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ASPECTS OF THE BIOLOGY OF THE ABALONE

HALIOTIS LAEVIGATA AND HALIOTIS SCALARIS

by

Scoresby Arthur SHEPHERD,
B.A. LL.B. M. Env. St.

A thesis in total fulfillment of the requirements of the degree of
Doctor of Philosophy at Deakin University.

School of Sciences
Submitted December 1987
CANDIDATE'S CERTIFICATE

I certify that the thesis entitled "Aspects of the biology of the abalone Haliotis laevigata and Haliotis scalaris and submitted for the degree of Doctor of Philosophy is the result of my own research, except where otherwise acknowledged, and that this thesis (or any part of the same) has not been submitted for a higher degree to any other university or institution.

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Other acknowledgements are added in those parts of the text containing reprints of published papers or preprints of other papers prepared, submitted or accepted for publication. For those papers with joint authorship, I set out below in detail the contribution of the joint author(s).

Chapter 2.

Ms Jean A Turner was my enthusiastic assistant during the period 1982-5 and shared the field work with me. I am grateful to her for instruction on the obscurities of crustose coralline taxonomy and laboratory preparation of much crustose coralline material. I am responsible for analysis of the data and preparation of the paper.

Chapter 3.

Mr P.S. Clarkson was my part time assistant with Ms J A Turner during part of 1985. The former assisted me with gonad studies of H. scalaris, and most ably assisted in the field. Ms J A Turner assisted with the field work. Data analysis and preparation of the papers were done by me. Mr A G J Mower assisted with data collection and Mrs K Hill performed the weighted linear regressions on the growth data.

Chapter 5.

Ms J Cannon was my assistant for three months. She did the field work necessary for estimation of density of abalone and shared in other field and laboratory work. Data analysis and preparation of the paper were done by me.
Chapter 7

My co-author carried out the statistical analyses relating to the fecundity data and explored numerous possibilities for analysis of data that fail to meet the assumption of homogeneity of residual variances. The remainder of the work, except as mentioned in the paper is mine.
SUMMARY

The abalone *Haliotis laevigata* Donovan is commercially exploited in southern Australia; *Haliotis scalaris* Leach is a smaller, non-commercial species. This thesis describes the early life history of both species and other aspects of the fishery biology of *H. laevigata* required for fishery management.

Both abalone species recruit onto a crustose coralline substratum variously from spring to winter. After settlement the growth rate of both species is linear for a number of years (1.7mm/month for *H. laevigata* and 1.1mm/month for *H. scalaris*). Crustose coralline algae are the main food during the first year of life but thereafter the diet switches largely to drift algae and seagrass. Survival of newly-settled cohorts differed between years and between species. Overall, it appeared to be density independent at low densities but density-dependent at high densities.

Recruitment strength (measured at 2-1/2 - 3 years of age) and natural mortality of adults in a closed population was measured over 17 years at West I. There were sequences of strong and weak recruitments, but no relationship with presumed spawning stock size was apparent. Adult natural mortality rates ranged from 0.02 to 0.86 and were strongly density dependent. Stingrays were a major, and octopuses a minor, cause of mortality.

The fecundity of *H. laevigata* was investigated at a number of sites and was adequately described by linear regressions of fecundity on total weight. Fecundity ratios and growth rate differed between sites and fecundity appears subject to phenotypic and genotypic variation.

The short and long term movement of *H. laevigata* was also examined. In short term studies sexually mature individuals aggregate during the spawning season but disperse randomly at other times of the year. In the longer term the amount of movement depends on availability of crevice space and size. Movement is also directional and, at one site, was towards that of the approaching swell.
A method is described for estimating density of abalone by using a free-range search technique and adjusting for individual variation in power and efficiency of different divers and in differing degrees of habitat heterogeneity. The method is useful for estimating recruitment strength and density of abalone in surveys of abalone stocks.
CHAPTER 1

INTRODUCTION

Population biology is the study of the dynamics or numbers of a species. It tries to answer questions about why a population changes in abundance. It is concerned with life cycles because a population cannot be described without also describing its growth, birth and death rate, and reproduction. It is concerned with the physical and biotic environment of the population because that influences its growth and survival. It is also concerned with the selective processes that lead to ecological and evolutionary change.

The classical view of the dynamics of a population stemmed from the observation that, because nearly all populations have persisted for many generations, they must in a practical sense be stable. In consequence there developed an equilibrium view of populations (Hutchinson 1978; Chesson and Case 1985). According to this theory:

1. populations are limited by competition
2. population parameters (growth, mortality etc) are described by deterministic equations, and
3. the environment is spatially and temporally homogeneous.

In consequence populations are in an equilibrium state. In fished stocks the models used to describe such populations were yield per recruit models and stock-recruitment equations.

Modern orientations have extended, rather than replaced, the traditional theories. They recognise that there are substantial temporal and spatial variations in population parameters; that the environment is not homogeneous, but fluctuates widely; that a great deal of chance variation occurs; that there can be very large variations in the levels of resources and competitors.

Many studies have shown that there is often little correspondence between empirical data and theory (Rothschild 1986). In practice it is usually very difficult, if not impossible to delineate the boundaries of a population (or unit stock); and rarely is it possible to demonstrate a relation between a stock and its recruits.
The modern approach thus emphasizes dynamic rather than static features, complexity rather than simplicity, variability rather than uniformity of life history traits, and so denies that populations are in equilibrium.

Theories which include these and other features are called non-equilibrium theories (Diamond and Case 1985). These theories lead to the paradox that populations, that seem to be stable in the sense that they have persisted for many generations, are in fact not so, or at any rate are stable only within very large bounds. A review of 49 long-term studies on populations (Connell and Sousa 1983) confirm that few populations are stable, and that most fluctuate wildly in numbers.

The processes that regulate a population are not only of intrinsic interest, but are of pressing practical importance in the case of a species that is exploited. If, for example, a species is exploited when its population number has reached a low ebb, it may well be driven to extinction. The collapse of many fisheries, in particular abalone fisheries, around the world, reinforce the view that some species may be inherently unstable and prone to collapse.

This thesis is an enquiry into the factors that control populations of two abalone species, one of them exploited commercially, in South Australia. Because the number of possible factors are very large it is necessary initially to distinguish direct effects from indirect effects, in the same way that Andrewartha (1970) distinguished the inner from the outer strands of the ecological net that embraces every population.

The first distinction necessary is the recognition of 3 phases in an abalone's life history: the adult, egg-producing phase, the larval phase and the juvenile phase. Each phase takes place in a different habitat and so is presumably subject to different constraints, and different environments. Each phase must therefore be examined independently if a holistic picture is ultimately to emerge.
Fig. 1.1: A Pawlik diagram showing the relationship between different stages of the life history.
Paulik (1973) suggested graphical procedures to facilitate such examination. The dynamic behaviour of a population with several life history stages can be assessed by establishing a co-ordinate system in 4 quadrants (Fig. 1). Quadrant 1 contains the stock-recruitment relation i.e. the number of recruiting young produced by a given population. Quadrant 2 contains the relation between spawning biomass and number of eggs produced. Quadrant 3 contains the relation between number of eggs and the number of settling larvae and quadrant 4 the number of settling larvae to the number of recruits. The diagram shows how transitions from one quadrant to the next ultimately affect the stock-recruitment relation. Transitions that are density independent are represented by a straight line, and those that are density dependent by a curved asymptotic function. The introduction of random variation (noise) in the system is shown in 2 quadrants. The noise in one part of the system may be dampened as shown in Quadrant 3 or magnified as shown in Quadrant 4. The diagram shows that each stage has its unique set of regulatory mechanisms and that environmental or chance variability can produce distortions or noise at each stage.

The regulatory mechanisms e.g. density dependence induce stability in the whole system, whereas the noise contributes a destabilising component. The long-term stability or otherwise of a population is the net outcome of these processes acting at different loci.

In the case of abalone populations our enquiry into the factors that control a population must be reduced to sets of questions about the factors controlling the different stages of the life history. In the succeeding sections of this chapter I describe the abalone species, the fishery, the status of existing knowledge, the specific goals of this study and the contributions of succeeding chapters to these goals.

**ABALONE**

Abalone are gastropods of the Family Haliotidae (genus *Haliotis* Linnaeus 1758) and have been fished in southern Australia commercially since about 1966, and for several thousand years before that as part of a subsistence fishery by aboriginals (Shepherd 1986). Of the 90 or so described species, five occur in southern Australia.
Fig. 1.2: Map of South Australia showing the zones of the fishery.
The species taken commercially are *Haliotis laevigata* Donovan (greenlip) and *Haliotis rubra* Leach (blacklip); the smaller non-commercial species are *Haliotis cyclobates* Peron, *Haliotis roei* Gray and *Haliotis scalaris* Leach (Shepherd 1973).

**THE FISHERY**

The commercial fishery in abalone is operated by licensed divers who search for and gather them by hand, using hookah equipment. There are presently 35 divers divided among 3 zones (Fig. 2). The total annual catch is 800-900 tonnes (in-shell weight) divided about equally between the two commercial species currently worth about $14 million.

The fishery is controlled by a number of methods designed to control effort. These are:

1. licence limitation
2. quotas (only in western zone and since 1985)
3. legal minimum length
4. closures.

Abalone fishing grounds were mapped by the author in 1979 and the State's waters were divided into about 250 subdivisions. Divers submit monthly catch returns specifying the daily abalone catch and the subdivision in which it was taken. These returns then form the basis of data on catch (according to zone, sub-zone and subdivision) and catch per unit effort of the fishery (see review by Shepherd 1984).

Increasing exploitation of abalone in 1981 due to increasing diver efficiency gave rise to concern that the parental stock may become depleted and cause a recruitment failure. This condition is called recruitment over fishing. To meet this situation quotas were imposed in the Western Zone where the risk seemed most grave.
RESEARCH

Research commenced in South Australia in 1969 and addressed those questions for which answers were needed in traditional fisheries models i.e. yield-per-recruit and egg-per-recruit analyses. Studies were directed to the adult stage and included investigation of distribution and ecology (Shepherd 1973) reproduction (Shepherd and Laws 1974), growth (Shepherd and Hearn 1983) and mortality (Shepherd et al. 1982). Thus at the time of commencement of this study much was known about the biology of the adult phase, with some notable gaps. Nothing was known of the behaviour of abalone in relation to spawning, or of the fecundity of abalone. Further, knowledge of the natural mortality rate and of movement was still inadequate. Nothing at all was known of:

(1) the settlement process of abalone, the habitat in which settlement occurred or the ecology of newly settled abalone (quadrants 3-4, Fig. 1);
(2) interannual variability in recruitment (quadrant 1, Fig.1) or its causes, or
(3) the egg mortality function.

The research reported in this thesis was largely undertaken during the period 1982 to 1987. In some chapters data obtained before 1982 are included with analyses of later data.

The principal study sites were at West Island, representing the central, and Waterloo Bay, representing the western regions of the fishery for H. laevigata. Numerous earlier studies have been carried out at both sites and provide a corpus of accumulated information on their ecology.

The specific objectives of this study within the framework described above are:

- the fill in gaps in the knowledge of the adult phase in order to adequately describe the egg production function (Fig.1);
- to elucidate key features of settlement and survival of juvenile abalone in order to describe the juvenile mortality function (Fig.1).

The egg mortality function as yet remains unexamined.
Chapter 2 described the technique that was developed to find juvenile abalone soon after settlement, and their habitat preference for a crustose coralline substratum. A method to quantify settlement strength is also described and some information given on predators of small abalone. Chapter 3 describes the growth of juveniles of 2 co-occurring species by identifying and following cohorts over time. This facilitates a description of the natural mortality rate of juvenile abalone in the first three years of life (chapter 4) by enabling measurement of change in density of cohorts over time. Chapter 5 completes the description of the ecology of juveniles with a description of their food and feeding. Part 1 thus constitutes a preliminary description of the juvenile mortality function (Fig.1).

Part 2 is concerned with the adult phase. Chapter 6 develops techniques to measure the strength of recruitment (at age 2) and is a first step toward an empirical description of the relation between stock size and recruitment of an abalone population. A quite simple technique is described for measuring the natural mortality rate of adult abalone. The chapter analyses accumulated census data and provides an insight into the density dependent mechanism that controls the upper size limit of an unfished population.

Chapter 7 provides an understanding of the egg production function. A simple linear relation between fecundity and abalone weight appears to be general. However, substantial variation in relative fecundity between and even within populations is found, and emphasizes the complexity that exists even in an apparently simple relationship. A hypothesis accounting for this variability is proposed.

Chapter 8 further considers the natural mortality of adult abalone and shows how the determination of long term movement is an essential part of any attempt to measure natural mortality.

Aggregative behavior, described in Chapter 9, is the mechanism underlying fertilisation success and so is an important element of the egg production function (Fig.1). This has important implications when adult densities become very low.
**ABALONE LIFE HISTORY**

![Diagram of abalone life history]

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**Fig. 1.3:** Life history of the abalone *Haliotis laevigata.*
Chapter 10 considers an important methodological problem namely the empirical measurement of density which is fundamental to the stock-recruitment function of Fig. 1. Finally, the progress of the whole study toward the objectives is reviewed in Chapter 11.

ABALONE LIFE HISTORY

Fig. 3 gives a generalised picture of the life-cycle of *H. laevigata* and its predators, with particular reference to West Island. *H. scalaris* differs only in that adults never emerge from a cryptic habitat.

Abalone are broadcast spawners and shed gametes into the seawater where fertilisation occurs. The eggs hatch into lecithotrophic larvae, initially a trophophore that appears to be positively phototactic, and later a veliger. The larval ecology of southern Australian species is poorly known. The larval stage of *H. laevigata* appears to last from 2-5 days (D Morrison pers. comm.), whereupon it settles on crustose coralline algae (Ch. 2) where it begins to feed on bacteria, diatoms and the epithelial tissue of the coralline itself. The feeding growth and mortality of juveniles is described in Chapters 3, 4 and 5. At an age of 2½ to 3 years juveniles are more easily visible by divers and the size of the recruiting cohort is measurable (Ch. 6). At about age 4 sexual maturity is attained, but few gametes are produced in the first year or two of sexual maturity (Ch. 7). Because gametes are shed freely into the water a mechanism is needed to bring the sexes together during spawning to maximise fertilisation success. The aggregative behaviour of *H. laevigata* is described in Chapter 9.

The predators of abalone differ according to size. Settling veligers are probably taken by anemones and other sit-and-wait predators (Appendix 1); newly settled abalone are taken by hunting predators (see references in Ch. 2) which include terebellids, nemerteans and copepods. Crabs are potential minor predators (Appendix 1), and the wrasses *Pseudolabrus tetricus* and *Plectilabrus laticlavius* major predators of small abalone to about 30 mm length (Ch. 2). Above this size stingrays are major predators and octopuses minor predators (Chs. 6, 8).
References


**Captions to Figures**

**Fig. 1.1:** A Paulik diagram showing the relationship between different parts of the abalone life history.

**Fig. 1.2:** Map of South Australia showing the zones of the fishery.

**Fig. 1.3:** Life history of the abalone *Haliotis laevigata.*
CHAPTER 2

SETTLEMENT AND RECRUITMENT

Introductory Remarks

It is well known that the number of recruits to an abalone population vary widely from year to year, even though the number of adults (especially in a fished population) may vary little (see Ch.6). The origin of this variation is to be found in the two antecedent phases of the life history described by the egg mortality function and the juvenile mortality function (Fig.1).

At present variation arising in the planktonic phase can only be guessed. However, environmental factors such as sea temperature variations, wind, current and predators are all expected to play a part. The large number of possible factors suggest that the number of settling larvae will have great variance.

After settlement the number of juveniles will be reduced further by factors that include competition for food and predators, and eventually a much small number will survive to be recruits either to the fishery, or as defined in Ch.6, an age of $2^{1/2} - 3$ years when they become accessible to a diver. Is the number of surviving recruits determined largely by planktonic events (the egg mortality function) or by events after settlement (the juvenile mortality function)? The question has practical importance because if the former is true then the number of recruits will bear little relationship with the number of adults in any locality. But if events after settlement are more critical then local factors assume much greater importance in determining the population size. The extent of larval dispersal is a key factor here that will determine the relative importance of the two phases and ultimately the relationship between recruits and adults at a local scale.

This paper makes two significant contributions toward a description of the settlement phase of the abalone life history.
First, the author successfully developed in 1982 an underwater magnifier which was successfully used to search for newly settled abalone on various substrata at West Island from 1983 to 1987. An improved version of the magnifier, equipped with a light (Mladenov and Powell 1986) has been used since 1987.

Other methods of quantitatively measuring density of newly settled abalone have been developed since publication of the within paper. Prince and Ford (1985) dipped boulders in anaesthetic after removal to the surface and reported an increase of over 50% in sampling efficiency. McShane and Smith (1988) used an underwater pump to vacuum the substratum and collect small abalone. Both methods are destructive and require many hours of laboratory sorting per sample and proved to be unsuitable for use in South Australia (unpublished data). Further comparison of results obtained with a magnifier and with Prince and Ford's (1985) method, described in Ch. 4, suggest little difference in efficiency between them.

The second contribution was the development of a standardised collector with which to monitor abalone larval settlement. In pilot studies during 1982, several benthic structures of different designs were constructed and placed on the bottom to 'collect' newly settled abalone. The only successful one was a structure of natural boulders set within a frame on a concrete base but designed to allow the passage of sediment through it.

These proved satisfactory for the purpose of the experiments described in this chapter but, over time, the structures acquired crustose animal communities which out-competed the crustose coralline algae on which the abalone larvae settled. This led to a search for a better understanding of the function of other animals sharing the under-boulder habitat with small abalone, namely chitons and archaeogastropods. The food and feeding of these molluscs and simple experiments to examine the effect of their removal on crustose coralline algae are described in Appendix 2. It was found that standardised collectors of boulders were only maintained with a healthy crustose coralline substratum if the suite of chitons and archaeogastropods that together 'graze' the rocky substratum and the coralline surface was also maintained within the structure.
References


STUDIES ON SOUTHERN AUSTRALIAN ABALONE (GENUS HALIOTIS). VI. HABITAT PREFERENCE, ABUNDANCE AND PREDATORS OF JUVENILES

S.A. SHEPHERD and J.A. TURNER

Department of Fisheries, 135 Pirie Street, Adelaide, South Australia 5000

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Abstract: The two abalone species Haliotis laevigata Donovan and H. scabra Leach settle on crustose coralline algae on boulders at West Island, South Australia. Peak settlement of H. laevigata is from November to February, and of H. scabra from February to June but settlement strength is very variable between years for both species. Experimentally placed boulders established the preference of these abalone species for a crustose coralline algal substratum and demonstrated the use of such structures to monitor quantitatively the settlement of abalone in time and space. The association of juvenile abalone with crustose coralline algae appears to be important for food and as a refuge from predators. Wrasses are important predators of juveniles but do not take individuals < 3 mm long.

Key words: Abalone, larval settlement; recruitment; Haliotis

INTRODUCTION

A critical but poorly known aspect of the life history of most marine invertebrates is the habitat requirements of their newly settled larvae, whose ability to discriminate between different substrata may be crucial to their subsequent survival. An understanding of the habitat needs of larvae of commercially important species such as abalone is basic to the management of natural stocks and to the development of methods for their artificial culture.

Crofts (1929) noted that the smallest individuals of the abalone Haliotis tuberculata occur on crustose coralline algae, an observation since confirmed for other halitids (Shepherd, 1973; Saito, 1981), while laboratory experiments on H. rufescens and H. fulgens (Morse et al., 1979a,b; 1980) have demonstrated that crustose coralline algae induce metamorphosis and settlement of their veligers. There have, however, been no previous studies on the natural habitat preferences of newly settled abalone. This paper describes such studies on the greenlip abalone H. laevigata Donovan, taken commercially in southern Australia, and on H. scabra Leach, a smaller non-commercial species. Both species settle on boulders at West Island, South Australia (35° 37' S: 138° 35' E) (Shepherd, 1973) where a population of H. laevigata has been monitored since 1969 (Shepherd, in prep). We describe the microhabitat and abundance of juveniles of these species at 4-5 m depth in Abalone Cove over three years. Experimentally placed boulders were used to verify observations on selection of substratum
and to determine the relative importance of predation. The size range of young abalone taken by wrasses was obtained directly by field experiments and analysis of gut contents.

Materials and Methods

The north shore of West Island is a boulder slope containing rounded boulders mostly 30–40 cm greater diameter by 20–30 cm lesser diameter from ≈ 0.5 to 5 m depth. A number of different microhabitats defined by the epifauna and flora occur on and under the boulders and are described by Kangas & Shepherd (1984). In the present study the microhabitats are divided into the following categories: erect algae; crustose coralline algae; non-calcified crusts of red and brown algae; encrusting animals (ascidians, bryozoans and sponges); and bare areas. Per cent cover for these categories are from Kangas & Shepherd (1984).

A magnifier consisting of two ×1650 power (15 diopter) aspheric lenses mounted in a Perspex holder (Fig. 1) was used to search for very small abalone. This magnifier differs from the immersion type described by Pratt (1973) by having an air space between the lenses. The magnification underwater is ≈ 2.5 to 3 times. Using this magnifier, we carefully searched the whole of the upper and lower surfaces of boulders at 4–5 m depth for small abalone (≤ 1 mm) and measured their length with vernier calipers. Numbers seen (15 min)⁻¹ searching time were noted. The aspect (whether upper or lower surface) and the substratum on which the abalone was found were also recorded.

Sampling was stratified to include boulders that rested on sand, and those that rested on top of other boulders. Average total searching time per census was 93 min (40–80 min when densities of small abalone ≤ 5 mm long were < 1 per 30 min searching time and 80–230 min at higher densities), and censuses were at about monthly intervals, or more frequently during the period of maximum settlement.

Erect algae growing on the boulders were carefully removed and placed in plastic bags and later searched for small abalone under a low power microscope (×12–25). Densities of adult H. laevigata are higher at the western than the eastern end of the site studied, whereas H. scalaris is more or less uniformly scattered throughout the area. Searching was carried out at the eastern and western ends of the area to test for differences in the numbers of small abalone between each area.

On 2 November 1982 an experiment was set up to examine the effect of crustose coralline algae and the natural boulder fauna on the settlement and survival of abalone.
within a group of nine island boulder structures. The structures were placed on sandy bottom near the base of the boulder slope at the site studied. Each structure consisted of boulders placed within a metal frame 60 cm x 60 cm set on a double concrete base designed to let sediment pass through it (Fig. 2).

Three of the structures contained bare boulders (BB) taken from nearby sandy bottom in which they were buried. Three contained boulders (CC) with crustose coralline algae growing on them, and from which all animals (grazing chitons, and gastropods, terebellid worms, anemones and encrusting bryozoans and sponges) had been removed. The last three contained boulders with their accompanying fauna (CCF). The structures were arranged as shown in Fig. 2. Using the magnifier described above,

Fig. 2. Upper, photograph of experimental structure (60 x 60 cm) at West Island; note holes in upper concrete slab allowing trapped sediment to pass through the habitat. Lower, arrangement of structures.
we searched the upper and lower surfaces of boulders in each structure for small abalone ($<5$ mm long) on four occasions between December 1982 and May 1983. We standardized searching time to 15 min per structure except for the BB structures, which could be completely searched in about half that time.

The results for each of the searches were considered to be independent because individuals present at one census would have grown out of the size class sought by the next census (Shepherd & Hearn, 1983; Shepherd et al., 1985). The results for each treatment were accordingly pooled over time.

RESULTS

NATURAL BOULDER HABITAT

The community on the upper surface of boulders at 4–5 m depth is distinctly different from that below. Above boulders there is an algal community of three strata: an upper stratum mainly of Cystophora monilifera J. Agardh or Ecklonia radiata (C.Ag.), J. Agardh, a middle stratum of erect geniculate coralline algae (mainly Halimeda rosea (Lamarck) Garbarry & Johansen, Amphiprora anacaps (Lamarck) Decaisne, and Chelosporum elegans (H. & H.) Aresch., and a crustose stratum of non-calcified brown (mostly Archaeolithodema sp.) and red (Cryptosia sp.) algae, and crustose coralline algae of the genera Sporolithon, Lithothamnion, Leptophyton, Mesophyllum, Tenerae and Clathromorphum. On the under surface of boulders there are crustose algae as described above and crustose ascidians, bryozoans and sponges. Grazing chitons (Kangas & Shepherd, 1984), archaeogastropods (Clarkson & Shepherd, 1985), terebellids, and anemones are also present. The mean per cent cover of algae and of the principal categories of crustose organisms are given in Table 1.

Two species, Halosia laevigata and H. scalaris were present on the boulders, but could confidently be distinguished by differences in shell shape only when longer than $\approx 1$ mm. Individuals 0.5–1 mm long with translucent shells and without poroholes were found only on crustose coralline algae. They were sometimes active and moved at speeds of up to $2–3$ mm $\cdot$ sec$^{-1}$ on, but never beyond the edge of, the crustose coralline substratum. Possibly disturbance of the boulders during searches provoked this movement.

At a length of $\approx 5–7$ mm H. laevigata moves from crustose coralline surfaces of boulders to the under sides of boulders partly buried in sand. In contrast, H. scalaris remains on crustose corallines until it is $15–20$ mm long. Hence length frequency distributions for H. laevigata (e.g. Fig. 3) rarely record it at a length $>5$ mm.

A summary of the results of searches in the natural habitat for small abalone ($<5$ mm long) by species and by host substratum from November 1982 to November 1983 is given in Table 1. Nearly all (94%) were found on crustose coralline algae either on upper or under sides of boulders or on vertical surfaces. Three were found on non-calcified crusts and none in any other microhabitat. None was found on any erect algae.
### Table I

Per cent cover of organisms above and below boulders at 5 m depth in Abalone Cove, West Island, and numbers of *H. lernaea* and *H. scalata* < 5 mm recorded in each microhabitat from November 1982 to November 1983: *a* bryozoans, ascidians, sponges; *b* these crusts are mostly an undescribed species of *Archaeolithodera* (Phaeophyta) but include species of *Crosor* (Rhodophyta) and probably other genera.

<table>
<thead>
<tr>
<th></th>
<th>Boulder under surface</th>
<th>Boulder upper surface</th>
<th>Vertical rocky surfaces with crustose corallines</th>
<th>Crustose corallines: position on boulder not specified</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Crustose corallines</td>
<td>Non-calcified crusts*</td>
<td>Geniculate corallines and erect algae</td>
<td>Bare rock</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Bare rock</td>
<td>Crustose corallines</td>
<td>Bare rock</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Non-calcified crusts</td>
<td></td>
</tr>
<tr>
<td>Mean % cover ± SE</td>
<td>34 ± 0.7</td>
<td>9 ± 0.5</td>
<td>28 ± 2.1</td>
<td>3</td>
</tr>
<tr>
<td><em>H. lernaea</em></td>
<td>29</td>
<td>1</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Species uncertain</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>H. scalata</em></td>
<td>13</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

*Crustose corallines*; position on boulder not specified.
The proportional abundance of small abalone on under and upper sides of boulders changed with size and differed between species. No _H. laevigata_ > 2 mm long were found on the upper sides of boulders, and for smaller individuals 12 were found on the upper and 26 on the under sides of boulders (these include all data until 1985 other than for 4 individuals found on vertical faces). Because crustose corallines have more than twice the total per cent cover on under as on upper sides the distribution of individuals <2 mm long does not differ from that expected under the hypothesis of random settlement on crustose corallines in proportion to their per cent cover ($\chi^2 = 0.29$; n.s.). The change in ratio of those found on upper to those on under sides for the two size classes 0.5–2 mm and 2–5 mm was, however, highly significant (Cochran's, 1954, test; $\chi^2 = 126$; $P < 0.001$). In contrast _H. scalaris_ was found on upper sides of boulders to a size of 6.5 mm, although the largest ones were hidden under a _Halimia_ turf. The ratio of those found on upper to those on under sides of boulders was examined for 3 size classes (0.5–3 mm, 3–5 mm, and 5–10 mm) and changed from 2.5 to 0.3 ($N = 43$ for all data to 1985). The distribution on boulders of the smallest size class differed significantly from that expected under the hypothesis of random settlement on crustose corallines in proportion to their cover ($\chi^2 = 6.7$; $P < 0.01$). The change in ratio for the 3 size classes was also highly significant (Cochran's, 1954, test; $\chi^2 = 252$; $P < 0.001$).

To test whether more juvenile _Halimia laevigata_ settled near conspecific adults we examined two subsets of the data in Table I taken from areas of high (3 to 4 m$^{-2}$) and low (0.5 to 1.5 m$^{-2}$) adult mean densities. After minor adjustment to equate searching time, 53% of juvenile _H. laevigata_ were found in the low density area and 47% in the high density area. The hypothesis that juveniles were present in equal numbers in the two areas was accepted ($\chi^2 = 0.17$; n.s.), and it was concluded that the relative abundance of adult conspecifics does not influence density of settling _H. laevigata_.

**Experimental Structures**

In the experimental structures 26 individuals were recorded on CC boulders, 43 on CCF boulders and 2 on the BB boulders (Table II). The two on BB were found on small (< 1 cm$^2$) patches of crustose corallines which had grown after the experiment had commenced.

The null hypothesis that the total number of animals found in each type of structure was equal was tested and rejected ($\chi^2 = 36.5$; $P < 0.001$). For this test we standardized the census data as numbers found $\cdot$ (15 min)$^{-1}$ and considered the 4 time periods as replicates. We then tested whether the number found on the CCF boulders differed significantly from that on the CC boulders and rejected the hypothesis of equality of numbers ($\chi^2 = 4.21$; $P < 0.05$). Lastly we tested whether the abundance of juveniles (in numbers $\cdot$ (15 min)$^{-1}$) was greater in the boulder structures (CC and CCF pooled) than on the natural boulder slope. Significantly more occurred in the structures than among the natural boulders than expected from the relative searching times ($\chi^2 = 18.5$; $P < 0.001$).
ABUNDANCE OF SMALL ABALONE

The size distribution of *H. laevigata* and *H. scalaris* at each sampling date from November 1982 to August 1983 is shown in Fig. 3. These data include the results of sampling the natural boulder habitat as well as the structures. The presence of individuals 0.5–2 mm long is accepted as indicative of recent settlement; this is based on a growth rate of \( \approx 1 \text{ mm} \cdot \text{wk}^{-1} \) for *H. laevigata* (Shepherd & Hearn, 1983) and 0.4 mm \cdot wk\(^{-1}\) for *H. scalaris* (Shepherd et al., 1985). On this basis settlement of *H. laevigata* occurred from November 1982 through to May 1983, and between December and March in 1984 and 1985 (Fig. 4); settlement of *H. scalaris* occurred from January through to June 1983. The period of settlement of both species closely accords with their respective spawning seasons (see Shepherd & Laws, 1974, for *H. laevigata* and Shepherd et al., 1983, for *H. scalaris*).

A plot of the numbers of small abalone \( \leq 5 \text{ mm} \) recorded per 15 min searching time (Fig. 4) gives a measure of the relative strength of settlement of both species from October 1982 to June 1985. For this purpose unidentified individuals \( < 1 \text{ mm long} \) were assigned to the two species in proportion to the relative abundances of larger individuals (1–5 mm long) at that sampling date. The possibility of error here is slight, because the numbers in this category were low during the period of settlement overlap.

Settlement of *H. laevigata* was relatively strong in 1982–1983 (with peak densities in November 1982) and weak in the next two years. Settlement of *H. scalaris* occurred in the 1983 season but was not detected at all in 1984 and 1985. Shepherd (in prep.) associated the recruitment strength of *H. laevigata* with maximum summer sea temperature anomalies.
PREDATION ON SMALL ABALONE

Two principal predators of small abalone are the wrasses *Pseudolabrus tetricus* (Richardson) and *Plectolabrus latilabius* Richardson (Shepherd & Clarkson, in prep.). The various fish, crustacean and molluscan predators of abalone listed by Shepherd (1973) and other potential predators like flatworms are rare or absent at the site studied at West Island. Possible predation by nemerteans and small crabs has not yet been evaluated.

We attempted to assess the effect of fish predation on abundance of small abalone by caging boulders or placing net coverings over them. Two pilot experiments were conducted each for 2 months in 1983 and 1984. At the conclusion of each experiment fewer small abalone were found in the covered boulders than in the uncovered (in one experiment significantly fewer: Mann-Whitney, U-test, $P < 0.05$), results opposite to those expected.

A continual problem, peculiar to situations of strong swell and abundant algal drift, was the accumulation of trapped drift algae and sediment in the covered boulders (despite regular cleaning). We concluded that the results obtained were probably an artifact of the changed environment. Partially covered boulders as cage controls were
unsatisfactory because they became the residence of several species of fish. Schmidt & Warner (1984) experienced similar problems with cages. Caging was, therefore, abandoned in favour of studies on the feeding and prey size preferences of the wrasse *Pseudolabrus tetricus*.

In experiments conducted during monitoring of the boulder community, boulders were overturned and the small abalone under them were measured. *P. tetricus* was then allowed to search the exposed underside of the boulder and select prey abalone. Data on the size range of abalone (a) not taken, (b) taken, and (c) the object of an unsuccessful attack for different size classes of wrasse are given in Fig. 5.

*P. tetricus* is a visually searching predator and takes abalone predominantly in the size range 10–30 mm. Abalone <10 mm are rarely taken presumably because their cryptic colour provides camouflage and protection. Some of the smallest ones taken were not on the crustose coralline and this probably facilitated recognition. Analysis of gut contents of 62 *P. tetricus* (Shepherd & Clarkson, in prep.) showed that small individuals 15–20 cm long took gastropods with a mean size of 4.5 mm (± 1.5 mm). These gastro-
pods, however, lived among the algal turf where the wrasse foraged for amphipods which comprised most of the diet, and so were presumably taken incidentally. The only abalone found in the gut of *P. tetricus* was 6.5 mm long. We cannot, however, infer from this that abalone are rarely taken because the wrasses whose guts were analysed were taken away from the site studied, in places where abalone were less frequent. We conclude that predation by this wrasse on abalone \(\leq 5\) mm long is a rare event.

![Graph showing the length of abalone taken, not taken, or unsuccessfully attacked by different length classes of the wrasse *P. tetricus*](image)

Fig. 5. Size range of small abalone not taken, taken, or unsuccessfully attacked by different length classes of the wrasse *P. tetricus*; broken lines indicate the approximate upper and lower boundaries of size range of abalone taken.

The wrasse *Pseudolabrus latiflavus* is a cryptic species and shy of divers and it was not possible to test its visual acuity experimentally in the field. It has, however, a similar diet to *Pseudolabrus tetricus* (unpubl. data) and our conclusions for the latter species should also apply to it.

**Discussion**

Our data and observations show that to a size of at least 5 mm these two species of abalone are largely restricted to a crustose coralline substratum. The smallest individuals recorded had a shell length of \(\approx 0.5\) mm, when the shell was colourless and lacked pore-holes. Numerous studies (see review by Koike, 1978) have shown that the shell develops within 1–4 days of larval settlement and pore-holes appear within another 20–30 days, when the shell is \(\approx 2\) mm long (Leighton, 1974; Koike, 1978). Shells acquire a pink colour during this period as feeding on crustose corallines proceeds (Morse *et al.*, 1980; Kitting & Morse, in prep.). Our observations of the smallest
individuals are, therefore, likely to have occurred within the first two weeks or so of larval settlement. Because small abalone are highly mobile we cannot strictly infer settlement behaviour from later observations. The following considerations, however, suggest that our conclusion on substratum specificity of small abalone can be extrapolated back to the time of larval settlement. Following Underwood (1979) three explanatory models of abalone larval behaviour can be postulated: 1) they settle preferentially on crustose coralline algae; 2) they settle haphazardly and then migrate to a crustose coralline substratum; 3) they settle haphazardly and differential mortality eliminates them from other substrata. The most likely cause of differential mortality is selective predation in unsuitable habitats. The only known predators of abalone larvae are terebellid polychaetes, certain copepods, and nematodes (Morse et al., 1979b; Ebert & Houk, 1984). Of these, we only saw terebellids under boulders and in particular among the CCF boulders. Another possible predator might be the anemone Anthothoe alboalbumata (see Sebens & Koehl, 1984) also present among these boulders. But in the experimental structures significantly greater numbers overall of small abalone were found in the CCF boulders with these predators than in those without (CC boulders) suggesting that predation by these sessile species is minor. Similarly, our data on wrasse predation show that abalone ≤ 5 mm long are unlikely prey. Consequently the third model of larval behaviour (haphazard settlement and differential mortality) seems unlikely.

The second model (haphazard settlement and migration) is excluded by the absence of small abalone on the bare boulders in the experimental structures.

From this we conclude that the substratum specificity of small abalone is most plausibly explained by substratum preference of the settling larvae. This is supported by the numerous studies of Morse and associates (Morse & Morse, 1984) in which they demonstrate preferential settlement of abalone larvae on crustose coralline algae and offer a molecular basis for such preference. They found that γ-amino butyric acid (GABA) and its analogues are agents (chemical signal) inducing metamorphosis behaviour and settlement of competent larvae of Haliotis Rufescens and H. fulgens. Only certain crustose red algae have GABA mimic molecules available at their surface, and so account for the contact dependent and substratum specific settlement of abalone larvae.

The rôle of crustose red algae inducing settlement of, or as a preferred substratum for, abalone larvae has not been tested outside the laboratory and this study is the first such field investigation.

The association between small abalone and crustose coralline algae is significant in two ways.

1) The combination of a smooth substratum (at the scale of a newly settled abalone) providing maximum adhesion for the foot, a shaded surface and cryptic colouration of the abalone constitutes an effective defensive strategy against visually searching predators.

2) The mucous exudate from the crustose corallines (Giraud & Cabioch, 1976) may,
and epiphytic diatoms do, provide a source of food for newly settled abalone (Kitting & Morse, in prep.; and see review by Shibui, 1972). This resource is also shared by chitons and archaeogastropods (Kangas & Shepherd, 1984; Clarkson & Shepherd, 1985) but is unlikely to be limiting, at least at our site because of the low densities of molluscs found.

There may also be a reciprocal benefit to the crustose coralline by the abalone removing fouling epiphytes (Adye, 1973; Steneck, 1978; Paine, 1980; Kitting & Morse, in prep.) but this possibility needs further investigation.

It is possible that cues other than or in addition to the presence of crustose corallines may induce settlement of abalone larvae. Saito (1981) found newly settled H. discus hannai on crustose corallines (although he did not critically examine other microhabitats). Yet Momma (1973) in experiments with veligers of the same species found that maximum settlement was on certain diatom films, while Seki & Kanno (1981a,b) showed that the mucous trails of adult abalone induced settlement. In our case, lack of any significant difference in the abundance of juvenile H. laevigata between areas of high and low adult density discounts the likelihood that larvae are attracted to or by conspecific adults. But the possibility that 1 and 2-yr-old conspecifics, which are more mobile than adults (Shepherd, 1973) and thus are likely to leave trails, attract settling veligers needs investigation.

Possible explanations for the changing ratios, with increasing size of individuals on upper to under sides of boulders and for the differences in these ratios between the two species include behavioural differences, biased sampling, and differential mortality. Biased sampling does not appear to be a factor over the size ranges compared because all possible microhabitats were exhaustively sampled. Differential mortality cannot be excluded in the light of our limited knowledge, but the simplest explanation is that the two species differ in behaviour at settlement (e.g. in response to light) and become increasingly cryptic after settlement, but at different rates.

Studies of abalone recruitment have been hampered in the past by the lack of a quantitative technique to measure the strength of larval settlement. The CCF experimental structures used in this study were more effective than both the natural boulder habitat and the CC structures in terms of densities of young abalone recorded (Table II). One of the several factors which may have contributed to the superiority of the CCF structures is the progressive decline of crustose coralline cover through epiphytic overgrowth on the CC structures due to absence of grazing (Clarkson & Shepherd, 1985). Saito (1981) also observed that small abalone disappeared when their crustose coralline substratum became covered with epiphytes and sediment. Thus, if a healthy crustose coralline substratum can be maintained, experimental structures offer a simple, replicable, uniform technique to measure settlement strength of abalone larvae in time or space.

This paper adds to a growing list of species in four phyla which are thought to settle selectively on crustose coralline algae. In addition to numerous haliotids the list now includes three species of chiton (Barnes & Gonor, 1973; Morse et al., 1979a; Rumrill
& Cameron, 1983), a trochid (Heslinga, 1981), a spirorbid worm (Gee, 1965), a limpet (Branch, 1975), an octocoral (Sebens, 1983), a scleractinian coral (Harrigan, 1972) and a seastar (Barker, 1977). Thus, this relationship between animal and a family of plants has apparently evolved independently in different places among different species. The benefits to the animal are functional, i.e. the substratum serves as a food resource, a refuge, or an indicator of suitable habitat. An intriguing question for future research is whether the relationship is species-specific, i.e. whether settling larvae can discriminate between crustose coralline taxa and so further identify an optimal habitat.

Acknowledgements

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References


CHAPTER 3

GROWTH

Introductory Remarks

Two species of abalone *H. laevigata* and *H. scalaris* were found to settle in the boulder habitat at West Island (Ch2).

Although, the species of principal concern is *H. laevigata*, information on *H. scalaris* was necessary to be able to confidently distinguish the two species soon after settlement, and this required an understanding of the spawning cycle of *H. scalaris*. Second, *H. laevigata* was not nearly as common as *H. scalaris* and so more difficult to study. It therefore seemed prudent to gather data at little extra cost on both species, with an increased probability of providing satisfactory results on at least one of them. Underwood (1985 p27) emphasises the wisdom in carrying out needed research on the most amenable species available. And, in any event, a comparison of two related species in the same habitat has intrinsic interest.

The growth rate of abalone is an important parameter to measure, necessary for aging of individuals (Ch 5) and estimating natural mortality rates (Ch 4). Because there is no known way of aging shells of either of these two species, other methods must be found. Those used here are cohort analysis supported by mark-recapture experiments. Cohort analysis is useful only when the modes are conspicuous; where they become diffuse the standard errors increase (see Fig.3) and reduce confidence in their precision. For this reason it is prudent to use two independent methods in the natural environment.

References


STUDIES ON SOUTHERN AUSTRALIAN ABALONE (GENUS HALIOTIS) V. SPawning, SETTLEMENT AND EARLY GROWTH OF H. SCALARIS

This note describes the spawning cycle of *Haliotis scalaris* Leach and the settlement density and growth of juveniles of the species at West Island (35°37'00"S, 138°35'00"E), South Australia. This spawning cycle differs markedly from that previously described for the species at Tiparra Reef*. South Australia and is therefore of considerable interest.

Samples of 9-12 sexually mature female *H. scalaris* 65-80 mm long were collected at Abalone Cove, West I., at about monthly intervals from February 1983-July 1984. The entire visceral mass was preserved in 10% formalin and sea-water and later sectioned in the laboratory. Cross-sections of the gonad and digestive gland were traced on transparent plastic, the cut-out sections weighed, and the respective areas of gonad and digestive gland calculated. A gonad index was then calculated with the formula Gonad index = 100 (Area of gonad)/(Total area of section). The annual reproductive cycle of this species at West J. proved to be synchronous within the population so that measurement of oocyte-ova diameters to distinguish the stages of the reproductive cycle was unnecessary (see Shepherd & Laws* for details of the method).

Sea surface temperature data were obtained with a mercury thermometer at about monthly intervals at West I.

A hand lens, designed for use underwater with about 3x magnification (the optics are described by Shepherd & Turner in prep.) was used to search for *H. scalaris* on crustose coralline algal substrate, the preferred substrate for settlement of this species (Shepherd & Turner in prep.). Searches were done for 60-100 minutes at about monthly intervals in the boulder habitat at West I. at 4-5 m depth and the lengths of all individuals to about 25 mm long recorded to 0.1 mm.

Changes in the mean monthly gonad index of *H. scalaris* from February 1983-May 1984, together with sea surface temperature data are given in Fig. 1. The index increases from winter to mid-summer and declines abruptly from late summer through to autumn. The increase indicates maturation and increase in size of oocytes in the gonad, and the decline of the index indicates the onset of synchronous spawning in the population. Spawning appears to have commenced later in 1983 than in 1984 and to have been more complete. In 1984 the gonad never became completely spent but commenced to increase in size again in July.

Thus *H. scalaris* has a late summer to autumn spawning season (February-May) which is synchronous throughout the population, and appears to begin at about the time of maximum summer sea temperature. This spawning cycle contrasts strikingly with the asynchronous cycle of *H. scalaris* at Tiparra Reef where spawning potentially occurs throughout the year.

![Fig. 1](image_url)

**Fig. 1.** (upper)—mean monthly sea surface temperatures (smoothed curve); (mid)—monthly distribution of gonad indices with standard errors; (lower)—density of small *H. scalaris* ≤ 5 mm at study site.

![Fig. 2](image_url)

**Fig. 2.** Length frequency distributions for *H. scalaris* at West Island from February 1983 to May 1984.

Of the various environmental factors that are known to influence the spawning cycles of abalone e.g. temperature,^2^ photoperiod,^1^ and food abundance,^1^ only the latter shows a marked difference between the two sites. Diet food algae are seasonally in short supply at Tiparra Reef but abundant throughout the year at West I.,^1^ but this is unlikely to account for the differences in spawning between the sites. Further studies of *H. scalaris* are necessary, especially in other parts of its geographic range, to elucidate the problem. *H. rubra* Leach also shows marked, but unexplained, differences in spawning cycle between these two sites. The only other abalone species that we know of with a similarly variable spawning cycle between localities is *Haliotis rufescens* Swainson.*^2^
The density of small H. scalaris (measured in mean numbers of individuals ≤5 mm recorded per 15 min searching time) is given in Fig. 1. Maximum settlement apparently occurred in March 1983. The relatively high densities recorded from July to September 1983 are of larger individuals (3–5 mm) and do not indicate recent settlement.

Fig. 3. Plot of mean length (with standard errors) of 1983 cohort of H. scalaris from March 1983 to May 1984. A polynomial regression of best fit to the means is shown.

Length frequency data from February 1983–May 1984 (Fig. 2) show that very small H. scalaris (1–3 mm long) were present from February–June 1983 indicating settlement in that period. This is in good agreement with the spawning season described above. No small H. scalaris were found in the 1984 spawning season, suggesting settlement was very poor and not detectable.

Shepherd (in prep.) associated the similar poor recruitment of H. laevigata Donovan at West 1 in 1984 with the lower maximum summer sea temperature in 1984 compared with 1983. The settlement failure of H. scalaris in 1984 may also be associated with lower summer sea temperatures in that year or with the incomplete spawning or a combination of them.

The change in mean size of the 1983 cohort from March 1983–May 1984 (Fig. 2) enables an estimate to be made of the growth of the cohort in the first year. The equation of best fit empirically fitted to the data is given in Fig. 3. On the basis that settlement occurred between 1 February and 30 June 1983, a mean birth date for the cohort can be fixed at 15 April 1983. From the regression (Fig. 3) the mean length of the one year old animal is therefore about 18.5 mm. Comparison of this growth rate with that of other haliotids suggests that it is relatively rapid for a species whose maximum size (at West 1) is only about 100 mm.

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S. A. SHEPHERD, P. S. CLARKSON and J. A. TURNER, Department of Fisheries, 135 Pirie Street, Adelaide, S. Aust. 5000.

STUDIES ON SOUTHERN AUSTRALIAN ABALONE (GENUS HALIOTIS) IX.
GROWTH OF H. SCALARIS

The non-commercial abalone *Haliotis scalaris* Leach is a common species occurring in a cryptic habitat under rocks in southern Australian coastal waters. As part of long-term studies on the recruitment and survival of abalone in this habitat at West Island, South Australia (35° 37'S; 138° 35'E), we describe here the growth rate of *H. scalaris* during the first four years of life. The earlier noise described the spawning cycle, recruitment and juvenile growth in the first year only of this species at West Island.

An underwater hand lens was used to search for newly settled *H. scalaris* on a crustose coraline substratum on and under boulders roughly 20 × 30 cm diameter at the study site (extending over a distance of about 60 m) where previous studies were made. Sampling was stratified spatially at 4 and 5 m depths in five sections of the site and twenty samples, each covering 0.25 m², were taken at each visit. Sampling consisted of measuring and recording the size of all abalone within a quadrat frame 0.25 m² in area. Diving time was about five hours per visit except that, on the October 1986 and December 1986-January 1987 visits, about 35 hours in all were spent searching for abalone.

The MIX interactive computer program was used to separate modes of multimodal distributions and fit Gaussian component distributions with maximum likelihood techniques. Probability values exceeding 0.05 indicate statistically satisfactory fits. Some individuals were also tagged with small plastic tags fixed to the shell with superglue to verify the growth rate.

Length frequency distributions from under-boulder censuses from December 1984-January 1987 are given in Fig. 1; those obtained during 1983 and 1984 have been published previously. There was a strong recruitment (i.e. numbers of individuals 1–5 mm long recorded) in 1983, a very weak recruitment in 1984 (only detected as individuals grew into larger size classes), a weak settlement in 1985 and a stronger one in 1986. The modes of length frequency distributions (Fig. 1) are plotted over time in Fig. 2, and the progression of the modes is taken to indicate the growth rate.

A linear regression by the least squares method was fitted to the modal means for all years combined, each modal mean being weighted by the reciprocal of its standard error. The regression equation of best fit is

\[ L = 0.00584 + 0.0373A \quad (R^2 = 0.98) \]

where \( L \) = length in mm and \( A \) = age in days. The standard error of the slope is 0.0009 and of the constant is 0.520. The mean growth rate of the successive cohorts (derived from the equation) is 1.13 mm per month (S.E. = 0.03 mm). The \( X \)-intercept (January 1) is a theoretical rather than a biologically realistic mean birth date. Earlier studies suggest that settlement of the species occurs predominantly from January to June. If this is so, the growth rate in the first few months after settlement must be faster than that indicated above.

The mean growth rate of four tagged individuals (plotted in Fig. 2) is 1.12 mm per month (S.E. = 0.10 mm) which is not significantly different from the growth rate inferred from modal progressions. This growth rate is slower than that of *H. laevigata* in the same habitat, but similar to numerous other species of abalone whose early growth has been examined.

We are grateful to Jean Turner, P. S. Clarkson and C. H. Deane for diving assistance. Funds supporting the study came from Fishing Industry Research Trust Account (FIRTA).

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H. scalaris

Dec. 84  
\( N = 52 \)  
\( \chi^2 = 14 \)  
\( P = 0.43 \)

Feb. 85  
\( N = 48 \)  
\( \chi^2 = 15 \)  
\( P = 0.96 \)

Mar. 85  
\( N = 34 \)  
\( \chi^2 = 20 \)  
\( P = 0.80 \)

Jun. 85  
\( N = 41 \)  
\( \chi^2 = 31 \)  
\( P = 0.88 \)

Dec. 85  
\( N = 56 \)  
\( \chi^2 = 50 \)  
\( P = 0.30 \)

Feb. 86  
\( N = 38 \)  
\( \chi^2 = 47 \)  
\( P = 0.17 \)

Apr. 86  
\( N = 49 \)  
\( \chi^2 = 28 \)  
\( P = 0.98 \)

May 86  
\( N = 128 \)  
\( \chi^2 = 52 \)  
\( P = 0.47 \)

Oct. 86  
\( N = 161 \)  
\( \chi^2 = 87 \)  
\( P = 0.003 \)

Dec. 86-Jan. 87  
\( N = 116 \)  
\( \chi^2 = 67 \)  
\( P = 0.15 \)

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Fig. 1. Length frequency distributions of H. scalaris at West I. from December 1984 to January 1987. Triangles represent the position of the modes of the fitted Gaussian distributions. Annual cohorts are distinctively shaded.
Fig. 2. Plots of modes (and standard errors) of annual cohorts from 1983 to 1986. The mean growth of tagged individuals is shown (x...x).
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Studies on Southern Australian Abalone (Genus *Haliotis*). VIII*

Growth of Juvenile *H. laevigata*

S. A. Shepherd

Department of Fisheries, 135 Pirie Street, Adelaide, S.A. 5000.

Abstract

The growth of juvenile *H. laevigata* was studied by analysis of sequences of length-frequency distributions obtained in below- and above-boulder habitats at West Island, South Australia. The mean growth rate overall is 1.69 mm month$^{-1}$ and is linear with length for the first 5 years, but thereafter declines with increasing length. The mean growth rate of four groups of marked *H. laevigata* aged 1 and 3 years is 1.62-1.87 mm month$^{-1}$, and thus supports the estimation of growth rate from analysis of length-frequency distributions.

Introduction

Settlement and early growth are important but neglected aspects of life histories of abalone. Knowledge of both is necessary for an understanding of the recruitment process which is itself critical for proper management of abalone fisheries. The greenlip abalone *Haliotis laevigata* Donovan is the basis of an important fishery in southern Australia and has been the subject of numerous biological studies (Shepherd 1973; Shepherd and Hearn 1983; Shepherd and Turner 1985; and references cited).

This paper examines the growth of juvenile *H. laevigata* at West Island, South Australia (35°37'S, 138°35'E), the site of most earlier studies by this author, by analysis of length-frequency distributions and by limited marking of juveniles. The growth rates so obtained are compared with earlier estimates obtained in mark-recapture studies (Shepherd and Hearn 1983). The methods used here have previously been used by Poore (1972), Shepherd et al. (1985) and Clavier and Richard (1986) for the study of juvenile growth of other abalone species.

Materials and Methods

The north shore of West Island is a slope covered by rounded boulders of 30-40 cm greater diameter and 20-30 cm lesser diameter. The study site extends for about 60 m along the shore and is bounded on the seaward side by bare sand and seagrass beds. *H. laevigata* recruits onto crustose coralline algae covering boulders at 4-5 m depth (Shepherd and Turner 1985) and remains cryptic until it reaches a length of 40-60 mm. Censuses of the population were done by two independent sampling methods: (a) by searching under boulders and (b) by searching the upper sides of boulders and crevices between them.

*Under-boulder censuses*

Regular searches for newly-settled abalone were made annually from November to June among boulders at the study site from 1983 to 1987 by using a magnifier (Shepherd and Turner 1985) to find individuals from about 0.5 mm long. Sampling sites were located to cover each of five sections of the


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study site at depths of 4 and 5 m. From 1985, searches were made of rocks within a 0·25 m² quadrant,
placed haphazardly in each section, twice at 4 m depth and twice at 5 m depth, to give a total coverage
of 5 m². Sampling time under water averaged 1 h m² and it was sometimes necessary to complete the
sampling over two visits. In November 1986, much more extensive sampling was undertaken involving
> 25 h under water. To minimize the decrement in diver performance due to cold (Fowler and Shepherd
1974), divers used local heating pads (Chan and Burton 1982).

Above-boulder censuses

A census of all accessible individuals of *H. laevigata* >40 mm long resting above boulders or in
crevices was made throughout the study site at about 3-monthly intervals; the data were recorded on
plastic strips by using the gauge described by Shepherd (1985). The time for each census was about 2 h.

Small abalone <30 mm long were marked by fixing numbered plastic tags to the shell with Selleys
superglue (cyanoacrylate) and larger (50–70 mm long) individuals were marked by fixing numbered
plastic tags to the backs of shells with a nylon rivet inserted through the proximal pore hole. The latter
method has the great advantage that marking can be performed under water without removing the
abalone from the rock.

The method of Macdonald and Pitcher (1979) incorporated in the MlX interactive computer program
was used to fit and separate modes of length-frequency distributions. The procedure fitted Gaussian
component distributions and used maximum likelihood methods to separate them. Probability values
> 0·05 indicate statistically satisfactory fits. In above-boulder censuses the largest animals were lumped
into one or two groups and parameters were constrained to the extent necessary to ensure biologically
reasonable fits (Macdonald, 1987).

Results

Length-frequency distributions from under-boulder censuses of *H. laevigata* at West
Island from December 1982 until November 1986 are given in Fig. 1. A strong settlement
of *H. laevigata* occurred from December 1982 to March 1983 (the 1983 cohort) as shown by
the abundance of juveniles 0·5–2·0 mm long. In contrast, the settlements of 1984, 1985
and 1986 were relatively weak. The 1983 cohort remained clearly identifiable in under-
boulder censuses until the May–June 1985 census when the modal mean was 46 mm.
Similarly, the 1984 to 1986 cohorts were identifiable until the final census in November
1986.

Length-frequency distributions for above-boulder censuses of *H. laevigata* (Fig. 2) are
multi-modal and, over time, show progressions of the first two modes. Plots of modal
progressions for both above- and below-boulder censuses combined (Fig. 3) show the shift
in size of various modes and in particular the transition of the 1983 cohort from an under-

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<th>Final mean length (mm)</th>
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<td>32.5 (3.9)</td>
<td>38.4 (7.3)</td>
<td>1.76 (0.20)</td>
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<td>1969–71</td>
<td>35</td>
<td>383</td>
<td>62.0 (1.0)</td>
<td>88.8 (1.6)</td>
<td>2.12 (0.084)</td>
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</tbody>
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Table 1. Mean growth rates of marked individuals of *H. laevigata* at West Island
S.e. in parentheses

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S. A. Shepherd
Fig. 1. Sequential length-frequency distributions of *H. laevigata* resulting from under-boulder censuses at West Island from December 1982 to November 1986. Annual cohorts are distinctively shaded. Triangles (△) are the modes of fitted Gaussian curves.

and provides a highly satisfactory fit to the data ($r^2 = 0.98$, $P < 0.0001$). The mean growth rate from the equation for the first 5 years of life of *H. laevigata* is 1.69 mm month$^{-1}$ (s.e. 0.03 mm). The growth rate of marked individuals agrees closely with this rate. Individuals in the 1983 and 1985 cohorts marked during 1986 showed mean growth rates of 1.5–1.8 mm month$^{-1}$ (see Fig. 3 and Table 1). However, the growth rates of individuals over the same size range (50–70 mm) marked from 1969–71 (extracted from data of Shepherd and Hearn 1983) was significantly higher ($t = 2.79$, $P < 0.01$) than that recorded in 1986 (see Table 1).

It is concluded that the modes of under-boulder length-frequency distributions indicate year classes and can be used to measure growth. The modes of above-boulder length-frequency distributions need to be interpreted more cautiously. The initial modes (i.e. those <110 mm) in Fig. 2 appear to indicate year classes in all cases except that of March 1987
where conflation of two weak age classes appears to have occurred. Modes at larger sizes (>110 mm) contain several age classes (see Shepherd and Hearn 1983) so that shifts in them would not reliably measure growth. To illustrate the growth of individuals >110 mm long, the von Bertalanffy growth curve found for this species at West Island is plotted in Fig. 4.

The linear growth rate of juvenile *H. laevigata* resembles that of other abalone (Newman 1968; Poore 1972; Sainsbury 1982; Clavier and Richard 1986).

**Discussion**

Analysis of size distributions has often been used to estimate the growth rates of abalone (Newman 1968; Poore 1972; Ichiki *et al.* 1977; Sainsbury 1982; Shepherd *et al.* 1985), but satisfactory separation of year classes depends on an annual brief period of settlement and sufficiently rapid growth with little variation within year classes. The biology of *H. laevigata* satisfies these conditions, allowing a description of growth in the natural environment during the first 5 years of life.

In an earlier study, Shepherd and Hearn (1983) estimated a mean growth rate of 3.25 mm month⁻¹ for *H. laevigata* during the first year, and a mean length of 39 mm at 1 year. Growth of the smallest individuals 12–20 mm long was even faster, averaging 3.9 mm month⁻¹. These rates are almost twice those recorded in this study and had been obtained from abalone kept in experimental cages from which all other algivorous molluscs
Fig. 3. Plot of modal mean lengths against time for below- and above-boulder censuses combined from the data in Figs 1 and 2 for the 1983 to 1986 cohorts. The modal progression at the transition from below- to above-boulder censuses for 1983, 1984 and 1985 age classes is shown by dashed lines and the mean growth of tagged individuals is shown by dotted lines. Vertical lines represent standard errors of the modal means.

had been removed and to which suitable algae had been introduced to ensure an abundant food supply (Shepherd and Hearn 1983). In contrast, the present growth rates were recorded in the under-boulder habitat where other grazing gastropods and chitons (many with diets which overlap widely with that of this abalone) occur in densities exceeding 185 m$^{-2}$ (Kangas and Shepherd 1984; Clarkson and Shepherd 1985).

Experimental studies have shown that the growth rate of limpets can be reduced by increasing the densities of other grazers, because of a reduction in the amount of food available to the limpets (Black 1977; Choa 1977; Underwood 1979; Creese 1980). While it is difficult to assess the availability of food that consists of both drift and attached algae (Shepherd and Cannon 1988), competition for preferred algae among grazers is certainly implied by the results of the grazer-removal experiments at the study site described by Clarkson and Shepherd (1985). Thus, it is possible that the high densities of other grazing molluscs at the study site so reduce the abundance or quality of food algae available to this abalone species as to depress its growth rate below the level recorded in the cage experiment of Shepherd and Hearn (1983).

The higher mean growth rate of tagged individuals of the 2+ age class in 1969-71 compared with that in 1986 may be an artifact of the tagging method. In 1986, rivets, which
Fig. 4. Plot of modal means of the 1982 to 1986 cohorts against age. The continuous straight line is the regression line fitted to the data, and the dashed line is from the von Bertalanffy growth curve after Shepherd and Hearn (1983). For the linear regression equation, \( L = 0.628 + 0.0557 \times T \) and \( R^2 = 0.98 \).

Projected up to 3 mm inside the shell, may have caused irritation and reduced the growth rate below that observed in the 1969–71 experiments in which tags were glued to the shell.

Of special interest here is the relationship between settlement strength as inferred from the recorded abundance of recruits 1-2 mm long in under-boulder censuses (Shepherd and Turner 1985) and the subsequent appearance of the year class in above-boulder censuses. These data show that strong (e.g. 1983) and weak (e.g. 1984) year classes appear some 2\( \frac{1}{2} \) years after settlement as the initial mode observed in above-boulder censuses. This suggests that relatively easily obtainable above-boulder census data could be used to estimate past settlement strength in a population, provided the age of the cohort is known. If validated by further research, it may also be a powerful tool with which to predict future recruitment strength into the fished section of the population. This would be of great benefit in managing an abalone fishery.

Acknowledgments

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CHAPTER 4

JUVENILE SURVIVAL
Central to the problem of stock-recruitment relations is to understand the relative importance of pre-settlement events and those which occur on the substratum between settlement and the time when recruitment is measured. This chapter addresses the latter question.

Settlement *stricto sensu* is defined as the point when an individual takes up residence on the substratum (Connell 1985). This is difficult to measure even for a sessile species and much more so for a mobile one. The measurements of 'settlement' described in Ch 2 were done strictly during an early post-settlement period when individuals were probably 2-4 weeks old. So the mortality rates described below run from this post-settlement period until an age of 2 1/2 or 3 years according to species. As with growth, reliance should not be placed exclusively on only one method of estimation of mortality. In fact, a pilot grid experiment of the kind described by Beinssen and Powell (1979) was set up in November 1986 for one year to examine the movement and mortality of juveniles. Too late for inclusion in this thesis, the data showed considerable movement of juvenile abalone among boulders and cast doubt on the usefulness of a grid-type experiment to measure juvenile mortality. The real problem with studies in a boulder habitat is the enormous amount of underwater time necessary for sampling (one hour m^-2), and the large number of samples required due to relatively low densities.

Determination of the relation between settlement and recruitment some 2 1/2 - 3 years later will, of course, require a longer time period than was available for the completion of this thesis. Nevertheless, survival data for four consecutive years for two abalone species, as described below, does suggest that recruitment patterns reflect settlement patterns in accordance with the model of Connell (1985). If continuation of the study verifies this tentative conclusion, there are important ramifications for the direction of future work. Measurement of settlement itself will have little utility and it will be sufficient to measure recruitment at some later and more convenient stage, with considerable saving in terms of underwater diving effort.
Reference


STUDIES ON SOUTHERN AUSTRALIAN ABALONE

(GENUS HALIOTIS) XIII. SURVIVAL OF JUVENILES

by

S A SHEPHERD

DEPARTMENT OF FISHERIES

135 PIRIE STREET

ADELAIDE, S AUST. 5000
ABSTRACT

The survival of newly-settled cohorts of two abalone species, *Haliotis laevigata* and *Haliotis scalaris* in a boulder habitat at West Island, South Australia, was measured from 1983 to 1987 by sequential sampling of the habitat to census the density of cohorts. In 1983, a year of relatively strong settlement, the survival was low (10 - 17%) in the first six months but thereafter was high (83 - 93%) until an age of 2-1/2 years for *H. laevigata* and three years for *H. scalaris*. In later years settlement of both species was light and survival variable; it ranged from 46 to nearly 100% and was independent of density.

INTRODUCTION

An understanding of recruitment variability is a central problem in the dynamics of exploited stocks. There is fundamental uncertainty whether recruitment strength is determined primarily by the size of the parent stock as assumed by most stock recruitment models (Beverton and Holt, 1957) or by environmental factors (Hancock, 1973). Recent studies have shown that the recruitment of abalone is highly variable from year to year (Sainsbury, 1982; Tegner, et al., 1988; Ch6) leading to doubts whether a stock-recruitment relationship exists at the level of stocks that are fished. On the other hand, Prince et al. (1987) have provided evidence of a close link between local spawning stock size and recruitment strength. Studies are now needed to determine the role of variable survival of newly settled individuals in recruitment variability in abalone.

*Haliotis laevigata* Donovan is an exploited abalone species and *Haliotis scalaris* Leach a smaller non-commercial species that occur in a boulder habitat at West Island, South Australia (35°37' S, 138°35' E.) and recruit onto crustose coralline algae from about November to July annually. Shepherd and Turner (1985) described a method of quantifying post-settlement strength (measured at a size of 0.5 - 1.0 mm length) of those two abalone species and measured cohort size of new settlers from 1983 to 1985. This paper describes the survival of these and later cohorts over the succeeding 2 - 3 years.
Materials and Methods

Field

The north shore of West Island is a slope covered by rounded boulders of 30 - 40 cm greater diameter and 20 - 30 cm lesser diameter. The study site extends for about 60 m along the shore and is bounded on the seaward side by bare sand and seagrass beds. *H. m. gigata* and *H. scalaris* recruit onto crustose coralline algae covering boulders at 4 - 5 m depth (Shepherd and Turner, 1985) and remain cryptic until a length of 40 - 60 mm. Censuses of the population were done by searching the boulders with an underwater magnifier, and recording all individual abalone from about 0.5 mm length.

Sampling sites were located to cover each of five sections of the study site at depths of 4 and 5 m. In 1983 and 1984 divers recorded the time taken per boulder searched but from December, 1984 searches were made of boulders within a 0.25 m$^2$ quadrat placed haphazardly in each section, twice at 4 m depth and twice at 5 m depth, to give a total coverage of 5 m$^2$. This sampling intensity proved inadequate for cohorts present in very low densities and, whenever possible, it was increased according to the same sampling strategy.

The earlier data were subsequently converted to density estimates (nos. 0.25 m$^{-2}$) by measuring the time taken to search boulders within the quadrat. The mean time was 20.4 minutes per quadrat (s.e. 1.4; 10 replicates).

Length frequency data for each species resulting from the censuses were decomposed by modal analysis into age classes as described in Ch 6 and Shepherd et al. (1988) and the numbers of each cohort per unit area determined.

If the mortality rate is constant, plots of the natural logarithm of density of a cohort vs time should give a linear decline whose slope is $-M$, the coefficient of natural mortality (Gulland, 1969).

An assumption of the method is that diver efficiency at finding small abalone does not change over the size range examined. Because the cryptic colouration and crustose coralline habitat dependence of individuals 1 - 5 mm long cast doubt on this, an experiment was
carried out at West 1. in March 1986 in which the diver searched 20 boulders for small abalone in the normal way with the magnifier and recorded the number, size and specific identity of all individuals found. The boulders were then each placed into individually numbered plastic bags, which were sealed and taken to the laboratory on shore. Each boulder was washed in dilute formalin and seawater and the surface carefully brushed; all epibiotes, retained by a 0.55 mm mesh sieve, was examined under a low power microscope. Twenty abalone 1-5 mm long were recorded during underwater examination of the boulders and three more were recorded in the laboratory. However, two of those found underwater were not subsequently recorded in the laboratory. After adjusting for the slight probability of an individual being missed in both below- and above-water examinations, the mean efficiency of the diver can be shown to be

\[
\frac{20}{23.3} = 0.86
\]

it was assumed that there was no change of diver efficiency in finding individuals > 5 mm long which are readily visible to the diver with the naked eye.

A second assumption is that no migration occurs within or from the study site. Because the site is bounded by sand on one side, unsuitable shallow boulder habitat on the other and granite blocks at each end, no migration from the site seems possible. However, Shepherd and Cannon (1988) provided evidence that \( H. \text{ scalaris} \) recruits onto boulders at 3 m depth and, later, at an age of 3 years and above, migrates to deeper water. Further, \( H. \text{ laevigata} \) begins, at an age of 2 1/2 years, to emerge from an under-boulder to a crevice habitat. For these reasons, changes in density of cohorts were analysed to age 3 years in the case of \( H. \text{ scalaris} \) and to age 2 1/2 years in the case of \( H. \text{ laevigata} \). The mean birthdate of \( H. \text{ scalaris} \) was taken to be 1 April (Shepherd et al., 1985) and of \( H. \text{ laevigata} \) to be 1 January (Shepherd 1988).

Because sampling intensity varied during the course of the study, due to weather and availability of divers, in this preliminary analysis the data points representing mean densities, are each weighted according to the number of quadrats per sample. A more complete
Fig 4.1 Plots of density of cohorts of *H. laevigata* (on a logarithmic scale) vs time.
Fig 4.1 Plots of density of cohorts of *H. laevigata* (on a logarithmic scale) vs time.
analysis will need to consider the highly non-normal distribution of abundances of individuals per quadrat.

RESULTS
Plots of changes in density of cohorts (on a logarithmic scale) versus time for *H. laevigata* and *H. scalaris* are given in Figs. 1,2 and presented in Table 1.

Inspection of the plots shows several features. First, densities may increase during the period of larval settlement. This is expected where there are several waves of settlement during a spawning season, but not if there is only a single episode of settlement. In the one year of strong settlement (1983) this is evident only for *H. scalaris*. Second, there may be an early steep decline in density, indicative of an early high mortality rate. This is evident for both abalone species but only during 1983. Third, from about 6 months from date of birth the decline of density is more or less log-linear, suggesting a constant mortality rate over time. This last conclusion is much obscured by the variability in the data and it should be noted that this variability is high when mean densities are low. This is to be expected because in low densities the chance occurrence of a single individual can make a large difference to the mean of the sample.

Mortality rates were accordingly calculated by linear regression analysis from an age of 6 months to 2-1/2 years of age (for *H. laevigata*) and three years of age (for *H. scalaris*) (see methods). The results, with corresponding survival values, are given in Table 2.

The values for the 1983 cohort are probably the most reliable because of the relatively strong settlement in that year. Of special interest is the low survival in the first 6 months and the high subsequent survival. In the three succeeding years densities were very low and the above pattern was not repeated except for the 1984 cohort of *H. laevigata*. All values for the cohorts from 1984, 1985 and 1986 must be regarded with caution and taken only as suggestive of trends.
Fig. 4.2: Plots of density of cohorts of *H. scalaris* (on a logarithmic scale) vs time.
Fig. 4.2: Plots of density of cohorts of *H. scalaris* (on a logarithmic scale) vs time.
Thus, survival of the 1984 cohorts for both species appears to have been high, whereas it was relatively low for the 1985 cohorts. The data sets for the 1986 cohorts are incomplete and comment is premature.

DISCUSSION
In a review of settlement and survival of benthic animals Connell (1985) concluded that "knowledge of the relative importance of pre-settlement vs post-settlement processes in marine benthic communities is minuscule .... Measurement of initial settlement should be one of the prime aims of benthic ecology." Such knowledge is critical for abalone as well. It is not known whether the cause of variation in recruitment (see Ch.6) is due to variability in the arrival of settling larvae (planktonic events) or to the mortality of juveniles after settlement. This study is the first known attempt to measure the natural mortality rate of abalone species from the earliest detectable post-settlement stage over several years.

It demonstrates that poor recruitment now described for several abalone species (Sainsbury, 1985; Breen, 1986; Ch 6) may be due to low rates of initial settlement rather than post-settlement mortality. It also suggests that strong settlements may be the exception rather than the rule because 1983 was the only relatively strong settlement for both abalone species in the four years to 1987.

However, some caution is needed in this interpretation. Because density of settlers is estimated some 2 - 4 weeks after settlement, the possibility cannot be excluded that a high, but variable mortality occurs during this period and causes the subsequent observed variability. If this were true some patchy survival of the supposed high density settlement might be expected in the study site; this was not seen in any of the years of apparent poor settlement.

The early steep decline of density recorded for the 1983 cohorts must produce conservative estimates of early survival. Judging from the appearance of the smallest individuals 0.5 mm to 1 mm long (Shepherd and Turner, 1985) there were major and minor episodes of settlement at different times by both _H. laevigata_ and _H. scalaris_. Because measurements of density at any one time record only the survivors of
Table 1: Sampling dates, number of quadrats sampled and mean densities of cohorts of *H. laevigata* and *H. scalaris*.

*Estimated (see text)*

<table>
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<td>17.12.82</td>
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<td>10*</td>
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<td></td>
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<td>1.06</td>
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<td>21.2.84</td>
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<td>0.60</td>
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<td>1.07</td>
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<td>10*</td>
<td>0.45</td>
<td>0.28</td>
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<td>13.12.84</td>
<td>22.5</td>
<td>0.49</td>
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<td>1.33</td>
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<td>26.1.85</td>
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<td>0.54</td>
<td>0.07</td>
<td>0.04</td>
<td></td>
<td>0.90</td>
<td>0.23</td>
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<tr>
<td>31.3.85</td>
<td>33</td>
<td>0.40</td>
<td>0.06</td>
<td>0.04</td>
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<td>0.75</td>
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<td>24</td>
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<td>0.08</td>
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<td>1.16</td>
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<td>30.12.85</td>
<td>49</td>
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<td>0.06</td>
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<td>0.82</td>
<td>0.02</td>
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<td>0.15</td>
<td>0.12</td>
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<td>0.04</td>
<td>1.04</td>
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<td>0.14</td>
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<td>30</td>
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<td>0.17</td>
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<td>22.3.87</td>
<td>37</td>
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<td>0.08</td>
<td>0.24</td>
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<td>0.08</td>
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<td></td>
<td></td>
<td>0.05</td>
<td></td>
<td></td>
<td>0.32</td>
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previous settlements, it follows that declines in density while settlement of new settlers is still occurring must under-estimate the mortality rate.
Table 2: Survival(S) and mortality(M) rates of juvenile *H. laevigata* and *H. scalaris* at West Island. A dash indicated that no realistic estimate was possible on the data

<table>
<thead>
<tr>
<th>Cohort</th>
<th>S (0-6mths)</th>
<th>S yr⁻¹ (6mths-21/2yrs)</th>
<th>M yr⁻¹ (±1 SE)</th>
<th>S (0-6mths)</th>
<th>S yr⁻¹ (6mths-3yrs)</th>
<th>M yr⁻¹ (±1 SE)</th>
</tr>
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<tbody>
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<td>1983</td>
<td>0.17</td>
<td>0.83</td>
<td>0.18(0.09)</td>
<td>0.51</td>
<td>0.93</td>
<td>0.07(0.07)</td>
</tr>
<tr>
<td>1984</td>
<td>0.10</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-0.05(0.32)</td>
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<tr>
<td>1985</td>
<td>-</td>
<td>0.46</td>
<td>0.77(0.17)</td>
<td>-</td>
<td>0.61</td>
<td>0.49(0.35)</td>
</tr>
<tr>
<td>1986</td>
<td>-</td>
<td>0.58</td>
<td>0.54(0.16)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 3: Summary of studies on survival of abalone seed transplants.

<table>
<thead>
<tr>
<th>Species with Reference</th>
<th>Length Range (mm)</th>
<th>Survival (%)</th>
<th>Comment</th>
</tr>
</thead>
<tbody>
<tr>
<td>Haliotis discus hannai</td>
<td>10 - 20</td>
<td>25 - 30 in 2 years</td>
<td>Placed on natural and artificial reefs</td>
</tr>
<tr>
<td>Saito (1979)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Momma et al. (1980)</td>
<td>15</td>
<td>17</td>
<td>Placed in concrete crib filled with boulders (S. A. Shepherd pers. observation).</td>
</tr>
<tr>
<td></td>
<td>21</td>
<td>33</td>
<td></td>
</tr>
<tr>
<td>Miyamoto et al. (1982)</td>
<td>&lt;22</td>
<td>&lt;10</td>
<td>After 491 days in natural habitat.</td>
</tr>
<tr>
<td></td>
<td>&gt;22</td>
<td>23 - 31</td>
<td></td>
</tr>
<tr>
<td>Haliotis discus discus</td>
<td>15 - 50</td>
<td>13 (several years)</td>
<td>On concrete artificial reefs (cited by Tegner and Butler (1985)).</td>
</tr>
<tr>
<td>Sakemoto et al. (1982)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>23 - 28</td>
<td></td>
</tr>
<tr>
<td>H. rubra</td>
<td>9 - 22</td>
<td>50 - 60 after 28 days</td>
<td>Released into boulder habitat. Handling mortality was 20%.</td>
</tr>
<tr>
<td>P. Whyte &amp; R.W. White</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(pers. comm.)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>H. rufescens</td>
<td>45 - 71</td>
<td>58 - 67</td>
<td>(Estimated from dead shell collection.) Released in Macrocystis forest.</td>
</tr>
<tr>
<td>Tegner &amp; Butler (1985)</td>
<td></td>
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</tbody>
</table>
Further, while the experiment to measure the efficiency of the diver at finding small abalone 1 - 5 mm long indicated only a slight decrement, it should be noted that some rocks (eg those partly buried in sand and those too large to be removed to the laboratory) were not tested, nor can they always be easily searched under water. It is, therefore, likely that the true density of settlers is somewhat higher than the data suggest. This would explain the apparent increase or the absence of any decline in density during the first year as recorded in some cohorts.

Although other studies on the natural mortality of juvenile abalone in wild populations are very scanty (see Tegner and Butler 1985), there are numerous studies on the survival of hatchery-reared seed abalone transplanted onto natural or artificial reefs, or confined in cages (Table 3). Survival rates in such studies are commonly 20-50% per annum for individuals 10 - 20 mm long (ie, 6 - 12 months old). The survival of *H. laevigata* and *H. scalaris* at this size was 46 - 93% per annum ie, about twice these rates. Schiel and Welden (1987) found that hatchery-reared abalone show behavioural differences from wild abalone and this could account for the higher mortality of the former when placed onto subtidal reefs.

The mortality rates (6 months - 2 1/2 or 3 years as the case is) for these two abalone species show no correlation with initial cohort density (*r = -0.30 n.s.); however, in the year of strong settlement there was evidence of a much higher early mortality of new settlers. The results are, therefore, consistent with the hypothesis proposed by Connell (1985) based on studies of barnacles, that when settlement is light, the mortality rate of juveniles is independent of density but when heavy it is density-dependent. To substantiate the hypothesis for these abalone species requires data for several more years and increased sampling intensity, especially when recruitment is light. Yet the trend is encouraging and suggests that it may be possible to use numbers of recruits (measured by Shepherd (1988) at 2 1/2 years old) as an indicator of density of settlers which is much more difficult to measure.

**Acknowledgements**

Substantial diving assistance was given by A.C.J. Mower, A. Dalgetty, Jean Cannon, J.A. Turner and statistical advice by Mrs K. Hill.
REFERENCES


Captions to Figures

Fig 4.1 Plots of density of cohorts of H. laevigata (on a logarithmic scale) vs time.

Fig 4.2 Plots of density of cohorts of H. scalaris (on a logarithmic scale) vs time.
CHAPTER 5

FOOD AND FEEDING OF JUVENILES

It has long been known that small abalone are found only on crustose coralline algae, but the nature of the relationship has only recently been elucidated.

In Chapter 2, it was shown that the substratum specificity of abalone occurred at the smallest size observable from which it was inferred that larvae settled onto crustose coralline algae. It was also suggested that the mucous exudate from and the epibiota on these encrusting algae provided food for newly settled abalone.

This paper takes the relationship much further. Abalone feed substantially on crustose corallines during the first year of life and to a less extent in the second year. As their dependence on crustose coralline algae declines, drift algae becomes of increasing importance to both abalone species.
Studies on southern Australian abalone (genus *Haliotis*)
X. Food and feeding of juveniles

by S.A. Shepherd and
Jean Cannon

Department of Fisheries
GPO Box 1625
Adelaide, South Australia 5001

ABSTRACT

The natural diet of juvenile *Haliotis laevigata* Donovan and *Haliotis scalaris* Leach was examined at West I, South Australia. Crustose coralline algae are the principal food eaten by both species from a length of 5 to 10 mm. From 10-20 mm length the diet switches to dead seagrass blades and drift algae such as *Lobosira bicuspida* and *Asparagopsis armata*; geniculate coralline algae also become more important with increasing length. Large brown algae such as *Ecklonia radiata*, *Sargassum* spp. and *Cystophora* spp. which dominate the habitat are avoided.

Crustose corallines are rasped from the rocky substratum whereas the drift algae lie between and under boulders where they are captured by the abalone.

From about three years of age, both abalone species occur in higher densities in deeper water where they are presumed to migrate to feed on the preferred food - algae, which are abundant there as drift.

INTRODUCTION

The need to understand the recruitment process in commercial species of abalone has focused increasing attention on the ecology of juveniles. The food and feeding of juveniles is an important aspect of niche that has been little studied, and is also of increasing relevance in mariculture. The food of newly metamorphosed abalone larvae has been examined by Garland *et al.* (1984) and the availability of food on crustose coralline algae by Lewis *et al.* (1985). Other studies of juvenile feeding of abalone are by Tomita and Tazawa (1971), Leighton (1972) and Bucher (1984).

*Haliotis laevigata* Donovan and *Haliotis scalaris* Leach recruit onto crustose coralline algae on and under boulders at West I, and remain in the same micro-habitat for several years (Shepherd and Turner 1985, Shepherd in prep). Subsequently these abalone species move to less cryptic sites where they feed on drift algae (Shepherd 1973).
In this paper we describe the food eaten by juveniles of these abalone species at the study site at West I, South Australia (35° 37'S; 138° 35'E) where the earlier studies on their recruitment have been done (Shepherd 1973). A map of the site is given by Kangas and Shepherd (1984).

**MATERIALS AND METHODS**

The north shore of West I is a boulder slope with rounded boulders mostly of 30-40 cm greater diameter and 20-30 cm lesser diameter from 0.5 to 5 m depth. Sixty-one *H. laevigata* and 114 *H. scutaria* from 4-70 mm long were taken in October and November 1986 during diving dives. Each abalone was dissected and the contents of the digestive tract spread out onto a slide under a coverslip and examined under a binocular microscope (x20). A grid with 25 intersections was placed under the slide and the alga at each intersection was identified to species or species-group to give the relative abundance by volume of food alga. Algae were categorised as crustose corallines, filamentous algae, green, brown or red macro-algae and seagrass according to the functional group approach previously used at the site for other molluscan herbivores (Steneck and Watling 1982, Kangas and Shepherd 1984). The presence of crustose calcareous material in the gut contents was tested with dilute HCl. For macro-algae and seagrass it was possible in most cases to identify the taxon to species.

Densities of *H. laevigata* and *H. scutaria* were estimated by counting and measuring all individuals *in situ* in 36 to 40, 0.25m² quadrats placed haphazardly at 3, 4 and 5 m depths on the boulder slope at the study sites. Individuals were then aged by using the age-length curve derived for each species (Shepherd 1988, Shepherd et al. 1988). Drift algae were collected during the period at the same depths by qualitative and quantitative methods; the former covered the whole study site and were used to calculate the relative abundances of algal species with depth, and the latter (five replicates of 0.25 m² at each depth interval) to determine absolute abundances of algal drift. MeV's (1961) selectivity index (E) was calculated with the following formula:

\[ E = \frac{r - p}{r + p} \]

where \( r \) = the relative abundance of a prey item in the gut and \( p \) = the relative abundance of the same item in the habitat. A positive value indicates preference and a negative value avoidance. The index ranges from -1 to +1.

**RESULTS**

The proportional abundance of algal or seagrass species groups in the digestive tract of *H. laevigata* and *H. scutaria* grouped in 10 mm size classes is shown in Fig. 1. No individual <5 mm long was found to have macro-algae or calcareous fragments of crustose corallines in the gut. At 5-10 mm length the diet of both species is largely calcareous fragments of crustose coralline algae. From 10-22 mm length the abalone switch increasingly to a diet of erect algae and by 25-30 mm length crustose corallines are of little importance as food. From about 25-70 mm changes in the diet are minor for both abalone species. Comparison of the size diagrams in Fig. 1 shows high similarity in the diet between abalone species, except that *H. laevigata* to a length of 20 mm takes relatively more crustose coralline algae.

The seagrasses eaten (Fig. 1) are mainly dead blades of *Heterozostera tasmanica*, and occasionally *Posidonia sinuosa* or *Amphibolis antarctica*. Green macro-algae eaten are mostly *Caulerpa brownii*, brown macro-algae mostly *Lobosira bicuspida*, with a little *Pachydictyon paniculatum*, and red macro-algae mostly *Asparagopsis armata* with small amounts of *Placozoon* sp. 'Filamentous algae' are polyphylectic and include ectocarpoid species and *Polysiphonia* sp. Genculate corallines are mostly *Halimione portulacoides*, with lesser amounts of *Amphiroa anceps*, *Chetiakorum elegans* and *Jania* sp. Crustose corallines were not identified.

The mean relative percentage composition of drift algae at 3-5 m depth at the study site (Fig. 2) shows that, at the time of the study, red algae (mostly *Asparagopsis armata*) and species of brown macro-algae were the most common drift algae. The attached algal flora in the habitat is an upper
stratum of *Ecklonia radiata* and *Cystophora* spp. and a middle stratum largely of geniculate (erect) corallines (see also Kangas and Shepherd 1984).

Elasticity indices were calculated for the 5 groups of drift algae or seagrass consumed using the average proportion of each group consumed by each abalone species over the length range 20-70 mm at 4-5 m depth. The results (Fig. 2) show that the large brown macro-algae (*Ecklonia*, *Cystophora* spp. and *Sargassum* sp.) and to a less extent seagrass are avoided, red algae (both fleshly species and geniculate corallines) are taken more or less in proportion to their abundance, and *Lobosira*, a smaller brown alga, is strongly favoured.

The vertical distribution with depth of successive age classes of *H. scalaris* and *H. laevigata* (Fig. 3) shows that whereas densities of 0+ to 2+ age classes differ little over the depth range examined, the 3+ and older age classes of both species are in higher densities at 4 and 5 m depths.

**DISCUSSION**

The diet of individuals < 5 mm long could not be investigated by the methods used. However, Garland et al. (1985) and Norman-Bourdeau et al. (1986) have shown that abalone in the length range of 0.5 - 2.5 mm scrape the surface of crustose corallines and rasp the cuticle, consuming both epibiota (Lewis et al. 1985) and part of the epithelium. This study shows that from a size of about 5 mm the abalone radula must be able to penetrate more deeply and remove crustose material. Padilla (1985) demonstrated, contrary to earlier hypotheses (e.g. Steneck and Walling 1982), that less force is required by the radula to remove crustose coralline algae than macro-algae. Thus, until a length of at least 10 mm crustose coralline algae and their epibiota are the main source of food of these abalone and so provide a basis for their coralline habitat dependence earlier observed by Shepherd (1973), and Shepherd & Turner (1985).

The food algae eaten by these abalone could be obtained by rasping the rock surface or by catching drift algae. Of the 7 categories of food eaten (Fig. 1) only crustose corallines can be unambiguously concluded to have been taken by rasping. Crustose corallines are epiphytic on *Posidonia* and *Amphibolus* leaves, but the amounts of these seagrasses taken are negligible, and would at best account for only a small fraction of the coralline algae in the gut. Filamentous algae are variously epiphytic or epiphytic on drift seagrass, and could be taken by either mode of feeding. The remaining categories of food are only present as detrital drift.

Neither species of abalone have ever been observed to emerge at night on the upper surfaces of boulders, or to feed on or under boulders by day. However, we have observed while diving during a moderate swell that juveniles adopt the feeding posture (elevated shell and extended foot) described by Shepherd (1973) for adult abalone, apparently preferring to catch passively rather than search actively for food. Hence we conclude that at this site both abalone species from a length of 10-20 mm, feed largely on drift algae trapped between or under boulders. The dependence of both abalone species on drift algae may explain why their diets are nearly identical in species composition.

This study does not address the question of possible bias due to the effects of differential digestion of algae. Because coralline algae and seagrass may remain identifiable in the gut for a longer time than, for example, small pieces of filamentous algae, our results may under-estimate the importance of the latter. However, we sought to minimise such bias by ensuring that all collections were taken in morning dives.

A mixed algal diet in which corallines and red algae are important has been reported elsewhere. Bucher (1984) found that juvenile *H. rubra* fed and grew more rapidly on a diet of red algae than on either *Ecklonia* or *Sargassum*. Tomita and Tazawa (1971) found that *Haliotis discus hannai* in its first year ate corallines and the seagrass *Phyllospadix*, and in its second year a mixed diet of seagrass, *Dictyota* and numerous red algae. *H. laevigata* reaches a length of about 20 mm in one year, and *H. scalaris* about 14 mm (Shepherd et al. 1985, Shepherd, 1988) so that their shift in diet, as for *H. discus hannai*, occurs at about one year of age. An important difference, however, is that *H. discus hannai* also feeds on considerable amounts of animal matter in its first year.
The factors determining food selection are poorly known. Both chemical attractants and deterrents have been identified in algae (Harada and Kawasaki 1982, Harada et al. 1984, Steinberg 1984, 1985) but the role of each remains uncertain. The feeding rate of adult *H. laevigata* on the various available brown algae at West I. is inversely correlated with the phenolic levels of the species concerned (Shepherd and Steinberg in prep.) suggesting that the amount of phenolics in brown algae may be of importance in determining algal preferences.

The differential abundances of age classes of both abalone species over the depth range examined suggest either that animals migrate to deeper water with increasing age or that differential mortality or settlement has occurred. While these last two possibilities cannot be excluded, the most likely explanation is that older individuals move toward the sand line at 4.5 to 5 m depth; here the preferred drift food, *Lobospira*, a brown alga, *Asparagopsis* and other red algae, are in high abundance. Current experiments are testing this hypothesis.

ACKNOWLEDGEMENTS

Mr A.G.J. Mower assisted with the fieldwork and the Commonwealth Department of Community Services provided funds for the second author. Dr R.W. Day, Mr S.M. Clarke and anonymous referees improved the manuscript.

LITERATURE CITED


FIGURE 1  Proportional abundance of species groups in the digestive tract of (a) *H. laevigata* and (b) *H. scalaris* from 5-70 mm long. Horizontal bars give the standard errors for each size class. Note that the vertical scale from 0-20 mm length is exaggerated to show detail. The approximate age-class is shown on the right vertical scale.
FIGURE 2 Distribution with depth of 5 categories of drift algae trapped between and under boulders, and IVlev's selectivity index values for each group.

FIGURE 3 Distribution of density of five age classes of *H. scalaris* and four age classes of *H. laevigata* at the study site at West I. Standard errors are shown by symbols: 0.40 — 0.60 — squares; 0.25 — 0.40 — triangles; < 0.25 — circles.
CHAPTER 6

RECRUITMENT AND MORTALITY

Recruitment and mortality are two of the most important parameters of a population requiring measurement, and are the most difficult to obtain. This chapter proposes two relatively simple ways of measuring them.

Ideally, recruitment should be estimated as early as possible after larval settlement in order to minimise the effects of post-settlement mortality. However, the later it is left, the simpler it becomes (except of course when the cohort merges with previous year classes). At an age of 2 1/2-3 years, *H. laevis* begins to emerge from its under-boulder habitat and this is a convenient time to measure recruitment. It was shown in Ch 3 that at this age, the cohort is usually detectable as the initial mode in a length-frequency distribution resulting from an above-boulder census taken by a diver; this allows an estimation of its numbers in a census. Other necessary conditions are described below.

If it is also true, as suggested in Ch 4, that recruitment strength reflects settlement strength, then the value of the method is even greater, because it no longer becomes necessary to measure settlement at much greater cost in terms of diving time. Further, the historical data for about 16 years of recruitment would be of great value in an attempt to unravel the effect of environmental (pre-settlement) events on recruitment. There are hints that summer sea temperature anomalies influence settlement strength but the relationship is diffuse and it seems that, if involved at all, other as yet unknown factors must also be involved. The solution to this problem would in turn shed light on the elusive stock-recruitment relation.

Natural mortality is also difficult to measure. The method used by Shepherd et al (1982) employing a Cormack analysis is unacceptably demanding in terms of diving time over a number of years. The method proposed in this Chapter is much simpler and requires no tagging to be carried out. However, it does require a knowledge of the growth rate, and assumes a closed population.
Overall, the long-term study of recruitment and mortality, and the agents of mortality sheds light on the processes regulating a natural population. No stock-recruitment relation emerges from the study, but this may simply be because the stock size has never fallen below some critical level, or because of one or other of the reasons discussed below.

Future manipulative studies which artificially decrease (or increase) the presumed spawning stock and observe the effect on recruitment may be useful in better defining the relation between recruitment and stock.

Reference
STUDIES ON SOUTHERN AUSTRALIAN ABALONE (GENUS Haliotis) XI.

RECRUITMENT AND MORTALITY OF H. laevigata OVER 17 YEARS AT WEST ISLAND

WITH NOTES ON PREDATORS OF ADULTS

S.A. Shepherd

Department of Fisheries

135 Pirie Street

ADELAIDE South Australia 5000

RUNNING TITLE: RECRUITMENT AND MORTALITY OF H. laevigata

key words: Abalone, Haliotis, recruitment, mortality, population dynamics, predators, predator-prey interactions, density-dependent mortality, dead shell production.
ABSTRACT

The recruitment strength and natural mortality of an isolated, unfished population of the abalone *Haliotis laevigata* Donovan at West Island, South Australia, were estimated from 1970 to 1987. Recruitment, judged by the appearance of 2 year old abalone, varied widely from year to year but no evidence was found that estimates of spawning stock size was a significant variable contributing to this variability. During that period the population size oscillated up and down twice; the increases were due to successive years of strong recruitment and the declines to the dampening effect of density dependent mortality, which ranged from 0.02 to 0.86 per annum. The changing mortality rates were attributed to the behavioural response of stingrays to abalone densities.

Analysis of dead shells collected from the study site for 5 years indicates that stingrays may cause 70-94% of the total mortality of abalone 3 years and older, and octopuses, crabs and unknown causes the remainder.

INTRODUCTION

Although recruitment and mortality are principal mechanisms regulating the size of natural populations of animals, they are difficult to measure and hence are poorly understood among marine invertebrates and molluscs in particular. A knowledge of these mechanisms, and of the factors influencing them, is essential to establish guidelines for the management of exploited species. In this paper the term recruitment means the process in which the young abalone first become accessible to the research diver at an age of 2 1/2 - 3 years.

Studies to measure these parameters have usually been over a relatively short time so that their variability and density dependent effects (the latter often assumed) (Hancock 1973, Shepherd and Cushing 1981) have rarely been established.

The greenlip abalone, *Haliotis laevigata* Donovan is a sedentary species occurring along the southern Australian coast in disjunct populations which are exploited commercially mostly between 134° and 139° east longitude (Shepherd 1973). Spawning occurs from spring to autumn (Shepherd and Laws 1974) and the lecithotrophic larvae settle
mostly during summer after a brief planktonic stage, on crustose corallines on boulders in the same general area as adults (Shepherd 1973, Shepherd and Turner 1985). Juveniles are cryptic until they reach a length of 50-70 mm at an age of 3 years (Shepherd 1988) when they emerge from crevices into a more open habitat where they become more accessible to a diver.

This paper describes methods of estimating recruitment strength and adult mortality rates of a population of *H. laevigata* from sequential length frequency data, and gives estimates of these parameters for a closed population at West Island, South Australia, from 1970 to 1987. Dead shell production was measured at the site for 5 years and the agents of mortality inferred.

**MATERIALS AND METHODS**

**Field Measurements**

The study site extends for 60 m along the shore at the base of a boulder slope within the West Island marine reserve (35° 36' 25" S., 138° 35' 27" E.) where earlier studies in the series have been made. Unsuitable habitat at each end of the site prevents emigration from the area censused.

Censuses of *H. laevigata* were made by the author and assistant at intervals of 2 to 5 months (with a few longer gaps) from November 1970 to 1988. The diver moved carefully over the whole area and measured all accessible individuals. Because densities of *H. laevigata* were very low outside the study site, the census included the bulk of the population. Before 1978 measurements were made with a vernier caliper, and the data written on a slate, but after that the diver used a gauge which impressed on a plastic strip each datum on length (Shepherd 1985), with considerable saving of time underwater.

Variability in census data is due largely to the variable water turbidity. Turbidity decreases distance of sight and decreases contrast, and may also affect the orientation of the diver (Marcotte and Browman 1986). Where visibility declined below 1.5 m data were excluded and the census repeated.
Recruitment

The recruitment of 2+ year old animals was estimated from the census data obtained between May and December each year. The MIX interactive computer programme (MacDonald and Pitcher 1979) was used to fit and separate modes of length-frequency distributions. The procedure fitted Gaussian component distributions and used maximum likelihood methods to separate them. The 2+ cohort is approximately 40-60 mm long at 2 1/2 years of age (Shepherd 1988). Because censuses did not record individuals < 40mm long this cohort could only be censused between about May and December each year when it had grown past 40 mm length. Modal fits were generally satisfactory for the 2+ cohort, but success at distinguishing older cohorts was variable (Shepherd 1988). Where recruitment strength in successive years was markedly disparate or poor, modes for the 3+ cohort either merged with the older or younger cohort or were absent altogether.

To determine the relationship between numbers of the 2+ cohort found in a census and the total size of the cohort, tagging experiments were carried out in different years to obtain Peterson estimates of cohort size.

Where a number of marked abalone (T) are released and there are n sightings in a later census of that cohort of which m are tagged, then the size of the cohort (N) is

\[ N = \frac{T \cdot n}{m} \]

and the standard error is

\[ s.e.(N) = \left( \frac{T^2 n(n-M)}{m^3} \right)^{1/2}. \] (Bailey 1951, Pauly 1984).

In these tagging experiments a number (12-26) of 2+ year old animals was marked and released throughout the study site in 9 experiments between May and October of 1972, 1973 and 1985-7. After allowing 2 months for adequate mixing of marked and unmarked individuals, a second census of the site was carried out and the values of n and m determined.
Fig. 6.1 - Sighting probabilities of *H. laevigata* marked at age 2 years during censuses of the study site at West Island.

The number shown against each datum indicates the total number at that age known to be alive.
Mortality

Due to the problems of fitting modes to length-frequency distributions discussed above the 3+ cohort and older age classes were separated from the 2+ cohort by knife-edge separation (Hancock 1965), in the light of the known growth curve for this species (Shepherd 1988). The cut off point was chosen at 65 mm for the 3+ age class (June census) increasing monotonically to 90 mm one year later. The natural logarithm of all individuals > 3 years of age was regressed against time to give a slope of \(-M\), the natural mortality rate (Gulland 1969). The annual period selected was from the May or June census of each year to that 12 months later. One assumption of the method is that each age class is equally available to the diver. This was tested by examining the probability of encounter of marked individuals aged from 3 to 6 years.

A sub-set of tagging data from Shepherd et al. (1982) together with some later data, consisting of animals tagged at 2 years of age were examined and sighting probabilities in censuses obtained (Fig. 1). This was done simply by summing the number of times tagged individuals of a given age were sighted during censuses and dividing the result by the number of censuses those tagged individuals were known to be alive. For this purpose a tagged animal was assumed to have died immediately after the last census in which it was recorded.

The mean sighting probability was 0.346 from ages 2 1/2 to 3 1/4 with a sudden increase to a mean value of 0.624 for older age classes; the two mean proportions were significantly different (P<0.001). Sighting probabilities did not change significantly (determined by regression of proportions on age, using transformation of \(y^\prime\) to \(\arcsin \sqrt{y^\prime}\)) after 3 1/2 years of age, so that the assumption of equal availability is met. However, because the first datum in each set was from the May or June census that included animals < 3-1/2 years old it was necessary to weight the numbers of this year class to offset its lower availability. It was assumed that the probability of encounter increased linearly from 0.346 at age 3 1/4
Fig. 6.2 - Length frequency distributions of *H. laevigata* marked at age 3 years and surviving to 5 years of age. S.D. = standard deviation.
years to 0.624 at 3 1/2 years for the purpose of calculating the
weighting ( = 0.624 where p is the probability of encounter for a
given census during the period 31 March to 30 June).

A second assumption of the method is that the growth rate of
individuals is approximately uniform. If growth were highly variable
then a knife-edge selection might exclude the slowest growing 3 year
olds or include fast growing 2 year olds and so introduce bias.
Plots of length frequency distributions of individuals marked at 3
years of age and surviving to 5 years of age (a subset of data from
Shepherd and Hearn 1983) are shown in Fig. 2. Standard deviations
increase only slightly from 3 to 4 years of age, so this assumption
seems to be satisfied. Other assumptions are that mortality is
independent of age and constant over the time interval chosen. The
former of these is met (Shepherd et al. 1982). As to the latter it
is likely that natural mortality is higher during summer and autumn
than in winter and spring (unpublished data). If this is so a linear
regression may over-estimate the mortality rate. The bias, however,
is likely to be small compared with the variability inherent in the
technique.

Shell Production

In December 1981 all accumulated shells and shell fragments of H. 
lazyigata were removed from the study site, and thereafter until June
1987 at about bi-monthly intervals, deposits of fresh shell and
fragments were collected. 'Old' shell, characterised by a dull inner
surface and often encrustations, were occasionally exposed above the
sand and were removed but not included in the counts.

Shells were measured and examined for breakage patterns. Only those
parts of the shells with a body whorl were included for determination
of dead shell production; their length was estimated in 10 mm size
classes by reference to a standard set of shells. Shells were
classified as (1) unbroken, (2) with chipped edges and (3) broken.
Fig. 6.3 - Length frequency distributions of *H. laevigata* from November 1970 to September 1987.
The potential shell production of individuals ≥ 65 mm long (i.e., 3 years old and older) was estimated by subtracting the number of individuals alive at the end of each annual period from those alive at the beginning. These were calculated from the regressions from which mortality rates were obtained (Fig. 4) and the results were then divided 0.624, the sighting probability of individuals > 3 1/2 years old (Fig. 1), which is equivalent to the censusing efficiency of the diver.

Biomass

In this study abalone biomass is used as an index of potential total number of eggs produced, because fecundity is linear with weight (Shepherd and Hill 1988). The biomass of individuals in different size classes was calculated by converting numbers in each length class (from length-frequency data) to weight by using the equation derived by least squares linear regression analysis for *H. laevisagata* at West Island.

\[ W = 0.045 L^{3.41} \quad (N = 34; r^2 = 0.95) \]

where \( W \) = total weight in g and \( L \) = shell length in cm. The population size in 1976 was not known directly, but was extrapolated from the 1977 census by using the mean mortality rate calculated for the period 10.vi.75 to 21.ix.77.

RESULTS

Length frequency distributions resulting from the censuses, numbers of adults (here defined as those > 3 1/2 years old), and number of recruits (2 1/2 - 3 years old) from November 1970 to June 1987 are given in Figs. 3,4.

The changes in adult population size over time are most usefully shown by a Ricker plot of the logarithm of current adult population size against that one year earlier. A Ricker plot for the adults of this population (at the time of each mid-year census) is shown in Fig. 5. The diagonal line represents the equilibrium point when the population is constant. The adult population increased in numbers after 1970 (when fishing for abalone ceased) and since then has gone through one complete, and a second incomplete, cycle. The processes causing these changes, recruitment and mortality, are described below.
Fig 6.4  Plots of numbers of adult (> 3 1/2 years old) H. laevigata from November 1970 to June 1987. Regression lines are given for each annual period. Recruitment strength (R) at age 2 1/2 - 3 years is shown by the vertical bars. Lines = standard errors. Absence of standard errors indicates that they were greater than the recruitment value itself, or, by reason of some constraint, were not given by the programme (MacDonald & Pitcher 1979).
Recruitment

Numbers in the 2+ cohort were generally highest in the mid-year (May-June) census, and declined later in the year as the effects of mortality became apparent. The mid-year census was therefore accepted as the best and earliest estimate of a recruitment index of the population. The Petersen estimates of total 2+ cohort size ($\hat{N}$) show a near-linear relation between 'n', the number in the cohort recorded in a census, and $\hat{N}$ (Fig. 6). These estimates were obtained at different times and in different conditions of swell and visibility and demonstrate that the proportion of the cohort available to a diver is independent of environmental factors and density.

Further, there is no tendency for proportionately more recruits becoming available to a diver at high densities, as might be expected if abundance of crevices was a limiting resource.

Recruitment strength was highly variable with peaks occurring during the periods 1971-73 and 1980-83 (see Fig. 4). A plot of recruitment strength against the biomass of individuals > 110 mm long (the length at which aggregation of spawning adults begins - see Shepherd (1986)) (Fig. 7) shows no significant relationship and gives no hint of the shape of the stock-recruitment curve.

ADULT MORTALITY

Annual instantaneous mortality coefficients and their standard errors are given in Table 1 for 1970 - 1987. Plots of the decline in numbers of all age classes > 3 1/2 years combined for approximately annual periods, are given in Fig. 4. These mortality rates were compared with those obtained from the analysis of sightings of marked individuals for two overlapping periods (Table 2) from Shepherd et al. (1982). The two data sets are independent because marked individuals were taken from outside the study site and were not included in the censuses. Although the estimates cannot be compared by formal statistics the overlap of standard errors indicates there is no significant difference between them. There is the obvious caveat, however, that estimates with wide standard errors and those for the years when there were few censuses (eg. 1975-77) should be accepted with caution.
Fig. 6.5 - Plot of Petersen estimates of total size ($\hat{N}$) of 2+ age class vs $n$, the number of sightings per census of individuals in the same age class.

$N = -6.8 + 3.02n$

$R^2 = 0.99$
A plot of annual mortality rates against the number of the 3+ and older age classes at the beginning of each period examined (Fig. 8) shows a significant correlation ($r = 0.617; P<0.01$) and suggests that the mortality rate is density dependent.

**DEAD SHELL PRODUCTION**

A total of 698 shells, excluding old ones, was removed from the study site over the 5 1/2 year period January 1982 to June 1987. Broken shells accounted for 66% of the total, unbroken shells 23% and those with chipped edges 11%. The size distribution of shells in these categories is shown in Fig. 9. Broken shells are mostly in the length range 60-160 mm and are the result of attack by the rays *Dasyatis brevicaudata* (Hutton) and *Myliobatis australis* (Macleay) (Shepherd 1973). It is common for shells to be broken into many fragments by these rays and in the only two observed attacks the ray swam off with the abalone onto sandy bottom and consumed it there. Hence some loss of shells from the area through stingray attack is likely.

The causes of mortality resulting in intact shells are uncertain. The sea-star *Coscinasterias calamaria* (Gray) leaves undamaged shells, but it is rare at West Island and predation by it on *H. laevigata* has never been observed. The octopus, *Octopus flindersi* (Cotton) is a known predator (Shepherd 1973), but it does not appear to drill a hole, as is typical of other octopus species (personal observations of attacks, and see Pilson and Taylor (1961), Ambrose and Nelson (1983)). Hence the occurrence of intact shell, although probably a result of its predation, cannot be unambiguously attributed to it.
Fig. 6.6 - Sequential Ricker plot on a logarithmic scale of $N_{t+1}$ vs. $N_t$. The diagonal represents the equilibrium point.
TABLE 1 - Annual mortality coefficients of *H. laevigata* and the periods for which they were calculated.

<table>
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<tr>
<th>PERIOD</th>
<th>NUMBER OF DAYS</th>
<th>M</th>
<th>s.e.</th>
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<tr>
<td>4.11.70 - 2.7.71</td>
<td>238</td>
<td>0.37</td>
<td>0.23</td>
</tr>
<tr>
<td>2.7.71 - 11.7.72</td>
<td>374</td>
<td>0.02</td>
<td>0.09</td>
</tr>
<tr>
<td>11.7.72 - 29.5.73</td>
<td>322</td>
<td>0.36</td>
<td>0.18</td>
</tr>
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<td>29.5.73 - 29.5.74</td>
<td>365</td>
<td>0.54</td>
<td>0.08</td>
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<td>29.5.74 - 10.6.75</td>
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<td>0.86</td>
<td>0.34</td>
</tr>
<tr>
<td>21.9.77 - 27.5.78</td>
<td>249</td>
<td>0.35</td>
<td>-</td>
</tr>
<tr>
<td>27.5.78 - 24.8.79</td>
<td>454</td>
<td>0.54</td>
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<td>24.8.79 - 8.7.80</td>
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<td>340</td>
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<td>0.22</td>
<td>0.11</td>
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<tr>
<td>29.5.86 - 24.6.87</td>
<td>391</td>
<td>0.32</td>
<td>0.13</td>
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TABLE 2 - A comparison between mean annual mortality estimates given by Shepherd et al. (1982) for marked *H. laevigata* (aged 3 years and over) and this paper for unmarked *H. laevigata* aged 3 1/2 years and over at West Island. Standard errors are in brackets.

Shepherd et al. (1982)

<table>
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<th>PERIOD</th>
<th>CORMACK (1964) METHOD</th>
<th>SANDLAND &amp; KIRKWOOD METHOD</th>
<th>THIS PAPER</th>
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<td>Nov. 1970 - Apr. 1974</td>
<td>0.26 (0.06)</td>
<td>0.28 (0.03)</td>
<td>0.31 (0.12)</td>
</tr>
<tr>
<td>Nov. 1970 - Jan. 1975</td>
<td>0.38 (0.17)</td>
<td>0.38 (0.04)</td>
<td>0.39 (0.16)</td>
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</tbody>
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Fig. 6.7 - Plot of recruitment strength vs biomass (kg) of spawning population (> 110 mm long) at West Island for period 1971-1985.
<table>
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<td>Stingray sightings</td>
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<td>11</td>
<td>4</td>
<td>9</td>
</tr>
<tr>
<td>Octopus sightings</td>
<td>1</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>No. whole shells found</td>
<td>30</td>
<td>15</td>
<td>44</td>
<td>20</td>
<td>6</td>
</tr>
<tr>
<td>No. broken and chipped shells found</td>
<td>71</td>
<td>92</td>
<td>126</td>
<td>47</td>
<td>95</td>
</tr>
<tr>
<td>TOTAL</td>
<td>101</td>
<td>107</td>
<td>170</td>
<td>67</td>
<td>101</td>
</tr>
<tr>
<td>Maximum shell production</td>
<td>159</td>
<td>204</td>
<td>223</td>
<td>67</td>
<td>104</td>
</tr>
<tr>
<td>No. shells lost from site</td>
<td>58</td>
<td>97</td>
<td>53</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Maximum no. taken by rays</td>
<td>129</td>
<td>189</td>
<td>179</td>
<td>47</td>
<td>98</td>
</tr>
<tr>
<td>%</td>
<td>91</td>
<td>93</td>
<td>80</td>
<td>70</td>
<td>94</td>
</tr>
</tbody>
</table>
Fig. 6.8 - Plot of annual mortality rates of H. laevigata for the periods set out in Table 1 vs the number of individuals 3 1/2 years of age at the beginning of each such period.
Recruitment

Numbers in the 2+ cohort were generally highest in the mid-year (May-June) census, and declined later in the year as the effects of mortality became apparent. The mid-year census was therefore accepted as the best and earliest estimate of a recruitment index of the population. The Petersen estimates of total 2+ cohort size (\(\hat{N}\)) show a near-linear relation between \(n\), the number in the cohort recorded in a census, and \(\hat{N}\) (Fig. 6). These estimates were obtained at different times and in different conditions of swell and visibility and demonstrate that the proportion of the cohort available to a diver is independent of environmental factors and density.

Further, there is no tendency for proportionately more recruits becoming available to a diver at high densities, as might be expected if abundance of crevices was a limiting resource.

Recruitment strength was highly variable with peaks occurring during the periods 1971-73 and 1980-83 (see Fig. 4). A plot of recruitment strength against the biomass of individuals > 110 mm long (the length at which aggregation of spawning adults begins - see Shepherd (1986)) (Fig. 7) shows no significant relationship and gives no hint of the shape of the stock-recruitment curve.

Shells with chipped edges are mostly in the length range 30-80 mm. This kind of damage has usually been attributed to crabs (Cox 1962, Kojima 1981, Tegner and Butler 1985), but Mower and Shepherd (1988) showed that although there are 4 crab species at West Island that can take abalone and typically chip the shell's edges during capture, abalone > 40 mm long are unlikely prey. It is considered that shells > 50 mm long in this category are taken by rays.

Shells < 50 mm length are poorly represented in the collection of shells. This is because major predators of this size group are wrasses (unpublished data; Shepherd and Turner 1985) which crush and ingest the shell. In order to quantify the extent of predation by stingrays on this abalone, the number of shells lost from the study site must be estimated. It is assumed that this loss is due to stingray attack. Table 3 gives the estimated maximum shell
Fig. 6.9 - Length frequency distribution of dead shell collections of *H. laevigata* from the study site from 1982-87.
production at the site (see Methods), the actual numbers of shells (whole and broken) found, and by subtraction the estimated number of shells lost. These are then added to the numbers of broken shell found to give an estimate of the maximum numbers taken by stingrays. During the period 1982 - 1987 between 70% and 94% of individuals > 3 1/2 years old were estimated to be taken by stingrays. The size distribution of dead shells (Fig. 9) for 1982-87 differs significantly from the size distribution of live animals, obtained by averaging all censuses taken during the same period (Kolmogorov-Smirnov test comparing the two distributions - D = 0.33; P<0.01), suggesting that mortality is relatively more intense on larger than on smaller abalone. However, an assumption of this conclusion is that differential loss of shells between size classes does not occur. There is no known explanation why the number of shells estimated to have been lost from the study site was high in the first 3 years but negligible in the last 2 years.

Hines and Pearse (1982) used annual shell production figures to estimate the natural mortality of abalone. For this to be possible for species like *H. laevigata* where loss of dead shell occurs, it would be necessary to estimate independently that loss.

**SIGHTINGS OF PREDATORS**

All sightings of stingrays (with estimates of their size) and octopuses during dives were recorded from July 1982 to June 1987. Stingrays were known to rest in certain caves near the study site and these were inspected on each dive. Octopuses did not occupy specific caves or middens and sightings were chance encounters. The number of sightings of these predators (Table 3) were few in 1982-83 but peaked in the following year and then decreased.

The cumulative number of stingrays seen annually was significantly correlated with the maximum shell production (mortality presumed due to stingrays) (Spearman Rank, $r_s = 0.9; P = 0.05$) but the number of octopuses seen was not correlated with the number of whole shells found. Thus sightings of stingrays appear to be a crude measure of intensity of predation by them. The occurrence of whole shells probably represents octopus predation and other unknown causes.
DISCUSSION

Recruitment

Variability in recruitment is common among many marine invertebrates (Hancock 1973) and the few long term studies on abalone populations suggest this is also true for them. Forster et al. (1982) monitored the population size of *Haliotis tuberculata* L. from 1968-1980 and found a marked long term decline in numbers. They related this and earlier historic declines to summer sea temperature anomalies affecting recruitment. Kojima et al. (1978) observed fluctuations of 6 to 12 year intervals in the catch of *Haliotis discus discus* Reeve over 70 years. Sainsbury (1982 a,b) found heavily skewed length frequency distributions of *Haliotis iris* Martyn and suggested that population size fluctuations occurred because a sporadic good recruitment was followed by long periods of poor recruitment. Tegner et al. (1988) found high variation in recruitment of *Haliotis rufescens* Swainson in a 5-year study. Conversely Hines and Pearse (1982) reported stable populations of *H. rufescens* and *H. waldilensis* Stearns from 1972-1981 with constant mortality and recruitment rates.

The absence of any clear relationship between recruitment and size of the presumed parent stock does not imply that none exists, which is not credible. It is possible that (1) the measure of the spawning stock at West Island is in error (Walters and Ludwig 1981) or (2) that recruitment is a poor measure of settlement strength due to density dependent mortality of pre-recruits (see Connell 1985), or (3) that pre-settlement events play a dominant role in determining settlement strength. Upon the first possibility Prince et al. (1987) provided evidence of a relation between local stock size and recruitment. The population of *H. laevigata* is some 15-20 km from neighbouring populations, so it is likely that the spawning stock at West Island is the principal source of recruits. In support of this the West Island stock is genetically distinct from that at Cape Jervis 30 km west (L. Brown pers. comm.). Even so, the effective spawning stock size is uncertain.
*H. laevigata* at West Island attains sexual maturity at 100 mm length (Shepherd and Laws 1974) but aggregation for spawning does not begin until it is 110 mm long or attain a maximum until 120 mm long (Shepherd 1986). Because fertilisation success declines exponentially with distance between spawning individuals (Pennington 1985) the effective spawning stock may be only larger aggregated individuals. Only a stock size calculated with a cut off point at 110 mm length is plotted here but other cut off points (100 mm, 120 mm) were tried and made little difference to the results.

Upon the 3rd possibility, Hancock (1973) in his review of marine invertebrates concluded that pre-settlement events played a paramount role in determining settlement strength. Later studies or reviews (eg. Butler and Keough 1981, Underwood and Denley 1984, Caffey 1985, Connell 1985) have all emphasized the unpredictability of recruitment and there still appears to be no published evidence of any stock recruitment relationship between density of adults and number of recruits for any mollusc (see Underwood 1979), Forster et al. (1982) and Shepherd et al. (1985) both suggested that below average summer sea temperatures may reduce settlement strength of abalone species but the data do not support this hypothesis for *H. laevigata* at West Island. The role of sea temperature and other pre-settlement events can only be adequately investigated when quantitative data on settlement or the early post-settlement stage (eg. Shepherd and Turner 1985) are available for a number of years.

**Mortality**

The mortality rates observed have shown far greater variation than has previously been reported for abalone species, but no other studies have been conducted for such an extended period of time. High mortality rates are given for abalone species by Tutschulte (1976), Doh et al. (1977) Van Sickle (1977) and Hines and Pearse (1982) and low rates (< 0.25) by Beinsson and Powell (1979), Breen (1980), Sainsbury (1982a) and Tegner et al. (1988). Variability in mortality rates between years may be more wide-spread than has previously been supposed.

The data on dead shell collections suggest that mortality is biased toward the larger size classes, possibly because large shells are weakened by boring sponge (*Ciona*) attack (Shepherd 1973), although
Shepherd et al. (1982) found no significant age dependence. Further studies on both young and very old abalone are needed to elucidate this problem.

The correlation between adult density of abalone and the natural mortality rate may be a density dependent effect, and three hypotheses can be advanced to explain the mechanism. They are:

1. competition for food,
2. competition for shelter, or
3. a predator-prey interaction.

Hypothesis (1) is rejected because there is no evidence that food is limiting. Drift algae are abundant throughout the year, usually in masses up to 1 m high. Only during prolonged calm periods are they temporarily unavailable to abalone (Shepherd 1973).

Hypotheses (2) and (3) cannot be rigorously separated and may interact. Stingrays are the major predator, but can only take individuals resting wholly or partly in the open. They do not have access to the crevice refuge where a few large, but mostly smaller abalone occur (Shepherd 1973). At high population densities relatively more abalone might be vulnerable to predation by rays (Hypothesis (2)). But because more individual rays were seen during the years of higher abundance, rather than simply the same few individuals being seen more often, it follows that predator density must have changed with prey density. A high hunting success rate may have induced more visiting rays to remain in the vicinity (see Curio 1976) as implied by Hypothesis (3). Thus Hypothesis (3) alone or with Hypothesis (2) is the most satisfactory explanation for the apparent dependence of the mortality rate on density.

**Management Implications**

This isolated, unfished abalone population has shown a surprising resilience during the 17 year study. Two pulses of strong recruitment 8-9 years apart have caused rapid growth of the population, but the strongly density dependent mortality rate has dampened the oscillations and kept the population within stable limits. How do these results relate to exploited populations of abalone? First, if predator behaviour is the correct mechanism for the density dependent regulation of population size, as inferred by
this study, then it is likely that in a fished population the natural mortality rate would be lower and would fluctuate less, because of the much lower densities to which abalone are fished down. Natural mortality coefficients of 0.2 - 0.3 recorded early in this study, when numbers were low, may be more applicable to exploited populations than the higher values recorded at higher abalone densities.

Second, the erratic recruitment patterns with sequences of good and bad recruitments reinforces earlier suggestions (Sainsbury 1982 a,b) that abalone populations are inherently unstable, and fisheries on them prone to recruitment overfishing. A feature of most, if not all, pristine abalone populations is their top heavy size distributions (accumulations of old animals) and high densities, sometimes 50-100 times those of fished populations. Such high densities no doubt provide resilience in natural populations in the face of prolonged recruitment failures.

May (1981, 1985) shows that as fishing intensity increases in a natural population "the influence of environmental noise (and therefore the unpredictability of next year's catch) increases". Thus, as an abalone population is fished down fluctuations in catch resulting from irregular recruitments would become more evident. This combination of heavy fishing and the unpredictability of recruitment may underlie the recorded collapses of many abalone fisheries (Breen 1986, Harrison 1986, Tegner et al. 1988).

The maintenance of an appropriate minimum size alone, as advocated by Harrison (1986) may not provide enough protection against recruitment failure (Breen 1986) and it may be necessary to use additional measures, such as quotas and prolonged closures (Sluczanowski 1986) to maintain egg production and ensure adequate recruitment in the long term.

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helpful comments on earlier drafts of this manuscript. Part of the study was supported by the Fishing Industry Research Committee.

REFERENCES


CAPTIONS TO FIGURES

Fig. 6.1 - Sighting probabilities of *H. laevigata* marked at age 2 years during censuses of the study site at West Island. The number against each datum is the sample size.

Fig. 6.2 - Length frequency distributions of *H. laevigata* marked at age 3 years and surviving to 5 years of age. S.D. = standard deviation.

Fig. 6.3 - Length frequency distributions of *H. laevigata* from November 1970 to September 1987.

Fig. 6.4 - Plots of numbers of adult (≥ 3 1/2 years old) *H.* from November 1970 to June 1984. Regression lines are given for each annual period. Recruitment strength (R) at age 2 1/2 - 3 years is shown by the vertical bars. Lines = standard errors. Absence of standard errors indicates that they were greater than the recruitment value itself, or, by reason of some constraint, were not given by the programme (MacDonald & Pitcher 1979).

Fig. 6.5 - Sequential Ricker plot on a logarithmic scale of $N_{t+1}$ vs. $N_t$. The diagonal represents the equilibrium point.

Fig. 6.6 - Plot of Petersen estimates of total size ($\hat{N}$) of 2+ age class vs $n$, the number of sightings per census of individuals in the same age class.

Fig. 6.7 - Plot of recruitment strength vs biomass (kg) of spawning population (≥ 110 mm long) two years before for period 1971-1985 at West Island.

Fig. 6.8 - Plot of annual mortality rates of *H. laevigata* for the periods set out in Table 1 vs the number of individuals ≥ 3 1/2 years of age at the beginning of each such period.

Fig. 6.9 - Length frequency distribution of dead shell collections of *H. laevigata* from the study site from 1982-87.
CHAPTER 7

FECUNDITY

Management of abalone fisheries has hitherto placed exclusive reliance on yield-per-recruit analyses that seek to maximise biomass yield and assume uniform recruitment. The collapse of numerous abalone fisheries around the world, and the collapse of some minor stocks in South Australia have cast doubts on the belief that abalone stocks, in which females produce a large number of eggs, are insensitive to recruitment over-fishing. Sluczanowski (1984, 1986) and Breen (1986) have suggested that a collateral goal of management should be to maintain high levels of egg production in exploited populations (at the cost of some production) in order to maintain resilience in the face of environmental uncertainty. Determination of the factors that control abalone populations includes a description of the egg production function (Ch.1) and its variability. This paper describes fecundity weight relations for a number of abalone stocks and explores the factors that may contribute to their variability.

References


STUDIES ON SOUTHERN AUSTRALIAN ABALONE (GENUS HALIOTIS)

XI ADAPTIVE SIGNIFICANCE OF DIFFERENT FECUNDITIES AND SEX RATIOS OF H. LAEVIGATA

by

S A SHEPHERD AND K HILL

Department of Fisheries
135 Pirie Street
ADELAIDE 5000

SUMMARY

Fecundity and sex ratios of Haliotis laevigata Donovan were examined at a number of sites in South Australia. Linear regressions of fecundity on weight gave satisfactory fits to the data for all sites.

At two sites, stunted sub-populations had lower relative fecundities than sub-populations with normal growth, and transplants between two sub-populations verified that fecundity was subject to environmental control.

The proportional allocation of resources between investment in egg production and in growth, determined for each site, was found to vary between them. The hypothesis is proposed that sites constitute in varying degrees, larval traps according to their individual coastal configurations, and that relative investment in egg production varies inversely with the efficiency of such traps.

Sex ratios show a linear dependence on size at most sites. At four sites the proportion of females increases with increasing size, at two other sites there is the opposite trend and at one site the sex ratio is equal. Changing sex ratios are considered to be a consequence of differential growth between sexes and an expression of sexual differences in allocation of resources between egg production and growth.
Fig 7.1 Map of South Australia showing sampling sites.
INTRODUCTION
The fecundity of a species is an important life history trait that has co-evolved with other life history traits to provide the optimal tactic for a species in a given situation. Energy available as food to an individual must be shared between the competing demands of reproduction, growth and maintenance. The interactions and trade-offs that occur between these demands are reviewed by Stearns (1976, 1977) who described models that predict under what conditions reproductive effort (fecundity) is less than the maximum possible.

There is also the problem of distinguishing phenotypic variation within a population, arising from environmental factors (eg food supply) which may obscure genotypic differences (Grahame and Branch 1985).

Here we consider the fecundity of an abalone species at a number of sites, and at one site in different years, and differences in sex ratios between sites. Our purposes are:

1. to describe the relation between fecundity and weight.
2. to compare the allocation of resources between reproduction and growth by different populations and sub-populations in order to understand how they might relate to environmental conditions.

Because the fecundity and sex ratios of abalone in different conditions have not previously been published we propose an explanatory hypothesis for the allocation of resources between reproduction and growth as a focus for future studies.

The exploited abalone *Haliotis laevigata* Donovan is a K-selected species (Stearns 1976) which shows iteroparity, has a delayed first reproduction, a relatively long life and low mortality. It produces a large number of eggs hatching into lecithotrophic larvae which are planktonic for a short time before settling in suitable habitat (Shepherd and Turner 1985).
Fig 7.2  Map of Fleurieu Peninsula (above) with populations of *H. laevigata* indicated by arrows, and West Island (below).
Fig 7.3

Map of Tiparra Reef and locations sampled; inset shows distribution of *H. leevigata* in eastern Spencer Gulf.
Site Descriptions (Fig 1).
Sites were selected to show the widest possible range of environmental conditions, and locations within sites to reflect wide differences in food supply, and at the same time to be representative of the major fishing grounds for this abalone.

West L (Fig 2).

H laevigata occurs on the northerly side of the island, where a boulder shore meets the sand at 5m depth. Samples were taken from Abalone Cove where abalone densities are highest and algal food is abundant, and from Restless Point where densities are low, food algae scarce and individuals stunted (Shepherd 1973). Tidal currents flow east and west with a maximum tidal excursion of about 5km.

Tiparra Reef (Fig 3).
Rocky bottom of low relief interspersed with sandy areas colonised by seagrasses (mostly Posidonia spp and Amphibolis spp) occur over about 30km². Tidal currents flow generally north and south with a maximum tidal excursion of about 10km. Samples were taken from:

(a) South Bottom at 10m depth dominated by Sargassum spp with some Ecklonia. Food algae are sparse and populations of H laevigata sparse and stunted.
(b) Lighthouse Reef, described by Shepherd (1973) at 5m depth. Food algae may be seasonally in short supply.
(c) Coal Reef at the foot of a drop off where large quantities of food algae accumulate. H laevigata is abundant.

Abalone divers fish Coal Reef heavily, Lighthouse Reef lightly and South Bottom rarely if at all. The legal minimum length is 130mm.

Waterloo Bay (Fig 4).
Waterloo Bay is a partly enclosed Bay partially cut off from the open sea by a barrier reef (Shepherd and Womersley 1981). The sample was taken from the centre of the Bay where H laevigata and its food algae are abundant (Shepherd and Hearn 1983).
Fig 7.4 Islands of the Investigator Group, eastern Great Australian Bight and adjoining mainland with Waterloo Bay.
The Investigator, Group (Fig 4).
Ward 1 and Pearson 1 are isolated Islands and Hotspot an emergent reef; they are separated from each other by 10-40km distance. H. laevigata occurs in the sheltered lee sides of each. Detailed site descriptions are given by Shepherd and Womersley (1971) and Branden et al (1986).

MATERIALS AND METHODS

H. laevigata spawns synchronously from October to March (Shepherd and Laws 1974). Samples were collected for analysis in 1981, 1982 or 1985 between August and October, prior to the commencement of spawning when ova are large and rounded. Shell length and total weight (TW) were recorded for each female and the ovary and visceral mass excised and preserved in 10% formalin and sea water until firm.

After separation from the viscera, the ovary was weighed, subsamples of 1-4mg from its anterior, middle and posterior parts were taken and weighed to the nearest 0.1mg and the number of ova in each subsample counted with the aid of a grid under a low power binocular microscope. The mean egg weight was calculated and by simple proportion fecundity (the number of eggs per individual) estimated.

Transplant experiments were carried out at West 1 on 9th February 1985. Large females were marked underwater in Abalone Cove with plastic tags attached to the shell by wire through two adjacent proximal pores and translocated underwater to Restless Point some 300m west. Controls were marked and moved to different rocks within each site. Back-transplants (with controls) were done on the same day. Surviving transplants and controls were recovered on 2nd October 1985 and fecundity determined in the described manner.

Gonad indices in addition to fecundity were obtained for all females >130mm long in 1985 using the method described by Shepherd and Laws (1974). Briefly, the conical appendage was sectioned and the area of gonad (A) and digestive gland (G) measured, and Gonad Index (GI) calculated with the formula \( GI = 100A/(A + G) \).
Fig 7.5

Plots of fecundity versus weight with linear regressions for *H. laevigata* at various sites and locations within sites. Note differences in vertical scales. The regression for Coal Reef (Tiparra) is intermediate in slope between those of the other two locations and is omitted for the sake of clarity.
Population sex ratios were determined from samples collected by research staff or from examination of catches of commercial divers, during August or September when individuals can be sexed visually (Shepherd and Laws 1974). For each sample, sex ratios were obtained for successive 20 (in one case 30) mm size classes and Cochran's (1954) test used to test for a significant change in sex ratio with length.

Growth parameters of the von Bertalanffy growth curve for Restless Point, West 1, and for Ward 1 were calculated, using the method described by Shepherd and Hearn (1983), from growth increment data from individuals at liberty from 364 to 370 days. There were 32 data points for Restless Point and 56 for Ward 1.

Length frequency data for various sites were obtained during routine annual censuses of the sites.

Statistics
Linear regressions of fecundity on total weight were fitted to the data sets using BIOSTAT computer package. The slopes of the linear regressions are measures of relative fecundity (Bagenel 1973) and were used in analyses of covariance to compare relative fecundities between populations at different sites and in different years. An assumption of this analysis is homogeneity of residual variances (Snedecor and Cochran 1980, p 385). The Waterloo Bay data and the South Bottom (Tiparra Reef) data did not meet this assumption because the range of x-values was much less than the data with which a comparison was sought; they were accordingly excluded from the comparisons.

RESULTS
Linear regressions of Fecundity on weight were found to give satisfactory fits to the data. The regressions and data are plotted in Fig 5 and the parameters of the regressions given in Table 1. The slopes of the regressions are measures of relative fecundity (Bagenel 1973) and the x-intercept is the theoretical weight at which sexual maturity is reached.
Fig 7.6

Facundity of two sets of transplants and controls translocated between Restless Point and Abalone Cove at West I. The linear regressions and their 95% confidence regions for fecundity - weight relations for the two locations are shown.
Differences within Sites (West 1, Tiparra Reef)

At West 1, relative fecundity was significantly lower at Restless Point than at Abalone Cove in 1985 (P<0.001). Plots of transplants between the two locations (Fig 6) show that of the nine recoveries of transplants moved from Restless Point to Abalone Cove, the fecundity of five apparently increased because they were outside the 95% confidence region for the location of origin, and three of them were within the 95% confidence region of the receiving site. Of the six recoveries of back - transplants from Abalone Cove to Restless Point, all were well below the 95% confidence region of the site of origin. At each site the controls were within the 95% confidence region for that site.

The von Bertalanffy growth parameters (K, L∞) for Restless Point were 0.49 and 121mm respectively demonstrating that the population is stunted in comparison with that at Abalone Cove (Table 4) and this was supported by comparison of length frequency distributions taken at each site (Fig 7). At Restless Point, the maximum length is 135mm compared with 155mm at Abalone Cove.

At Tiparra Reef, the relative fecundity at the Lighthouse was nearly twice that at Coal Reef and this difference was significant (P<0.004). Relative fecundity at the South Bottom was less than half that at Coal Reef but could not be compared by formal statistics (see Methods). However, the 95% confidence intervals of the slopes do not overlap suggesting that the differences are highly unlikely to be due to chance.

A comparison of length frequency distributions for the three sites (Fig 7), shows a maximum size of 145mm at South Bottom compared with 160mm at the other sites, implying stunting of that population. The differences might be greater if the Lighthouse and Coal Reef locations were not heavily fished.
Fig 7.7  Length frequency distributions of H. laevigata at three locations at Tiparra Reef and two locations at West 1.
**Differences Between Sites** (Investigator Group)

The relative fecundities of populations at Ward 1, Pearson 1 and Hotspot did not differ from each other significantly (P = 0.13) and the hypothesis that they were equal was accepted. The relative fecundity of the Waterloo Bay population was much lower than those of the three sites, but could not be compared by formal statistics (see Methods). The 95% confidence interval of the slope of the Waterloo Bay data overlaps with that of Ward 1 by only 0.0003 suggesting that the differences are unlikely to be due to chance (Table 1).

**Differences Between Years** (Abalone Cove, West 1)

Data on fecundity of *H. laevigata* were available for 1981 and 1985. Relative fecundity did not differ significantly (P=1.0) in these years.

In addition, data on the Gonad Index (GI) of samples from the same site were available for previous years. The GI was found to be significantly correlated (r = 0.66; P<0.05) with fecundity of individuals 130-140mm long during the spawning season. This is expected from the relationship between fecundity and measures of gonad size found by Tutschulte and Connell (1981); hence variability of GI values between years should reflect the variability of fecundity between years. GI values for six years at West 1, are given in Table 2. The differences between years were tested by one way analysis of variance and were not significant (F=0.85; P>0.05). It is concluded that fecundity is unlikely to have differed significantly between years for that population.

These results contrast with those of Tutschulte and Connell (1981) who found significant differences between years for Californian abalone species. This might be due to the oceanographic peculiarities of the southern California Bight where temperature shifts due to El Nino effects cause large periodic fluctuations in algal abundance (Tegner and Dayton 1987; Tegner et al. 1988).
Table 1 Parameters of linear regressions of fecundity (E) on weight (W) for samples of *H. laevigata* from various sites. Equations are of the form $E = c + dW$. $W(o)$ is the theoretical weight at which sexual maturity is attained (see text).

<table>
<thead>
<tr>
<th>SITE</th>
<th>YEAR</th>
<th>N</th>
<th>c ± 95%CI</th>
<th>d ± 95%CI</th>
<th>W(o)(g)</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>West Island Restless Pt</td>
<td>1985</td>
<td>30</td>
<td>-0.19 ± 0.49</td>
<td>0.0050 ± 0.0016</td>
<td>38</td>
<td>0.57</td>
</tr>
<tr>
<td>Abalone Cove</td>
<td>1981</td>
<td>36</td>
<td>-0.36 ± 0.62</td>
<td>0.0151 ± 0.0024</td>
<td>25</td>
<td>0.82</td>
</tr>
<tr>
<td>Abalone Cove</td>
<td>1985</td>
<td>26</td>
<td>-0.31 ± 0.81</td>
<td>0.0143 ± 0.0031</td>
<td>22</td>
<td>0.80</td>
</tr>
<tr>
<td>Tiparra Reef South Bottom</td>
<td>1982</td>
<td>29</td>
<td>-0.65 ± 0.48</td>
<td>0.0069 ± 0.0027</td>
<td>94</td>
<td>0.52</td>
</tr>
<tr>
<td>Lighthouse</td>
<td>1982</td>
<td>35</td>
<td>-2.17 ± 1.06</td>
<td>0.0246 ± 0.0037</td>
<td>88</td>
<td>0.85</td>
</tr>
<tr>
<td>Coal Reef</td>
<td>1982</td>
<td>30</td>
<td>-0.86 ± 1.41</td>
<td>0.0154 ± 0.0051</td>
<td>56</td>
<td>0.58</td>
</tr>
<tr>
<td>Waterloo Bay</td>
<td>1982</td>
<td>32</td>
<td>-0.36 ± 0.57</td>
<td>0.0040 ± 0.0020</td>
<td>91</td>
<td>0.34</td>
</tr>
<tr>
<td>Hotspot</td>
<td>1983</td>
<td>25</td>
<td>-4.28 ± 2.21</td>
<td>0.0143 ± 0.0052</td>
<td>299</td>
<td>0.59</td>
</tr>
<tr>
<td>Ward Island</td>
<td>1983</td>
<td>27</td>
<td>-1.87 ± 1.81</td>
<td>0.0080 ± 0.0033</td>
<td>234</td>
<td>0.51</td>
</tr>
<tr>
<td>Pearson Island</td>
<td>1983</td>
<td>29</td>
<td>-2.51 ± 2.34</td>
<td>0.0113 ± 0.0039</td>
<td>222</td>
<td>0.56</td>
</tr>
</tbody>
</table>
Sex Ratio
Samples taken at seven sites were subjected to a $X^2$ test (Cochran 1954) to detect a linear dependence of the sex ratio on size. The results are given in Table 3. At three sites (West Island, Tiparra Reef and Waterloo Bay) the proportion of females increases with increasing size, at two sites (Ward I and Flinders I) there is a reverse trend, and at the Hotspot there is no significant change.

DISCUSSION

Fecundity
The relationship between fecundity and weight is satisfactorily represented by linear regressions as is the case for most other species of *Haliotis* (Newman 1967, Poore 1973, Hayashi 1980, McShane et al 1986, Ortiz and Gonzales 1986 and Gonzales and Ortiz 1986). On the other hand, Sainsbury (1982) found a polynomial relationship in which fecundity decreased in the largest size class implying that reproductive senescence occurred in the largest females.

Interpretation of the differences in fecundity between and within sites depends on assumptions about what constitutes a unit stock in abalone populations. This requires a consideration of what is known about larval dispersal of abalone. While much is known of the larval development of abalone, practically nothing is known of the behaviour of larvae in nature or of their dispersal capabilities. Indeed, there are very few reports of abalone larvae being taken in the plankton (Tanaka et al 1977, Tanaka et al 1986). The only direct evidence of very localised dispersion is that of Prince et al (1987) who found correlations between adult density of *H. rubra* and subsequent recruitment strength on a scale of tens of metres. These authors presented an elaborate argument in favour of the view that abalone larvae are demersal and disperse only over a few metres. The considerable evidence of phototaxis of the trophophore stage (Ito 1952, Leighton 1974, Yano and Ogawa 1977, Tanaka, 1978) which would favour extensive transport in surface water currents, was dismissed as a laboratory artifact.

On the other hand, there is little direct evidence of wider dispersal. Tanaka et al. (1986) found that trophophores and veligers were
dispersed over several hundred metres but were concentrated in near-shore eddy currents. Additional evidence comes from the observation that *Haliotis fulgens* settled in large numbers on floating oyster trays set several km downstream from the nearest larval source in Bahía Tortugas, Mexico (S.A. Shepherd personal observation).

Tegner and Butler (1985) considered surface drifters to be a good model for the larval transport of *H. rufescens* and *H. fulgens*, but concluded that long distance transport (i.e., for tens of km) of larvae was unlikely even assuming a swimming phase lasting up to nine days.

The extent of dispersal of *H. laevigata* larvae is not known, but consideration of the location of sites and known water currents suggests that transport of larvae between sites only 10 km apart would be minimal and even less likely for more distant sites. The four sites in the eastern Great Australian Bight are 10-60 km apart and prevailing currents are to the north west during the spawning season. The nearest population of *H. laevigata* to the south east of Waterloo Bay is about 30 km away and the offshore islands are even more distant. The transport of larvae from outside populations into Waterloo Bay seems highly unlikely.

West Island (Fig 2) is 10-20 km from neighbouring populations of *H. laevigata* and with a maximum tidal excursion of about 5 km (unpublished data) larval transport between populations seems unlikely. It is therefore postulated that each of the sites Pearson I, Ward I, Hotspot, Waterloo Bay and West I constitute 'larval traps' in which larvae released from local parent stock are trapped in near-shore eddies in local embayments. Genetic studies by L Brown (pers comm) on populations from these sites show differences between them and lend support to this hypothesis.

Tiparra Reef (Fig 3), differs from the other sites because it is a wholly submerged reef swept by strong tidal currents with a maximum tidal excursion of about 10 km (unpublished data). Dispersal of larvae for some km seems probable even on the assumption that they are demersal. If larval transport between sites is negligible as postulated above, then differences in fecundity between sites could have genetic as well as environmental components, whereas differences
within sites would be environmental only. The evidence for an environmental effect is clearest for West 1 where cross transplants between locations of healthy and 'stunted' sub-populations demonstrated the labile character of fecundity. The decline in fecundity was more dramatic in those transplanted to Restless Point than was the increase in fecundity of the back transplants. If not an artifact of sample size, this may have been due to the relatively large demands for maintenance by the former which were 130-140mm long i.e. larger than the mean Loo of abalone at Restless Point.

The existence of 'stunted' abalone i.e those with a below average maximum size is well known (Breen and Adkins 1979) and is attributable to a poorer supply or quality of food. Shepherd (1973) compared food eaten by *H. laevigata* at the same places at West 1 (Restless Point and Abalone Cove) and found experimentally, that less food was eaten in the stronger water movement conditions at Restless Point.

Because the prevailing swell conditions are much higher all year round at Restless Point than at Abalone Cove (Shepherd and Womersley 1970) a poorer food supply is probably perennial and would account for the lower maximum size attained in the growth studies. Breen and Adkins (1979) also observed that stunted abalone occurred in surf conditions. The Tiparra Reef populations showed similar lability in fecundity between locations and tended to confirm the features of stunted stocks found for West 1 namely, the concurrence of lower maximum size and lower fecundity.

The importance of food in the exogenous regulation of egg production has been shown in field and experimental studies on sea urchins (Gonor 1973, Keats et al 1984, Andrew 1986 and see review by Walker 1982) and molluscs (Spight and Emlen 1976, Thompson 1982).
## Table 2


<table>
<thead>
<tr>
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<th></th>
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</thead>
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<tr>
<td>Mean GI</td>
<td>0.79</td>
<td>0.77</td>
<td>0.72</td>
<td>0.81</td>
<td>0.76</td>
<td>0.75</td>
</tr>
<tr>
<td>1 S D</td>
<td>0.08</td>
<td>0.17</td>
<td>0.10</td>
<td>0.08</td>
<td>0.11</td>
<td>0.09</td>
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</table>

## Table 3

Change in sex ratios at seven sites. The change in sex ratio is shown by comparing that of the smallest and largest size classes respectively.

<table>
<thead>
<tr>
<th>SITE</th>
<th>NUMBER EXAMINED</th>
<th>SIZE RANGE (MM)</th>
<th>CHANGE IN FEMALE TO MALE SEX RATIO</th>
<th>$X^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>West Island</td>
<td>332</td>
<td>85-157</td>
<td>0.36 - 1.24</td>
<td>5.00</td>
<td>&lt;0.03</td>
</tr>
<tr>
<td>Tiparra Reef (South Bottom)</td>
<td>198</td>
<td>78-135</td>
<td>0.65 - 2.25</td>
<td>13.30</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Tiparra Reef (Coral Reef)</td>
<td>234</td>
<td>77-156</td>
<td>0.46 - 1.88</td>
<td>7.69</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Waterloo Bay</td>
<td>923</td>
<td>130-190</td>
<td>0.82 - 1.38</td>
<td>6.90</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Sheringa</td>
<td>200</td>
<td>130-188</td>
<td>0.71 - 1.00</td>
<td>12.02</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Hotspot</td>
<td>174</td>
<td>137-196</td>
<td>0.85 - 0.73</td>
<td>0.49</td>
<td>n.s</td>
</tr>
<tr>
<td>Ward Island</td>
<td>312</td>
<td>127-206</td>
<td>1.45 - 0.94</td>
<td>5.00</td>
<td>&lt;0.03</td>
</tr>
<tr>
<td>Flinders Island (South east side)</td>
<td>202</td>
<td>127-186</td>
<td>1.85 - 0.38</td>
<td>30.21</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
Fig 7.8

Plot of relative fecundity vs the anabolic growth parameter $K_{L,oo}$ for *H. laevicollis* at various sites. The line AB is the boundary of domain of possible values (see text).
Because the energy available to an animal must be shared between the competing demands of reproduction and growth (Cody 1966, Stearns 1975, 1977) differences in fecundity of this abalone between populations should be considered in the context of each population's allocation strategy. This can be shown by a plot of relative fecundity against the anabolic growth parameter K, Loo (see Table 4) for each population or sub-population (Fig 8).

If the allocation strategy for a given population has been selected to respond to the range of conditions experienced by it, and is population specific (Calow and Woolhead 1977), then samples from different sub-populations of a population should lie within a specific part of a domain bounded by a line AB (Fig 8) representing optimal conditions in terms of food availability. The Tiparra Reef and West 1 data would appear to conform to this model. Sub-populations from each site lie in a specific region in the left hand part of the domain. A second consequence is that, in optimal conditions for each population, there should be an inverse correlation between relative fecundity and the anabolic growth parameter. This is also true for all the populations sampled when the stunted populations are excluded from the comparison (r = -0.85 P<0.05).

An intriguing question arises as to the environmental factors which appear to have fixed the observed allocation ratios in these populations. We suggest the interpretive hypothesis that the allocation ratio for a given population is determined by the one factor which is the most critical of all for a species with planktonic larval dispersal, namely the survival of the larval stage. The substance of the argument is that if larval survival is high, then the population will evolve toward less than maximum fecundity. It may become more advantageous to invest more energy in faster growth and produce more eggs later in life (eg Creese 1980, Graham and Branch 1985). This hypothesis cannot be easily tested because of the very great difficulties of trying to measure larval survival. However, consideration of the coastal configurations of the different sites suggests that there may be differences in their efficiency as larval traps.
Table 4: Estimates of the parameters of the Von Bertalanffy growth curve for various sites with authority.

<table>
<thead>
<tr>
<th>SITE</th>
<th>K</th>
<th>L∞</th>
<th>K.L∞</th>
<th>AUTHORITY</th>
</tr>
</thead>
<tbody>
<tr>
<td>West I (Restless Point)</td>
<td>0.49</td>
<td>121</td>
<td>59.3</td>
<td>Growth data - this paper</td>
</tr>
<tr>
<td>West I (Abalone Cove)</td>
<td>0.48</td>
<td>138</td>
<td>66.2</td>
<td>Shepherd and Hearn (1983)</td>
</tr>
<tr>
<td>Tiparra Reef (Lighthouse)</td>
<td>0.41</td>
<td>131</td>
<td>53.7</td>
<td>Shepherd and Hearn (1983)</td>
</tr>
<tr>
<td>Tiparra Reef (South Bottom)</td>
<td>0.4</td>
<td>120</td>
<td>48</td>
<td>Shephard and Hearn (1983)</td>
</tr>
<tr>
<td>Waterloo Bay</td>
<td>0.59</td>
<td>148</td>
<td>87.3</td>
<td>Shepherd and Hearn (1983)</td>
</tr>
<tr>
<td>Hotspot</td>
<td>0.4</td>
<td>150-167</td>
<td>60-66.8</td>
<td>Analysis of length frequency data (unpublished)</td>
</tr>
<tr>
<td>Ward Island</td>
<td>0.41</td>
<td>167</td>
<td>68.5</td>
<td>Growth data - this paper</td>
</tr>
<tr>
<td>Pearson Island</td>
<td>0.4</td>
<td>150-167</td>
<td>60-66.8</td>
<td>Analysis of length frequency data (unpublished)</td>
</tr>
</tbody>
</table>
in Waterloo Bay water circulation practically ceases under conditions of low swell (unpublished drogue studies), and a large proportion of the larvae would be expected to be retained within the Bay.

At island sites such as Pearson I, Ward I, Hotspot and West I, near shore fine scale currents and eddies would be expected to retain a smaller proportion of larvae (Uda and Ishino 1958, Alldredge and Hammer 1980, Tanaka et al 1986). Finally at the most open site, Tiparra Reef, with no emergent reefs and few bottom topographic features to concentrate larvae, dispersal of larvae would be expected to be highest with a consequent very high loss. The range of allocation ratios observed for this suite of sites (Fig 8) correlate broadly with the range of coastal topographies described and the inferred efficiency of sites as larval traps and provide the basis for this speculative hypothesis. It is recognised that there is a complexity of trade-offs that determine resource allocation strategies (Parry 1981) and that it is a dangerous oversimplification to select one parameter when much of the life history remains poorly known. In particular, there is the risk of drawing unwarranted adaptationist conclusions of the kind criticised by Gould and Lewontin (1979). Nevertheless, the larval trap hypothesis is a useful framework in which to examine the puzzling variation of fecundity, and it needs to be tested at other sites.

Sex Ratios

While unequal sex ratios have been observed in a few abalone species (Sinclair 1963, Forster 1967, Giorgi and Demartini 1977, Ortiz and Marín 1976) and equal sex ratios in others (Crofts 1929, Boolootian et al 1962, Newman 1967, Young and Demartini 1970), there have been no studies of changes in the sex ratio with size or between populations except earlier notes by Shepherd and Laws (1974), Tutschulte and Connell (1981), and Shepherd and Hearn (1983).

The significance of a changing sex ratio with size is still not certain (Tutschulte and Connell 1981). Shepherd and Hearn (1983) found that female *H. m. gigas* grew 25% faster than males at Waterloo Bay and suggested that differential growth between the sexes was the most likely reason for the changing sex ratio there. Differential mortality between the sexes is possible but seems improbable because
there are no external physical or known behavioral differences between the sexes. Further, Shepherd (1986) found no evidence of differential mortality between the sexes at Waterloo Bay.

Cochard (1980) suggested that abalone may show labile gonochorism i.e. there was a possibility of an environmental influence on sex determination early in life. While this may be so, the simpler hypothesis remains tenable namely that differential sex ratios reflect differential growth between the sexes, implying that allocation strategies may vary between the sexes in different populations. This needs further study.

ACKNOWLEDGEMENTS
We are grateful to P S Clarkson, C H Deane, M Kangas and J A Turner for assistance in the field and laboratory. Mr C Cole kindly made his boat available for collection of abalone from Pearson l, Ward l, Hotspot and Flinders l. Dr P Sluczenowski fitted the von Bertalanffy growth curve to the data from Ward l.

REFERENCES


Young, J.S. and J.D. De Martini: The reproductive cycle, gonadal histology, and gametogenesis of the red abalone Haliotis rufescens (Swainson). Calif. Fish and Game 56, 298-309 (1970).
CAPTIONS TO FIGURES

Fig 7.1 Map of South Australia showing sampling sites.

Fig 7.2 Map of West Island and adjacent Fleurieu Peninsula. Arrows indicate location of populations of H. laevigate. The Abalone Cove study site is shaded.

Fig 7.3 Map of Tiparra Reef and locations sampled. Inset shows distribution of H. laevigate in eastern Spencer Gulf.

Fig 7.4 Islands of the Investigator Group, eastern Great Australian Bight and adjoining mainland with Waterloo Bay.

Fig 7.5 Plots of fecundity versus weight with linear regressions for H. laevigate at various sites and locations within sites. Note differences in vertical scales. The regression for Coal Reef (Tiparra) is intermediate in slope between those of the other two locations and is omitted for the sake of clarity.

Fig 7.6 Fecundity of two sets of transplants and controls translocated between Restless Point and Abalone Cove at West I. The linear regressions and their 95% confidence regions for fecundity - weight relations for the two locations are shown.

Fig 7.7 Length frequency distributions of H. laevigate at three locations at Tiparra Reef and two locations at West I.

Fig 7.8 Plot of relative fecundity vs the anabolic growth parameter Kc for H. laevigate at various sites. The line AB is the boundary of domain of possible values (see text).
CHAPTER 8

MOVEMENT AND MORTALITY

Waterloo Bay has been one of the principal sites for the study of the biology of *H. laevigata* (e.g. Shepherd and Hearn 1983) and is currently the site of a long term study of stock-recruitment relations. The Bay is taken to be representative of much of the greenlip abalone fishery habitat on the west coast of Eyre Peninsula in terms of productivity and growth. Hitherto however, there has been no information on natural mortality, one of the necessary inputs in yield-per-recruit analyses (Sluczanski 1986).

The study described below set out to measure natural mortality at three sites in Waterloo Bay with different degrees of protection (i.e. crevice abundance) against the major predator, the stingray. It transpired that movement of abalone differed substantially between sites and precluded adequate measurement of mortality. Nevertheless, the study provided information on the factors inducing differential movement which is valuable in understanding dispersal of abalone.

Hitherto it has been thought that the larval stage is exclusively the dispersal phase of abalone, and that juveniles and adults are sedentary. This study shows that extensive movement of adults is possible and may be an additional mode of dispersal. The study also has a bearing on the problem of delineation of a unit stock. If larval dispersal is very limited as recent studies suggest (e.g. Prince et al. 1988) then the movement of adults assumes considerable importance as a dispersal mechanism.

Despite the extensive movement of abalone, some information on natural mortality did emerge. Analysis of a subset of tagging data from 1969 to 1974 showed a survival of the 2+ cohort over 2 1/2 years of 56% per annum. This rate is unusually high compared with rates earlier described by Shepherd et al. (1982) for Tippera Reef and West Island and raises questions as to the validity of the assumptions, in particular that tag shedding rates were negligible. Current studies on *H. laevigata* in Waterloo Bay (S N Clarke pers. comm.) show that sand abrasion is much greater there than at the other sites and raise the possibility that tag loss is a significant factor.
Alternatively, rates of natural mortality may be much more variable (See Ch 6) than has usually been supposed. The annual survival of 79% at Site A1 for a very small sample may be more realistic. Further experiments are in progress in Waterloo Bay to measure natural mortality. In all the experiments described, the Bay has been closed to commercial fishing. However, some poaching has been reported and there was a suspicion in this study that the poor recoveries at Site C4 were due in part to such activity.

References


Movement of the Southern Australian abalone *Haliotis laevigata* in relation to crevice abundance

S. A. SHEPHERD  
Department of Fisheries, 135 Pirie Street, Adelaide, SA 5001, Australia

Abstract

The long-term movement of the abalone *Haliotis laevigata* was measured at three sites in Waterloo Bay, South Australia, characterized by differing amounts of available crevice space. Movement was negligible at a site where crevices were abundant, but extensive at a site without crevice space. At a site of limited available crevice space, the amount of movement increased as available crevice space decreased. In addition, the extent of movement was size dependent and movement was oriented in the direction of the approaching swell.

Current experimental designs for measuring natural mortality of abalone depend heavily on assumptions about their movement. An understanding of this behaviour is thus a prerequisite for designing experiments to measure the mortality rates of abalone or other sedentary animals.

The natural mortality rate at one site was estimated to be 0.59 (s.e.m. = 0.02; i.e. survival = 56% per year) and the disappearance rate (natural mortality and emigration) was independent of sex.

Introduction

An understanding of the long-term movements of abalone is critical for designing marking programmes to measure mortality and growth, which are important for managing abalone fisheries. Most authors have recorded little or no movement among abalone species (Momma & Sato 1969; Koike et al. 1970; Poore 1972; Shepherd 1973; Beinissen & Powell 1979; Clavier & Richard 1984), but Newman (1966) recorded much more extensive movements for *Haliotis midae*.

While most authors consider that movement is undertaken for feeding, few have attempted to elucidate the significance of this or of other factors. Clavier and Richard (1984) found that migration was oriented in the direction of swell and current, while Momma and Sato (1969, 1970) considered there were intrinsic behavioural differences between individuals, some being migratory, some homing and others sedentary.

This study set out to assess the mobility of *H. laevigata* Donovan in three different habitats in Waterloo Bay, South Australia (33°39'S, 134°54'E; see Fig. 1) for the purpose of testing the applicability of Beinissen and Powell's (1979) experimental design to measure the natural mortality rate. The design of Beinissen and Powell assumes that the movement of individuals is random, local, and consistent over time. The movement of *H. laevigata* was examined in relation to crevice space availability, size and sex, and over time. The rate of disappearance of marked individuals at each site is also described.

![Fig. 1. Map of Waterloo Bay showing study sites.](image-url)
Methods

Site descriptions

Site C3 (Fig. 2) at a depth of 10 m is an aeolianite plain with occasional outcrops 10–50 cm high and with numerous depressions where the harder surface crust has eroded away to form basins of variable size (mostly 5–20 m across) and depth (usually 20–50 cm deep). The sides of the basins overhang, forming deep undercuts or crevices penetrating up to 1 m under the crust.

Site C4, at a depth of 9 m is a nearly flat, featureless aeolianite plain with patches of rubble scattered throughout. A massive mooring chain traverses the site in a direction of about 10° to the right of the direction of approaching swell, and the gap between it and the substrate provides a long, narrow, linear crevice. Other crevices are rare.

Site A1 (Fig. 3), at a depth of 3 m is intermediate between Sites C3 and C4 in bottom topography. The area is partly a sand-swept plain without relief, but with patches of outcropping aeolianite 10–20 cm high which overhang in places at the margins to form shallow crevices.

The bottom topography and algal vegetation of Waterloo Bay is described by Shepherd and Womersley (1981).

*Haliotis laevigata* occurs in high densities of 40–80 per 100 m² at Sites C3 and C4 (Shepherd 1986) and at lower densities of 10–20 per 100 m² at Site A1 (Shepherd 1985). Abalone used in the marking experiments were obtained in each case as close as possible to the place of release.

In 1969 and 1970, 240 *H. laevigata* were marked with epoxy tags and released in suitable crevices at several adjacent points at Site C3 (Fig. 2) in Waterloo Bay and the position of marked individuals recorded on a map of the site at intervals of 6 months until October 1974.

On four occasions (April and October of 1982 and 1983) 50 individuals were marked and released at Site C4, and 30 at Site A1 (Fig. 3). Numbered plastic tags were attached to the growing edge of the shell near the spire with nylon nuts and bolts (2 mm in diameter), and made fast with quick-setting epoxy resin. Marked individuals were placed under a section of the mooring chain at Site C4, and in crevices surrounding a central release point at Site A1.

Sites were examined on the day following marking to determine marking mortality. On average, 10% of marked animals disappeared during this period, probably due to attack by sting-rays and octopuses which are common. The number lost was deducted from the
number released for the purpose of calculating the disappearance rate (see below).

In April 1984, exhaustive searches by four divers were made at each site for 10–12 man-hours to recover all marked abalone. Four 50 m surveyors' tapes were laid out at right angles to each other on the bottom, radiating out from the point of release. The distal extremities of the tapes were joined by ropes to enclose a square approximately 70 × 70 m, divided into four segments. Divers swam on compass course systematically on traverses 2 m apart and parallel to a tape through each segment to search for marked individuals. Subsequent searches extended for about 20 m beyond the outer boundaries of the enclosed areas. The position of marked individuals was recorded by reference to the co-ordinates on the tape and were considered accurate to within 2 m.

Data were plotted onto maps prepared for each site and the net distance and direction of movement was measured graphically for each individual.

The frequency of angular data in each of six 60° sectors of the circle was counted and a $\chi^2$ test was used to determine whether the observed frequencies differed significantly from those expected under randomness. Mean directions of movement, their confidence intervals and other circular statistics were calculated with formulae or graphs given by Batschelet (1981).

**Results**

**Movement**

*Site C3* Of 240 individuals marked in 1970 there were 203 sightings within the study area (Shepherd & Hearn 1983), as well as multiple sightings (up to eight times) of many individuals on consecutive visits at 6 month intervals. Almost all individuals rested permanently in the crevices described above. Of five individuals whose movement away from the site was recorded, one moved onto an aeolianite outcrop and the others moved laterally along the crevice margin. In each case the distance moved was less than 20 m.
Site C4  Dispersal of marked individuals was rapid, and sightings after 2 years ranged from 28% of those marked for 6 months to 2% of those marked for 24 months. The histograms in Fig. 4 show distances moved for each of the four groups with differing periods at liberty. There is a modal distance of 25-30 m moved by those at liberty for 6 months, and a maximum distance of 250 m. However, because systematic searching was not conducted beyond about 60 m from the point of release, it is likely that many individuals, especially those at liberty for more than 6 months, moved beyond the range of searching.

Site A1  The dispersal pattern of individuals differed between the four groups of releases. The groups at liberty for 2 years and 18 months moved least and did not differ significantly from each other ($\chi^2 = 2.3$, NS), however, dispersal increased for each group successively released after that time (Fig. 4). The null hypotheses that there was no difference between dispersal of the first three groups or all four groups were tested and rejected ($\chi^2 = 14.1$, $P < 0.01$ and $\chi^2 = 19.5$, $P < 0.005$, respectively). Differential dispersal between groups was not due to biased marking of small or large size classes (see below) because there were no significant differences between the size distributions of the four groups marked ($\chi^2 = 13.9$, NS).

Finally, tests were made to determine whether distances moved differed according to the size of abalone. Movement data combined for both sites were grouped in three size categories according to length at date of marking, with approximately equal numbers in each. The results (Fig. 5) show that movement was least in the smallest size class and increased with increasing size. The null hypothesis that the frequency distribution of movement did not differ between size classes was tested and rejected ($\chi^2 = 13.9$, $P < 0.01$). For this test, data on distance moved were grouped in three categories (0-5 m, 6-20 m and $> 20$ m).
pected under the hypothesis of random dispersal (at Site C4, \( \chi^2 = 26.5, P < 0.001 \), and at Site A1, \( \chi^2 = 17.3, P < 0.01 \)). It was concluded that movement was directional at both sites. The mean direction of movement at Site C4 was 17.6° to the left of the direction of approaching swell, and at Site A1 it was 18.1° to the right (Fig. 6). The 95% confidence angle of deviation was ± 33° at Site C4 and ± 50° at Site A1. Thus, at neither site did the sample mean direction differ significantly from the direction of approaching swell. The frequency distributions of directions moved did not differ significantly between the two samples (Kuiper's test [Batschelet, 1981] \( K = 241, P > 0.2 \)) so it is unlikely that unfavourable habitat, i.e. dense Cystophora stands to the north and east of the release area at Site A1 (Fig. 3), influenced the direction of movement at that site.

**Disappearance rate**

A plot of the natural logarithm of the number of marked individuals sighted over time gives a curve whose slope is \(-X\), where \(X\) is the sum of natural mortality, fishing mortality, tag loss and emigration. In this preliminary analysis, the survival of 79 individuals in the 2+ age class (65–95 mm long, see Shepherd & Hearn 1983), comprising a subset of mark-recapture data for Site C3, was examined over 5 years.
with approximately equal searching effort at intervals of 6 months. The curve for these data shows a log linear decline until individuals are 5+ years old and then a more rapid decline (Fig. 7). The slope of the linear part of the curve gave an $X$ value of 0.59 (s.e.m. = 0.02) or an annual survival of 56%. The mean length of the survivors in the 5+ year class was 135 mm (s.e.m. = 1.5 mm) and the minimum legal length of capture by abalone divers was 130 mm. Emigration and tag loss rates were negligible (this report and Shepherd et al. 1982) but the area was lightly fished by divers. The slope of the linear part of the curve is therefore an estimate of the natural mortality rate.

Where abalone are marked at successive time intervals and recovered at one time, as at Sites C4 and A1, then Beinssen and Powell (1979) showed that a regression of the natural logarithm of the ratio of number recaptured to number released against time has a slope of $-X$.

At Site C4, the rate of disappearance was 1.71 (s.e.m. = 0.27) or an annual 'survival' of 18%. As no fishing occurred during the period, this represents the natural mortality and emigration rates combined.

At Site A1 it was not possible to use Beinssen and Powell's (1979) method to estimate the disappearance rate because the emigration rate apparently changed over time (Fig. 4). However, the mean disappearance rate for the two groups at liberty for 24 and 18 months was 0.23, which equals an annual survival of 79% (assuming no emigration). However, the number of recoveries is too few to make this estimate of natural mortality reliable.

One hundred of the individuals tagged in October 1982 and 1983 were sexed; there were 52 males and 48 females. Of these, 14 males and 11 females were recovered. The ratio of the sexes recovered did not differ from that expected from the proportions of the sexes marked ($x^2 = 0.13$, NS) and it was concluded that there was no difference between the sexes in respect of mortality and emigration rates.

**Discussion**

The differences in movement between the three sites can be explained in terms of the quality and abundance of crevices. Movement was least at Site C3 where large and deep crevices were abundant. The results at this site paralleled those at West Island and Tiparra Reef which have a similar abundance of crevices and where movement was minimal or absent (Shepherd 1973; Shepherd et al. 1982). Conversely, maximum movement was recorded at Site C4 where there were no crevices and intermediate movement was recorded at Site A1 where crevices were smaller and fewer. The simplest explanation is that *H. laevigata* moves continually until it finds a crevice, after which movement ceases. This is supported by short-term experiments over 3 days carried out at Site C4 where movement of almost all the population was observed (Shepherd 1986).

Hunger is also considered to be a stimulus that causes abalone to move (Poore 1972; Hines & Pearse 1982) and it is possible that the experimental manipulations which locally increased abalone densities at each site, induced the marked abalone to disperse to places of lower density where presumably there was less competition for food. At best, this might explain initial dispersal but it cannot explain the long-term differences in mobility of abalone between sites.

The change in distance moved over time at Site A1 may be a saturation effect, that is, when 'crevice space' became scarce as existing crevices filled up, an increasing proportion of successive additions of marked individuals dispersed in search of available crevices. It certainly became increasingly difficult to
find crevice space for successive releases of abalone.

The differential dispersal with size may occur because crevice space becomes increasingly limiting with increasing size of abalone, or may be due to the intrinsic behaviour of this abalone. Lesser movements by smaller abalone were observed by Newman (1966) and Clavier and Richard (1984).

Two features of crevices may account for the crevice-seeking behaviour of this abalone. First, crevices provide a refuge from sting-rays, one of the main predators of this species, and second, they tend to trap drift algae on which this abalone feeds (Shepherd 1973). The relative importance of these, or other unrecognized, features can only be determined experimentally. The crevice-seeking behaviour of abalone, although well known in general terms, has been examined critically only by Hines and Pearse (1982) for Californian species and by Shepherd (1973) for Haliotis ronu Gray. Both studies showed that the size of the abalone occupant was dependent on crevice dimension, and Hines and Pearse (1982) found no evidence of migration out of specific crevices.

The directional movement of this species into the swell suggests a rheotactic basis for orientation. This is consistent with the knowledge that this species is sensitive to water movement and adopts a catching behaviour as water movement increases (Shepherd 1973). Rheotaxis has been described for several species of gastropod (see Gendron 1977 and references cited therein) but for only one other species of abalone, H. tuberculata Linn., which also orient and moves toward the swell direction (Clavier & Richard, 1984).

The estimate of the natural mortality rate for Site C3 is more than double that of Site A1 or those previously reported for H. laevigata (Shepherd et al. 1982). Further studies are needed to measure the natural mortality rate in different habitats and to therefore define its relations with environmental factors such as availability of shelter.

The experimental procedure of Beinssen and Powell (1979) to measure natural mortality assumes random, local movements of individuals and consistency in rates of movement over time. Their study was conducted at a site having a flat reef-top but with many deep vertical crevices, in a forest of the preferred food-alga Phyllospora comosa (S.A. Shepherd pers. obs.), where these conditions may have been met although they were not discussed. In the present study, the movement of H. laevigata proved to be extensive and non-random, and varied with size of animal and availability of crevice space. These factors will need to be taken into account in designing experiments to measure the natural mortality of this abalone, or other similar sedentary animals.

Acknowledgments

I am grateful to P.S. Clarkson, C.H. Deane, and J.A. Turner for diving assistance and Drs W.G. Inglis, B.J. Mills, P.S. Sluzcanowski and R.W. Day for criticism of the manuscript. The study was supported with funds from the Fishing Industry Research Trust Account.

References


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CHAPTER 9

AGGREGATION

The aggregative behaviour of abalone is important partly because it may increase fishing mortality, but more importantly because it has a bearing on the problem of stock-recruitment relations. Measurement of stock size implies that all sexually mature females in a population contribute to egg production in accordance with the fecundity weight relationship derived for that population. However, the measure of interest is not egg production *simpliciter* but production of fertilised eggs. Fertilisation efficiency depends *inter alia* on the proximity of males and females to each other, and declines with increasing distance between them. The significance of distance between individuals in relation to water movement affecting fertilisation success has recently been shown by the study of Pennington (1985). He carried out field and laboratory experiments to measure fertilisation success in sea urchins in different water movement conditions. Highest fertilisation success was achieved in low water current speeds. When individuals were <20cm apart, 60-95% of eggs were fertilised, but at greater distances less than 15% of eggs were fertilised.

These findings are relevant to attempts to measure fertile egg production of the West Island population of *H. laevigata* (Ch 5). Shepherd and Laws (1974) showed that at West Island, *H. laevigata* attains sexual maturity at 95mm, although few eggs are then produced. However aggregation is only partial at a length of 110-120mm and at a maximum only for individuals >120mm long. Thus only a portion of the sexually mature stock is likely to contribute to zygote production.

One detail of the following paper is incorrect, in the light of the findings on growth of juvenile *H. laevigata* (Ch 3). The age classes in Fig 2 should be 4, 5 and 6 years respectively instead of 3, 4 and 5.
References


Studies on Southern Australian abalone (genus *Haliotis*)

VII. Aggregative behaviour of *H. laevigata* in relation to spawning

S. A. Shepherd

Department of Fisheries; 135 Pirie Street, Adelaide, Southern Australia 5000, Australia

Abstract

The aggregative behaviour of the abalone *Haliotis laevigata* Donovan was examined at two localities in South Australia from 1981 to 1984. Sexually mature individuals display aggregative behaviour just before and during the spawning season, but tend to be randomly distributed at other times of the year. Sexually immature individuals show no such behaviour and are regularly to randomly dispersed. The tendency to aggregate increases with increasing age on attainment of sexual maturity. Experimental manipulations of adults only temporarily interrupts the dispersion pattern at a given time. The implications of the behaviour in managing exploited stocks are discussed.

Introduction

Abalone, like most other archaeogastropods, release their eggs directly into the surrounding seawater, where fertilisation occurs (Fretter and Graham, 1962; Webber, 1977). Behavioural mechanisms which bring male and female together could, therefore, be expected to have evolved to facilitate synchrony of release of gametes, and increase the successful fertilisation of spawned eggs. Such mechanisms that have been described include pairing of individuals and the formation of aggregations (Webber, 1977).

If spawning, or its approach, induces aggregative behaviour, then this tendency would be more pronounced during the spawning season and after attainment of sexual maturity. This study set out to determine the pattern of dispersion of adult *Haliotis laevigata* Donovan, and changes in that pattern both seasonally and between length classes.

The commercially exploited abalone *Haliotis laevigata* occurs on rocky bottom and is often associated with crevices (Shepherd, 1973). Populations were examined at West Island (35°36'25"S; 138°35'27"E) and Waterloo Bay (33°39'S; 134°54'E) South Australia, both closed to fishing during this study. The spawning season of this abalone is from October to March (Shepherd and Laws, 1974).

The pattern of dispersion of *Haliotis laevigata* at West Island from November 1981 to March 1984 is described, as well as the results of experimental manipulations of the dispersion pattern at Waterloo Bay at the beginning and end of the spawning season.

Materials and methods

West Island

*Haliotis laevigata* Donovan occurs among boulders mostly 30 to 40 cm long by 20 to 30 cm wide, at the base of a boulder slope (Shepherd, 1973). The area studied extended 55 m along the base of the slope over a band width of 1 m. A 50 m tape and the sandline marked the upper and lower boundaries of the band, and permanent marks were set at each end. Adult abalone densities were 3 to 4 m⁻² for about one half of the area and about 1 m⁻² for the other half. At about 3 mo intervals (more frequently in spring) a diver counted all abalone that he could find in a 1 m² quadrat placed contiguously and sequentially through the area. Numbers of abalone were recorded in three cumulative length classes, viz. >100 mm, >110 mm and >120 mm; small abalone <100 mm long are not all sexually mature (Shepherd and Laws, 1974) and were excluded.

The variance to mean (v:m) ratio applied to numbers in the three length classes in each quadrat (Greig-Smith, 1957) was used as an index of dispersion to measure the dispersion pattern. At the scale selected (1 m²) the value 1 indicates a random pattern, and larger values clumping or aggregation. The significance of aggregation was tested by a Student’s 𝑡 test and a χ² goodness-of-fit test. Cumulative length classes were examined, because the dispersion pattern of the two smaller length classes (100 to 110 mm,
110 to 120 mm) independent of larger length classes as little biological interest.

From the growth curve of *Haliothis laevigata* at West Island (Shepherd and Hearn, 1983) with knife-edge separation between age-classes, the length range at Age 3 is 90 to 109 mm and at Age 4 is 110 to 119 mm. Thus, the length classes examined correspond crudely with the 3.4 and $\geq 3$ yr-old individuals. The correspondence between length and age is more satisfactory for the 3 yr age class than for older ones, which are increasingly confounded due to the decreasing annual growth increment with increasing age.

In addition, at the same site the diver measured the nearest-neighbour distances between all individuals that he could find > 100 mm long; these were recorded for the same three length classes, i.e., 100 to 110 mm, 110 to 120 mm and $\geq 120$ mm. Measurement of distances between individuals within, and nearest neighbours outside, the area were included to avoid bias due to the edge-effect.

Nearest-neighbour measurements were analysed by using the dispersal coefficient ($R$) of Clark and Evans (1954), calculated as follows:

$$R = \frac{\sum r}{N} \times 2 \sqrt{d},$$

where $r$ = distance between each individual and its nearest neighbour, $N$ = number of abalones and $d$ = density of the species in the area. Mean density values were obtained from the quadrat data.

An $R$ value of 0 corresponds to complete aggregation. 1.0 to a random distribution and 2.15 to regular dispersion. The statistic has biological meaning because, in any distribution, the mean observed distance to nearest-neighbour is $R$ times as great as expected in a random distribution. Thus, an $R$ value of 0.5 indicates that nearest neighbours are, on average, half as far apart as expected under conditions of randomness (Clark and Evans, 1954). Simberloff’s (1979) modification to the formula, allowing for the diameter of the animal, is unnecessary, because the diameter of this abalone (10 to 15 cm) is less than half the expected mean nearest-neighbour-distance between points. The value of $R$ was calculated separately for the three length classes 100 to 110 mm, 110 to 120 mm and $\geq 120$ mm, and the significance of the values tested by the formula given by Clark and Evans (1954).

**Waterloo Bay**

On 27 October 1983 and 27 April 1984, a 2 m grid of weighted polypropylene rope was laid down in an area 10 m x 10 m on calcrete limestone in the centre of the Bay at about 9 m depth. Low ridges or peaks, of about 15 cm relief, and 1 to 2 m apart occurred through the area and *Haliothis laevigata* occurred in shallow troughs between them. The position of all *H. laevigata* initially in the area was measured by reference to the grid and marked on a map, and all individuals (except those < 100 mm long) were removed. Mean densities in the plot at the start of the two experiments were 0.33 and 0.26 m$^{-2}$ respectively for individuals $\geq 120$ mm, and 0.76 and 0.54 m$^{-2}$ respectively for all individuals.

Individuals > 120 mm, some taken from outside the area, were marked by a groove in the shell and placed on the bottom in a regular array at each intersection of a 1 m grid superimposed on the original grid, except that none were placed within 2 m of the perimeter. Thus, 49 individuals, each 1 m apart, were uniformly distributed over a 6 x 6 m grid. A nearby area of 8 m$^2$ served as a control. After 3 d, the location of all abalones in the 10 x 10 m area and the control site was recorded as X and Y coordinates on each 2 x 2 m grid.

The v:m ratio was calculated on 1 m$^2$ quadrat data for (a) the whole population recorded in the 100 m$^2$ area, and (b) the subset $\geq 120$ mm long. The $R$ statistic was obtained for those (a) $\geq 120$ mm long and (b) < 100 mm long (those 100 to 120 mm long having been removed). These length classes were selected for comparison because 100 mm is about the length when individuals first become sexually mature, and 120 mm when all are sexually mature (Shepherd and Laws, 1974).

**Results**

**West Island**

Changes in the two statistics for *Haliothis laevigata* from 1981–1984 are shown in Fig. 1. In most months sampled, the v:m ratio for the largest length class (\( \geq 120 \)) mm showed a significant departure from randomness toward aggregation. Values tended to be higher in November and December than at other times of the year. The incorporation of smaller length classes sharply increased the v:m ratio from November to December, but had a variable effect at other times. Except for three samples (see below), the v:m ratio for the three cumulative length classes from November 1981 to March 1984 (Fig. 1) all showed significant aggregation. Values of the $t$ test used for significance ranged from 2.0 to 18.3 with sample sizes of 48 to 58 quadrats. Of the three samples which did not show significant aggregation (24 May 1982 for those $\geq 110$ mm, $t=1.44$ NS; 29 March 1983 for those $\geq 120$ mm, $t=1.6$ NS and 2 March 1984 for those $\geq 120$ mm, $t=1.6$ NS), the second was significant according to the $\chi^2$ test ($\chi^2=6.02; P<0.05$). The $R$ statistic measures the pattern of dispersion of each length class. The largest ($\geq 120$ mm) length class is significantly aggregated from September to March each year (in each case $P<0.01$, except January 1983 when $P<0.05$) and at other times randomly dispersed (Fig. 1). The intermediate (110 to 120 mm) length class is significantly aggregated ($P<0.05$) for some but not all sampling dates in the period September-March, and the smallest length class is mostly randomly, but sometimes regularly (e.g. November 1982, $P<0.001$) dispersed.
Fig. 1. *Haliotis laevigata*. (a) Changes in variance-mean ratio for a population of abalone at West Island, 1981-1984. (b) Changes in $R$ statistic during same period. Filled symbols indicate a significant ($P < 0.05$) departure from randomness, and open symbols a random dispersion.

The results are more readily interpreted by conversion of the length classes to approximate age (see "Materials and methods"), notwithstanding the partial confounding of older (4 and 5 yr) age classes that occurs, and then plotting the change in the $R$ statistic with increasing age (Fig. 2). It is apparent that the dispersion pattern shifts gradually from a regular or random one prior to Age 3 to an aggregated one during the spawning season at Ages 4 and 5. Between spawning seasons the pattern reverts to a random one.

Waterloo Bay

Changes in the v:m ratio and the $R$ statistic before the October experiment, immediately after the manipulation of location and density of large ($\geq 120$ mm) abalone, and at the end of the experiment, are given in Table 1.

At the commencement of the experiment, $R$ statistics (Table 1) indicate that large abalone were aggregated and small abalone were randomly distributed in the area. The manipulation resulted in a regular distribution pattern of all abalone throughout the area. After 3 d, the position of only 5 out of 49 abalone remained unchanged and large abalone were significantly aggregated, but small ones remained randomly dispersed. The v:m ratio showed the same changes in dispersion of the largest length class ($\geq 120$ mm), although the whole population shifted from a random to an aggregated pattern of dispersion. Because the experimental clearing of large abalone from the perimeter of the area and the edge-effect may have biased the two statistics, they were recalculated after excluding data from all 1 m$^2$ quadrats around the perimeter of the area. The differences (Table 1) were trivial. There were some changes in the statistics for the control, probably due to the relatively small sample size, but no strong trend is evident.

The April experiment gave very different results for both statistics and showed no evidence of aggregation (Table 2). Immediately prior to the experimental manipulation, abalone were randomly distributed (except in the control where numbers of small ones caused a temporary aggregation pattern in the sample). After 3 d, the position of only 5 out of 49 abalone remained unchanged, and the distribution was random in the plot and the control.

Discussion

The two statistics used to describe the dispersion pattern for *Haliotis laevigata* show the same trends although they do not always agree in detail. Where they disagree, the $R$ statistic is probably the more reliable, partly because it is based on distance measurements and partly because the v:m ratio is known to be sensitive to quadrat size and density (Greig-Smith, 1957).

A number of mechanisms have been proposed to explain why marine invertebrates aggregate (Hutchinson, 1953). They are (a) habitat heterogeneity and (b) various facilitation behaviours by which individuals benefit in some way by the closeness of conspecifics. Examples of
Table 1. *Haliotis laevigata*. Values of the v:m ratio and *R* statistic before, immediately after, and 3 d after a manipulation of the dispersion of abalone in an experimental plot ("Plot") at Waterloo Bay on 27 October 1983. The dispersion pattern (regular, random or aggregated) is shown, with results of significance tests (*P* < 0.05; **P** < 0.01; ***P*** < 0.001); pop: population.

<table>
<thead>
<tr>
<th>Date and site</th>
<th>v:m ratio</th>
<th>R statistic</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>≥ 120 mm</td>
<td>Total pop</td>
</tr>
<tr>
<td>27 Oct. 1983</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot</td>
<td>1.41</td>
<td>1.22</td>
</tr>
<tr>
<td>Control</td>
<td>2.26</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td>Reg***</td>
<td>Reg**</td>
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<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>30 Oct. 1983</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot (10 m × 10 m area)</td>
<td>1.82</td>
<td>1.49</td>
</tr>
<tr>
<td>Control</td>
<td>2.03</td>
<td>1.48</td>
</tr>
<tr>
<td></td>
<td>Reg***</td>
<td>Reg**</td>
</tr>
<tr>
<td>30 Apr. 1984</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot (10 m × 10 m)</td>
<td>0.98</td>
<td>1.00</td>
</tr>
<tr>
<td>Control</td>
<td>0.96</td>
<td>2.86</td>
</tr>
<tr>
<td></td>
<td>Reg***</td>
<td>Reg**</td>
</tr>
</tbody>
</table>

* The 10 × 10 m plot after exclusion of 1 m² quadrats from the perimeter

Table 2. *Haliotis laevigata*. Values of the v:m ratio and *R* statistic before and after a manipulation of the dispersion of abalone in an experimental plot at Waterloo Bay on 27 April 1984. See Table 1 for further details.

<table>
<thead>
<tr>
<th>Date and site</th>
<th>v:m ratio</th>
<th>R statistic</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>≥ 120 mm</td>
<td>Total pop</td>
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<tr>
<td>27 Apr. 1984</td>
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<td>Plot</td>
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<td>Control</td>
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<td>2.86</td>
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<tr>
<td></td>
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<td>Reg**</td>
</tr>
<tr>
<td>30 Apr. 1984</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plot (10 m × 10 m)</td>
<td>0.97</td>
<td>0.98</td>
</tr>
<tr>
<td>Control</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>

These behaviours are: food sharing, group defence, and spawning. These are each considered in relation to abalone.

If the habitat is heterogeneous, a species will tend to occur in a restricted number of favourable sites and may then show an aggregated dispersion. This is better known for intertidal than subtidal molluscs (Underwood, 1976a, b). The preferred habitat of *Haliotis laevigata* is in a crevice, and if none is present it appears to move about slowly until it finds one (Shepherd, 1973, and in preparation). At West Island, crevices occur between every pair of boulders, which are spread throughout the study site. There is no reason to think that the physical characteristics of crevices vary in the area or influence the
dispersion pattern of abalone. At Waterloo Bay, the low ridges scattered throughout the area also seem unlikely to affect the dispersion of abalone.

Of the three facilitation mechanisms, food-sharing is unlikely because drift alga on which this species feeds is in superabundance (Shepherd, 1973; Shepherd and Hearn, 1983), and individuals have rarely been observed sharing the same piece of drift alga. This contrasts with the study of Duggins (1981), who recorded a high incidence of sharing of drift algae between species of sea-urchins.

Aggregation is well established as a group defence mechanism for species such as sea-urchins, whose spines can form a formidable array to a predator (Pears and Arch, 1969; Bernstein et al., 1983). However, it is a tactic of doubtful utility for adult abalone, whose major predator is the sting-ray (Shepherd, 1986). The evidence is rather the other way, namely that aggregation is a disadvantage because predators are more successful when searching for clumped, than for randomly dispersed, prey (Timbergen et al., 1967; Croze, 1970; Taylor, 1977).

In this study, a spawning mechanism is the simplest explanation for aggregation. The clumping pattern becomes established only with increasing size after attainment of sexual maturity, is strongest during the spawning season, and relaxes between spawning seasons. Field manipulations only temporarily interrupt the pattern in the spawning season and demonstrate that it is not a merely passive response to environmental factors. Two other studies on abalone have also related this behaviour with spawning. Breen and Adkins (1980) observed aggregations of Haliotis kamtschatkana Jones, in which individuals sought local elevations on the bottom, and even climbed on top of one another while spawning. Uno et al. (1972) found that the intensity of aggregation of H. steboldii Reeve decreased after the spawning season.

Because Haliotis laevigata lives in places of vigorous water movement (Shepherd, 1973) and fertilisation of gametes is external, aggregation may function as a mechanism for maximising contact between eggs and sperm and hence secure a high fertilisation rate. Kikuchi and Uki (1974) found optimum fertilisation at sperm densities of 100 000 to 190 000 ml⁻¹. Dilution of sperm below such concentrations would occur at a relatively short distance from spawning males.

The aggregative behaviour of abalone may have practical significance in managing fish stocks. Fishing mortality rates are likely to be higher for aggregated abalone than more randomly dispersed ones (Breen and Adkins, 1980), and this may have a strong effect in excessively reducing the adult stock and thus affecting recruitment.

Recruitment overfishing is a problem which has affected many abalone stocks (Doi et al., 1977; Wyner et al., 1977; Breen, 1985), and Sluczanowski (1984) has suggested that enhancement of egg production is an important goal in managing these fisheries. A seasonal closure of this fishery during the spawning season would be an effective step to achieving a dual goal of increasing egg production and reducing fishing effort.

Acknowledgements. I am grateful to P. Clarkson, C. H. Deane and J. Turner for assistance in the field and for useful discussions, and to Dr P. R. Sluczanowski and Dr W. G. Inglis for helpful comments on the manuscript. Funds supporting the study were received from the Fishing Industry Research Trust Account.

Literature cited


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CHAPTER 10

MEASURING DENSITY

The use of catch per unit effort (CPUE) as a measure of abalone abundance depends inter alia on assumptions about the random mixing of fished and unfished populations; these do not hold in abalone stocks and CPUE is in fact, known to be insensitive to changes in density of abalone and is thus unreliable as an indicator of stock density. Indeed Harrison (1983) has explained changes in CPUE in terms of mechanical efficiency of divers, and changes in skill, Prince and Hilborn (pers. comm.) add location of fishing grounds (distance from home port) and diver motivation as factors influencing catch rates. Breen (1980) and Fedorenko and Sprout (1982) reviewed the problems of CPUE as a measure of density of northern abalone. Factors considered by them included:

(1) differences in efficiency between divers and over time;
(2) the unreliability of fishermen's logs;
(3) the tendency for quotas to decrease effort intensity;
(4) the variation of effort intensity between sites according to exposure to harsh weather conditions.

They concluded that CPUE was not useful as a direct index of relative abundance in H. kamtschatkana. These factors apply to all diving operations where a species is gathered by hand, and are applicable to the South Australian fishery. For these reasons CPUE is considered unreliable and at best a crude guide to changing abundance of abalone (Fedorenko and Sprout 1982).

The search for a method of assessing stock abundance and recruitment, independent of catch return information supplied by divers, led the author to develop a method adapted for use on the many deep-water off-shore populations of H. laevigata of the eastern Great Australian Bight. The method estimates abundance by a free range search technique carried out over a given time interval and converts this to a real density in the light of the known power of the research diver. The method has obvious advantage in deep-water (>20m) where diving time is very limited, and is probably the only method practicable at such sites. For shallower sites (such as Waterloo Bay) more conventional methods such as line transects are more accurate and therefore to be preferred.
However, even in Waterloo Bay, where clumping of abalone is extreme, mainly due to habitat heterogeneity the free range technique gives acceptable results.

Waterloo Bay was used in this study simply because its bottom topography has been described and is thus well-known (Shepherd and Womersley 1981), and because it was shallow and convenient to carry out the various experiments described. A serious disadvantage of the free range technique is the need to calibrate each diver and to re-calibrate him if a change in his power or efficiency is suspected.

Results of annual surveys of stocks using the method at numerous sites are given by Shepherd (1984).

References


POWER AND EFFICIENCY OF A RESEARCH DIVER, WITH A DESCRIPTION OF A RAPID UNDERWATER MEASURING GAUGE: THEIR USE IN MEASURING RECRUITMENT AND DENSITY OF AN ABALONE POPULATION

S.A. Shepherd
Department of Fisheries
135 Pirie Street
Adelaide, South Australia 5001

Experiments to measure the power, measuring time and efficiency of research divers are described. Power values for individual divers ranged from 15 to 27 m² min⁻¹ (mean 20.5 m² min⁻¹), measuring time from 2.9 to 6.2 seconds and the searching ability component of efficiency from 0.67 to 0.78. The power of a diver is affected by swell and algal cover.

Another component of efficiency, namely the diver’s ability to discriminate between habitat types shows no significant variation between divers but varies according to site characteristics, an needs to be taken into account.

The results are used to estimate densities of abalone by the free-range search method at several sites in Waterloo Bay, South Australia, and are compared with transect line censuses. The free-range search method tends to give higher estimates of density but has the advantage of substantial savings of time underwater.

INTRODUCTION

Surveys of extensive areas of reef are often necessary to establish population parameters of sedentary demersal species of economic importance. Quantitative methods most often used are quadrats or line transects and movie or still photography (see Dart and Rainbow 1976 and Kenchington 1978 for reviews). None of these methods is appropriate where the species sought is cryptic, aggregated and in low average densities; in such conditions the coverage of a very large area is necessary to obtain reliable results.

In determining the most appropriate technique, the pattern of distribution of
the species in question, and the amount of information required must be considered and weighed against the physical and logistic limitations imposed by working underwater. It is well known that an underwater study is several times more time-consuming and expensive than a comparable terrestrial one.

The free-range search technique (Kenchington 1978) where the diver searches freely over the bottom, is the most efficient in locating the maximum number of individuals of the species sought in a given time, because divers use their knowledge of the species' habitat to direct their searching and so maximise the use of time underwater. The difficulty of the method is that estimates of the density of the species cannot be readily derived from such data, unless the power and efficiency of the diver are known.

The greenlip abalone Haliotis laevigata Donovan lives on open rocky bottom usually near or in crevices (Shepherd 1973) and is fished for commercially in South Australia. Population studies of this abalone species in Waterloo Bay (33°39'S; 134°54'E) have been undertaken to investigate stock size and recruitment in different parts of the Bay. Surveys to estimate density were carried out in April 1982 and April 1983. The topography of the Bay and environmental features are described by Shepherd and Womersley (1981).

In this paper I describe experiments to calibrate the power and efficiency of research divers and apply the results to census data obtained by divers using the free-range search technique to locate and measure abalone with a gauge developed for the purpose. The power of a diver may be defined as the effective area covered by him per unit time (Reinsen 1979). Efficiency refers to the ability of the diver (a) to discriminate between 'abalone' and 'non-abalone' habitat, and (b) to find abalone in 'abalone' habitat. These two components are described below.

MATERIALS AND METHODS

A grid of 5 columns and 5 rows was established in Waterloo Bay and buoys were dropped at each intersection to mark a diving site (Fig. 1). At each of the 21 sites one or more divers swam for a total of four to six replicate periods of 10 minutes measuring all abalone (H. laevigata) that were seen, with the gauge described below.

![Figure 1. Waterloo Bay divided by a grid into sub-areas.](image-url)
Description of Gauge

The measuring gauge, of brass, (Fig. 2) consists of a slider on an arm which holds a strip of soft plastic (or waterproof paper) 2.5 cm x 25 cm, backed by a vinyl facing strip. A needle is inserted below a thumbplate to a flexible stainless steel arm. Pressure on the thumbplate impresses a hole in the plastic when a measurement is made. The flexible arm can be moved laterally to impress measurements on different parts of the strip. The gauge is operated easily by the diver with one hand and will record up to 100 measurements. The strip can be rapidly changed by the diver underwater. Measurements on the plastic can be 'read' under a low power microscope or microfiche reader.

Figure 2. Brass measuring gauge used to measure abalone in situ.

Power and Difficulty Coefficient of a Diver

Beinssen (1979) showed that the diving time of a research or commercial diver can be divided into two components; searching time and measuring time. The latter is proportional to the number measured.

Thus: \[ T = S + mN \] \hspace{1cm} (1)

where \( T \) is total diving time, \( S \) is searching or swimming time, \( m \) is measuring time per abalone, and \( N \) is the number of abalone measured. Equation (1) can be rewritten

\[ S = T - mN \]

\[ \text{hence} \quad Sr = Tr - mrN \] \hspace{1cm} (2)

where \( r \) is the power of the research diver.

Because different conditions of surge and algal density affect the swimming speed (and hence power) of a diver, a further variable 'd' must be introduced as a difficulty coefficient for different sites according to the prevailing surge and algal density at a given site. The parameter 'a' is a difficulty constant unique to each ith diver and represents the extent to which his power is affected by swell and algal density.

If data are available on area (A) searched and number (n) of abalone measured for a given period of time by a diver 'i' in areas with different densities of abalone and in different conditions of surge and algal density, \( r_i, m_i \) and \( d_i \)
can be estimated by regressing the area searched by him in a given time against
the number of abalone measured. Since \( A = S r \), the equation becomes:

\[
A_t = T r_t - m_t r/N + a t d \hspace{1cm} (3)
\]

An assumption is that diver proficiency is constant over time. In this study
the same group of experienced divers were used in order to minimise within
diver variability, (i.e. any increasing proficiency of a diver over time as he
\big) gains experience).

Preliminary experiments have shown that in Waterloo Bay the diver can
effectively cover a swathe about 1 m while searching for abalone; beyond the
boundaries of the swathe below him he sees only about 30% of the abalone in the
adjoining 1 m swatches (unpublished data). The power of a diver was measured
directly by requiring him to swim successively along each side of a 50 m tape
laid on the bottom and measure those individuals within 1 m of the tape. After
10 minutes the diver recorded, by reference to the tape, the distance covered.
If both traverses were completed in less than 10 minutes, then the diver moved
several metres to one side of the tape and continued as before until 10 minutes
expired. For each diver, data on numbers measured and distance covered were
obtained at different sites in 1982 and 1983. Values of the coefficient of
difficulty 'd' were estimated for each site in Waterloo Bay on a composite 5
degree scale, comprising indices* of surge and algal density, and were based on
the environmental data given by Shepherd and Womersley (1981). Equations of
the form described above were fitted to the data for each diver by multiple
regression analysis by using an iterative non-linear estimation procedure in the
GLIM (Generalised Linear Interactive Modelling) computer package.

Diver Efficiency

While searching for abalone in a patchy environment a diver searches for
suitable habitat, and abalone within that habitat. The efficiency of a diver
therefore has two components operating at different scales:

(1) Habitat Discriminatory Ability (HDA). In a heterogeneous environment the
habitat can be stratified as:

(a) 'Abalone habitat' (Ha) comprising mostly bottom of low relief (<1m
high), and

(b) 'Unsuitable Habitat' (Hu) comprising a variety of habitats where
abalone do not occur e.g. sand patches, reef of moderate to high
relief (>2m high).

These categories of habitat type can be readily distinguished by a diver
and the mean proportion of each type estimated by measuring the proportion
of linear length of each habitat type lying under a transect line set out
randomly on the bottom. Hence the proportion of Ha (\( P_{ha} \)) at a given site
is given by:

\[
P_{ha} = \frac{Ha}{Ha + Hu} \hspace{1cm} \text{(4)}
\]

*The index of surge is little surge - 0; average conditions - 1; strong surge
- 2. The algal density index is low - 0; average - 1; high - 2. The composite
index ranged from 0 for sites in the inner part of the Bay to 4 at the entrance
and near the Bar (Fig. 1).
P·ha was obtained for each site by laying a 50m transect line on the bottom at random (with 5 replicates) and directly measuring the total linear lengths of habitat types Ha and Hu.

A diver, while searching with the free-ranging technique, selectively searches in abalone habitat and avoids as far as possible unsuitable habitat (Fig 3). In a patchy environment, however, it may be necessary to swim over unsuitable habitat and hence a proportion of the diver's searching time is spent both in suitable and unsuitable habitats.

![Diagram of diver's track while searching for abalone.](image)

**Figure 3.** Schematic diagram of diver's track while searching for abalone.

The proportional area of each habitat type (Ha and Hu) covered by a diver can be measured by the swimming time spent in each. This was done by using a stop-watch underwater during a normal search and recording the number of seconds spent swimming over various habitats. The proportion of total time spent (\(PT\)) by a diver 'i' in abalone habitat is given by:

\[
PT_i = \frac{SA_i}{SA_i + SU_i} \quad \quad (5)
\]

Where \(SA_i\) is his swimming time in abalone habitat and \(SU_i\) is his swimming time in unsuitable habitat. This ratio is the effective (i.e. searched) proportion of total area covered that represents abalone habitat. The habitat discrimination index (HDI) is given by:

\[
HDI = \frac{P_{TI}}{P_{ha}} \quad \quad (6)
\]
and measures the diver's ability to discriminate between habitats during searches for abalone.

Between diver differences in $P_{ij}$ were measured in Waterloo Bay at a site (D2) of marked habitat heterogeneity (i.e. high rocky bottom relief of 2 - 3m with small scattered deep depressions containing abalone).

Two sub-areas, one with higher abalone density, and the other with lower abalone density were chosen and four divers carried out 6 replicate (2 in high and 4 in low, density areas) censuses by the free-range search technique. The results (in numbers of abalone measured) were analysed by analysis of variance after standardising for different powers, measuring times and searching abilities (see below) of divers. Comparing numbers of abalone found by different divers was thought to be a simpler and equally effective measure of a diver's $P_{ij}$ as attempting to record individual time spent in different habitats.

(2) Searching Ability. The second component of efficiency is the diver's ability to find abalone. This was measured by comparing the number of abalone >50nm long seen by a diver in a 100m$^2$ area (in strip each side of a 50 m tape in various parts of Waterloo Bay and in different conditions of water movement and algal cover, with the total number present. The latter was obtained by a thorough search of the same area by an independent diver. The ratio of number found ($n_i$) by diver $i$ to the total number present ($t$) is a measure of the diver's efficiency ($E_i$), i.e.

$$E_i = \frac{n_i}{t} \quad \text{..........................(7)}$$

Abundance of Abalone

When the number ($N$) of abalone and the area ($A$) are known, estimates of density ($D$) can be derived. However both $N$ and $A$ must be weighted by the respective components of diver efficiency. The number ($N_i$) seen by the $i^{th}$ diver must be divided by $E_i$ his searching ability to give the total number ($N_T$), i.e.

$$N_T = \frac{N_i}{E_i} \quad \text{..........................(8)}$$

The area ($A_i$) covered by him must be multiplied by $H D I_i$ to give the true area ($A_T$), i.e. $A_T = \frac{A_i}{H D I_i}$

By substituting from Equations (3) and (8) the density ($D$) is derived.

$$D = \frac{N_T}{A_T} = \frac{N_i}{E_i H D I \left(T r_i - a_i + \frac{r_i N_i}{N} + \frac{a_i d}{N} \right)} \quad \text{..........................(9)}$$
RESULTS

Power and Difficulty Coefficient

Results of multiple non-linear regression analyses of area searched against number of abalone measured and the difficulty coefficient at various sites are given for six divers in Table 1. Power values ranged from 15 to 27 m² per minute, measuring time per abalone from 2.9 to 6.2 seconds and the difficulty constant from -13.8 to -34.3. It is of interest that the power of a diver is correlated with his difficulty coefficient ($r=0.84; P<0.05$). This simply means that a fast swimming diver is slowed down more by adverse conditions than a slower swimming diver.

Table 1. Parameters of multiple regressions for divers with values of power of a diver, measuring time per abalone, difficulty constant and efficiency estimates. Standard errors are given in brackets. $R^2$ values are given for each estimate with probability level ($^* P<0.05$; $^{**} P<0.01$; $^{***} P<0.001$)

<table>
<thead>
<tr>
<th>Diver</th>
<th>Power(r) (m² min⁻¹)</th>
<th>Measuring time (m) (secs)</th>
<th>Difficulty Coefficient (a)</th>
<th>$R^2$</th>
<th>Efficiency (Search Ability)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>27.0 (3.1)</td>
<td>2.9 (0.5)</td>
<td>-34.3 (11.0)</td>
<td>0.76</td>
<td>0.67 (0.01)</td>
</tr>
<tr>
<td></td>
<td>8.7 $^{**}$</td>
<td>5.4 $^*$</td>
<td>3.1 (8%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B</td>
<td>15.0 (0.6)</td>
<td>4.0 (0.3)</td>
<td>-13.8 (2.0)</td>
<td>0.92</td>
<td>0.74 (0.03)</td>
</tr>
<tr>
<td></td>
<td>24.0 $^{***}$</td>
<td>12.5 $^{***}$</td>
<td>6.9 $^{**}$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>18.7 (1.1)</td>
<td>3.1 (0.3)</td>
<td>-14.7 (4.1)</td>
<td>0.77</td>
<td>0.78 (0.02)</td>
</tr>
<tr>
<td></td>
<td>16.7 $^{***}$</td>
<td>8.9 $^{**}$</td>
<td>3.6 (6%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>D</td>
<td>18.5 (1.5)</td>
<td>3.1 (0.8)</td>
<td>-16.6 (3.3)</td>
<td>0.90</td>
<td>0.73 (0.03)</td>
</tr>
<tr>
<td></td>
<td>12.3 $^{***}$</td>
<td>4.0 $^*$</td>
<td>5.0 $^*$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>20.7 (1.0)</td>
<td>6.2 (0.4)</td>
<td>-17.9 (3.1)</td>
<td>0.89</td>
<td>0.77 (0.02)</td>
</tr>
<tr>
<td></td>
<td>20.0 $^{***}$</td>
<td>14.9 $^{***}$</td>
<td>5.8 $^*$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F</td>
<td>23.1 (1.9)</td>
<td>5.9 (0.5)</td>
<td>-26.5 (6.3)</td>
<td>0.90</td>
<td>0.77 (0.06)</td>
</tr>
<tr>
<td></td>
<td>12.1 $^{***}$</td>
<td>9.4 $^{**}$</td>
<td>4.2 $^*$</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Efficiency

The results of the experiment to measure between diver differences in HDI (Table 2) showed no significant differences between divers, but significant differences between densities. It was concluded that divers' ability to recognize abalone habitat does not differ significantly between divers.

HDI values differ between sites according to the degree of habitat heterogeneity. This can be shown by plotting $P_{Tj}$ versus $P_{Ha}$ for various sites in Waterloo Bay (Fig. 4). Values of $P_{Ha}$ approaching 0 or 1 indicate minimum habitat heterogeneity in terms of abalone habitat, whereas intermediate values indicate maximum heterogeneity. Note that maximum values of HDI ($P_{Tj}/P_{Ha}$) occur at intermediate values of $P_{Ha}$ i.e. in high habitat heterogeneity.

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Table 2. Effect of diver and abalone density on number of abalone recorded by divers.

<table>
<thead>
<tr>
<th>Source</th>
<th>SSQ</th>
<th>DF</th>
<th>MSQ</th>
<th>F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diver Density</td>
<td>19.4</td>
<td>3</td>
<td>6.5</td>
<td>0.35</td>
</tr>
<tr>
<td>Density</td>
<td>2518.7</td>
<td>1</td>
<td>2518.6</td>
<td>116.49</td>
</tr>
<tr>
<td>Diver x Density</td>
<td>55.8</td>
<td>3</td>
<td>18.6</td>
<td>0.86</td>
</tr>
<tr>
<td>Explained</td>
<td>2593.9</td>
<td>7</td>
<td>370.5</td>
<td>17.14</td>
</tr>
<tr>
<td>Residual</td>
<td>345.9</td>
<td>16</td>
<td>21.6</td>
<td>127.8</td>
</tr>
<tr>
<td>Total</td>
<td>2939.8</td>
<td>23</td>
<td>127.8</td>
<td></td>
</tr>
</tbody>
</table>

The values for the searching ability of six divers are given in Table 1. Values ranged from 0.67 to 0.78. Divers with high power values tended to have lower searching ability but the inverse correlation between the parameters was not significant (r = -0.64; n.s.). The searching ability values for diver E were further examined for correlation with environmental variables. However, no correlation was found with underwater surge (r = -0.28; n.s.) or underwater visibility (r = 0.38; n.s.) and it was concluded that over the ranges of these factors tested they did not affect a diver's searching ability. However it should be noted that no experiments were conducted when visibility declined below about 2m.

Figure 4. A plot of proportion of total diver time spent in abalone habitat (P_{Ti}) against proportion of abalone habitat (P_{ha}).

Abundance of Abalone

Using Eq. 9 estimates of the density of recruits (1+ yrs) and of the total population of H. Iaevigata at 5 sites in Waterloo Bay are given for 1982 and 1983 (Table 3).
Table 3: Comparison of abalone density estimates between free-range method (this paper) and transect line. Density in nos 100m⁻². Standard errors in brackets n.o. = not obtained.

<table>
<thead>
<tr>
<th>Site</th>
<th>1982 Free-range census</th>
<th>1983 Free-range census</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Recruits (1+ yrs)</td>
<td>Total</td>
</tr>
<tr>
<td>A1</td>
<td>1.0 (0.2)</td>
<td>15.4 (4.1)</td>
</tr>
<tr>
<td>A2</td>
<td>0.1 (0.1)</td>
<td>11.3 (4.7)</td>
</tr>
<tr>
<td>A3</td>
<td>0.3 (0.3)</td>
<td>10.3 (4.3)</td>
</tr>
<tr>
<td>B2</td>
<td>2.7 (1.0)</td>
<td>40.2 (8.7)</td>
</tr>
<tr>
<td>B3</td>
<td>5.8 (1.9)</td>
<td>43.0 (3.4)</td>
</tr>
</tbody>
</table>

They are compared with estimates of density obtained by 4-6 replicate counts along a transect line at each site. The total time underwater for the free-ranging census per site was about half that for the respective transect line census because it takes 8-10 minutes to lay out and retrieve a 50m tape on the bottom. Thus there are significant savings in time underwater without any marked increase in the standard errors. Although density estimates by the two methods are highly correlated (r = 0.91; P<0.001) the free-ranging census method in all examples except one gave higher estimates than the transect line census.

DISCUSSION

This study is the first to estimate by direct means the power and search ability of divers in differing conditions of swell and algal cover, and to determine the searching behaviour of divers in a heterogeneous environment. The experimental procedure to estimate r (the diver following a tape) could affect the kind of habitat searched by him, but not his power, which is determined by his swimming speed. This is affected by swell, which increases drag, and algal cover which impedes searching. The mean estimate of power for the six divers - 20.5 m² min⁻¹ (- 122.5 m² h⁻¹) is close to the estimates obtained by Beinssen (1979) for the research diver - 1306 (s.e. 73) m² h⁻¹. However, Beinssen (1979) did not estimate variability between divers or environmental effects on r or consider the effect of habitat heterogeneity. These differences are substantial and need to be taken into account if different divers are used and in different weather conditions or in different habitats.

A difficulty of the free-range search method, (shared also by Beinssen's (1979) method) is that it uses distance between abalone (measured by swimming time) to estimate density. If abalone were dispersed randomly the measure would be unbiased, but because abalone are aggregated in favourable sites the measure will tend to over-estimate density (Pielou 1969, Lamarcraft et al. 1983). It is likely that the consistent over-estimation of density for the 5 sites (Table 3) is due to the aggregation of this abalone. However if the within-site spatial pattern of distribution at a given site is constant over time, the estimates should give reasonable comparisons of relative density (or recruitment) at a site from year to year. If the spatial pattern changes (as during a closure to fishing) then it may be important to obtain data on the size of aggregations and the distances between them.
The method is applicable to any sedentary, benthic organism occurring in low
densities, but for more abundant organisms, quadrats or line transects would
give better estimates of density.

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CHAPTER 11

CONCLUSIONS

To what extent has the study met the objectives given in Chapter 1? In this chapter I review what has been achieved and what needs to be done. The initial question posed by this thesis: namely What are the factors regulating an abalone population? - as shown by the Paulik diagram in Ch.1, must be reduced to analyses of functional relations in the three sequential phases of the life history. Here I review each phase, and consider the achievements and what still needs to be done.

Juvenile mortality function

The findings of Part 1 represents a major contribution to an understanding of the juvenile mortality function. Chapter 2 describes a method for measuring quantitatively density of settlement at an early post-settlement stage when the effects of post-settlement mortality are slight.

An important collateral finding is the dependence of newly settled abalone on a crustose coralline micro-habitat. This was verified by the description of the food and feeding of juveniles (Ch.5). A practical consequence of this habitat dependence is that searching for juveniles can be concentrated on one micro-habitat with savings in diving time. Overall the technique for measuring post-settlement strength, especially by using standardised collection frames, as described, will enable valuable quantitative comparisons of settlement strengths for experimental purposes. However, a disadvantage is that data collection is costly in terms of diving time and this probably precludes widespread use of the technique as a monitoring tool.

The quantification of settlement strength facilitated the measurement of juvenile mortality. But first it was necessary to age individuals and this required a study of growth (Ch.3). The presence of two abalone species in the same habitat posed some problems in distinguishing them especially at a small size, but offered the benefit of being able to compare their subsequent growth. Lastly in Ch.4 the analysis of 4 year's survival data on 2 species provides an insight into the nature of the juvenile mortality function for one
site. The results suggest that juvenile mortality is independent of density, although some density dependence may operate at high densities of settling abalone. There are two caveats: first the time series is as yet inadequate for a firm conclusion, and at least another 4 years data are required; second, the method of measuring natural mortality needs to be verified by an independent method such as the Deinissen-Powell technique.

The significance of the above findings is that the juvenile mortality function is likely to be the locus where dampening will occur but high variability is unlikely to be induced. That is, that very strong settlements will be dampened down by density-dependent mortality so preventing the population increasing beyond bounds. So far there is no evidence for the opposite mechanism, namely that very poor settlements will have very high survival, so promoting a tendency for recruitment to level out from year to year. It follows that the cause of high variability in recruitment is to be found in the egg mortality function, rather than the juvenile mortality function. A practical consequence of this for monitoring abalone stocks is that it is sufficient to monitor recruitment when abalone reach about 3 years of age, enter the habitat of adult abalone, and become accessible to a diver.

Egg production function
A description of this function requires measurement of adult density of abalone, measurement of adult mortality rates, examination of the fertilisation process and the measurement of population fecundity.

A methodological problem (how to measure adult densities in the field) is addressed in Ch.10. Adult natural mortality rates are examined in Chs 6 and 8. Ch.6 shows that adult mortality is not uniform, as is usually assumed, but may vary greatly, at least in an unshifted population. Here an apparent density dependent mortality operates both as a dampening mechanism preventing the population increasing beyond bounds and as a buffer against extinction by permitting the population to persist at low levels with little further decline in numbers.
Measurement of natural mortality is not easy and often requires measurement of long term movement as well. This aspect, with suggestions as to the basis of abalone movement, is addressed in Ch.8. Overall, natural mortality rates of 0.2-0.3 appear to be general in exploited populations.

A further important consideration is the success of fertilisation of eggs. This question was addressed not directly, but by examining the aggregation behaviour of abalone which is a pre-requisite for successful fertilisation of eggs. An implication of the study (Ch.9) is that if adult densities fall below some critical level, when individuals are too far apart to find each other, fertilisation will decline to nearly zero (see egg production function in Ch.1, Fig.1).

The last element is fecundity itself. A study of its relation with weight (Ch.7) led to the general conclusion that a simple linear relationship is valid for nearly all populations. This simple relation is made more complex by the variability that occurs between and within populations, due to variability in food supply and possibly genetic differences as well. In general the egg production function appears to be the simplest and most regular of the several functions in the abalone life history, and with the least variability. Nevertheless, some strings remain untied and need to be addressed; more precise methods need to be found to measure densities of adults in the field, or at any rate the method developed (Ch.10) needs validation by further experiments; adult mortality rates are not well enough known for many places; and finally, the genetic component of variability between populations in fecundity needs to be examined by transplant experiments.

Stock Recruitment Relations
The Paullik diagram connects the sequence of links in the life history of abalone and brings together the opposite ends of the chain; namely stock and recruitment. In 2 phases of the sequence, there are strongly stability - Inducing, density dependent processes, that collectively provide redundancy and control the population. If regulation in one phase fails, compensation will occur in the next. The independence of the successive phases ensures that failure at one stage is unlikely to be repeated later in the system. At West 1, we have seen how strong pulses of recruitment are evident in censuses.
for several years but are eventually reduced by a high adult mortality rate. Conversely when the adult population is low the natural mortality rate falls to a low level and the population persists during periods of recruitment failure. But the Paullik diagram does not take into account the de-stabilising component of the system, namely the relation between the several life history phases and the environment. At West Island environmental factors operating in the egg mortality phase appear responsible for the high variability in recruitment. The resultant impression is that there is no relation at all between stock size and recruitment, which of course cannot be true. The only conclusion that can be drawn from the West Island data is that the population is on the plateau of the stock-recruitment curve, and well above the critical level of stock density, below which there must be a direct relation between stock abundance and number of recruits. The determination of the 'critical' level of density and the environmental factors that cause the great variability in recruitment remain as two fundamental, and as yet elusive, goals of research into abalone.

The former question can be answered by examining over a number of years the recruitment pattern of a collapsing stock, or alternatively of several replicate stocks maintained at high, medium and very low levels of density. Note that both kinds of experiments require an understanding of what constitutes a unit stock. As yet there is little understanding of this subsidiary question. Electrophoretic studies of *H. laevigata* by L Brown (pers. comm.) show small, but significant differences in the frequencies of the less common alleles between the isolated populations described in Ch.7, and support the view that these populations constitute unit stocks. But field studies need to be carried out to establish the extent of larval dispersal at several scales.

Determination of the environmental factors that influence settlement success is even more formidable and will only be understood after long term studies, and in the light of knowledge of oceanographic and other events that trigger spawning. So far this is not known for any abalone species, although anecdotal evidence suggests that very calm seas are a critical element. This problem is one aspect of the egg
mortality function (Ch.1) which is outside the scope of this thesis, but remains as the principal barrier to an understanding of the relation between stock and recruitment.

It is important here to distinguish between monitoring and understanding the performance of a system and predicting how it will work. This thesis has elucidated much of the temporal and spatial dynamics of two abalone species from larval settlement through adulthood, and has described their interactions with other species and environment. The groundwork is now laid for the pursuit of the next goal - understanding the egg mortality function, which will complete the functional descriptions of the life history phases and hence provide a holistic account of the relation between stock and recruitment. Only then can we achieve a complete understanding of, and an ability to predict, the dynamics of abalone populations.
APPENDIX I


Anthozoans are ubiquitous on rocky substrata in temperate waters yet there have been few studies of their natural diet in southern Australia or elsewhere. The anemone *Anthothoe albocincta* (Stuckey) is the most common anemone at West Island, South Australia (35°37'S, 134°52'E) and occurs on the northern side of the island at 4-5 m depth, at a mean adult population density of 12.5 m⁻² (SE = 2.8), with a mean column diameter of 10.1 mm (size range 7-14 mm). The species is described and figured by Thomas & Shepherd.

During the course of an experimental investigation of the settlement of abalone we examined the role of this anemone as a potential predator of settling abalone larvae. This species, like most anemones, is a passive suspension feeder that captures prey, usually zooplankton, brought to the tentacles by ambient currents.

The habitat of *A. albocincta* is usually near the sandline on rocky substrata, under boulders or at the entrance of crevices. The tentacles project into the current and the tentacular crown fans outwards and downward to a width of one millimetre, enabling the tentacles to sieve the water passing between them. Up to 200 conical tentacles to 15 mm long are borne at the oral disc. Distance between the larger, inner tentacles is about 2-4 mm at the mid points and 8 mm at the tips. The finer, outer tentacles are spaced 0.5-1 mm apart at the mid point and up to 2 mm apart at the tips. Particles captured are passed from the outer to inner tentacles and then to the mouth. Mean mouth size of the sample was 2.3 mm but it can expand considerably.

We observed nocturnal rhythm in the expansion and contraction of tentacles and usually 60-90% of *A. albocincta* were expanded day and night. In this respect this anemone resembles most other studied subtidal temperate species that have zooxanthellae.

In this note we describe the coelenteron contents of a sample of 38 adult *A. albocincta* taken at West I during December 1984 when competent abalone larvae are expected to settle. Samples were preserved in formalin and sea-water and subsequently examined in the laboratory under 40x magnification with a dissecting microscope. Mesenterial filaments of *A. albocincta* are numerous and it was necessary to dissect each anemone and scrape the filaments to free partially digested prey.

The coelenteron contents of the sample of *A. albocincta* are given in Table 1. Crustacean appendages and other crustacean fragments are the most abundant items but positive identifications were not possible due to partial digestion; their size and shape suggested that many of them are probably amphipods. Judging from the abundance of complete and fragmented crustaceans found in the coelenteron, the abundance of common taxa is in the order: amphipods, ostracods and copepods. Of the non-crustacean items, invertebrate eggs are the most abundant by far, with bivalve and gastropod larvae and foraminifers less common. There are also quantities of macro-algal fragments and fragments of encrusting organisms such as sponge, hydroids and coralline algae (included in red algae in Table 1). The mean length range of prey categories is from 0.17 mm to 2.08 mm with standard deviations ranging from 1/3 to greater than the means.

The size distribution for all prey items (Fig. 1) is skewed to smaller sizes with a mode at 0.4-0.6 mm. However this

<table>
<thead>
<tr>
<th>Table 1. Coelenteron contents of Anthothoe albocincta.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
</tr>
<tr>
<td>n</td>
</tr>
<tr>
<td>----</td>
</tr>
<tr>
<td>Amphipods</td>
</tr>
<tr>
<td>Cladocerans</td>
</tr>
<tr>
<td>Copepods</td>
</tr>
<tr>
<td>Isopods</td>
</tr>
<tr>
<td>Mysis</td>
</tr>
<tr>
<td>Ostracods</td>
</tr>
<tr>
<td>Crustacean appendages</td>
</tr>
<tr>
<td>Other crustacean fragments</td>
</tr>
<tr>
<td>Gastropod larvae</td>
</tr>
<tr>
<td>Bivalve larvae</td>
</tr>
<tr>
<td>Annelids</td>
</tr>
<tr>
<td>Nematodes</td>
</tr>
<tr>
<td>Foraminifera</td>
</tr>
<tr>
<td>Sponge fragments</td>
</tr>
<tr>
<td>Bryozoan fragments</td>
</tr>
<tr>
<td>Invertebrate eggs</td>
</tr>
<tr>
<td>Green algae (fragments)</td>
</tr>
<tr>
<td>Brown and red algae (fragments)</td>
</tr>
<tr>
<td>Dinoflagellates</td>
</tr>
<tr>
<td>Spines, spicules</td>
</tr>
<tr>
<td>Shell fragments</td>
</tr>
<tr>
<td>TOTAL</td>
</tr>
</tbody>
</table>
The coelenteron contents of this anemone is similar in terms of taxonomic prey categories to that of other temperate anemones studied, and we likewise conclude that the diet of this anemone, in summer at least, is principally of decapod crustaceans and larvae of benthic organisms. Its ability to capture plankton over a wide size range and, in particular, active species like amphipods, implies that it is capable of capturing weakly swimming prey such as abalone larvae in the size range 0.25-0.5 mm. Nevertheless, while this anemone may be a potential predator of abalone larvae, its importance as a predator depends on presently unknown ecological factors such as the sieving efficiency of the tentacular crown. Its effect on the density of settling larvae may in fact be slight, since a study of abalone settlement using experimental boulder structures found more newly settled abalone on structures with anemones present than on structures from which they had been removed.

We thank the Department of Fisheries for a student grant, Michelle Jenkins for technical help and Dr R. Black for helpful criticism of the manuscript.

S. A. SHERPHERD and J. D. GRAY, Department of Fisheries, 135 Pirie Street, Adelaide, South Australia, 5000.
THE CRAB FAUNA OF WEST ISLAND, SOUTH AUSTRALIA:
THEIR ABUNDANCE, DIET AND ROLE AS PREDATORS OF ABALONE

By A. G. J. MOWER & S. A. SHEPHERD*

Summary


Twenty-three species of crabs are recorded from West Island, South Australia. The vertical distribution and densities of sixteen species occurring on the boulder slope at Abalone Cove on the northern side of the Island, are described and the diets of the five most common species enumerated. Four of the species are mainly herbivorous but eat small amounts of animal matter and one species is omnivorous. Four of the species also ate small abalone in cage experiments and represent potential agents of abalone mortality.

KEY WORDS: crabs, abalone, diet, predation.

Introduction

The need to understand the recruitment process in abalone, necessary for the proper management of abalone fisheries has focused increasing attention on the ecology of juveniles and in particular of the agents of mortality. Dead abalone shells are frequently found damaged in different ways, but there is dispute whether this is caused by crabs, or is due to natural causes such as abrasion (Hines & Pearse 1982; Tegner & Butler 1985).

Studies on the ecology of juvenile Haliotis laevigata Donovan, and Haliotis scalaris Leach have been in progress at West Island, South Australia (35°36'25"S; 138°35'27"E) since 1983 (Shepherd & Turner 1985) but their predators are still largely unknown. Several crab families, which are represented at West Island, are known to attack and feed on molluscs, often inflicting shell damage (Skilleter & Anderson 1986; Vermeij 1977; Zisser & Vermeij 1978; Williams 1982).

This study describes the abundance and diet of the crab species present on a boulder slope at West Island the site of earlier studies, and gives the results of preliminary experiments to determine whether crabs eat abalone and the type of damage to the shell inflicted by them. An ancillary purpose was to accumulate information on a group of consumers, leading to a better understanding of the benthic food-web of the Island.

Materials and Methods

Twenty samples were taken at 1 m depth intervals from 1-5 m depths on the boulder slope of the study site on the northern slope of West Island (see Kangas & Shepherd 1984). A quadrat, 0.25 m² in area, was placed on the boulders and the area within the perimeter was searched systematically for crabs by removal of all boulders down to the sandy substratum. The sand below the boulders was then sifted by hand to collect any burrowing species.

Animals collected were identified to species and preserved in 70% alcohol. Subsequently the gastric mill was removed in the laboratory and the contents mounted on microscope slides in Karo, a light corn syrup. Only gastric mills subjectively estimated to be more than half full were examined in order to avoid biased estimates due to differential retention time of different prey items in the mill (Williams 1981).

Slides were placed on a grid and the material under each of 25 grid intersections was identified to the lowest taxonomic category possible. This method estimates the percentage composition of food items by volume (Berg 1979). Subsequently plant material was classified as green, brown or red macro-algae, filamentous algae (a polyphyletic group), genticulate corallines, comprising species in the genera Jania, Halimeda and Cheilosporum, seagrass, comprising Posidonia or Heterozoster, and unidentified matter. Animal material was classified as sponge, foraminifers, echinoderms, molluscs, crustaceans, and unidentified matter. The presence of sand grains was also recorded.

A series of "no choice" feeding experiments was conducted in plastic cages set on the sea-bed at West Island to determine whether crabs attacked abalone in the absence of other food, and to determine the nature of shell damage inflicted. In each cage 4-6 juvenile H. scalaris over a range of sizes were placed on boulders in the cage with a number (usually 4) of crabs of a given species. Controls with abalone but without crabs, were placed in an adjoining cage and all cages were recovered after intervals of 5-21 days. In addition observations were made on the period of activity of four species of crabs kept in aquaria.

* Department of Fisheries, 135 Pirie Street, Adelaide, S. Aust. 5000.
<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANOMURANS</td>
<td>— Porcellana dispar (Stimpson) B, 1-5</td>
</tr>
<tr>
<td>Porcellanidae</td>
<td>— Lomis hirta (M. Edwards) B, 1-5</td>
</tr>
<tr>
<td>Lithodidae</td>
<td>— Paguristes frontalis (M. Edwards) B, 3-5</td>
</tr>
<tr>
<td>Paguridae</td>
<td>— Paguristes sulcatus (Baker) B, 1-5</td>
</tr>
<tr>
<td></td>
<td>— Paguristes brevirostris (Baker) B, 5</td>
</tr>
<tr>
<td></td>
<td>— Pagurus sp. 1 B, 5.</td>
</tr>
<tr>
<td></td>
<td>— Pagurus sp. 2 B, 5.</td>
</tr>
<tr>
<td></td>
<td>— Galathea australiensis (Stimpson) B, 1-5</td>
</tr>
<tr>
<td>Gallatheidae</td>
<td>— Huemia protus (de Haan) F, 10.</td>
</tr>
<tr>
<td>BRACHYURANS</td>
<td>— Naxia austral (Latrielle) B, 1-5; E, 13.</td>
</tr>
<tr>
<td>Majidae</td>
<td>— Panzylus latipes (Baker) B, 2-4</td>
</tr>
<tr>
<td>Goneplacidae</td>
<td>— Lithochea bispinosa (Kinahan) B, 3.</td>
</tr>
<tr>
<td>Hymenosomatidae</td>
<td>— Halicarcinus ovatus (Stimpson) B, 2-4</td>
</tr>
<tr>
<td>Dramidae</td>
<td>— Petalamera lateralis (Gray) B, 3.</td>
</tr>
<tr>
<td>Xanthidae</td>
<td>— Pilumnus rufopunctatus (Stimpson) B, 1-5</td>
</tr>
<tr>
<td></td>
<td>— Pilumnus fissifrons (Stimpson) B, 1-5</td>
</tr>
<tr>
<td></td>
<td>— Heteropilumnus fimbriventer (M. Edwards) B, 4</td>
</tr>
<tr>
<td></td>
<td>— Actaea peroni (M. Edwards) B, 3-4</td>
</tr>
<tr>
<td></td>
<td>— Actaeo calculesa (M. Edwards) B, 3.</td>
</tr>
<tr>
<td></td>
<td>— Megameteo carinatus (Baker) B, 1-5</td>
</tr>
<tr>
<td></td>
<td>— Brachynamus octodentatus (M. Edwards) terrestrial</td>
</tr>
<tr>
<td>Portunidae</td>
<td>— Necrocarcinus tuberculosus (M. Edwards) B, 4-5</td>
</tr>
</tbody>
</table>

## Results

Twenty-three species of crabs, in 11 families, have been recorded in this and earlier collections at West Island (Table 1). Of these 20 were found on the boulder slope in this study. The vertical distribution of density of the six commonest species (density more than 0.1/m²) on the boulder slope is shown in Fig. 1. The two species of *Pilumnus* were not readily distinguishable in the field and are plotted together in Fig. 1. *P. fissifrons* was much less common than *P. rufopunctatus*. *Porcellana dispar* escaped rapidly on disturbance and our sampling technique is therefore likely to have underestimated its density.

There are two very abundant species, *Lomis hirta* and the hermit crab *Paguristes sulcatus*, with densities of 10-15/m², and four moderately abundant species *Pilumnus rufopunctatus, Paguristes brevirostrus, Megameteo carinatus, and Paguristes frontalis*. The remaining species are quite rare with densities of less than 0.1/m².

Five of the six most common species were used for dietary analysis. The mean percentage composition of food in the gut of a sample of 15 of each of these species is given in Table 2. The percentage discarded for gut analysis, where the gastric mill was less than half full is also indicated.

Two species (*Paguristes sulcatus and Pilumnus rufopunctatus*) are almost wholly herbivorous, two species (*Lomis hirta and Paguristes frontalis*) are mainly herbivorous but take small amounts of animal matter, and one species, *Megameteo carinatus* takes about equal amounts of plant and animal matter. Most collections were taken in morning dives, and it seems likely that the high incidence of empty gastric mills recorded by nocturnally active species (Table 2) is related to their nocturnal feeding and rapid fore-gut clearance (Table 3).

The results of "no choice" feeding experiments (Table 3) show that four out of five common species captured and are small abalone mostly in the length range 15-32 mm. Two species of crab chipped the

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![Fig. 1. Distribution of density of crabs on the boulder slope, in Abalone Cove, West Island.](image-url)
Table 2. Mean percentage composition of contents of gastric mill of five species of crabs. In each case sample size is 15.

<table>
<thead>
<tr>
<th>Macro-algae</th>
<th>Lomis hirta</th>
<th>Paguristes sulcatus</th>
<th>Paguristes frontalis</th>
<th>Pilumnus rufopunctatus</th>
<th>Megametope carinatus</th>
</tr>
</thead>
<tbody>
<tr>
<td>green</td>
<td>3</td>
<td>5</td>
<td>3</td>
<td>6</td>
<td>-</td>
</tr>
<tr>
<td>brown</td>
<td>50</td>
<td>36</td>
<td>7</td>
<td>49</td>
<td>5</td>
</tr>
<tr>
<td>red (non-germicate)</td>
<td>60</td>
<td>24</td>
<td>14</td>
<td>13</td>
<td>2</td>
</tr>
<tr>
<td>(germicate coralline)</td>
<td>6</td>
<td>9</td>
<td>9</td>
<td>7</td>
<td>16</td>
</tr>
<tr>
<td>TOTAL % ALGAE</td>
<td>73</td>
<td>95</td>
<td>80</td>
<td>88</td>
<td>49</td>
</tr>
<tr>
<td>sponge</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>foraminiferan</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>echinoderm</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>mollusc</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>crustacean</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>12</td>
</tr>
<tr>
<td>unclassified</td>
<td>7</td>
<td>2</td>
<td>12</td>
<td>1</td>
<td>23</td>
</tr>
<tr>
<td>TOTAL % ANIMAL</td>
<td>20</td>
<td>5</td>
<td>15</td>
<td>6</td>
<td>49</td>
</tr>
<tr>
<td>sand grains</td>
<td>7</td>
<td>-</td>
<td>-</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>% with gastric mill &amp; half full</td>
<td>30</td>
<td>17</td>
<td>12</td>
<td>52</td>
<td>65</td>
</tr>
</tbody>
</table>

Table 3. The size range of predatory crabs and prey abalone, and the sizes of abalone, consumed and nature of shell damage inflicted and other details of "no choice" feeding experiments of crabs on abalone. Data on period of activity are from aquarium observations.

<table>
<thead>
<tr>
<th>Species</th>
<th>Lomis hirta</th>
<th>Paguristes sulcatus</th>
<th>Paguristes frontalis</th>
<th>Pilumnus rufopunctatus</th>
<th>Megametope carinatus</th>
</tr>
</thead>
<tbody>
<tr>
<td>carapace width of crab (mm)</td>
<td>11-18</td>
<td>8-12*</td>
<td>13-17*</td>
<td>10-15</td>
<td>18-35</td>
</tr>
<tr>
<td>abalone presented (length range - mm)</td>
<td>11-53</td>
<td>6-40</td>
<td>10-49</td>
<td>9-35</td>
<td>15-40</td>
</tr>
<tr>
<td>abalone taken (length - mm)</td>
<td>22-27</td>
<td>28, 40</td>
<td>25, 32</td>
<td>-</td>
<td>15-19</td>
</tr>
<tr>
<td>damage inflicted</td>
<td>growing edge sometimes chipped</td>
<td>none</td>
<td>growing edge chipped</td>
<td>-</td>
<td>growing edge chipped</td>
</tr>
<tr>
<td>number of experiments</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>duration (days)</td>
<td>5, 13</td>
<td>5, 13</td>
<td>12</td>
<td>12</td>
<td>13, 21</td>
</tr>
<tr>
<td>time of activity</td>
<td>none kept</td>
<td>day time</td>
<td>day time</td>
<td>night time</td>
<td>night time</td>
</tr>
</tbody>
</table>

* inferred from size of shell occupied.

Growing edge of the shell (Fig. 2) presumably during the process of capture. The controls showed no mortality of abalone and no chipped shells were observed on any individual.

Discussion

The factors influencing the vertical distribution of crabs are unclear and few comments can be made. Lomis hirta is morphologically strongly compressed in the dorso-ventral plane and clings tenaciously to the rock surface. It is thus well adapted to withstand strong water movements that occur in shallow water of 1-2 m depth where it is most abundant. It also has pincer antennal appendages suggesting that it also can filter feed planktonic organisms. Megametope is a burrowing crab mostly found below the sand surface under boulders and this may account for its apparent preference for depths of 4-5 m where sand accumulates between and under boulders.

Fig. 2. Chipped shells of Haliotis scalaris eaten by crabs during cage experiments.
Despite the bias toward herbivory in most species, whose feeding was studied, the cage experiments show that all except 
*Pilumnus rufopunctatus* can capture abalone and that the only damage inflicted by these crab species is slight chipping of the 
growing edge of the shell. This kind of damage is similar to that inflicted on abalone by crab species of the genera 
*Gaetea* and *Charybdis* (Kojima 1981), 
*Loxorhynchus* and *Cancer* (Tegner & Butler 1985) and 
*Macropipus ruber* (Clavier & Richard 1985). 

"No choice" experiments do not indicate whether or how many abalone are actually taken by a 
potential predator. The incidence of dead juvenile 
abalone shells with chipped edges in the under-
boulder habitat is low and only about 1-2/m² 
(Shepherd unpubl.) and this suggests that predation 
by these crabs is not high. This contrasts with the 
studies of Kojima (1981) and Tegner & Butler (1985) 
who reported that from one third to one half of 
the total mortality of young abalone was attributable to crab predation. Similarly Clavier & 
Richard (1985) considered crabs a principal predator 
of *Haliotis tuberculata.*

**Acknowledgments**

Messrs. L. Gray, A. Bennett, V. Karo all gave 
assistance in the field. We are grateful to Dr P. 
Abrams for identifying *Pagurus brevirrostrus* and 
to Dr. D. J. G. Griffin for identifying earlier 
collections of crabs from West Island. We thank Mr 
R. K. Lewis for criticism of the manuscript.

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southern Australian abalone (genus *Haliotis*). VI. 
Habitat preference, abundance and predators of 

morphology of the chelipeds, mouthparts and gastric 
mill of *Ozius truncatus* (Milne Edwards) (Xanthidae) 
and *Leptograpsus variatus* (Fabricius) (Grapsidae) 

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APPENDIX 2


Distribution and feeding of archaeogastropods in a boulder habitat at West Island, South Australia

by P.S. Clarkson and S.A. Shepherd

Department of Fisheries, G.P.O. Box 1625, Adelaide, South Australia 5001

ABSTRACT

The vertical distribution and feeding of eleven species of archaeogastropod were examined on a boulder slope at West Island, South Australia. Most species occur throughout the depth range, but species which feed on drift seagrass and algae occur in higher density at about 4m depth.

All species are herbivorous and feed variously on geniculate and crustose coralline algae, Petrosella crusts, macrophytes and drift seagrass and algae. There are minor differences between the species in microhabitat and type of food eaten.

Removal experiments show that, in the short term, these archaeogastropods (together with chitons) control the growth of filamentous algae on the upper sides of boulders.

INTRODUCTION

Subtidal boulders contain a complex community of erect and crustose algae, crustose animals and mobile grazing and predatory animals. Herbivorous molluscs in particular, play an important role in regulating benthic algal structure by controlling algal growth (Luckens 1974, Lubchenko 1978, Rafaelli 1979, Brawley and Adey 1981, Underwood and Jernakoff 1981). In order to elucidate the mechanisms controlling such a complex system it is necessary first to identify functionally similar groups of organisms and then to discover their effect by manipulations. This paper primarily addresses the former of these objects. It describes the distribution and feeding of some archaeogastropod molluscs in a subtidal boulder community, at West Island, South Australia and adds to an accumulating corpus of information on its biology, e.g. the algal communities (Shepherd and Womersley 1970), grazing by a chiton guild (Kangas and Shepherd 1984), and ecology of abalone (Shepherd 1973, Shepherd and Turner in prep.).
MATERIALS AND METHODS

The north shore of Abalone Cove, West Island, (35° 36' 25" South; 138° 35' 27" East) is a boulder slope with boulders, mostly 30 - 40 cm x 20 - 30 cm, and 20 cm high from about 0.5m depth to 5m at low water. At six depth intervals, 0.5m and from 1 to 5m at 1m depth intervals, 10 boulders were thoroughly examined, and the archaeogastropods (excluding limpets) on both the boulder upper and under surfaces, and on rocks below the boulder, identified and counted. This survey was conducted in March 1983 and again in September 1983. In order to estimate the density of archaeogastropods, the area of each boulder was taken to be its projection on the horizontal plane.

Archaeogastropods were collected between May and September 1983, and preserved in 10% formal sea-water. The stomach contents of samples of each species were extracted and spread out on a slide or petri dish for microscopic examination. The contents were scanned along several parallel lines, and the material under the cross of the eyepiece at equidistant points identified to morphological group.

Plant material was categorised as coralline algae (geniculate and encrusting), Petroderma crusts*, filamentous algae, brown, red or green macroalgae, and seagrasses, in accordance with the functional group approach of Steneck and Watling (1982).

A night dive was made on 21/6/83, and the presence or absence of normally cryptic species on the upper surfaces of boulders noted.

Percentage similarity (Bray and Curtis 1957) between the diets of 11 species was calculated and a dendrogram grouping species by the nearest neighbour method (Field and McFarlane 1968) was used to discover associations in terms of diet between species.

In a short term manipulation four experimental structures were set up on sandy bottom adjoining the subtidal boulder slope on 19 September 1983. Each structure consisted of a concrete base and 10 - 15 boulders all contained within a metal frame. The boulders were covered with crustose corallines and Petroderma sp., but all grazing animals (archaeogastropods and chitons) were removed from them. The controls were boulders which remained undisturbed at the base of the boulder slope and were subject to grazing by gastropods and chitons. We did not specifically control for disturbance of boulders because other experiments concurrently in progress showed that similar structures of boulders but with grazing molluscs on them, remained in the same condition in terms of algal cover as natural boulders.

The growth of erect algae on boulders was sampled by carefully taking the boulder from the water and scraping off the algae and trapped sediment on the upper surface from an area of 25cm², with four replicates on different boulders. Algae were dried at 50°C for 24 hours to give dry weight biomass.

RESULTS

The distribution of macro-algal communities described by dominance criteria, on the boulder slope in Abalone Cove is given in Fig. 1. Above and below boulders crustose red and brown algae, encrusting sponge, bryozoans, and ascidians (see Kangas and Shepherd (1964) for detailed distributional data) are abundant throughout the depth range.

Seventeen species of archaeogastropods (excluding limpets and abalone) were recorded on the boulder slope. Information on depth range, mean density, size range, and number of gut contents of species analysed are given in Table 1; six of the species were too rare to allow a study of their feeding. The depth distribution and density (averaged for the two surveys) of the 11 commoner species above and below boulders are given in Fig. 2.

Only three of the species (see Fig 2) occur on the upper, as well as under, surfaces of boulders during daylight hours. No additional species were recorded on the upper surfaces of boulders during the single night dive.

* refers to non-calcified algal crusts mostly of the genus Petroderma.
Two species showed substantial differences in abundance between the March and September censuses (Fig. 3). The G. preissiana population was mainly juveniles in September and adults in March, implying a recruitment at 4-5m depth and later upward migration. D. odontis tends to occur in clusters and the differences in Fig. 3 may be a sampling artifact.

The proportional abundance of different food types in the gut of 11 species is shown in Fig. 4. All species are herbivorous, with several food types commonly present in the gut. In some species small amounts of animal matter (mostly sponge but forams in the case of P. ventricosa and G. imbricata) are present in the gut, and are probably taken incidentally.

The dendrogram (Fig. 5) showing dietary similarities between species discloses several species groupings, some of which coincide with microhabitat differences between species. In general there is high overlap in diet between groups.

The first group, C. plebejus, E. aspersus and E. preissiana shares the same microhabitat on the underside of boulders and feeds mainly on sea-grass and crustose coralline algae. Extensive Posidonia beds and occasional patches of Heterozostera tasmanica occur on adjoining sandy bottom, and drift blades of these seagrasses and algae are abundant under and between boulders.

The species feed on drift, but not living, seagrasses. Except for G. preissiana, which eats considerable amounts of Zonaria spp. (27%), they eat little macroalgae.

The second group T. undulatus, T. torquatus and P. ventricosa live on the upper sides of boulders (except small P. ventricosa) and graze mostly on macrophytes and geniculate coralline algae (mostly Halicryptus spp.) The macrophytes eaten differ according to species. T. undulatus feeds on Ecklonia, (28%) on whose fronds it is commonly found, and green algae of the genus Caulerpa (27%). The other species take mostly brown algae of the genera Cystophora (sporelings and juveniles), Halopteris, Dictyota, Pachydictyon and Lobospira. The last two genera are common in the drift (Shepherd 1973) and are probably taken as detritus.

The species of the third group, D. odontis and B. squamifera, occur on the upper sides of boulders and feed substantially on crustose corallines and the same genera of brown macroalgae listed for the previous group.

Of the fourth group, C. limbatus lives on the under sides of boulders and G. imbricata in sand or gravel under boulders. Both species graze on crustose and geniculate corallines as well as taking drift seagrass and some brown macroalgae.

The last species S. antiquipes lives on the under sides of boulders or in fissures, where it feeds exclusively on drift macroalgae and seagrass, as do the abalone Haliotis scalaris and H. laevigata in the same habitat (Shepherd 1973).

Experimental Removal of Archaeogastropods

By 23 November 1983, after 65 days, a low turf of erect, filamentous algae to about 5 mm high, mostly Polysiphonia sertularioides had grown on the upper surfaces of the boulders in the four structures kept free of grazing molluscs. Mean biomass (d.w.) of the turf algae was 19 mg cm\(^{-2}\) (s.e. 4 mg) and of the trapped sediment 87 mg cm\(^{-2}\) (s.e. 4 mg). On boulders subject to natural grazing there was no algal turf and little sediment (3.7 mg cm\(^{-2}\), s.e. 0.6 mg). On the same date three of the turf-covered boulders from the structures were replaced among other boulders at the base of the boulder slope. When inspected on the following day a number of D. odontis and B. squamifera and their grazing trail marks were observed on the turf. By 30 November 1983 the algal turf was gone exposing the crustose layer of apparently dead crustose corallines. Ungrazed boulders in the structures were still covered by filamentous algae and sediment, and the original grazed control boulders still retained a healthy layer of crustose algae. It was concluded that in the absence of grazing molluscs filamentous algae covered upper surfaces of boulders and, with entrapped sediment, smothered the crustose algal layer.
DISCUSSION

Guilds of grazing archaeogastropods have received little attention in the literature and this is the first such study for southern Australian waters. The diversity of species matches that of chitons at the same site (Kangas and Shepherd 1984) and they are similarly distributed throughout the depth range. In contrast with the chitons, however, these archaeogastropods appear to prefer a habitat free of sediment and so decline in abundance at 5m depth, where rock is buried by sand. However, the abundance of drift seagrass, epiphytes and drift macroalgae at 4 - 5m depth may account for the increased abundance at about 4m deep of those species (M. plebejus, P. ventricosa and S. antipodes) which feed on them.

Hawkins and Hartnell (1983) considered that most archaeogastropods are generalist grazers feeding on whatever is available. However, Steneck and Watling (1982) suggested that the rhipidoglossan radula of archaeogastropods, with its lack of buccal strength and inherent weaknesses in tooth structure was ill-adapted to rasping leathery macrophytes or coralline algae. While the species considered in this paper have a much more varied diet than predicted by Steneck and Watling's scheme, the minor differences between their diets suggest some choice of food. Given the need for caution in inferring food preferences from gut contents, the abundance of macroalgae, corallines, crustose species and algal drift in the habitat imply that consistent differences are likely to be real ones, particularly if they coincide with micro-habitat differences between species. However, filamentous algal species, rare in the boulder habitat, may be preferred by several of the grazers, as demonstrated by the rapidity with which they were grazed from the ungrazed boulders replaced on the boulder slope.

The removal experiment suggests that archaeogastropods and chitons together control the growth of filamentous algae on the rock surface. The chitons Chiton diaphorus and Chiton calliozonus (Kangas and Shepherd 1984) and the archaeogastropods D. odontis and B. squamitera observed in this study all graze on the upper surfaces of boulders and appear to be the principal agents of such control. Sediment and algal films are known to inhibit the growth of crustose algae (Slocum 1980 and review of Hatcher 1983) and the decline of crustose corallines and Petroderma on ungrazed boulders is consistent with this. Thus grazing by these archaeogastropods might be expected to influence considerably the algal community structure. This can best be shown by longer term experiments.

This study and that of Kangas and Shepherd (1984) show that at least 22 species of archaeogastropods and chitons share the same boulder habitat and have strongly overlapping diets. How is this co-existence maintained? It is possible that they have partitioned their resources in subtle ways and are in stable co-existence without serious inter-specific competition (Kohn 1959, Ayal and Safriel 1962). Alternatively they may be able to tolerate a high similarity in requirements without their co-existence becoming precarious (MacArthur 1972). Another possibility, that is more easily testable, is that predators prevent the molluscan populations increasing to a level where competition for resources may occur. Studies on the effect of predation by wrasses, which are abundant in the area, and known to feed on these molluscs would be valuable.

ACKNOWLEDGEMENTS

We are grateful to Ms. J. Turner and M. Kangas for assistance in the field, to Mr. C.H. Deane for preparing the figures, and to Professor H.B.S. Womersley for algal identifications. Funds supporting the study were received from Fishing Industry Research Trust Account.

LITERATURE CITED


Table 1 Species of grazing gastropods on the boulder slope at West Island, with depth range, mean density, mean size and size range, and number of gut contents analysed. In each case the length measurement is columnar length.

<table>
<thead>
<tr>
<th>Species</th>
<th>Depth (m)</th>
<th>Mean Density (Nos. m⁻²)</th>
<th>Range (mm)</th>
<th>Mean Length (mm)</th>
<th>Number Used in Feeding Study</th>
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<tbody>
<tr>
<td>Scutus antipodes (Montfort)</td>
<td>4 - 5</td>
<td>2.9</td>
<td>30-90</td>
<td>61.1</td>
<td>8</td>
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<tr>
<td>Clanculus (Euricanculus) limbatus (Quoy and Gaimard)</td>
<td>1 - 5</td>
<td>10.2</td>
<td>13-21</td>
<td>19.1</td>
<td>10</td>
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<tr>
<td>Clanculus (Mesocanculus) plebeius (Philippi)</td>
<td>0.5 - 5</td>
<td>44.6</td>
<td>6-8</td>
<td>7.3</td>
<td>10</td>
</tr>
<tr>
<td>Diloma (Chlorodiloma) odontis (Wood)</td>
<td>0.5 - 5</td>
<td>5.5</td>
<td>16-22</td>
<td>18.8</td>
<td>10</td>
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<tr>
<td>Gibbula (Notogibbula) preissiana (Philippi)</td>
<td>1 - 5</td>
<td>12.7</td>
<td>7-8</td>
<td>7.8</td>
<td>10</td>
</tr>
<tr>
<td>Granata imbricata (Lamarck)</td>
<td>1 - 5</td>
<td>6.2</td>
<td>24-35</td>
<td>28.2</td>
<td>10</td>
</tr>
<tr>
<td>Euchelus aspersus (Philippi)</td>
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<td>2.3</td>
<td>7-10</td>
<td>8.7</td>
<td>10</td>
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<tr>
<td>Turbo (Subnella) undulatus (Solander)</td>
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<td>9.8</td>
<td>22-40</td>
<td>33.8</td>
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<tr>
<td>Turbo (Ninella) torquatus (Gmelin)</td>
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<td>1.1</td>
<td>28-74</td>
<td>43.0</td>
<td>8</td>
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<tr>
<td>Bellastra squamifera (Koch)</td>
<td>3 - 5</td>
<td>5.7</td>
<td>13-15</td>
<td>14.3</td>
<td>10</td>
</tr>
<tr>
<td>Phasianella ventricosa (Swainson)</td>
<td>2 - 5</td>
<td>12.9</td>
<td>8-14</td>
<td>28.2</td>
<td>10</td>
</tr>
</tbody>
</table>

Rare species not used in feeding study

- Cantharidus (Phasianotrochus) eximius (Perry)
- Thalotia (Prothalamia) lehmanni (Menke)
- Thalotia (Prothalamia) pulcherrima (Wood)
- Clanculus (Macroclanculus) undatus (Lamarck)
- Clanculus (Mesocanculus) consobrinus (Tate)
- Stomatella auncula (Lamarck)
Fig 1. Map of West I, showing the algal communities of the boulder slope in Abalone Cove. The granite blocks shown are prominent topographic features bearing similar algal communities to surrounding boulders.
Fig 2. Distribution with depth of density of archaeogastropods on the upper (hatched) and lower (blank) sides of boulders.

Fig 3. Distribution with depth of density of *G. preissiana* and *D. odontis* in March (continuous line) and September (dashed line) 1983.
Fig 4. Mean percentage composition of food categories in the gut of 11 species of archaeogastropod grouped according to affinities in diet (see Fig. 5).
Distribution and feeding of chitons in a boulder habitat at West Island, South Australia

by Mervi Kangas and
S.A. Shepherd

Department of Fisheries, G.P.O. Box 1625, Adelaide,
South Australia

ABSTRACT

The vertical distribution and feeding of sixteen species of chiton was examined on a boulder slope at West Island, South Australia. There is a trend of increasing abundance and diversity of species with depth, with most species present at 4-5 m depth where boulders are partly buried by sediment.

Six species are herbivorous, seven omnivorous and three carnivorous. There are generalist and specialist feeders within those feeding types. Specialist feeders include species which eat predominantly drift seagrass (one species), crustose coralline algae (four species), Petrodema crusts (one species), sponge (one species) and amphipods (one species).

A comparison of the distribution with depth of abundance of food organisms attached to the upper and under-surface of boulders with the depth distribution of chitons, shows that the food supply is unlikely to limit the abundance of chitons or affect their distribution. However, drift seagrass and algae, eaten by several species, are abundant only at 4-5 m depth; this may be a factor contributing to the abundance of some chitons at this depth.

INTRODUCTION

Subtidal crevice faunas and floras, although rarely studied, are ecologically important because crevices provide a refuge and a place for recruitment of many mobile species, including those of economic value such as abalone and sea urchins (Shepherd 1973; Tegner and Dayton 1977, 1981; Brock 1979).

Chitons are prominent members of the mobile fauna of crevices, and in southern Australia, the chiton fauna is notably rich in species (Hyman 1967, Boyle 1977). Chitons have usually been considered to be herbivorous grazers (Simpson 1976, Boyle 1977, Steneck and Watling 1982), although omnivory and even carnivory are known to occur (Barnawell 1969, McLean 1962, Langer 1983).
A boulder slope in Abalone Cove, West Island, South Australia (35°36'25"S., 138°35'27"E.) (Fig. 1) has an over-boulder flora of erect and crustose algae, and an under-boulder sessile fauna of crustose sponges, bryozoans, and ascidians and a mobile fauna of chitons and gastropods. The chitons, in particular, are numerically abundant and diverse, with 22 species present.

This study is part of an investigation of the role of chitons in this complex community whose biological interactions are of likely importance. The broad components of the habitat above and below boulders, the distribution and density of chitons along a depth gradient, and the diet of 16 chiton species are described and the diet related to the presence and abundance of food in the habitat. The algal ecology of West Island is described by Shepherd and Womersley (1970).

**MATERIALS AND METHODS**

**Distribution and Abundance of Organisms**

The north shore of Abalone Cove, West Island, is a boulder slope containing boulders, mostly 30-40 cm x 20-30 cm and 20 cm high, from about 0.5 m depth to 5 m at low water. At six depth intervals (0.5 m and at 1 m depth intervals from 1 to 5 m), 20 boulders taken from different locations along the boulder slope were overturned and the chitons on the under surface and on rocks below the boulder were identified and counted. In order to estimate the density of chitons, the area of each boulder was taken to be its projection on the horizontal plane. In addition, exhaustive searches were made over the depth range for less common species. Estimates of the mean percentage cover of crustose organisms on and under boulders were obtained by laying a transparent sheet of plastic marked with a 2.5 cm grid on the boulder and counting the number of squares occupied by each organism. Estimates of cover of upper (> 20 cm high) and middle (1-20 cm) algal strata on the upper side of boulders were also made.

**Food and Feeding**

Samples of each species of chiton were collected between January and April 1983, and preserved in 10% formal seawater. The whole of the digestive tract, from stomach to anus, was removed from each animal, the contents spread on a slide and examined microscopically. The slide was scanned along several parallel lines and the material under the cross of the eyepiece at equidistant points was identified to morphological group. Plant material was categorised as coralline algae (geniculate and encrusting), *Petroderma* crusts, filamentous algae, macroalgae and seagrasses, in accordance with the functional scheme proposed by Steneck and Watling (1982). Animal matter was placed in one of the following taxonomic groups: sponge, bryozoans, ascidians, hydroids, serpulid worms and amphipods. According to the amount of food in the gut, 20-90 identifications of food items were made for each individual. The basis for evaluating the accuracy of the method is given by Curtis (1960). Shepherd and Boudouresque (1984) tested the accuracy of the method experimentally and showed that gains in accuracy decline sharply after 50 identifications, so do not justify additional effort.

Within species differences in the food eaten with depth were examined for four species by analysing the gut contents of five individuals per species at different depths. The differences were analysed statistically with the non-parametric Mann-Whitney U-Test.

* This refers to crusts of non-calcified algae, mostly of an undescribed species of the genus *Petroderma*. 

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*102 M. Kangas & S.A. Shepherd*
A night dive was made on 24 February 1983 and the species on the upper surfaces of boulders noted.

**RESULTS**

**The Boulder Habitat**

The boulder slope at West Island has an upper stratum of Ecklonia radiata and Cystophora monilifera from about 2-5 m depth (Fig. 1), with a middle stratum of geniculate corallines mostly from 4-5 m depth.

The distribution of mean percentage cover of algae of the middle and lower (i.e. crustose) strata with depth on the upper surfaces of boulders is shown in Fig. 2, and of crustose organisms on the under surfaces of boulders in Fig. 3. Upper surfaces of boulders have an almost 100% cover of encrusting algae and geniculate corallines often below the canopy of Ecklonia and Cystophora, whereas the under surfaces have a somewhat diverse encrusting fauna and flora with a total cover of 50-90% (Fig. 3).

**Distribution and Feeding of Chitons**

Twenty-four species of chiton occur subtidally and one species intertidally. Sixteen species examined by us are listed in Table 1 according to feeding type, together with data on depth range, mean density, size range and number of gut contents analysed. The remaining nine species are listed in the Appendix, but they were either too rare to allow feeding studies of them or were in seagrass. The vertical distribution of the more abundant species is shown in Fig. 4. The number of species is least in shallow water, but increases with depth, so that at 4-5 m depth where boulders are partly buried in sediment, most species are present and attain their highest density.

However, Ischnochiton australis, and to a lesser extent, Ischnochiton elongatus and Chiton calliozonus, have lower densities at intermediate than in deeper or shallower depths. The decrease in density of these species was not an artifact of sampling because replicate samples at 3 m depth gave the same results.

The proportion of different food organisms in the gut of sixteen species of chiton is shown in Figs. 5-7. Six species are herbivorous, with 75% or more of plant material in the gut (Fig. 5). They include generalist feeders (I. australis, I. cariosus and Plaxiphora albida) and specialist feeders (Ischnochiton torri, Chiton diaphorus and Callochiton crocinus) which feed predominantly on seagrass, crustose corallines, and Petroderma crusts respectively.

Omnivorous species (Fig. 6) eat both plant and animal matter. In three of them (C. calliozonus, Chiton torrius, and Chiton tricostalis), the diet is predominantly crustose coralline algae. The remaining four species (Ischnochiton elongatus, Ischnochiton lineolatus, Cryptoplastr striata and Loricula cimolia), show more diversity in the kind of food eaten and variability in their proportions within species. Hence it is likely that these species are generalists which feed opportunistically according to the local availability of food.

Three species are mainly carnivorous (Fig. 7), with 75% or more of animal material in the gut. Notoplax speciosa is almost exclusively a sponge feeder, Ischnochiton smaragdinus eats bryozoans and ascidians as well as sponge. Loricea angusta feeds largely on amphipods, but also consumes other animal and plant material. According to Ludbrook and Goullitt (1984) the latter species traps amphipods by rapidly clamping the previously elevated girdle to the substrata.

Four species (Table 1) crawl on to the upper surfaces of boulders at night, and a fifth, I. australis, on to the sides of boulders, presumably to feed. The remaining species are cryptic, by night as well as by day.

Differences with depth in the proportions of major food categories eaten were
examined for four species. The differences were significant for one or more food categories in three species (Table 2). Drift seagrass (mostly *Heterozostera tasmanica*) is only abundant at 5m depth and the availability of this appears to largely account for the differences in the diet of *L. australis*, *L. cariosus* and *L. lineolatus* with depth.

**DISCUSSION**

In a recent review, Steneck and Watling (1982) suggested that chitons are herbivores which largely specialise on perennial (leathery) macrophytes or crustose corallines. This overlooks numerous earlier studies, summarised by Boyle (1977), which show that some chitons may consume considerable amounts of animal matter. This is the first account of the distribution and diet of a chiton ‘guild’ in Australian waters, and it shows an astonishing diversity of species, with a wide variety of feeding types co-existing over a narrow habitat range. The feeding types include herbivores, omnivores and carnivores, and there may be generalist or specialists within those categories. Of special interest is the carnivorous species, *L. angasi*, which captures live amphipods; this has otherwise been recorded only for the Californian species, *Placiphorella velata*, Dall (McLean 1962).

Food resources on the boulders (attached algae and crustose animals) are abundant at all depths and apparently more than sufficient for the chiton populations dependent on them. Hence food is unlikely either to limit the abundance of these species or influence their distribution. An exception is drift seagrass, which only occurs at 4-5 m depth. *L. torri*, a specialist feeder on this resource, occurs only at these depths, and may thus be one species whose vertical distribution is limited by the distribution of its preferred food.

The low abundance of *L. australis* at intermediate depths on the boulder slope (Fig. 4) is enigmatic. The unusual escape behaviour of this species which curls up and falls off a rock if disturbed (Lудbrook and Gowlett 1984), would enhance their survival of individuals when boulders are rolled about during storms, and may account for the abundance of this species in very shallow water.

It is surprising that only four species emerge at night apparently to feed. Presumably there is an abundant supply of food on the undersides of boulders for the other species, so that they do not need to make feeding excursions.

The abundance and diversity of chitons at 4-5 m depth may be due in part to their apparent preference for a habitat under boulders partly buried in sediment, and partly to the abundance of drift algae and seagrasses, which a majority of these chitons eat.

Some authors (Adiey 1973, Steneck 1977, Brock 1979, Paine 1980) have suggested that grazing may be important in maintaining the stability of crustose communities by enhancing the growth of competitively inferior species such as coralline algae, or removing superior competitors for space such as ascidians. The wide range of feeding types present among these chitons shows that they are capable of doing so but whether they in fact do so is currently being examined by manipulative experiments.

**ACKNOWLEDGEMENTS**

We are grateful for field assistance from Ms. Jean Turner and Mr. P. Clarkson. Professor H.B.S. Womersley kindly identified the *Petroderma* crusts and Miss Karen Gowlett gave much helpful advice on the taxonomy of chitons, and wrote the Appendix.

**LITERATURE CITED**


Chiton feeding


Table 1. List of species of chitons on the boulder slope at West Island, with depth range, mean density, mean size and size range, and number of gut contents analysed.

<table>
<thead>
<tr>
<th>Species</th>
<th>Depth Range (m)</th>
<th>Mean Density (Nos. m²)</th>
<th>Length Range (mm)</th>
<th>Number used in Feeding Study</th>
</tr>
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</table>


### Herbivores

<table>
<thead>
<tr>
<th>Species</th>
<th>Lower</th>
<th>Upper</th>
<th>Lower</th>
<th>Upper</th>
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</thead>
<tbody>
<tr>
<td>Ischnochiton</td>
<td>0.5-5</td>
<td>19.4</td>
<td>29-57</td>
<td>43.1</td>
</tr>
<tr>
<td>(Ischnoradzia)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>australis (Sowerby)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ischnochiton</td>
<td>2-5</td>
<td>6.3</td>
<td>24-37</td>
<td>29.5</td>
</tr>
<tr>
<td>(Heterozona)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cariosus Carpenter</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ischnochiton</td>
<td>4-5</td>
<td>0.1</td>
<td>21-40</td>
<td>31.8</td>
</tr>
<tr>
<td>(Autochiton) torri</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Iredale &amp; May</td>
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<tr>
<td>*Chiton</td>
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<td>(Rhyssoplax)</td>
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<td>diaphorus (Iredale &amp; May)</td>
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<td>crochinus Reeve</td>
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<tr>
<td>Plaxiphora albida</td>
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<tr>
<td>(Blainville) Intertidal</td>
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### Omnivores

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<td>6.0</td>
<td>18-29</td>
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<tr>
<td>elongatus (Blainville)</td>
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<td>Ischnochiton</td>
<td>2-5</td>
<td>10.0</td>
<td>25-36</td>
<td>23.9</td>
</tr>
<tr>
<td>lineolatus (Blainville)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Chiton</td>
<td>1-5</td>
<td>4.0</td>
<td>23-47</td>
<td>33.8</td>
</tr>
<tr>
<td>(Rhyssoplax)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>calliozonus Pilsbry</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Chiton</td>
<td>0.5-5</td>
<td>3.0</td>
<td>24-39</td>
<td>30.1</td>
</tr>
<tr>
<td>(Rhyssoplax) torrianus Hedley &amp;</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hull</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chiton</td>
<td>3-5</td>
<td>0.5</td>
<td>15-23</td>
<td>17.2</td>
</tr>
<tr>
<td>(Rhyssoplax) tricostalis Pilsbry</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cryptoplax striata</td>
<td>4-5</td>
<td>0.1</td>
<td>60-70</td>
<td>65.0</td>
</tr>
<tr>
<td>(Lamarck)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lorica cimolia</td>
<td>0.5-5</td>
<td>2.0</td>
<td>16-69</td>
<td>37.7</td>
</tr>
<tr>
<td>(Reeve)</td>
<td></td>
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</tr>
</tbody>
</table>
Chiton feeding

Carnivores

*Ischnochiton (Haplopax) smaragdinus (Angas)

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Encrusting Coralline algae</th>
<th>Mean % of Erect algae</th>
<th>Food in Gut Seagrass</th>
<th>Animal</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-4</td>
<td>1.5</td>
<td>18-25</td>
<td>21.3</td>
<td>10</td>
</tr>
</tbody>
</table>

Notoplax speciosa (H. Adams)

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Encrusting Coralline algae</th>
<th>Mean % of Erect algae</th>
<th>Food in Gut Seagrass</th>
<th>Animal</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-5</td>
<td>0.1</td>
<td>13-16</td>
<td>14.5</td>
<td>2</td>
</tr>
</tbody>
</table>

Loricella angasi (H. Adams)

<table>
<thead>
<tr>
<th>Depth (m)</th>
<th>Encrusting Coralline algae</th>
<th>Mean % of Erect algae</th>
<th>Food in Gut Seagrass</th>
<th>Animal</th>
</tr>
</thead>
<tbody>
<tr>
<td>3-5</td>
<td>0.1</td>
<td>21-47</td>
<td>36.7</td>
<td>7</td>
</tr>
</tbody>
</table>

* Observed above boulders during night

Table 2. Differences in feeding with depth of four species of chiton. Significance levels (Mann-Whitney U test) are shown as follows: * = P < 0.05; ** P < 0.01.

For I. australis the difference between 0.5 and 2.5 m were not significant; differences between 0.5 and 5 m and 2.5 m and 5 m were both significant at the level indicated.

APPENDIX

Additions to the chiton fauna of West Island

by Karen Gowlett, P.O. Box 362

BLACKWOOD, S.A. 5051

*Ischnochiton (Ischnochiton) variegatus (H. Adams & Angas) Rare, under smooth rocks in sandy pockets, at one metre depth.

*Stenochiton cymodocealis* Ashby. On seagrass *Amphibolis antarctica* at base of stems, usually buried in sand, at 5 m depth.

*Stenochiton longicymba* (Blairville). Under stones among seagrass beds of *Posidonia sinuosa*, at 5 m depth. This species is usually found in the leaf sheath of the seagrass.

*Callistochiton antiquus meridionalis* Ashby Rare, usually under bare rocks at 3-5 m deep.
Plaxiphora (Frembiya) matthewsi Iredale Usually under rocks in silty situations, at 5 m depth.

Cryptoplax iredalei Ashby Rare, in Abalone Cove, at 3 m depth.

Acanthochiton a cladophylla (Ashby) Rare, under rocks at 3 m deep.

Acanthochiton australis (Sykes) Rare, under rocks in sponge at 2-3 deep.

Acanthochiton australis (Blainville) Rare, under rocks in sponge at 2-3 m deep.

Fig. 1. Map of West I. and of the algal communities of the boulder slope in Abalone Cove.
Fig. 2. Distribution with depth of mean percentage cover of middle and lower strata on the upper surfaces of boulders in Abalone Cove, West I.

Fig. 3. Distribution with depth of mean percentage cover of crustose organisms on the under surfaces of boulders in Abalone Cove, West I.

Fig. 4. Distribution of density of chitons on the boulder slope at West I.
Fig. 5. Mean percentage composition of food categories in the gut of six species of herbivorous chitons.

Cr.c : Crustose corallines  
Ge.c : Geniculate corallines  
Fil : filamentous algae  
Mac : macroalgae  
Seag : seagrass  
Pet. : Petroderma  
Snd : Sand grains  
Asc : ascidians  
Bry : bryozoans  
Oth : other  
Spo : sponge
Fig. 6. Mean percentage composition of food categories in the gut of seven species of omnivorous chitons.

Notation as in Fig. 5.

Fig. 7. Mean percentage composition of food categories in the gut of three species of carnivorous chitons.

Notation as in Fig. 5.