsorbed after a spawning event.

As described for *H. rufescens* (Giorgi & DeMartini 1977), *H. midae* exhibited total spawning, partial spawning and total atresia of ripe gonads without spawning. This last pattern deviated from the norm described by Wells & Keesing (1989) where once an animal ripened it would automatically spawn.

The mean size at 50% sexual maturity for *H. midae* in the Eastern Cape was 53.83 mm SW (73.09 mm SL) attained at 2.7 years of age. This was in contrast to 80 mm SW for *H. midae* in the Western Cape (Newman 1967b) which was attained at an age of 7.06 years (Newman 1968). Two populations, at Cape Recife and Kelly's Beach, were heavily exploited by recreational divers, while the populations at Great Fish Point and Mgwalana were rarely fished. Equal sex ratios were described for all size classes above sexual maturity at all four locations. A 1:1 sex ratio under extreme fishing mortality is indicative of similar growth characteristics for males and females - this was confirmed in the ageing study. Differential gender growth can lead to one sex being recruited to the fishery sooner, thereby leading to a skewing of the natural sex ratio which can adversely affect reproductive output and have long term deleterious affects on recruitment (Ault 1985).

As is typical of broadcast spawners, *H. midae* was highly fecund although it exhibited a high degree of variation with respect to fecundity and animal size, and gonad weight and animal size. This was attributed to the inclusion of recovering or sub-ripe ovaries in the counts, nevertheless a linear relationship between gonad weight and fecundity was obtained. The low longevity of *H. midae* implied that fecundity would not decrease with age as described in other species (Giorgi & DeMartini 1977; Muller 1984) which live in excess of 25 - 30 years and where older animals contributed less due to the effects of senescence.

While abalone in captivity can be induced to spawn at any time after exposure to certain stimuli, the processes which control the breeding cycle and initiate spawning in nature are poorly understood. It is widely accepted that a combination of mainly exogenous environmental factors and to a lesser extent endogenous circadian rhythms and chemical processes influence breeding patterns, with temperature being the most important factor of all (Fretter & Graham 1964; Newman 1967b). Sea temperatures did not correlate well with the gonadal cycle and spawning season of *H. midae*, however, with a protracted breeding season this was to be expected (e.g. Young & DeMartini 1970). The exact role that temperature plays both in the Eastern Cape and the Western Cape remains uncertain due to the variable winds which cause periodic upwelling events in both regions. Future work needs to consider other factors whose influences and effects are more localized, such as food supply, currents and bottom conditions, tidal cycle, photoperiod, and population densities and structure (Giese 1959; Hayashi 1980a; Wilk *et al.* 1990). It seems, however, that once a single animal has spawned, the presence of hormones and gametes in the water can trigger spawning in other ripe individuals. If this is the case then it could explain that the significance of aggregations formed by some species during the spawning season (Shepherd 1986) was to ensure maximum possible fertilization rates in an unstable and often unpredictable environment.

Management considerations

Haliotis midae is highly susceptible to over exploitation along the Eastern Cape coast for the following reasons:

1. Although *H. midae* is capable of movement it is restricted to relatively small areas because of the patchiness of the reef along the coast and the high degree of microhabitat specificity exhibited by various size classes. These two aspects are also the reason for the observed discontinuous distribution of *H. midae* in the Eastern Cape, with the resultant small isolated populations being particularly sensitive to extreme fishing pressure.
2. These animals have a preference for shallow water. Although it is commonly found down to 10 meters and occasionally extends its range to 35 meters in the Western Cape (Barkai & Griffiths 1986), *H. midae* in the Eastern Cape is restricted to the rocky intertidal and shallow subtidal reefs down to a depth of between 4 and 5 meters.
3. Legal sized animals occupy exposed positions on rock faces and despite extensive settlement and growth of organisms on the shells, they remain highly visible. This aspect together with their restricted and shallow distribution makes them easily accessible to divers.
4. Many sub-legal sized individuals (105 - 113 mm SW) which are also exposed and highly visible, and which are damaged when they are mistakenly removed from the rocks, have minimal chances of survival after being returned. *Haliotis midae* bleed profusely because they lack coagulating agents in their blood, and if accidentally cut will bleed to death, if predators are not attracted to them first. A damaged shell also exposes the soft visceral and body parts to predators.
5. An asynchronous and protracted breeding season together with pelagic larval stages in the unstable rocky intertidal surf zone contribute to the unpredictable recruitment which characterises abalone species. Their patchy distribution, specific microhabitat requirements of larvae and juveniles together with a poor understanding of the environmental and endogenous processes which control spawning, contribute more to the inability to predict accurately when, where and to what extent recruitment will occur.

At present there are blanket restrictions imposed on *H. midae* along its entire distributional range based upon biological parameters obtained from animals in the cool Western Cape waters. The minimum legal size is set at a level above its size at 50 % sexual maturity (80 mm SW), the closed season coincides with the period when the majority of animals are at their peak of reproductive activity, and the bag limit is set at 4/man/day. Based on results from this study, the minimum size and closed season restrictions are inadequate for Eastern Cape animals. These restrictions should be re-evaluated if sustainable utilization of *H. midae* in the Eastern Cape is to be ensured. A reduction in the minimum legal size for East Cape coast animals,taking the size at 50 and 100 % maturity into account, should be considered. If the new size was to be implemented at the size attained one year after the animal reaches 100 % sexual maturity (as it is at the moment, based on Western Cape growth parameters), the new size would be approximately 93 mm SW and 119 mm SL, which is attained at 5.19 years of age. The faster growth rate also means that Eastern Cape populations have the potential to recover from the effects of fishing a lot quicker than their cold water conspecifics. While the existing closed season incorporates part of the spawning season of *H. midae* in the Eastern Cape, the animals are open to exploitation during their peak breeding period between April and June. A shift in the closed season to this period should be considered as a more effective management option in this region, although studies should first be conducted to ascertain whether *H. midae* is more vulnerable during the spawning period, e.g. to establish whether it forms spawning aggregations (Shepherd 1986; Breen & Adkins 1980). If this is the case then the closed season should incorporate the peak spawning period, however, if this is no the case then the effectiveness of a closed season during the breeding season must be questioned, and other options such as closed areas on a rotational basis amongst populations could be considered.

The concept of closed areas which are free from exploitation has been recognized as a viable management option for the *H. midae* fishery (Tarr 1992) with the establishment of abalone reserves at Betty's Bay and Dyer Island, and the Castle Rock Marine Reserve in False Bay (Tarr 1987; see Figure 2.1). The protection afforded the spawner stock in these closed areas would benefit the immediate and nearby populations, but depleted stocks further along the coast would only benefit if larval dispersion and/or adult migrations were extensive (Tegner & Butler 1985b). Newman (1966) concluded that *H. midae* had the potential to migrate over vast distances and replenish depleted stocks, however, his data was unreliable since it was based on tagged animals removed from their home scars and returned to a different site, and was also extrapolated from short term records. Migratory tendencies have been proven for three species of Japanese abalone, *H. sieboldii, H. gigantea* and *H. discus* (Koike *et al.* 1972), which moved from adjacent areas to repopulate a test area which had been cleared of all animals only 2 to 3 months previously. This would, however, have limited relevance to the Eastern Cape situation, as reefs are typically small, discontinuously distributed and separated by vast expanses of sand which preclude the movement of abalone. Stocks are instead maintained either by direct input from the resident spawner stock or by larval drift from nearby populations, although the extent to which the larvae of *H. midae* are capable of dispersing is yet to be determined.

In summary it is proposed that the minimum legal size in the Eastern Cape be reduced to 93 mm SW, and that the closed season in the Eastern Cape be temporarily moved to the 1st April - 31st June until the feasibility of closed areas for the small isolated Eastern Cape populations can be determined.

REFERENCES

ANONYMOUS. 1991. SA abalone TAC by area (Tons whole mass): 1992. *S. A. Shipping News & Fishing Industry Rev.* **46(6):** 19.

ANWAR, N.A., RICHARDSON, C.A. & SEED, R. 1990. Age determination, growth rate, and population structure of the horse mussel *Modiolus modiolus*. *J. Mar. Biol. Assoc. U. K.* **70:** 441-457.

ARNOLD, W.S., MARELLI, D.C., BERT, T.M., JONES, D.S. & QUITMYER, I.R. 1991. Habitat-specific growth of hard clams *Mercenaria mercenaria* (L.) from the Indian River, Florida. *J. Exp. Mar. Biol. Ecol.* **147:** 245-265.

AULT, J.S. 1985. Some quantitative aspects of reproduction and growth of the red abalone *Haliotis rufescens* Swainson. *J. World Maricul. Soc.* **16:** 398-425.

AULT, J.S. & DEMARTINI, J.D. 1987. Movement and dispersion of red abalone, *Haliotis rufescens*, in northern California. *Calif. Fish Game* **73(4):** 196-213.

BARKAI, R. & GRIFFITHS, C.L. 1986. Diet of the South African abalone *Haliotis midae*. *S. Afr. J. Mar. Sci.* **4:** 37-44.

BARKAI, R. & GRIFFITHS, C.L. 1987. Consumption, absorption efficiency, respiration and excretion in the South African abalone *Haliotis midae*. *S. Afr. J. Mar. Sci.* **5:** 523-529.

BARKER, M.F. 1977 Observations on the settlement of the brachiolaria larvae of *Stichaster australis* (Verrill) and *Coscinasterias calamaria* (Gray) (Echinodermata: Asteroidea) in the laboratory and on the shore. *J. Exp. Mar. Biol. Ecol.* **30:** 95-108.

BARLOW, L.A. 1990. Electrophysiological and behavioral responses of larvae of the red abalone (*Haliotis rufescens*) to settlement-inducing substances. *Bull. Mar. Sci.* **46(2):** 537-554.

BARNARD, K.H. 1963. Contributions to the knowledge of South African marine Mollusca. *Ann. S. Afr. Mus.* **47:** 304-306.

BARNES, J.R. & GONOR, J.J. 1973. The larval settling response of the lined chiton *Tonicella lineata*. *Mar. Biol.* **20:** 259-264.

BEAMISH, R.J. & MCFARLANE, G.A. 1983. The forgotten requirements for age validation in fisheries biology. *Trans. Am. Fish. Soc.* **112(6):** 735-743.

BECKLEY, L. 1988. Marine invertebrates. In: A field guide to the East Cape coast. pp73-88. (Eds.) R.A. Lubke, F.W. Gess & M.N. Bruton. Grahamstown Centre of the Wildlife Society of Southern Africa.

BENNETT, R., THANASSI, N. & NAKADA, H.I. 1971. Hepatopancreas glycosidases of the abalone (*Haliotis rufescens*). *Comp. Biochem. Physiol.* **40(B):** 807-811.

BERG, J. 1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobiusculus flavescens* (Gobiidae). *Mar. Biol.* **50:** 263-273.

BOLOGNARI, A. 1953. Richerche sulla sessualita di *Haliotis lamellosa* Lam. *Archo. Zool. Ital. Torino.* **38:** 361-402.

BOOLOOTIAN, R.A. FARMANFARMAIAN, A. & GIESE, A.C. 1962. On the reproductive cycle and breeding habits of two western species of *Haliotis*. *Biol. Bull. (Woods Hole).* **122(2):** 183-193.

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

BRANCH, G.M. 1975. Intraspecific competition in *Patella cochlear* Born. *J. Anim. Ecol.* **44:** 263-281.

BRANCH, G. & BRANCH, M. 1981. Rocky Shores. In: The living shores of Southern Africa. pp26-50. C. Struik, Cape Town.

BRANDEN, K.L. & SHEPHERD, S.A. 1982. A survey of stocks of the abalone *Haliotis roei* Gray on the western coast of Spencer Gulf, South Australia. 1. *S. Austr. Dept. Fish., Fish. Res. Paper.* **4.**

BREEN, P.A. 1980. Measuring fishing intensity and annual production in the abalone fishery of British Columbia. *Can. Tech. Rep. Fish. Aquat. Sci.* **947:** 49pp.

BREEN, P.A. 1986. Management of the British Columbia fishery for northern abalone (*Haliotis kamtschatkana). Can. Spec. Publ. Fish. Aquat. Sci.* **92:** 300-312.

BREEN, P.A. & ADKINS, B.E. 1979. A survey of abalone populations on the east coast of the Queen Charlotte Islands, August 1978. *Fish. Mar. Serv. MS Rep.* **1490:** 125pp.

BREEN, P.A. & ADKINS, B.E. 1980a. Spawning in a British Columbia population of northern abalone, *Haliotis kamtschatkana. Veliger.* **23:** 177-179.

BREEN, P.A. & ADKINS, B.E. 1980b. Observations of abalone populations in Emily Carr Inlet and Lotbiniere Bay, April 1980. *Can. Manuscr. Rep. Fish. Aquat. Sci.* **1576:** 17pp.

BREITBURG, D.L. 1984. Residual effects of grazing: inhibition of competitor recruitment by encrusting coralline algae. *Ecology.* **65:** 1136.

BROWN, L.D. 1991. Genetic variation and population structure in the blacklip abalone, *Haliotis rubra. Aust. J. Mar. Freshwater Res.* **42:** 77-90.

BUTTERWORTH, D.S., PUNT, A.E., BORCHERS, D.L., PUGH, J.B. & HUGHES, G.S. 1989. A manual of mathematical techniques for linefish assessment. *S. Afr. Natn. Sci. Prog. Rep.* **160:** 89pp.

CARLISLE, J.G. 1962. Spawning and early life history of *Haliotis rufescens* Swainson. *Nautilus.*

76(2): 44-48.

CLAVIER, J. & RICHARD, D. 1985. Etudes sur les Ormeaux dans la Region de Saint-Malo. *Association pour la Mise en Valeur du Littoral de la Cote d'Emeraude, France.* 285pp.

CLAVIER, J. & RICHARD, D. 1986. Growth of juvenile *Haliotis tuberculata* (Mollusca: Gastropoda) in their natural environment. *J. Mar. Biol. Assoc. U.K.* **66:** 497-503.

COCHARD, J.C. & FLASSCH, J.P. 1981. Etat des connaissances sur l'ormeau (*Haliotis tuberculata*). *Actes Colloq.* **12:** 55-59.

COMFORT, A. 1951. The pigmentation of molluscan shells. *Biol Rev.* **26:** 285-301.

COOPER, J., WIELAND, M. & HINES, A. 1976. Subtidal abalone populations in an area inhabited by Sea Otters. *Veliger.* **20(2):** 163-167.

COTTON, B.C. 1959. South Australian Mollusca. Archaeogastropoda. Suborder Rhipidoglossa In: Handbook of the Flora and Fauna of South Australia. pp29-32. Government Printer, Adelaide.

COX, K.W. 1962. California abalones, Family Haliotidae. *Dept. Fish Game. Fish. Bull. Calif.* **118:** 133pp.

CROFTS, D.R. 1929. *Haliotis. Liverp. Mar. Biol. Comm. Memoirs.* **29:** 1-74.

CROFTS, D.R. 1937. The development of *Haliotis tuberculata*, with special reference to organogenesis during torsion. *Phil. Trans. Roy. Soc. London. Ser. B.* **228:** 219-268.

DAY, J.H. 1974. A guide to marine life on South African shores. 2nd edition. Cape Town, Balkema. 300pp.

DAY, R.W. & FLEMING, A.E. 1992. The determinants and measurement of abalone growth. In: Abalone of the world. Biology, fisheries and culture. pp141-168. (Eds.) S.A. Shepherd, M.J Tegner & S.A. Guzman del Proo. Blackwell Scientific Publications, Great Britain.

DAY, R.W. & LEORKE, A.E. 1986. Abalone catches - what factors affect them. *Aust. Fish.* **45(10):** 32-36.

EBERT, E.E. & HOUK, J.L. 1984. Elements and innovations in the cultivation of red abalone, *Haliotis rufescens. Aquaculture.* **39:** 375-392.

EMMETT, B & JAMIESON, G.S. 1988. An experimental transplant of northern abalone, *Haliotis kamtschatkana*, in Barkley Sound, British Columbia. *Fish. Bull. U. S.* **87:** 95-104.

ERASMUS, J. 1992. A study of the internal shell structure and growth rings in the shell of the abalone *Haliotis midae*. Honours Project, University of Cape Town.

ERZINI, K. 1990. Sample size and grouping of data for length-frequency analysis. *Fish. Res. (Amst.).* **9:** 355-366.

FORSTER, G.R. 1962. Observations on the ormer population of Guernsey. *J. Mar. Biol. Assoc. U. K.* **42:** 493-498.

FORSTER, G.R. 1967. The growth of *Haliotis tuberculata*: results of tagging experiments in Guernsey. *J. Mar. Biol. Assoc. U.K.* **47:** 287-300.

FOURNIER, D.A. & BREEN, P.A. 1983. Estimation of abalone mortality rates with growth analysis. *Trans. Am. Fish. Soc.* **112:** 403-411.

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

FRETTER, V. & GRAHAM, A. 1962. British Prosobranch Molluscs. Their functional anatomy and ecology. Ray Society, London. 755pp.

FRETTER, V. & GRAHAM, A. 1964. Reproduction. In: Physiology of mollusca. Vol.1. pp127-164. (Eds.) K.M. Wilbur & C.M. Yonge. Academic Press, New York.

FRICKE, A.H. 1979. Kelp grazing by the common sea urchin *Parechinus angulosus* Leske in False Bay, Cape. *S. Afr. J. Zool.* **14(3):** 143-148.

FROST, W.E. 1977. The food of Charr *Salvelinus willughbii* (Gunther) in Windermere. *J. Fish Biol.* **11:** 531-547.

GARLAND, C.D., COOKE, S.L., GRANT, J.F. & MCMEEKIN, T.A. 1985. Ingestion of the bacteria on and the cuticle of crustose (non-articulated) coralline algae by post-larval and juvenile abalone (*Haliotis rubra* Leach) from Tasmanian waters. *J. Exp. Mar. Biol. Ecol.* **91:** 137-149.

GENADE, A.B., HIRST, A.L. & SMIT, C.J.1988. Observations on the spawning, development and rearing of the South African abalone *Haliotis midae* Linn. *S. Afr. J. Mar. Sci.* **6:** 3-12.

GIESE, A.C. 1959. Comparitive physiology: Annual reproductive cycles of marine invertebrates. *Annu. Rev. Physiol.* **21:** 547-576.

GIORGI, A.E. & DEMARTINI, J.D. 1977. A study of the reproductive biology of the red abalone, *Haliotis rufescens* Swainson, near Mendocino, California. *Calif. Fish Game* **63(2):** 80-94.

GLOVER, C.J.M. & OLSEN, A.M. 1985. Fish and major fisheries. In: Natural history of Eyre Peninsula. pp169-181. The Royal Society of South Australia.

GUZMAN DEL PROO, S.A. 1992. A review of the biology of abalone and its fishery in Mexico. In: Abalone of the world. Biology, fisheries and culture. pp341-360. (Eds.) S.A. Shepherd, M.J. Tegner & S.A. Guzman del Proo. Blackwell Scientific Publications, Great Britain.

HARRISON, A.J. 1986. Gastropod fisheries in the Pacific with particular reference to Australian abalone. *Can. Spec. Publ. Fish. Aquat. Sci.* **92:** 14-22.

HARRISON, A.J. & GRANT, J.F. 1971. Progress in abalone research. *Tasmanian Fish. Res.* **5(21):** 10pp.

HAYASHI, I. 1980a. The reproductive biology of the ormer, *H. tuberculata*. *J. Mar. Biol. Assoc. U.K.* **60:** 415-430.

HAYASHI, I. 1980b. Structure and growth of a shore population of the ormer, *Haliotis tuberculata*. *J. Mar. Biol. Assoc. U.K.* **60:** 431-437.

HAYASHI, T. 1955. Studies on the age determining characters of shellfish. I. Observations by sectioning of the shell (1). *Bull. Hokkaido. Reg. Fish. Res. Lab.* **12:** 43-48. (In Japanese).

HECHT, T. & BRITZ, P.J. 1992. The current status, future prospects and environmental implications of mariculture in South Africa. *S. Afr. J. Sci.* **88:** 335-342.

HINES, A.H. & PEARSE, J.S. 1982. Abalones, shells and sea otters: dynamics of prey populations in Central California. *Ecology* **63(5):** 1547-1560.

HORSTMAN, D.A., MCGIBBON, S., PITCHER, G.C., CALDER, D., HUTCHINGS, L. & WILLIAMS, P. 1991. Red tides in False Bay, 1959-1989, with particular reference to recent blooms of *Gymnodinium* sp. *Trans. Roy. Soc. S. Afr.* **47(4&5):** 611-628.

HUMASON, G.L. 1979. Animal tissue techniques. W.H. Freeman and Company, San Fransisco.

HYNES, H.B.N. 1950. The food of freshwater sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.* **19:** 36-58.

HYSLOP, E.J. 1980. Stomach contents analysis - a review of methods and their application. *J. Fish Biol.* **17:** 411-429.

INO, T. 1952. Biological studies on the propagation of the Japanese abalone (genus *Haliotis*). *Bull. Tokai Reg. Fish. Res. Lab.* **5:** 29-102. (In Japanese).

INOUE, M. & OBA, T. 1980. Circuli on the shell as an age determination and growth of the Japanese abalone, *Haliotis gigantea*. *Bull. Kanagawa Prefect. Fish Res. Stn.* **1:** 107-113. (In Japanese).

KEESING, J.K. & WELLS, F.E. 1989. Growth of the abalone *Haliotis roei* Gray. *Aust. J. Mar. Freshwater. Res.* **40:** 199-204.

KOIKE, Y., YAMAKAWA, H., ISHIDA, S. & UNO, Y. 1972. Ecological studies on the propagation of Japanese abalones (Genus *Haliotis*) - II. Recruitment of abalones in the natural environment after catching. *Bulletin de la Societe franco-japonaise d'oceanographie.* **10(2):** 50-55.

KOJIMA, H. 1976. A study on the growth of the shell of *Haliotis discus discus* (Gastropoda; Haliotidae) I. Age and growth. *Aquaculture.* **23:** 61-66.

KOJIMA, H., NAKAHISA, Y., TANIMOTO, H. & ISIBASI, K. 1977. A study on the stock of Japanese black abalone, *Haliotis discus discus* in Tokushima Prefecture I. Growth of shells. *Bull Tokai Reg. Fish. Res. Lab.* **90:** 25-37. (In Japanese).

KUROGANE, K., SAGARA, J., HAMADA, S. & TANAKA, Y. 1974. On the growth of tagged abalone, *Haliotis gigantea* Gmelin, in the Manazuru fishing port. *Bull Tokai Reg. Fish. Res. Lab.* **77:** 7-19. (In Japanese).

LEE, T.Y. 1974. Histological study on gametogenesis and reproductive cycle of abalones of the Korean coasts. *Bull. Pusan Fish. Coll. (Nat. Sci.).* **14(1):** 59-67.

LEIGHTON, D.L. 1961. Observations of the effect of diet on shell coloration in the red abalone, *Haliotis rufescens* Swainson. *Veliger.* **4(1):** 29-32.

LEIGHTON, D.L. 1966. Studies of food preference in algivorous invertebrates of southern California kelp beds. *Pac. Sci.* **20:** 104-113.

LEIGHTON, D.L. 1971 Grazing activities of benthic invertebrates in Southern California kelp beds. *Beih. Nova Hedwigia.* **32:** 421-453.

LEIGHTON, D.L. 1972. Laboratory observations on the early growth of the abalone, *Haliotis sorenseni*, and the effect of temperature on the larval development and settling success. *Fish. Bull. U. S.* **70(2):** 373-381.

LEIGHTON, D.L. 1974. The influence of temperature on larval and juvenile growth in three species of Southern California abalones. *Fish. Bull. U. S.* **72(4):** 1137-1145.

LEIGHTON, D. & BOOLOOTIAN, R.A. 1963. Diet and growth in the black abalone, *Haliotis cracherodii. Ecology.* **44(2):** 227-238.

LINDBERG, D.R. 1992. Evolution, distribution and systematics of Haliotidae. In: Abalone of the world. Biology, fisheries and culture. pp3-18. (Eds.) S.A. Shepherd, M.J. Tegner & S.A. Guzman del Proo. Blackwell Scientific Publications, Great Britain.

LINNAEUS, C. 1758. Systema natura. Tom. 1. Regnum anumale. Edito decima, reformate. Holmiae, 824pp. Facsimile reproduction; *Brit Mus. (Nat. Hist.)*, 1939.

LISSMANN, H.W. 1945. The mechanism of locomotion in Gastropod molluscs I. Kinematics. *J. Exp. Biol.* **21:** 58-69.

LOMBARD, H.W. 1977. Die bevolkingsdinamika van en energievloei deur *Turbo sarmaticus* op twee rotsstrande in die Oos-Kaap. M. Sc. Thesis, University of Port Elizabeth.

LUBKE, R.A. 1988. Introduction. In: A field guide to the Eastern Cape coast. ppxiii-xvii. (Eds.) R.A. Lubke, F.W. Gess & M.N. Bruton. Grahamstown Centre of the Wildlife Society of Southern Africa.

MACDONALD, P.D.M. 1987. Analysis of length-frequency distributions. In: The age and growth of fish. pp371-384. (Eds.) R.C. Summerfelt & G.E. Hall. Iowa State University Press, Ames, Iowa.

MACDONALD, P.D.M. & PITCHER, T.J. 1979. Age groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. *J. Fish. Res. Board Can.* **36:** 987-1001.

MACGINITIE, N. & MACGINITIE, G.E. 1966. Starved abalones. *Veliger.* **8(4):** 313.

MANAHAN, D.T. & JAECKLE, W.B. 1992. Implications of dissolved organic material in sea water for the energetics of abalone larvae *Haliotis rufescens*: a review. In: Abalone of the world. Biology, fisheries and culture. pp95-106. (Eds.) S.A. Shepherd, M.J. Tegner & S.A. Guzman del Proo. Blackwell Scientific Publications, Great Britain.

MCLEAN, N. 1970. Digestion in *Haliotis rufescens* Swainson (Gastropoda: Prosobranchia). *J. Exp. Zool.* **173:** 303-318.

MCSHANE, P.E. & SMITH, M.G. 1988. Measuring abundance of juvenile abalone, *Haliotis rubra* Leach (Gastropoda: Haliotidae); Comparison of a novel method with two other methods. *Aust. J. Mar. Freshwater Res.* **39:** 331-336.

MCSHANE, P.E., SMITH, M.G. & BEINSSEN, K.H.H. 1988. Growth and morphometry in abalone (*Haliotis rubra* Leach) from Victoria. *Aust. J. Mar. Freshwater Res.* **39:** 161-166.

MOMMA, H. 1973. Optimal conditions for collecting swimming larvae of *Haliotis discus hannai. J. Hokkaido Inst. Maricul.* 105-110. (In Japanese).

MONTGOMERY, W.L. & GERKING, S.D. 1980. Marine macroalgae as foods for fishes: an evaluation of potential food quality. *Environ. Biol. Fish.* **5:** 143-153.

MORALES, J.M.T. & ORTIZ, J.L.C. 1989. Growth of *Haliotis fulgens* in Bahia Tortugas, Bahia California Sur, Mexico. *Fish. Res. Pap. Dept. Fish. (S. Aust.).* **24:** 10-15.

MORSE, A.N.C. & MORSE, D.E. 1984. Recruitment and metamorphosis of *Haliotis* larvae induced by molecules uniquely available at the surface of crustose red algae. *J. Exp. Mar. Biol. Ecol.* **75:** 191-215.

MOSS, G.A. & TONG, L.J. 1992. Effect of stage of larval development on the settlement of the abalone, *Haliotis iris. N. Z. J. Mar. Freshwater Res.* **26:** 69-73.

MOTTET, M.G. 1978. A review of the fishery biology of abalones. Washington Report. *Fish. Tech. Rep.* **37.** 81pp.

MULLER, S. 1984. Studies on the ecology, feeding, growth and reproduction of *Haliotis spadicea* Donovan, 1808. M.Sc. Thesis, University of Port Elizabeth. 195pp.

MULLER, S. 1986. Taxonomy of the Genus *Haliotis* in South Africa. *Trans. R. Soc. S. Afr.* **46(1):** 69-77.

MUNOZ LOPEZ, T. 1976. Resultados preliminares de un metodo para determinar edad en abulones (*Haliotis* spp.) de Baja California. *Memorias del Simposio sobre Recursos Pesqueros Masivos de Mexico Ensenada B.C. del 28 al 30 de Septiembre, 1976.* 281-301.

MURAYAMA, S. 1935. On the development of the Japanese abalone, *Haliotis gigantea*. *J. Coll. Agric.* **13(3):** 227-236.

NEWMAN, G.G. 1966. Movements of the South African abalone *Haliotis midae*. *Investl. Rep. Div. Sea Fish. S. Afr.* **56:** 19pp.

NEWMAN, G.G. 1967a. Abalone research in South Africa. *Fish. Bull. S. Afr.* **4:** 28-34.

NEWMAN, G.G. 1967b. Reproduction of the South African Abalone *Haliotis midae*. *Investl. Rep. Div. Sea Fish. S. Afr.* **64:** 24pp.

NEWMAN, G.G. 1968. Growth of the South African abalone *Haliotis midae*. *Investl. Rep. Div. Sea Fish. S. Afr.* **67:** 24pp.

NEWMAN, G.G. 1969. Distribution of the abalone (*Haliotis midae*) and the effect of temperature on productivity. *Investl. Rep. Div. Sea Fish. S. Afr.* **74:** 7pp.

NORTH, W.J. & PEARSE, J.S. 1970. Sea urchin population explosion in southern California waters. *Science.* **167:** 209.

OBA, T. 1964. Studies on the propagation of an abalone, *Haliotis diversicolor supertexta* Lischke - II. On the development. *Bull. Jpn. Soc. Sci. Fish.* **30(10):** 809-819. (In Japanese).

OLLEY, J. & THROWER, S.J. 1977. Abalone - an esoteric food. *Adv. Food. Res.* **23:** 143-185.

OLSEN, D.A. 1968. Banding patterns in *Haliotis* - II. Some behavioral considerations and the effect of diet on shell coloration for *Haliotis rufescens, Haliotis corrugata, Haliotis sorenseni,* and *Haliotis assimilis*. *Veliger.* **11(2):** 135-139.

PARKER, R.R. 1963. Effects of formalin on length and weight of fishes. *J. Fish. Res. Board Can.* **20:** 144-155.

PARSONS, D.W. & MACMILLAN, D.L. 1979. The escape response of abalone (Mollusca, Prosobranchia, Haliotidae) to predatory Gastropods. *Mar. Behav. Physiol.* **6:** 65-82.

PAUL, A.J. & PAUL, J.M. 1981. Temperature and growth of maturing *Haliotis kamtschatkana* Jonas. *Veliger.* **23:** 321-324.

PAUL, A.J., PAUL, J.M., HOOD, D.W. & NEVE, R.A. 1977. Observations on food preferences, daily ration requirements and growth of *Haliotis kamtschatkana* Jonas in captivity. *Veliger.* **19(3):** 303-309.

PEARSE, J.S. 1978. Reproductive periodicities of Indo-Pacific invertebrates in the Gulf of Suez. IV. The chitons *Acanthopleura haddoni* Winckworth and *Onithochiton lyelli* (Sowerby), and the abalone *Haliotis pustulata* Reeve. *Bull. Mar. Sci.* **28(1):** 92-101.

PECK, L.S. 1989. Feeding, growth and temperature in the ormer, *Haliotis tuberculata* (L.). *Prog. Underwater Sci.* **14:** 95-107.

PECK, L.S. & CULLEY, M.B. 1990. Structure and density of *Haliotis tuberculata* populations around the coasts of Jersey, Channel Isles. *J. Mar. Biol. Assoc. U. K.* **70:** 67-75.

PILSON, M.E.Q. & TAYLOR, P.B. 1961. Hole drilling by octopus. *Science.* **134:** 1366-1368.

POORE, G.C.B. 1972a. Ecology of New Zealand abalones, *Haliotis* species (Mollusca: Gastropoda). 1. Feeding. *N. Z. J. Mar. Freshwater. Res.* **6(1 & 2):** 11-22.

POORE, G.C.B. 1972b. Ecology of New Zealand abalones, *Haliotis* species (Mollusca: Gastropoda). 2. Seasonal and diurnal movement. *N. Z. J. Mar. Freshwater Res.* **6(3):** 246-258.

POORE, G.C.B. 1972c. Ecology of New Zealand abalones, *Haliotis* species (Mollusca: Gastropoda). 3. Growth. *N. Z. J. Mar. Freshwater Res.* **6(4):** 534-559.

POORE, G.C.B. 1973. Ecology of New Zealand abalones, *Haliotis* species (Mollusca: Gastropoda). 4. Reproduction. *N. Z. J. Mar. Freshwater Res.* **7(1 & 2):** 67-84.

PRINCE, J.D. 1991. A new technique for tagging abalone. *Aust J. Mar. Freshwater* Res. **42:** 101-106.

PRINCE, J.D. & FORD, W.B. 1985. Use of anaesthetic to standardize efficiency in sampling abalone populations (Genus *Haliotis*; Mollusca : Gastropoda). *Aust. J. Mar. Freshwater. Res.* **36:** 701-706.

PRINCE, J.D., SELLERS, T.L., FORD, W.B. & TALBOT, S.R. 1987. Experimental evidence for limited dispersal of haliotid larvae (Genus *Haliotis*; Mollusca : Gastropoda). *J. Exp. Mar. Biol. Ecol. **106:** 243-263.*

PRINCE, J.D., SELLERS, T.L., FORD, W.B. & TALBOT, S.R. 1988. A method for ageing the abalone *Haliotis rubra* (Mollusca: Gastropoda). *Aust. J. Mar. Freshwater Res.* **39:** 167-175.

PRITCHARD, A. 1982. Paua shell - harvest and utilisation problems. *Fish. Res. Div. Occas. Publ.* **41:** 26-27.

PUNT, A.E. 1992. PC-yield user's guide (version 2.2). *BEP Report.* **No. 26:** 36pp.

QUAYLE, D.B. 1971. Growth, morphometry and breeding in the British Columbia abalone (*Haliotis kamtschatkana* Jonas). *Tech. Rep. Can. Fish. Res. Bd.* **279:** 1-19.

RHO, S. & PARK, C.K. 1975. Studies on the propagation of the abalones. II. The spawning season of *H. discus hannai* Ino, in the adjacent areas of Yeosu. *Bull. Korean Fish. Soc.* **8(4):** 234-241.

RICHARDSON, C.A., SEED, R. & NAYLOR, E. 1990. Use of internal growth bands for measuring individual and population growth rates in *Mytilus edulis* from offshore production platforms. *Mar. Ecol. Prog. Ser.* **66:** 259-265.

RICKER, W.E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. *J. Fish. Res. Board Can.* **26:** 479-540.

RICKER, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Fish. Res. Board Can. Bull.* **191:** 382pp.

ROPES, J.W. 1988. Ocean quahog *Arctica islandica.* In: Age determination methods for Northwest Atlantic species. pp129-132. (Eds.) J. Pentilla & L.M. Dery. *NOAA Technical Report NMFS.* **72:** 129-132.

ROPES, J.W. & JEARLD, A. JR. 1987. Age determination of ocean bivalves. In: The Age and Growth of Fishes. pp517-530. (Eds.) R.C. Summerfelt & G.E. Hall. Iowa State University Press, Ames, Iowa.

ROPES, J.W. & SHEPHERD, G.R. 1988. Surf clam *Spisula solidissima.* In: Age determination methods for Northwest Ayalntic species. pp125-128. (Eds.) J. Pentilla & L.M. Dery. *NOAA Technical Report NMFS.* **72.**

SAINSBURY, K.J. 1980. The effects of individual variation on the von Bertalanffy growth equation. *Can. J. Fish. Aquat. Sci.* **37:** 241-247.

SAINSBURY, K.J. 1982. Population dynamics and fishery management of the paua, *Haliotis iris.* 1. Population structure, growth, reproduction, and mortality. *N.Z. J. Mar. Freshwater Res.* **16:** 147-161.

SAITO, K. 1981. The appearance and growth of 0-year old ezo abalone. *Bull. Jpn. Soc. Sci. Fish.* **47:** 1393-1400. (In Japanese).

SAKAI, S. 1960. On the formation of the annual ring on the shell of the abalone, *Haliotis discus* var. *hannai* Ino. *Tohoku J. Agric. Res.***11:** 239-244. (In Japanese).

SAKAI, S. 1962a. Ecological studies on the abalone *Haliotis discus hannai* Ino. I. Experimental studies on the food habit. *Bull. Jpn. Soc. Sci. Fish.* **28(9):** 766-779. (In Japanese).

SAKAI, S. 1962b. Ecological studies on the abalone *Haliotis discus hannai* Ino. IV. Studies on the growth. *Bull. Jpn. Soc. Sci. Fish.* **28(9):** 899-904. (In Japanese).

SAKATA, K. & INA, K. 1992. Algal feeding stimulants for abalone. In: Abalone of the world. Biology, fisheries and culture. pp182-192. (Eds.) S.A. Shepherd, M.J. Tegner & S.A. Guzman del Proo. Blackwell Scientific Publications, Great Britain.

SCHIEL, D.R. & BREEN, P.A. 1991. Population structure, ageing, and fishing mortality of the New Zealand abalone *Haliotis iris. Fish. Bull. U.S.* **89:** 681-691.

SCHNUTE, J. & FOURNIER, D. 1980. A new approach to length-frequency analysis: growth structure. *Can. J. Fish. Aquat. Sci.* **37(9):** 1337-1351.

SEAGRIEF, S.C. 1967. The seaweeds of the Tsitsikamma Coastal National Park. National Parks

Board of the Republic of South Africa. 147pp.

SEAGRIEF, S.C. 1988. Marine algae. In: A field guide to the Eastern Cape coast. pp35-72. (Eds.) R.A. Lubke, F.W. Gess & M.N. Bruton. Grahamstown Centre of the Wildlife Society of Southern Africa.

SEARCY-BERNAL, R., SALAS-GARZA, A.E., FLORES-AGUILAR, R.A. & HINOJOSA-RIVERA, P.R. 1992. Simultaneous comparison of methods for settlement and metamorphosis induction in the red abalone (*Haliotis rufescens*). *Aquaculture.* **105:** 241-250.

SEKI, T & KAN-NO, H. 1981a. Observations on the settlement and metamorphosis of the veliger of the Japanese abalone *Haliotis discus hannai* Ino, Haliotidae, Gastropoda. *Bull. Tohoku Reg. Fish. Res. Lab.* **42:** 31-37. (In Japanese).

SEKI, T. & KAN-NO, H. 1981b. Induced settlement of the Japanese abalone *Haliotis discus hannai* veliger by the mucous trails of the juvenile and adult abalones. *Bull. Tohoku Reg. Fish. Res. Lab.* **43:** 29-36. (In Japanese).

SHAW, W.N. 1982. The culture of molluscs in Japan. III. Abalone culture. *Aquacult. Mag.* **9(43).**

SHAW, W.N. 1991. Abalone farm in Northern California. *Aquacult. Mag.* 92-97. September/October 1991.

SHEPHERD, S.A. 1973a. Competition between sea urchins and abalone. *Aust. Fish.* 4-7. June 1973.

SHEPHERD, S.A. 1973b. Studies on Southern Australian abalone (Genus *Haliotis*) I. Ecology of five sympatric species. *Aust. J. Mar. Freshwater. Res.* **24:** 217-257.

SHEPHERD, S.A. 1975. Distribution, habitat and feeding habits of abalone. *Aust. Fish.* 12-15. January 1975.

SHEPHERD, S.A. 1976. Breeding, larval development and culture of abalone. *Aust. Fish.* 7-10. April 1976.

SHEPHERD, S.A. 1986. Studies on Southern Australian abalone (Genus *Haliotis*). VII. Aggregative behaviour of *H. laevigata* in relation to spawning. *Mar. Biol.* **90:** 231-236.

SHEPHERD, S.A. 1988. Studies on Southern Australian abalone (Genus *Haliotis*). VIII. Growth of juvenile *H. laevigata. Aust. J. Mar. Freshwater Res.* **39:** 177-183.

SHEPHERD, S.A. 1990. Studies on Southern Australian abalone (Genus *Haliotis*). XII. Long term recruitment and mortality dynamics. *Aust. J. Mar. Freshwater Res.* **41:** 475-492.

SHEPHERD, S.A. & BREEN, P.A. 1992. Mortality in abalone: its estimation, variability and causes. In: Abalone of the World, Biology, fisheries and culture. pp276-304. (Eds.) S.A. Shepherd, M.J. Tegner & S.A. Guzman del Proo. Blackwell Scientific Publications, Great Britain.

SHEPHERD, S.A. & CANNON, J. 1988. Studies on southern Australian abalone (Genus

Haliotis). X. Feeding of juveniles. *J. Malacol. Soc. Aust.* **9:** 21-26.

SHEPHERD, S.A. & GODOY, C. 1989. Studies on Southern Australian abalone (Genus *Haliotis*) XI. Movement and natural mortality of juveniles. *J. Malacol. Soc. Aust.* **10:** 87-95.

SHEPHERD, S.A., GUZMAN DEL PROO, S.A., MORALES, J.M.T., BELMAR, J., BAKER, J.L. & SLUCZANOWSKI, P.R. 1991. Growth, size at sexual maturity and egg-per-recruit analysis of the abalone *Haliotis fulgens* in Baja California. *Veliger.* **34:** 324-330.

SHEPHERD, S.A. & HEARN, W.S. 1983. Studies on Southern Australian abalone (Genus *Haliotis*). IV. Growth of *H. laevigata* and *H. ruber*. *Aust. J. Mar. Freshwater Res.* **34:** 461-475.

SHEPHERD, S.A. & LAWS, H.M. 1974. Studies on Southern Australian abalone (Genus *Haliotis*). II. Reproduction of five species. *Aust. J. Mar. Freshwater Res.* **25:** 49-62.

SHEPHERD, S.A. & STEINBERG, P.D. 1992. Food preferences of three Australian abalone species with a review of the algal food of abalone. In: Abalone of the world. Biology, fisheries and culture. pp169-181. (Eds.) S.A. Shepherd, M.J. Tegner & S.A. Guzman del Proo. Blackwell Scientific Publications, Great Britain.

SHEPHERD, S.A., TEGNER, M.J. & GUZMAN DEL PROO, S.A. 1992. Preface. In: Abalone of the world. Biology, fisheries and culture. ppix-x. (Eds.) S.A. Shepherd, M.J. Tegner & S.A. Guzman del Proo. Blackwell Scientific Publications, Great Britain.

SHEPHERD, S.A. & TURNER, J.A. 1985. Studies on Southern Australian abalone (Genus *Haliotis*). VI. Habitat preference, abundance and predators of juveniles. *J. Exp. Mar. Biol. Ecol.* **93:** 286-298.

SIMONS, R.H. 1976. Seaweeds of Southern Africa: guide-lines for their study and identification. *Fish. Bull. S. Afr.* **7:** 1-113.

SINCLAIR, M. 1963. Studies on the paua, *Haliotis iris* Martyn in the Wellington district, 1945-46. *Zool. Publ. Vic. Univ. Wellington.* **35:** 1-16.

SLATTERY, M. 1992. Larval settlement and juvenile survival in the red abalone (*Haliotis rufescens*): an examination of inductive cues and substrate selection. *Aquaculture.* **102:** 143-153.

SLOAN, N.A. & BREEN, P.A. 1988. Northern abalone, *Haliotis kamtschatkana*, in British Columbia: Fisheries and synopsis of life history information. *Can. Spec. Publ. Fish. Aquat. Sci.* **103:** 46pp.

SLUCZANOWSKI, P.R. 1984. A management oriented model of an abalone fishery whose substocks are subject to pulse fishing. *Can. J. Fish. Aquat. Sci.* **41:** 1008-1014.

STEPHENSON, T.A. 1924. Notes on *Haliotis tuberculata*. I. *J. Mar. Biol. Assoc. U. K.* **13:** 480-495.

STEPHENSON, T.A. 1944. The constitution of the intertidal fauna and flora of South Africa.

Part II. *Ann. Natal Mus.* **10(3):** 261-358.

TANIGUCHI, K., KURATA, K. & SUZUKI, M. 1991. Feeding-deterrent effect of phlorotannins from the brown alga *Ecklonia stolonifera* against the abalone *Haliotis discus hannai. Nippon Suisan Gakkaishi.* **57(11):** 2065-2071. (In Japanese).

TANIGUCHI, K., KURATA, K. & SUZUKI, M. 1992. Feeding-deterrent activity of some laminariaceous brown algae against the ezo-abalone. *Nippon Suisan Gakkaishi.* **58(3):** 577-581. (In Japanese).

TARR, R.J.Q. 1987. Biology and management of South African perlemoen. *Underwater.* **3:** 41-42.

TARR, R.J.Q. 1989. Abalone. In: Oceans of life off Southern Africa. pp62-69. (Eds.) A.I.L. Payne & R.J.M. Crawford. Vlaeberg Publishers, Cape Town.

TARR, R.J.Q. 1992. The abalone fishery of South Africa. In: Abalone of the world. Biology, fisheries and culture. pp438-447. (Eds.) S.A. Shepherd, M.J. Tegner & S.A. Guzman del Proo. Blackwell Scientific Publications, Great Britain.

TEGNER, M.J. 1989. The California abalone fishery: production, ecological interactions, and prospects for the future. In: Marine invertebrate fisheries: their assessment and management. pp401-420. (Ed.) J.F. Caddy. John Wiley & Sons, Canada.

TEGNER, M.J., BREEN, P.A. & LENNERT, C.E. 1989. Population biology of red abalones, *Haliotis rufescens*, in southern California and management of the red and pink, *H. corrugata*, abalone fisheries. *Fish. Bull. U. S.* **87:** 313-339.

TEGNER, M.J. & BUTLER, R.A. 1985a. The survival and mortality of seeded and native red abalones, *Haliotis rufescens*, on the Palos Verdes Peninsula. *Calif. Fish Game.* **71(3):** 150-163.

TEGNER, M.J. & BUTLER, R.A. 1985b. Drift-tube study of the dispersal potential of green abalone (*Haliotis fulgens*) larvae in the southern California Bight: implications for recovery of depleted populations. *Mar. Ecol. Prog. Ser.* **26:** 73-84.

TEGNER, M.J. & BUTLER, R.A. 1989. Abalone seeding. In: Handbook of culture of abalone and other marine Gastropods. pp157-182. (Ed.) K.O. Hahn. CRC Press, Boca Raton, Florida.

TEGNER, M.J., DEMARTINI, J.D. & KARPOV, K.A. 1992. The California red abalone fishery: a case study in complexity. In: Abalone of the world. Biology, fisheries and culture. pp370-383. (Eds.) S.A. Shepherd, M.J. Tegner & S.A. Guzman del Proo. Blackwell Scientific Publications, Great Britain.

TEGNER, M.J. & LEVIN, L.A. 1982. Do sea urchins and abalones compete in California kelp forest communities? In: International echinoderms conference, Tampa Bay. pp265-271. (Ed.) J.M. Lawrence. A.A. Balkema, Rotterdam.

TENORE, K.R. 1976. Food chain dynamics of abalone in a polyculture system. *Aquaculture*. **8:** 23-27.

TOMITA, K. & TAZAWA, N. 1971. On the stomach contents of young abalone, *Haliotis discus hannai* Ino, in Reubun Island, Hokkaido. *Sci. Rep. Hokkaido Fish. Exp. Stn.* **13:** 31-38. (In Japanese).

TUNBRIDGE, B.R. 1967. Feeding habits of paua (*Haliotis iris* Martyn). *Fish. Tech. Rep. N. Z. Mar. Dept.* **20:** 17pp.

TUTSCHULTE, T.C. & CONNELL, J.H. 1981. Reproductive biology of the three species of abalones (*Haliotis*). *Veliger*. **23(3):** 195-206.

TUTSCHULTE, T.C. & CONNELL, J.H. 1988a. Feeding behaviour and algal food of three species of abalones (*Haliotis*) in southern California. *Mar. Ecol. Prog. Ser.* **49:** 57-64.

TUTSCHULTE, T.C. & CONNELL, J.H. 1988b. Growth of three species of abalones (*Haliotis*) in southern California. *Veliger*. **31:** 204-213.

UEDA, S. & OKADA, Y. 1940. Studies on the food of useful Gastropoda in Japan. 1. Two species of Japanese abalone, *Haliotis gigantea* Gmelin and *H. kamtschatkana* Jonas. *Bull. J. Soc. Sci. Fish.* **8:** 51.

WEBBER, H.H. 1970. Changes in metabolite composition during the reproductive cycle of the abalone *Haliotis cracheroidii* (Gastropoda: Prosobranchiata). *Physiol. Zool.* **43:** 213-231.

WEBBER, H.H. & GIESE, A.C. 1969. Reproductive cycle and gametogenesis in the black abalone *Haliotis cracheroidii* (Gastropoda: Prosobranchiata). *Mar. Biol.* **4:** 152-159.

WELBORN, J.R. & MANAHAN, D.T. 1990. Direct measurements of sugar uptake from seawater into molluscan larvae. *Mar. Ecol. Prog. Ser.* **65:** 233-239.

WELLS, F.E. & KEESING, J.K. 1989. Reproduction and feeding in the abalone *Haliotis roei* Gray. *Aust, J. Mar. Freshwater. Res.* **40:** 187-197.

WILBUR, K.M. 1964. Shell formation and regeneration. In: Physiology of Mollusca. Vol. 1. pp 243-282. (Eds.) K.M. Wilbur & C.M. Yonge. Academic Press, New York.

WILK, S.J., MORSE, W.W. & STEHLIK, L.L. 1990. Annual cycles of gonad-somatic indices as indicators of spawning activity for selected species of finfish collected from the New York Bight. *Fish. Bull U. S.* **88:** 775-786.

WRIGHT, M.B. 1975. Growth in the black abalone, *Haliotis cracherodii. The Veliger*. **18(2):** 194-199.

WRIGHT, R.R. 1982. Export value of paua shell to New Zealand. *Fish. Res. Div. Occas. Publ. (N.Z.)* **41:** 24-25.

YANO, I. & OGAWA, Y. 1977. Effects of light, temperature and hydrostatic pressure on vertical distribution of abalone larvae, *Haliotis gigantea*. *Bull. Tokai Reg. Fish. Res. Lab.* **91:** 19-27. (In Japanese).

YOUNG, J.S. & DEMARTINI, J.D. 1970. The reproductive cycle, gonadal histology, and gametogenesis of the red abalone, *Haliotis rufescens* (Swainson). *Calif. Fish Game.* **56(1):** 298-309.