FISHING INDUSTRY RESEARCH AND DEVELOPMENT TRUST ACCOUNT

FINAL REPORT FOR PROJECT 85/53

THE DEVELOPMENT OF AN INDEX FOR THE PREDICTION OF CATCHES OF BLACKLIP (*HALIOTIS RUBRA*) AND GREENLIP ABALONE (*H. LAEVIGATA*), AND A TECHNIQUE FOR AGEING ABALONE

Investigators
Mr J.D. Prince
Mr W. Nash
Mrs T.L. Sellers
Mr S. Talbot
Mr W.B. Ford

Institution
Tasmanian Department of
Sea Fisheries

Date of Commencement - 1st July 1985.

Date of Completion - 30th June 1988.

Objectives

The major aim of this project was to document the patterns of abalone settlement and recruitment, as well as the juvenile biology of abalone, in order to examine the factors determining these patterns. The overall objective was to examine the relationship between settlement/recruitment and the density of adult abalone.

It was hoped that a study of this kind could lead to a method for predicting stock abundance which could possibly be used for setting quota levels.

A subsidiary aim of this study was to use the data and samples gathered during the cause of this study to develop a technique for ageing Australian stocks of abalone.

Introduction

The scientific literature has generally accepted that abalone populations are characterised by low levels of settlement and recruitment (Tegner in press), that mortality is relatively low (Doi *et al.* 1977; Beinssen and Powell 1979; Sainsbury 1982; Shepherd *et al.* 1982; Fournier and Breen 1983) and uniform throughout life (Shepherd *et al.* 1982), and correspondingly that the natural productivity of these stocks is low (Tegner in press). In some studies it has been noted that one or more year classes are apparently missing (Forster et al. 1982; Sainsbury 1982) and this has led to the conclusion that abalone recruitment is relatively sporadic and irregular. It has been generally assumed that larval dispersal is relatively widespread (20-50km; Tegner & Butler 1985). No relationship had been observed between the abundance of breeding stock and the abundance of recruitment. On the basis of these observations and laboratory studies, together with generally held assumptions, it has been accepted that oceanographic and other environmental factors would be the major determinants of settlement and recruitment density (Fedorenko & Spout 1982; Tegner in press).

It was these widely held views which led to the original rationale for this project, which was to develop an index of settlement or recruitment abundance which could be used to predict broad scale trends in the future abundance of the fishable stock.

In addition, there was also no scientifically proven method of ageing abalone prior to this study, and it was generally accepted that the Australian species of abalone could not be aged. The FIRTA-funded review of Ward (1986) found that this was a major impediment of research into and assessment of abalone stocks in Australia.

Results

All the results of this study will have been published in the scientific

literature before the end of 1988 and copies of all these publications are attached to this report. These publications are:

1. Prince, J.D., Sellers, T.L., Ford, W.B., and Talbot, S.R. (1987). Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*; Mollusca: Gastropoda). *J. Exp. Mar. Biol. Ecol.* **106**: 243-263

2. Prince, J.D., Sellers, T.L., Ford, W.B., and Talbot, S.R. (1988). A method for ageing the abalone *Haliotis rubra* (Mollusca: Gastropoda). *Aust. J. Mar. Freshw. Res.* **30**: 167-75.

3. Prince, J.D., Sellers, T.L., Ford, W.B., and Talbot, S.R. (1988). Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca : Gastropoda). *J. Exp. Mar. Biol. Ecol.* **122**: 91-104.

4. Prince, J.D., T.L. Sellers, W.B. Ford, & S.R. Talbot, (in press). Recruitment, growth, mortality and population structure in a southern Australian population of *Haliotis rubra* (Mollusca:Gastropoda). *Mar. Biol.*

Some of these results have also been published in more popular forms and copies of these articles are also attached. These articles are:

DSF study throws new light on abalone. *FINTAS*, Sept. 1986 **9 (3).**

DSF finds a way to age abalone. *FINTAS*, Sept. 1987 **10 (3).**

To date these results have not been published in 'Australian Fisheries' although it is intended that this will occur during 1989. However, details of these results have already been disseminated relatively extensively through the abalone industry, both within Australia and internationally with oral presentations having been made at the following meetings:

Annual General Meetings of the Tasmanian Abalone Divers' Association.

Annual General Meeting of the Tasmanian Abalone Divers' Research & Development Trust.

Annual General Meeting of the NSW United Abalone Divers' Association.

General Meeting of all South Australian Abalone Divers

General Meeting of Victorian Central Zone Divers

Presentation to Dermersal Mollusc Research Group Meetings, SEFC.

CSIRO Seminar, Hobart

Annual General Meetings of the Australian Society of Fish Biology

Annual General Meeting of the New Zealand Abalone Divers' Co-operative

Invited Lecture to Faculty Members and Students of CICESE, Ensenada, Mexico

Informal seminar to Fisheries Biologists of The Fisheries Department of Baja California, Mexico

Informal seminar to the Fisheries Biologist of Californian Department of Fisheries and Game, Long Beach California

Arrangements are also being made to present much of this material in a seminar to the Western Australian Department of Fisheries. To date this material has only been presented to this Department through informal discussions. Much of this material will also be presented at the International Symposium on Abalone Research to be held in La Paz, Mexico in November, 1989.

Because all the results of this study have been published and are attached we do not intend presenting the results in detail within this report. Instead we are presenting a summarized account of the major achievements and findings of the study, together with a brief discussion of what we believe to be the implications of these findings. The reader is referred to the papers listed above for a detailed presentation of materials and methods, results and discussions. The numbers contained in the text below direct the reader to the particular paper (listed above) detailing the different facets of this study.

Summarized Results and Achievements

This study was primarily with blacklip abalone (*Haliotis rubra*) which is commercially the most important Australian species and consequently these results pertain strictly only to this species. However, it is already evident that many of these results apply to some extent to other abalone species including Australia's other major commercial species, greenlip (*H. laevigata*).

The major findings of this study are:

1. The major factor determining the abundance of recruitment and apparently settlement is the immediate density of breeding stock.

4

Approximately 70 percent of the observed variability in recruitment density could be explained by variations in the breeding stock density (1&3).

2. This result apparently indicates that larval dispersal is generally very restricted, occurring on a scale of meters or tens of meters (1&3).

3. Settlement and recruitment to abalone populations is more abundant than has been previously recognised, suggesting that most previous studies have used seriously deficient sampling techniques (4).

4. Mortality rates of juvenile abalone are also much higher than previously recognised, but decline with age or size. Hence, juvenile populations are relatively dynamic with high levels of turnover (4).

5. Juvenile growth is almost linear and cannot be described using von Bertalanffy parameters. Previous studies which have described the growth of juveniles and adults with a single von Bertalanffy curve have apparently underestimated the age of maturity by between one and three years (2 & 4).

6. Abalone populations apparently partition the habitat, with juveniles using the hidden under boulder habitat, where they remain until maturity. Upon reaching maturity abalone emerge into the open habitat where they become vulnerable to fishing pressure (4).

7. A simple and quick method of ageing abalone has been shown to work for southern Australian populations of blacklip abalone (2). Preliminary use of this technique suggests that it will work with most temperate water haliotid species, including all the other species taken commercially in Australian waters (*H. laevigata, H. roei* and *H. scalaris*).

Implications of These Results

The development of an ageing technique has major implications for abalone research worldwide, facilitating the study of growth, mortality and population structure in these species. Unfortunately, the deterioration of the shell in older individuals and in some areas may restrict the techniques' application to some extent. However, the technique is already proving extremely useful in studies of growth and reproduction and it is likely that the development of this technique alone may do more to advance the study of abalone biology than the results of any other recent study.

The other finding from this study with major implications is that recruitment density is directly related to the localized abundance of breeding stock, apparently through the mechanism of limited larval dispersal. The implication of this is that abalone fisheries are composed of an extremely large number of localized unit stocks, which may be prone to localized recruitment overfishing. Hence, fishery management policies should be designed to spread fishing pressure evenly over all stocks. Management and monitoring of abalone fisheries should also be adapted to this fine scale if they are to be relevant to the fishery.

However, the fact that the abundance of recruitment is apparently largely determined by the localized density of breeding stock apparently undermines the original intention of this project. The original intention was to develop ways of monitoring settlement and recruitment in order to predict the general abundance of fishable stock. Clearly the results of this study indicate that measurements of settlement or recruitment strength will be of extremely limited use to fishery managers because they will pertain to such limited areas.

This observation in itself suggests the possibility of developing alternate methods for assessing and monitoring these species, using knowledge of the relationship between stock and recruitment. The observation that stock-recruitment relationships operate on a small spatial scale indicates that over a large scale these relationships will also be extremely strong. This assumption is based on the premise that the variability of many smaller relationships will tend to cancel each other out when considered on a larger scale, producing an extremely stable relationship between overall levels of stock and recruitment. Hence, if the level of stock which maximizes recruitment could be determined and fishing pressure could be spread evenly over all unit stocks, an abalone fishery could be managed in order to maintain optimal levels of recruitment.

In turn, the fact that stock and recruitment operates on such a small scale indicates that stock-recruitment studies should be relatively easy for these species. Different experimental levels of stock could be established in a large number of small experimental sites and the relationship between stock and recruitment ascertained relatively rapidly. The major impediment to these studies is likely to be the difficulty of accurately measuring the abundance of animals which are strongly aggregated on such a small spatial scale.

Conclusions

The results of this study have largely precluded following the original intention of the study which was to develop methods which could be used to predict the future abundance of abalone stocks on a large scale, and enable managers to set quota levels with some confidence.

Instead of leading to an immediately useful management technique, this study has produced results which have significantly improved our understanding of abalone stock dynamics. The results suggesting extremely restricted larval dispersal indicate that, for abalone, unit stocks must be considered to have a scale of hundreds of metres rather than kilometres or greater. This has large ramifications for management practice and suggests new avenues for developing techniques of stock assessment.

This study has also produced a large body of general biological information which to a large extent challenge or extend many of the accepted ideas about abalone biology. The most significant of these being: (i) previous studies may have seriously overestimated juvenile growth; (ii) all of the breeding stock is exposed to fishing pressure unless protected by appropriate size limits; and (iii) abalone populations are more dynamic than previously thought.

Finally, the study has produced a proven method for ageing abalone. This technique should greatly facilitate future studies of the exploited stocks of abalone.

References

Beinssen, K., Powell, D. (1979). Measurement of natural mortality in a population of blacklip abalone, *Notohaliotis ruber*. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer*, **175**: 23-6.

Doi, T.S., Guzmán del Próo, S.A., Marín, V., Ortíz, M.Q., Camacho, J.A., Muñoz, y T.L. (1977). Analisis de la poblacion y diagnostico de la pesqueria de abulon amarillo (*Haliotis corrugata*) en el area de Punta Abreojos e Isla Cedros, B.C. *Serie cient. Dir. gen. Inst. nac.Pesca, Mex.* **18**

Fedorenko, A.Y. & P.E. Sprout, (1982). Abalone biology, fishery regulations, commercial catch (1952-1980), and current state of resource in British Columbia. *Can. Man. Rep. Fish. Aquat. Sci.,* No.**1658**: 1-74.

Forster, G.R., Potts, G.W., Swinfen, R. (1982). Changes in the ormer populations of Guernsey and Jersey. *J. Mar. Biol. Ass. U.K.* **62**: 717-727.

Fournier, D.A., Breen, P.A. (1983). Estimation of abalone mortality rates with growth analysis. *Trans. Am. Fish. Soc.* **112**: 403-11

Sainsbury, K.J., (1982). Population dynamics and fishery management of the paua, *Haliotis iris* I. Population structure, growth, reproduction, and mortality. *N.Z. J. Mar. Freshw. Res.*, **16**: 147-161.

Shepherd, S.A., Kirkwood, G.P., Sandland, R.L. (1982). Studies on Southern Australian abalone (genus *Haliotis*). III Mortality of two exploited species. *Aust. J. Mar. Freshw. Res.* **33**: 265-72.

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

Tegner, M.J. (in press). The California abalone fishery: Production, ecological interactions, and prospects for the future. *In* 'Scientific approaches to the management of invertebrate stocks.' (Ed. Caddy, J.F.) John Wiley and Sons.

Ward, T.J. (1986). Abalone biology and fisheries in Australia: A review of research. *Australian Fisheries Service, Canberra, Aust. Fish. Pap. No.* **86-12.**

Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*; Mollusca: Gastropoda)

J. D. Prince[1,2], T. L. Sellers[1], W. B. Ford[1] and S. R. Talbot[1]

[1]*Tasmanian Department of Sea Fisheries, Research Laboratory, Crayfish Point, Taroona, Tasmania, Australia 7006;* [2]*Zoology Department, University of Tasmania, G.P.O. Box 252C, Hobart, Tasmania, Australia 7001*

Abstract: The literature on haliotids generally assumes that these organisms have a short pelagic larval life with dispersal powers limited only by the time available before settlement. The results of an experiment designed to test this assumption are presented. The density of mature *Haliotis rubra* Leach was experimentally decreased along a 90 m section of shoreline. The resulting effect on recruitment patterns was examined in comparison with previous recruitment patterns. The results indicate that haliotid larvae may be strongly benthic with limited patterns of dispersal.

Key words: Abalone; *Haliotis*; Mollusca; Larva; Dispersal; Recruitment

INTRODUCTION

No studies on the dispersal ability of haliotid larvae have been published despite the fact that managers of haliotid (abalone) fisheries around the world are concerned with the possibility of recruitment failure (Mottett, 1978). The paucity of work in this area is due to the difficulty of finding haliotid larvae and juveniles within their natural environment (Tomita *et al.*, 1977; Breen & Adkins, 1980; Prince & Ford, 1985). From observations made under laboratory conditions it has generally been assumed that the lecithotrophic haliotid larvae are pelagic and disperse widely (Mottett, 1978; Fedorenko & Sprout, 1982; Sluczanowski, 1984; Tegner & Butler, 1985).

Recently developed techniques have made it possible to obtain samples of large numbers of haliotids within months of their settlement (Prince & Ford, 1985; Shepherd & Turner, 1985), allowing patterns of recruitment to be observed directly. Observations of recruitment patterns have indicated that they are extremely variable on a spatial scale of 20–200 m (Prince, unpubl. data). One explanation for this observation could be that larval dispersal is more restricted than has been assumed in the literature. Pelagic larvae are the most widespread form of larvae amongst benthic marine invertebrates (Thorson, 1950; Mileikovsky, 1971); free non-pelagic larvae (demersal development larvae) have,

however, been found in a range of marine organisms (e.g. see Millar & Hollis, 1963; Pearse, 1969; Gerrodette, 1981; Olson, 1985) including gastropods (e.g. see Shuto, 1983).

The ability to disperse is a major factor affecting the potential of species to recolonize areas from which they have been removed. This ability is of particular importance for commercially caught species (Mileikovsky, 1971) as it directly effects the resilience of a species to exploitation. The objective of the present study was to test whether larval dispersal may be relatively limited in natural populations of haliotids. A number of studies have tested this premise for a range of marine organisms other than haliotids by experimentally removing or introducing reproductive stock and observing subsequent settlement or recruitment patterns (Anderson & North, 1966; Dayton, 1973; Sebens, 1983; Dayton *et al.*, 1984; Olson, 1985; Vandermeulen & DeWreede, 1986).

No techniques exist for measuring directly abalone settlement. Connell (1985), however, presented evidence to suggest that, except at very high densities, invertebrate recruitment patterns were likely to reflect settlement patterns accurately. This principle, and the possibility of directly measuring haliotid recruitment using the technique of Prince & Ford (1985), suggested the possibility of experimentally manipulating breeding stock to test the dispersal ability of haliotid larvae. The current paper describes an experiment in which the density of mature *Haliotis rubra* Leach, was reduced along a 90 m section of shoreline and the resulting effect on juvenile recruitment examined. The logistics of conducting such an experimental programme within the natural environment are great and because of this replication was impossible. An attempt has, however, been made to use previous recruitment patterns in the same area as a form of temporal replication. The assumption is that patterns in the age structure of an area are the result of breeding stock density prior to experimental manipulation. Therefore they may give an historical comparison which can provide information as to the likely pattern of settlement without experimental manipulation.

H. rubra is ideally suited for this sort of experimental design. The movement of juvenile *H. rubra* is known to be extremely restricted. At a nearby site, in a boulder habitat similar to that used in this experiment, 6 to 50-mm (maximum length) abalone were found to move < 10 m from the point of release over 12 months, while 50 to 127-mm animals generally moved < 30 m in the same time (White & Whyte, pers. comm.). If factors such as growth and mortality are assumed to act relatively uniformly, within similar habitats on a spatial scale of hundreds of metres, the density of successive size classes can be expected to preserve patterns of past recruitment. These past patterns have been used in this experiment to provide a basis for comparing the experimental with the previously undisturbed state. While this does not meet the rigorous requirements of an experimental control or replication the logistics of this process are feasible.

The hypothesis being tested by this experiment is that the abundance of abalone recruitment is related to the immediate density of adult abalone. The logic is that if abalone larval dispersal is relatively large, then abalone recruitment will not necessarily depend on the immediate density of breeding stock. If larval movement is, however, restricted, then the occurrence of abalone recruitment will be determined by whether or not breeding abalone are present in an area.

MATERIALS AND METHODS

AREA STUDIED

The area studied at Ninepin Point, Tasmania (43°17'S : 147°10'E) is a uniform section of rocky coastline extending 70 m from high water mark to a depth of 6–9 m. The bottom is composed of three layers of boulders resting on silt. The boulders are of irregular shape and mostly 30–40 cm greater diameter by 10–20 cm lesser diameter.

The macroalgal community of the area has three strata; the upper strata (> 1 m) consists of *Macrocystis pyrifera* (L.) C. Agardh, the middle strata (0.15–1.0 m) is dominated by the species *Acrocarpia paniculata* (Turn.) Aresch., *Cystophora moniliformis* (Esper), Wom. & Niz., and *Sargassum verruculosum* (Mertens) C. Agardh, the lowest strata (0–0.15 m) is dominated by encrusting corallines. On the exposed surface of the boulders these corallines are overgrown by filamentous algae including *Cladophora* sp., *Ceramium* sp., *Polysiphonia* sp. and *Calithamnion* sp., and small fleshy algae of the genera *Zonaria*. In depths > 6 m algae of the genera *Peyssonnelia*, *Thamnoclonium* and *Caulerpa* commonly overgrow the crustose corallines which are abundant at these depths.

In this area *Macrocystis pyrifera* is of limited importance, being confined to a narrow (5–10 m in width), diffuse and irregular band ≈ 20 m from the shoreline in depths of 2–3 m. As a consequence, despite the presence of *M. pyrifera*, in depths < 4 m the algal community is typical of a fucoid association indicative of slight to moderate wave action (Sanderson & Thomas, 1987). This is in contrast to depths > 4 m where the characteristics of the algal community change, and only the lowest strata is found.

This entire section of shoreline has carried a natural population of *Haliotis rubra* at sufficient densities to support continuing amateur and professional fishing over the past 15 yr, suggesting regular recruitment of abalone.

BREEDING STOCK REMOVAL

The existence of recent recruitment and the size of the smallest abalone present before the experiment were established with one day sampling (3 August 1985) using the anaesthetic technique (detailed below). Following this the central 90 m section of shoreline was marked out for the removal of abalone breeding stock. To aid in the allocation of diving effort during the removal process, this area was divided into three segments, Sites 4, 5 and 6, respectively (Fig. 1), each ≈ 30 m long. These were delineated with chain laid on the seabed perpendicular to the shore from low water mark to the edge of the sandy substratum.

On five occasions between 10 August 1985 and 18 September 1985 all abalone found
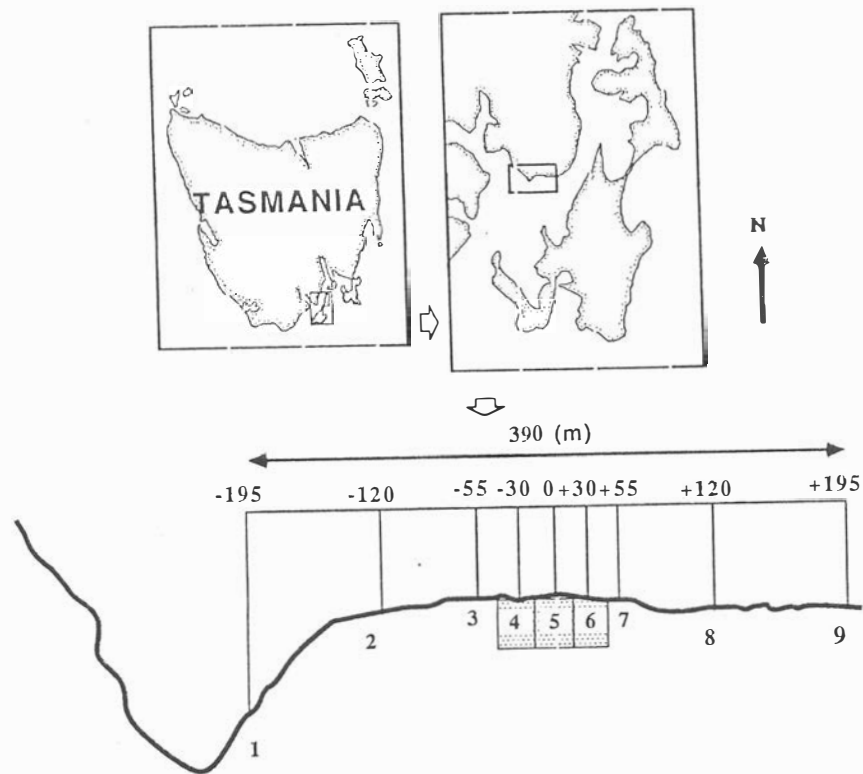
Fig. 1. The location and layout of the study site at Ninepin Point, Tasmania: shaded area indicates the area from which abalone were removed and the numbers indicate sampling sites; distances (m) are given from the centre of the removal area.

of > 60 mm maximum shell length were removed from each of the three sections by divers. Disturbance of the substratum during collection was minimal as abalone were only taken from the exposed boulder surfaces and no boulders were moved during the searches. It was recognized that a proportion of the > 60-mm abalone would not be detected by these searches, but minimal disturbance of the substratum was considered more important than maximal reduction of the population. The maximum length of each abalone captured was measured to the nearest millimetre. The number removed from each of the three 30-m segments and the total diver-hours expended in each area was recorded for each of the first four searches. The fifth and final search was of a shorter duration (total diver-h = 4.5) and on this occassion the catch and effort was not separated by area.

BREEDING STUDIES

From the initial removal (10 August 1985) subsamples of 20 abalone from each 10-mm size class were retained for gonad index studies. The methods used for this study are based on those of Hayashi (1980). After fixation in 10% formalin the visceral mass was sectioned beneath the visceral coil and the cross section placed against clear plastic and drawn. The relative areas of gonad and hepatic gland in the cross section were calculated by weighing the plastic outlines. The gonad index was calculated as the percentage of the area of the cross section made up by the gonad.

A further sample of 83 abalone, covering the size range indicated by the gonad index study to be mature, were collected between 10–16 September 1985 for analysis of fecundity. The fecundity at the site studied was also measured after the removal of breeding stock to determine the time of spawning at the site.

The method used to estimate fecundity was based on that of Sainsbury (1982). After fixation in 10% formalin the gonad was dissected from the hepatic gland and gently teased apart into 50–250 ml of sea water. The water was agitated until all the eggs were free and evenly dispersed; two or three 0.5 to 1.0-ml samples were then taken. Each sample was placed in a counting chamber marked with a grid and the yolked eggs in five standard squares were counted. Total fecundity was calculated by multiplying out the various subsampling factors.

POST REMOVAL SAMPLING

In February–March 1986 the abalone populations at nine sites were sampled. The sites (Fig. 1) covered 390 m of shoreline, and were situated at the centre of the segment of shoreline from which the breeding stock was removed (0 m, Site 5) and 30 m (Sites 4, and 6), 55 m (Sites 3 and 7), 120 m (Sites 2 and 8), and 195 m (Sites 1 and 9) either side of the centre. This spacing was selected so as to maximize the probability of observing any effect caused by removing the breeding stock.

The anaesthetic technique detailed by Prince & Ford (1985) was used to sample the abalone at these sites. Twenty areas of 1 m² at each site were selected by throwing a quadrat from an anchored vessel. Stratification was achieved between sites by anchoring the vessel 10 m offshore while selecting the initial 10 squares at each site, and 35 m offshore while selecting the remaining squares. If the square landed on an area where no substratum could be gathered, the boulders being too large or the substratum being entirely sand and silt, the square was retrieved and re-thrown. From each selected area a diver collected all the substratum possibly suitable for abalone, principally boulders and kelp. The few boulders too large to lift to the surface were searched underwater and all abalone collected.

The substratum material was placed in bins and bathed in a 1% solution of ethanol in sea water for a minimum of 10 min. This material was then brushed with a soft brush before being removed from the solution. After all the solid substratum removed from a square had been soaked, the contents of the bins were drained through 15-mm and 0.5-mm sieves. Abalone retained by the coarser sieve were collected and the sample held by the smaller sieve was returned to the laboratory for examination. These samples were washed through sieves of 9-, 4-, 2- and 1-mm aperture and the abalone preserved. The maximum shell length of all abalone collected were measured to the nearest 1 mm.

The length frequency data from the samples were analysed using the Macdonald and Pitcher mixture analysis 'Mix' (Macdonald & Pitcher, 1979; Macdonald & Green, 1985). The cut-off points between the different size distributions of abalone described by this analysis were taken as the points where two consecutive distributions overlapped. These points were calculated using the formula:

$$X = [(\overline{x}_2 + \overline{x}_1) \times 0.5] + [(s_1^2 \times s_2^2) \times \log_e (\pi_1/\pi_2)/(\overline{x}_2 - \overline{x}_1)]$$

where X is the cut-off point (mm) and $\overline{x}_i$, s_i^2, and π_i are the estimated means, standard errors, and proportions of the i-th distribution, respectively.

The densities of abalone detected showed a tendency to be positively skewed about the mean. A $\log(Y + 1)$ transformation was used to normalize the data. The differences in densities between areas was tested with a two-tailed Student's t-test using a significance level of 0.05. This method was also used to test the significance of correlations between adult and juvenile densities.

RESULTS

BREEDING STUDY

Analysis of the gonad index of abalone collected from the research site on 10 August 1985 showed that for the size classes examined (>60 mm) the index increases with size up to the length of 100 mm; a sharp increase was observed between 90 and 100 mm. Maximal values were found in abalone of 100–145 mm maximum length. The relationship between fecundity and maximum shell length for animals collected 10–16 September 1985 was best described by a single variable regression:

$$F = (0.028 \times ML) - 2.415$$

where F is fecundity measured in millions of eggs and ML is maximum shell length in millimetres. This relationship was found to be highly significant ($r = 0.62$; $n = 83$; $P < 0.001$). The intersection of this curve with the x-axis is at 87 mm, which is in relatively close agreement with the results obtained by examining the gonad index. These results indicate that the onset of sexual maturity in this area probably occurs when the abalone attain the length of 87 mm and that by the length of 100 mm virtually all the abalone are sexually mature.

A sample of 45 mature female abalone collected on 27 September 1985, indicated that a widespread spawning had occurred in the study area prior to this date. Over 50% of the gonads showed signs of extensive spawning, 26% had fecundities $<5\%$ that predicted by the above relationship. For this sample the relationship between maximum length and fecundity was not found to be significant ($r = 0.23$; $n = 45$; $P > 0.1$). This timing is consistent with the observations of Harrison & Grant (1971) made for

Tasmanian populations of *H. rubra* and suggests that a general spawning occurred within 9 days of the final search for breeding stock. The water temperature at the site studied at this time was $\approx 13\,°C$.

BREEDING STOCK REMOVAL

Between 10 August 1985 and 18 September 1985 divers spent 85.8 diver-h searching for abalone. A total of 3584 abalone were removed from the 90-m section of shoreline encompassing Sites 4–6, of which 3 274 (91%) were >87 mm (Fig. 2). Over the entire area catch rates fell from $104.0 > 87$ mm abalone $\cdot h^{-1}$ during the initial search to $9.8 > 87$-mm abalone $\cdot h^{-1}$ during the final search (Fig. 3). Using the number of abalone caught in each area and the size of the areas (1793, 1987 and 1674 m² for Areas 4, 5 and 6, respectively), the searches can be calculated to have reduced the density of mature abalone by 0.54, 0.51 and 0.77 abalone $\cdot m^{-2}$ in each area respectively. Catch rates declined from 98.7, 92.6, and $127.1 > 87$-mm abalone $\cdot h^{-1}$ during initial searches, to 10.2, 7.4 and $16.2 > 87$-mm abalone $\cdot h^{-1}$ in Areas 4, 5 and 6, respectively, during the fourth search.
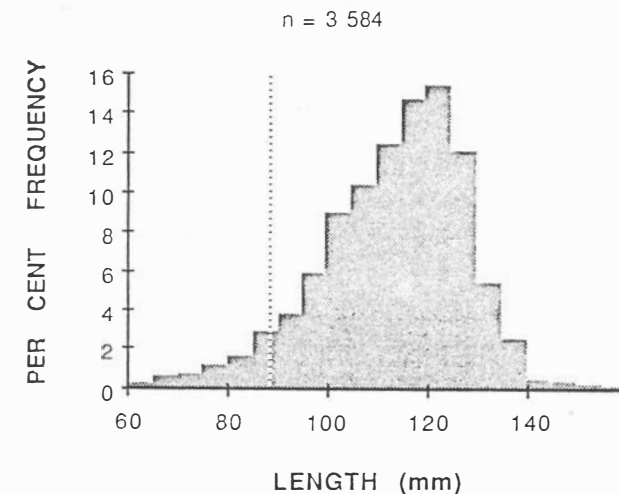
n = 3 584

Fig. 2. Length–frequency histograms for *Haliotis rubra* collected during searches of the removal area: dotted line indicates the size of first maturity (87 mm).

Accepting the catch rates as an index of relative abundance the estimated decrease in abundance of mature abalone in each area between the first and fourth visit is 89.7, 92.0 and 87.3%, respectively. From these data it can be estimated that the density of mature abalone within each area before the searches was ≈ 0.60, 0.55, and 0.88 abalone $\cdot m^{-2}$, respectively. It can also be estimated that after the searches the remaining density of mature abalone in each area was 0.06, 0.04, and 0.11 abalone $\cdot m^{-2}$,
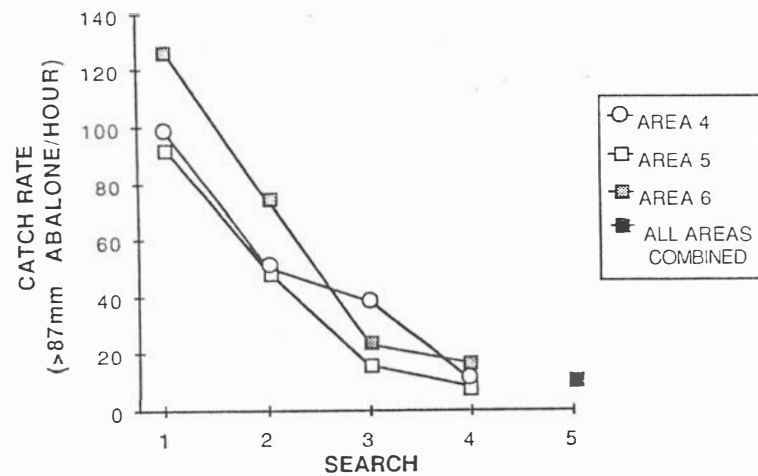
Fig. 3. Catch rates of *Haliotis rubra*, in each section of the removal area, during each period of searching: data were not separated by area for the fifth search.
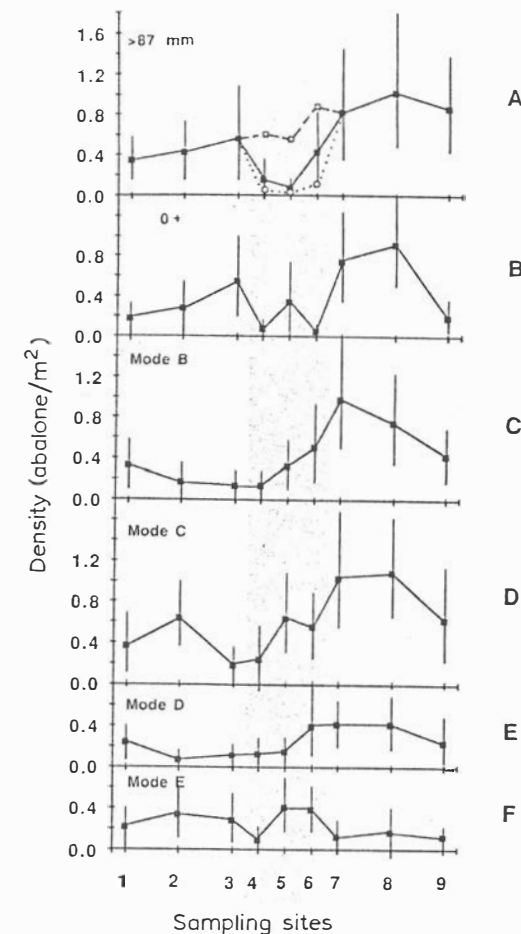

Fig. 4. The density of *Haliotis rubra* measured at each sampling site in February–March 1986, using the anaesthetic technique (solid line): A, >87-mm abalone, broken line indicates estimated density before searches, dotted line indicates estimated density during spawning; B, 0^+ mode; C, Mode B; D, Mode C; E, Mode D; F, Mode E; bars indicate ±95% confidence interval; shading indicates sites from which mature abalone were removed.

respectively. In making these estimations only the catch rate data from the first four searches have been used, as these data were not separated by individual area during the short (4.5 diver-h) final search. The final catch (44 > 87-mm abalone) has been proportioned equally between the areas. Any bias caused by this process is likely to be negligible due to the small number of abalone removed by the final search.

The movement of *H. rubra* is known to be relatively limited and widespread spawning commenced within 9 days of the final search. So it can be safely assumed that the estimated densities of mature abalone after the searches approximate the density that was present in each area during spawning.

POST REMOVAL SAMPLING

Fig. 4A shows the density of mature (> 87 mm) abalone measured at each site in February–March 1986, four months after spawning had occurred. Sites 1–3 had a generally low level of mature abalone when compared with Sites 7–9. The effect of removing breeding stock from Sites 4–6 (Sites 4–6 pooled) was still clearly evident at the time of sampling, with the density of mature abalone being significantly lower ($t = 4.15$; $P < 0.001$) than the mean density at the other sites (Sites 1–3, 7–9 pooled). The effect of migration back into the area since the removal is indicated by the shape of the depression in densities, with the highest value (Site 6) being adjacent to the highest adjoining outside value (Site 7) and the lowest value being at Site 5, furthest from the source of immigrating abalone.

Fig. 5 shows the length frequency histograms for all 0 to 60-mm abalone collected during anaesthetic sampling in 1-mm size classes. The figure presents the results of preliminary sampling conducted in August 1985 and the sampling conducted in

February and March 1986. These latter data are shown grouped for Sites 1–3, 4–6, 7–9 and for all sites pooled.

When the Macdonald & Green (1985) MIX program was used to describe the 0 to 42-mm length-frequency data the best fit was achieved with 10 log-normal size distributions, with means at 3.3, 8.4, 12.3, 15.1, 19.7, 23.7, 27.7, 33.2, 36.4, and 40.0 mm ($\chi^2 = 7.54$; d.f. = 13; $P = 0.87$). Because the smallest abalone collected during the preliminary samples, in August 1985, was 5 mm in length the smallest size group observed in February and March ($\bar{x} = 3.3$ mm) clearly settled after the removal of
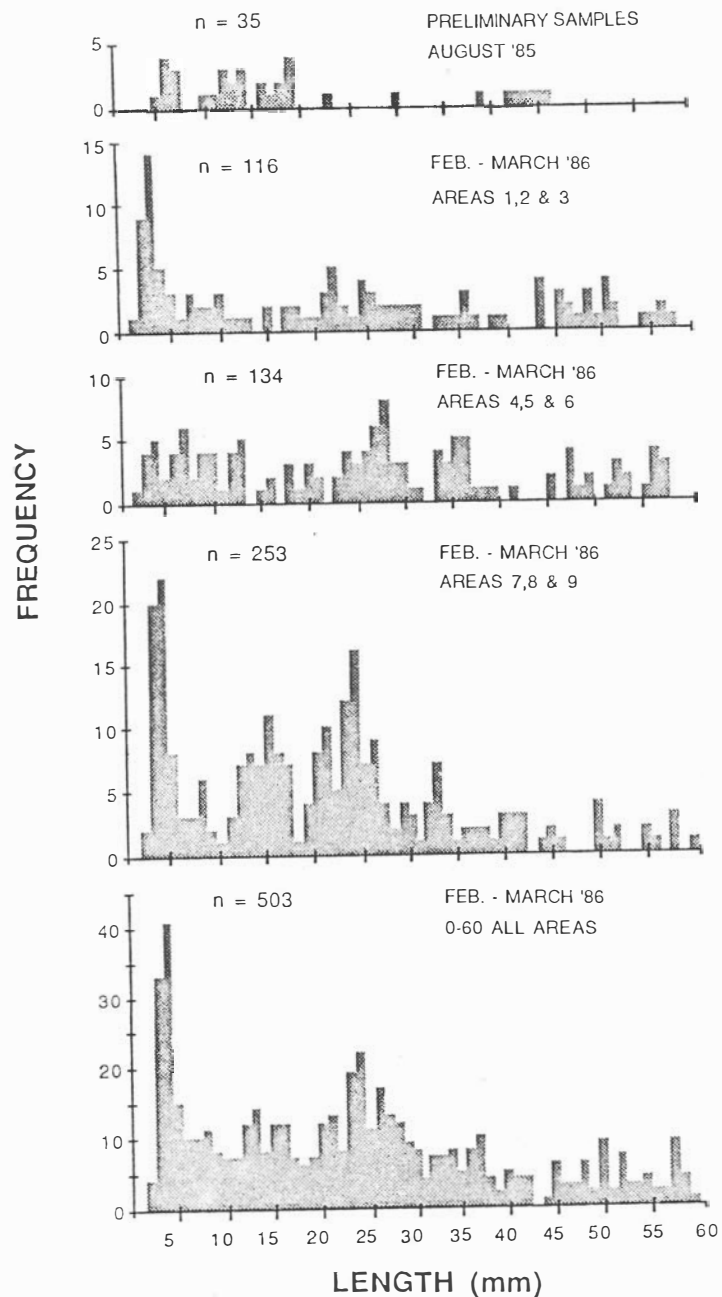
Fig. 5. Length–frequency histogram for all 0–60 mm *Haliotis rubra* sampled with the anaesthetic technique during August 1985 and February–March 1986; the February–March samples are grouped for Sites 1–3, 4–6, 7–9, and all sites combined.

breeding stock. The estimated cut-off point between the first and second distribution is 6 mm.

The next best description of the 7 to 42-mm data grouped the 2nd–4th, 5th–7th and 8th–10th of the former distributions, respectively, and described these data as three distributions. In this latter analysis the estimates converged with the estimated means of each distribution being 14.4, 25.0, and 36.1 mm ($\chi^2 = 37.1$; d.f. = 30; $P = 0.174$). To increase the numerical abundance of each size class this grouping of the smaller distributions has been used. The cut-off points between the three larger distributions (17 and 31 mm) have, however, been calculated using the estimated parameters of the smaller component distributions. The size group 43–60 mm is clearly distinct from the smaller size groups and has been treated as a separate size class.

This cursory analysis of the length–frequency histogram is not meant to imply an age for any size group besides the 0 to 6-mm class. This smallest class was clearly not present in the August 1985 samples, but settled after the searches, consequently it can be concluded that they represent at least some portion of the 0^+ age class. No age can be attached to the other size classes. If growth rates are, however, assumed to be relatively uniform within the area studied it can safely be assumed that each size class represents some unknown grouping of ages. If this is accepted, and mortality is also assumed to be relatively uniform over the research area, each size group can be used to indicate the recruitment pattern which occurred over some period of the past. For this analysis the 0 to 6-mm size group will be referred to as the 0^+ and the size groups 7 to 17, 18 to 31, 32 to 42 and 43 to 60-mm will be referred to as Modes B, C, D and E, respectively.

Fig. 4B shows the measured density of the 0^+ mode across the sampled sites. The mean density for Sites 4–6 (Sites 4–6 pooled) was significantly lower than the mean of the other sites (Sites 1–3, 7–9 pooled; $t = 3.52$; $P < 0.001$). The density for the 0^+ size group at Sites 1–3 was also generally lower than at Sites 7–9. These results show that a reduced level of recruitment occurred at Sites 4–6 following the removal of mature abalone. This effect appears to have been extremely localized, with the reduction in recruitment only being evident within the removal area. This pattern corresponds to the density pattern of adult abalone at the time of spawning.

In contrast to the observed 0^+ densities, the density patterns observed for each of the other modes were generally similar to the pattern of mature abalone, estimated to have existed prior to the removal process. With the exception of Mode E all had higher values at Sites 7–9 and their density declined relatively smoothly towards Sites 1–3 (Fig. 4C–F). The density of Mode E showed no obvious trends across the sites. For each of these size classes no significant difference was found between the mean densities at Sites 4–6 (Sites 4–6 pooled) and the mean density of the sites outside (Sites 1–3, 7–9 pooled) the removal area (Mode B; $t = 1.18$; $P > 0.1$, mode C; $t = 1.22$; $P > 0.1$, Mode D; $t = 0.287$; $P > 0.1$, Mode E; $t = 1.13$; $P > 0.1$). These data indicate that no historical precedence exists for the recruitment pattern observed following the removal of breeding stock.

TABLE I

Estimated correlations between the density of the 0^+ size group, modes B, C, D and E, and the estimated density of mature (> 87 mm) abalone before and after the searches.

Regression variable Y	Regression variable X–density of > 87 mm abalone			
	Regression equation	Correlation coefficient (r)	t-statistic ($n = 9$)	2-tailed significance
Before removal				
0^+	$y = -0.01 + 0.55x$	0.42	1.22	0.256
Mode B	$y = -0.17 + 0.87x$	0.70	2.59	0.032
Mode C	$y = 0.03 + 0.84x$	0.63	2.15	0.064
Mode D	$y = -0.07 + 0.47x$	0.78	3.29	0.011
Mode E	$y = 0.34 - 0.16x$	0.30	0.83	0.430
After removal				
0^+	$y = 0.08 + 0.60x$	0.73	2.83	0.022
Mode B	$y = 0.20 + 0.46x$	0.58	1.88	0.096
Mode C	$y = 0.36 + 0.51x$	0.61	2.04	0.076
Mode D	$y = 0.16 + 0.17x$	0.45	1.33	0.219
Mode E	$y = 0.32 - 0.18x$	0.54	1.70	0.128

Linear regressions of the density of these smaller size classes at each site against the density of mature abalone at each site, both before the searches and at the time of spawning, have been estimated (Table I). In this analysis the estimates of the initial density of mature abalone at Sites 4-6 before the searches (0.60, 0.55, and 0.88 abalone $\cdot$ m^{-2}, respectively) have been used along with the estimated densities during spawning (0.06, 0.04 and 0.11 abalone $\cdot$ m^{-2}, respectively). The density of mature abalone estimated by the post removal sampling at Sites 1–3 and 7–9 have been used as the density at these sites both before the searches and at the time of spawning.

With the exception of Mode E, all the modes showed a positive correlation with the density of mature abalone both before and after the removal process. The density of Mode E was not significantly correlated with the density of mature abalone before the searches ($r = 0.30$; $n = 9$; $P > 0.1$) nor at the time of spawning ($r = 0.54$; $n = 9$; $P > 0.1$). The relationships between the density of mature abalone before the searches and the densities of Modes B ($r = 0.70$; $n = 9$; $P < 0.05$) and D ($r = 0.78$; $n = 9$; $P < 0.05$) at each site are significant, while the correlation with Mode C is high but not significant at this level ($r = 0.63$; $n = 9$; $P = 0.064$). The density of 0^+ at each site was not significantly correlated with the density of mature abalone before the searches ($r = 0.42$; $n = 9$; $P > 0.1$).

In direct contrast to the above, the density of mature abalone at each site during spawning was significantly correlated only with the density of the 0^+ ($r = 0.73$; $n = 9$; $P < 0.05$). These results indicate that the density pattern observed for the 0^+ was most closely related to the densities of mature abalone that existed at the time of spawning, while the density patterns of Modes B, C and D were most closely related to densities of mature abalone that existed before the removal process.

The results of this experiment clearly demonstrate that for *H. rubra* the density of recruitment is related to the immediate density of spawning abalone. The density of recruitment (the 0^+ mode) was significantly lower inside the area from which spawning stock were removed, than outside the area, a pattern which was not evident in the size groups of abalone spawned before this experiment was conducted. In addition, the density of recruitment both inside and outside the area was significantly correlated with the density of breeding stock at each site. Abalone populations have been observed to be stable over time (Hines & Pearse, 1982). Thus, the density pattern of the spawning stock before the searches was probably similar to those that existed when modes B, C, D and E were recruited. The density pattern of three of these size classes were more strongly correlated with this previous pattern of breeding stock than with the pattern created by the searches. This is consistent with the finding that for *H. rubra* recruitment is directly related to the immediate density of spawning abalone. The fact that the density of the fourth and oldest size class was not correlated with either density pattern of spawning stock may indicate that some change has occurred in this abalone population over time, or the effect of movement over time.

Patterns of recruitment may arise from two causes, differential settlement or differential mortality after settlement (Keough & Downes, 1982). Connell (1985) postulated that at high settlement densities, density dependent mortality may affect recruitment. In the present study density dependent mortality would have had a smoothing effect, producing a pattern of recruitment more uniform than the settlement pattern. This would have reduced the likelihood of observing a relationship between spawning stock and recruitment but it can be rejected as being the cause of this relationship.

It is possible to hypothesize that some other form of differential mortality acting on the recruited juveniles is the causal agent of the observed pattern. To do this it is, however, necessary to take into account the significant relationship between spawning stock density and recruitment density. Any hypothesized form of differential mortality must be inversely related to the density of adult abalone. In the literature there is no indication of any biological factor associated with adult abalone which promotes the survival of juvenile abalone after settlement. Consequently, it would appear unlikely that differential mortality can explain the observed recruitment pattern and that such patterns reflected the abundance of settlement at each site.

Accepting that the recruitment densities observed reflect actual settlement patterns four explanatory models can be postulated to explain these patterns: (1) settlement of abalone larvae is random; (2) settlement is attracted by physical, chemical or biochemical cues independent of the adult stock; (3) settlement is attracted by physical, chemical or biochemical cues associated with the adult abalone; (4) dispersal of larvae is extremely restricted (Underwood, 1979).

The first and second model are easily dismissed as being incompatible with the significant correlation that was observed between recruitment density and the density

of adults. The third model cannot be entirely discounted. Abalone larvae are known to settle on surfaces of coralline algae (Shepherd & Turner, 1985). It is possible that grazers such as abalone play an important rôle in keeping these surfaces free from epiphytes and available for settling larvae. Larvae have also been shown to settle on the slime trails of conspecifics (Seki & Kan-no, 1981a). Both these factors could possibly attract larvae to settle around adult abalone and such a phenomenon has been observed in the laboratory for a number of other gastropods (see Underwood, 1979). It should also be noted that Underwood stresses that this does not necessarily happen in the natural environment.

In the present study adult abalone were only removed from the exposed surface of boulders during the searches and small abalone were not collected. The crustose coralline algae on the exposed surface of the boulders were overgrown with epiphytes before the searches were conducted which is in contrast to the crustose coralline algae on the under surfaces of the boulders in the area. These latter corallines showed evidence of grazing before and after the searches and it was on these surfaces that the small 0+ abalone (< 5 mm) were usually found, suggesting that these were the settling sites. As large amounts of macroalgae other than crustose corallines were available above the boulders and these are the preferred food of *H. rubra* in this area (Prince, unpubl. data) it is improbable that the adult abalone found during the searches were grazing the coralline surfaces below the rocks or leaving many slime trails in this micro-habitat. The high proportion of the adult abalone population in the removal area, collected by searching the exposed surface of the boulders (> 85%) also suggests that adult abalone spend little time in the under-boulder habitat. In contrast, small abalone (< 60 mm) were rarely observed on the exposed surfaces of the boulders (despite > 20 h night diving) suggesting that if conspecific abalone have a rôle in conditioning settlement sites it is probably the juveniles which are the more important. It should also be remembered that spawning began within 9 days of the last search, so that the time available for any increased epiphytic growth on settling surfaces was relatively restricted. For these reasons it is unlikely that the removal of adult abalone significantly affected the epiphytic growth or the number of slime trails on potential settlement sites. Consequently it is improbable that the observed recruitment patterns resulted from settlement being attracted by cues associated with adult abalone. This conclusion is supported by Shepherd & Turner (1985) who, on the basis of their field study, discounted the likelihood of abalone larvae being attracted to or by conspecific adults.

The final model which can explain the settlement pattern inferred by this study is that abalone larval dispersal at the site studied was extremely restricted. This explanation suggests that significant numbers of larvae did not travel into the removal area from the spawning stock known to have been outside the area, a distance at Sites 4 and 6 of only 15 m. The literature for haliotids assumes that abalone larvae are pelagic (Mottett, 1978; Fedorenko & Sprout, 1982; Tegner & Butler, 1985), swimming to the surface after hatching. Matthews & Volframs (1978) studied a similar body of water near the area studied and showed that in depths < 10 m water movement is primarily wind driven.

From the relationship derived by that study, between wind strength, depth and water movement, and from meteorological data (Aust. Dept. Sci., unpubl. data) it is possible to estimate the magnitude of water movements in the area during the time when the abalone were spawning as $\approx 0.005-0.038 \ \mathrm{m \cdot s^{-1}}$. The movement can effectively be considered unidirectional for periods of 48–96 h (Matthews & Volframs, 1978). This would have resulted in a gross movement of between 430 and 3300 m for every 24-h period abalone larvae spent in the water column, depending on the depth at which they occurred. The gross distance moved by a cell of water indicates a magnitude of mixing and dispersal, for pelagic larvae, that is incompatible with the localized reduction in settlement observed in this experiment. Clearly, the assumption of a pelagic larval life for *H. rubra* is not supported by the settlement pattern inferred by this study. Considering the magnitude of the water movement the inverse of this assumption is suggested by these results. That is, haliotid larvae avoid dispersal.

The assumption that abalone larvae are pelagic in the natural environment rather than demersal is based solely on laboratory observations of haliotid larvae. Under laboratory conditions the trochophore is positively phototactic and swims slowly towards the surface (Ino, 1952; Leighton, 1974; Yano & Ogawa, 1977; Tanaka, 1978). Late stage veligers exhibit "tumbling behaviour", in which large numbers assemble in vertical columns and at irregular intervals spontaneously tumble to the bottom of the tank and disperse (Leighton, 1972; Grant, 1981; Grant & Sumner, in prep.). Mariculturists take advantage of these behaviour patterns by using surface collection techniques when transferring larvae between tanks (Ebert & Houk, 1984). Under laboratory conditions settlement of larvae generally occurs between 3–11 days post fertilization depending on temperature (Ino, 1952; Leighton, 1974; Ebert & Houk, 1984). These observations have all been made during mariculture research programmes and no controlled experiments have been published which test their accuracy or relevance to natural conditions. Instead, the relevance of these observations to the natural environment has been assumed, and they have been taken to indicate that naturally occurring abalone larvae are pelagic, having a dispersal phase before becoming competent to settle (precompetent phase) equivalent to the time taken to settle in the laboratory (Mottett, 1978; Fedorenko & Sprout, 1982; Sluczanowski, 1984; Tegner & Butler, 1985).

There is, however, no certainty that such an assumption can be made (Underwood, 1979). The preferred settlement conditions for abalone are still poorly understood and can only be crudely approximated in the laboratory (T. Dix, pers. comm.; J. Grant, pers. comm.). It is known that when faced with less than optimal settlement conditions invertebrate larvae postpone settlement (Thorson, 1950). It has also been shown that the discrimination of the larvae choosing settlement substrata decreases as larval life is prolonged (Knight-Jones, 1953). Because of this, the time from fertilization to settlement observed in the laboratory may be a gross over-estimate of the average length of larval life in the natural environment, where optimal settlement conditions occur. These estimates of the length of abalone larval life should be regarded as estimates of the maximum length of larval life rather than the minimum.

The minimum possible larval life length is actually the time required by the larvae to become physiologically capable of settling (Strathmann *et al.*, 1981) and this is the correct definition of the precompetent phase (Jackson & Strathmann, 1981). For abalone this is when the third tubule forms on the cephalic tentacles, and the ctenidium and first epipodial tentacle appear within the larval shell (Grant, 1981; Seki & Kan-no, 1981b). For *H. rubra* the length of the precompetent phase is ≈ 106 h at $16\,°C$ (Grant & Sumner, in prep.) although settlement in the laboratory does not normally occur until ≈ 142 h post fertilization. Even this does not give a true indication of what may be the minimum possible time available for dispersal. To estimate this it is necessary to consider the proportion of the precompetent phase during which the larvae are physiologically forced to swim freely. Abalone eggs are considerably heavier than water (Ino, 1952; Grant, 1981) and if dispersal occurs it is unlikely to occur before the trocophore hatch. In addition, abalone larvae are able to stop swimming and explore settlement surfaces by creeping from the time the two snout protruberances are formed (Seki & Kan-no, 1981b). For *H. rubra* the time between hatching and being capable of movement by creeping rather than swimming is only ≈ 43 h at $16\,°C$ (Grant & Sumner, in prep.; J. Grant, pers. comm.).

The second difficulty in assuming that the laboratory behaviour of larvae is the same as natural behaviour, is that the simple, smooth, sterile laboratory tanks in which the larvae are held are totally divorced from the biologically and physically complex bottom on which abalone naturally occur. Also the densities at which the larvae are held are probably several orders of magnitude higher than those found naturally (T. Dix, pers. comm.; J. Grant, pers. comm.; L. Tong, pers. comm.). In these conditions it cannot be assumed that larval behaviour is normal. Even if this assumption were made, the importance of stereotyped behaviour might be lessened by numerous conditions in the field (Moore, 1975; Young & Chia, 1982). It is probable that if the behaviour of cultured larvae correspond to the behaviour of larvae in the natural environment, then it may correspond to the behaviour of larvae that have hatched in smooth, simple conditions. It has been demonstrated that invertebrate larvae can be capable of a number of behaviour patterns stimulated by different settlement prospects (e.g., Harrigan, 1972; Young & Chia, 1982). A possible hypothesis is that larvae in the laboratory are attempting to disperse widely because they do not receive the cues which indicate the proximity of natural settling sites, while larvae that detect these cues may avoid or minimize dispersal.

Restricted dispersal of larvae is favoured amongst benthic marine invertebrates when the resources they require are uniformly available (Menge, 1975) and relatively free of temporal variation (Palmer & Strathmann, 1981). In this situation larvae that disperse have a lower probability of finding suitable habitats than non-dispersing larvae and face greater risks while they search (Sebens, 1983). After settlement there is little compensation for this cost as both types of animal are equally certain that their chosen habitat will continue to provide the resources they need (Palmer & Strathmann, 1981). No evidence exists in the literature to suggest that adult abalone reduce the suitability of habitat for larvae or juveniles, indicating that the resources required by abalone larvae are as likely to be available locally as further afield. In addition, the kelp communities in which abalone are found are temporally stable (Dayton *et al.*, 1984; Tegner, in prep.). Thus the resources required by abalone are both uniformly available and temporally stable. As a consequence it should be expected that abalone will have evolved morphological and behavioural adaptations which will restrict larval dispersal.

For morphological reasons the primitive Archaeogastropoda cannot easily produce complex egg capsules nor undertake internal fertilization (Yonge, 1947). For this reason direct development benthic egg capsules (in which larvae pass through all development stages) and viviparity, the two most common means of restricting larval dispersion (Thorson, 1950; Mileikovsky, 1971), are not commonly found in Archaeogastropoda (Underwood, 1979). Underwood (1979) hypothesized that small gastropods denied these methods and pelagic larvae by their extremely small body size, would be forced to develop by non-dispersal lecithotrophy. Similarly it can be hypothesized that archaeogastropods such as haliotids, ecologically favoured by non-dispersal but morphologically constrained from evolving direct development or viviparity, are likely to develop this form of demersal development larvae.

Circumstantial evidence exists suggesting that abalone have behavioural adaptations which aid in restricting larval dispersal. For example, the only observation contained in the literature, of wide-scale spawning in haliotids in the natural environment, occurred in calm conditions and after several days of very calm weather (Breen & Adkins, 1980). From anecdotal information provided by commercial divers in Tasmania *H. rubra* also appears to spawn during calm weather. These observations suggest that abalone populations possibly select conditions of low water movement for spawning, adaptive behaviour which would minimize dispersion of gametes, eggs, and larvae. *H. rubra* maintains its gonads in a ripe state for long periods (Harrison & Grant, 1971; McShane *et al.*, 1986) as do many haliotids (see Mottett, 1978) and this may enable spawning to coincide with short irregular periods of low water movement. A similar phenomenon has been observed in the limpet *Cellana radians* in which spawning coincides with localized conditions of water movement (Creese & Ballantine, 1983), although for this limpet the required condition is high water movement. A number of haliotid species have been found to have variable spawning times (Newman, 1967; Poore, 1973; Shepherd & Laws, 1974; Shepherd *et al.*, 1985). More specifically several workers have observed abalone populations short distances apart spawning at different times (Webber & Giese, 1969; Hayashi, 1980); this has also been observed for *Haliotis rubra* (McShane *et al.*, 1986). These observations suggest that locally specific cues such as water movement, may be important in stimulating spawning in haliotids, which would explain why the rôle of more universal cues such as water temperature, and day length is so ambiguous (e.g. see Webber & Giese, 1969; Shepherd & Laws, 1974; Shepherd *et al.*, 1985; McShane *et al.*, 1986). This hypothesis is consistent with the results of the current study where spawning occurred between 18 and 29 September 1986. During this time there was a 3-day period (21–23 September) when winds were generally offshore and lighter

(2.3 m·s⁻¹) than the average wind speed of September (7.6 m·s⁻¹), a highly significant difference ($t = 9.17$; d.f. = 198; $P < 0.001$; Aust. Dept. Sci., unpubl. data). It is possible that the spawning of the abalone in the area studied coincided with this calm weather.

The eggs produced by haliotids are considerably heavier than water and if released over a boulder substratum, can be expected to sink and roll down into the substratum before hatching. Lodging the eggs within the substratum would prevent the eggs being rolled across sandy substrata away from reef habitat, and ensure that larvae begin their life in a habitat suitable for settlement. The behaviour observed by Breen & Adkins (1980) and supported by the observations of Quayle (1971), where spawning abalone climbed up onto kelp and prominent points of the substratum before releasing ova, is also reported by commercial divers for *H. rubra*. As abalone are often found on the edge of a rocky substratum and sand, where drifting kelp accumulates (Shepherd, 1973), this behaviour in calm water conditions may maximize the probability that eggs land on, and lodge in a hard substratum, rather than falling onto a sandy substratum.

Yano & Ogawa (1977) studied the behaviour of the larvae of *H. gigantea* under controlled laboratory conditions and found that the trochophore are positively photo-tactic and negatively geotatic. This study found that 75 h after hatching 80% of the larvae were still in the top 10 cm of the water column. Tegner & Butler (1985) used these results to imply that in the natural environment haliotid trocophores are generally positively phototactic and swim to the surface of the water where they remain for up to 75 h. This, however, conflicts with the results of Tanaka (1978), who while confirming that 3- and 5-day-old larvae (post fertilization) of the same species are positively phototactic, found them to be most abundant in the bottom layer of still water laboratory tanks. In the laboratory the trocophores of *H. rubra* swim freely for ≈ 10 h at 16 °C; they stop swimming and sink if they encounter hard surfaces or turbulence (J. Grant, pers. comm.; C. Sumner, pers. comm.). If this behaviour also occurs in the natural environment it is extremely uncertain as to whether the trocophore normally swim to the surface of the water. An alternative hypothesis is that being positively phototactic helps the larvae to orientate within the substratum. This could enable the larvae to move from deep within the substratum where the egg may have lodged towards the lighter upper boulder layers where suitable settlement sites (crustose corallines) are most abundant.

In addition to being consistent with the results of this experiment, the hypothesis that haliotid larvae are adapted to avoid dispersal, also offers an explanation for the observations of Breen & Adkins (1980) who found no abalone larvae, despite towing a plankton net over a known spawning site 2 and 3 days after the spawning. It also explains the findings of Tomita *et al.* (1977) who, by using a plankton pump, found small numbers of larvae in six of 19 samples. In only two of these samples were the larvae more numerous in the surface layer than the bottom layer and both these samples were taken from depths < 3 m. This hypothesis is also consistent with the observation reported in Sluczanowski (1984) that in an isolated substock a positive relationship had been found between the biomass of fecund abalone and the recruitment of 1⁺ animals.

Restricted dispersal patterns for haliotid larvae are also consistent with the high levels of inbreeding observed in haliotid populations (Fujino, 1978; Fujio *et al.*, 1983).

The possibility that haliotid larvae generally avoid dispersal, rather than being pelagic and thus vagile, as at present assumed, has important implications for the management of abalone fisheries and deserves further consideration. Low dispersal rates would explain why many abalone fisheries have been so easily over-fished (Mottett, 1978). If larval dispersal is generally restricted, it is obvious that the potential for recolonizing areas which have been denuded of breeding stock by over-fishing, is extremely limited. The removal of small pockets of breeding stock would cause the overall productivity of a fishery to diminish, concentrating the fishing power of that industry on the remaining stocks, and making their collapse more likely.

REFERENCES

ANDERSON, E. K. & W.J. NORTH, 1966. *In situ* studies of spore production and dispersal in the giant kelp, *Macrocystis*. *Proc. Int. Seaweed Symp.*, Vol. 5, pp. 73–86.

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

CREESE, R. G. & W.J. BALLANTINE, 1983. An assessment of breeding in the intertidal limpet, *Cellana radians* (Gmelin). *J. Exp. Mar. Biol. Ecol.*, Vol. 67, pp. 43–59.

CONNELL, J. H., 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J. Exp. Mar. Biol. Ecol.*, Vol. 93, pp. 11–45.

DAYTON, P. K., 1973. Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. *Ecology*, Vol. 54, pp. 433–438.

DAYTON, P. K., V. CURRIE, T. GERRODETTE, B. D. KELLER, R. ROSENTHAL & D. VEN TRESCA, 1984. Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.*, Vol. 54, pp. 253–289.

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

FEDORENKO, A. Y. & P. E. SPROUT, 1982. Abalone biology, fishery regulations, commercial catch (1952–1980), and current state of resource in British Columbia. *Can. Man. Rep. Fish. Aquat. Sci.*, No. 1658, 74 pp.

FUJINO, K., 1978. Genetics studies on the Pacific Abalone. I. Inbreeding and overdominance as evidenced by biochemical polymorphism in a wild population. *Bull. Jpn. Soc. Sci. Fish.*, Vol. 44, pp. 357–361.

FUJIO, Y., R. YAMANAKA & P.J. SMITH, 1983. Genetic variation in marine molluscs. *Bull. Jpn. Soc. Sci. Fish.*, Vol. 49, pp. 1809–1817.

GERRODETTE, T., 1981. Dispersal of the solitary coral *Balanophyllia elegans* by demersal planular larvae. *Ecology*, Vol. 62, pp. 611–619.

GRANT, J. F., 1981. Abalone culture in Japan: development and current commercial practise. *Tasmanian Fish. Res.*, Vol. 23, pp. 1–17.

HAYASHI, I., 1980. The reproductive biology of the ormer, *Haliotis tuberculata*. *J. Mar. Biol. Assoc. U.K.*, Vol. 60, pp. 415–430.

HARRIGAN, J. F., 1972. Behaviour of the planula larva of the scleractinian coral *Pocillopora damicornis* (L.). *Am. Zool.*, Vol. 12, p. 723 only.

HARRISON, A. J. & J. F. GRANT, 1971. Progress in abalone research. *Tasmanian Fish. Res.*, Vol. 5, pp. 1–10.

HINES, A. H. & J. S. PEARSE, 1982. Abalones, shells, and sea otters: dynamics of prey populations in central California. *Ecology*, Vol. 63, pp. 1547–1560.

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

JACKSON, G. A. & R. R. STRATHMANN, 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development. *Am. Nat.*, Vol. 118, pp. 16–26.

KEOUGH, M. J. & B. J. DOWNES, 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia (Berlin)*, Vol. 54, pp. 348–352.

KNIGHT-JONES, E. W., 1953. Decreased discrimination during setting after prolonged planktonic life in larvae of *Spirorbis borealis* (Serpulidae). *J. Mar. Biol. Assoc. U.K.*, Vol. 32, pp. 337–345.

LEIGHTON, D. L., 1972. Laboratory observations on the early growth of the abalone, *Haliotis sorenseni*, and the effect of temperature on larval development and settling success. *Fish. Bull. NOAA*, Vol. 70, pp. 373–381.

LEIGHTON, D. L., 1974. The influence of temperature on larval and juvenile growth in three species of southern California abalones. *Fish. Bull. NOAA*, Vol. 72, pp. 1137–1145.

MACDONALD, P. D. M. & P. E. J. GREEN, 1985. *MIX 2.2.: An interactive program for fitting mixtures of distributions*. Icthus Data Systems, Hamilton, Ontario.

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

MATTHEWS, J. H. & A. VOLFRAMS, 1978. Investigating the physical aspect of bays and estuaries: a study of the hydrology and hydrodynamics of North West Bay. *Univ. Tas. Env. Stud. Occ. Pap.*, No. 7.

MCSHANE, P. E., K. H. H. BEINSSEN, M. G. SMITH, S. O'CONNOR & N. J. HICKMAN, 1986. Reproductive biology of blacklip abalone *Haliotis ruber* Leach from four Victorian populations. *Mar. Sci. Lab. Tech. Rep.*, No. 55, 13 pp.

MENGE, B. A., 1975. Brood or broadcast? The adaptive significance of different reproductive strategies in the two intertidal sea stars *Leptasterias hexactis* and *Pisaster ochraceus*. *Mar. Biol.*, Vol. 31, pp. 87–100.

MILEIKOVSKY, S. A., 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar. Biol.*, Vol. 10, pp. 193–213.

MILLAR, R. H. & P. J. HOLLIS, 1963. Abbreviated pelagic life of Chilean and New Zealand oysters. *Nature (London)*, Vol. 197, pp. 512–513.

MOORE, P. G., 1975. The role of habitat selection in determining the local distribution of animals in the sea. *Mar. Behav. Physiol.*, Vol. 3, pp. 97–100.

MOTTET, M. G., 1978. A review of the fishery biology of abalones. *Wash. Dept. Fish. Tech. Rep.*, No. 37, 78 pp.

NEWMAN, G. G., 1967. Reproduction of the South African abalone *Haliotis midae*. *Invest. Rep. Div. Sea Fish. S. Afr.*, No. 64, 24 pp.

OLSON, R. R., 1985. The consequences of short-distance larval dispersal in a sessile marine invertebrate. *Ecology*, Vol. 66, pp. 30–39.

PALMER, A. R. & R. R. STRATHMANN, 1981. Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. *Oecologia (Berlin)*, Vol. 48, pp. 308–318.

PEARSE, J. S., 1969. Slow developing demersal embryos and larvae of the Antarctic sea star *Odontaster validus*. *Mar. Biol.*, Vol. 3, pp. 110–116.

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

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

QUAYLE, D. B., 1971. Growth, morphometry and breeding in the British Columbia abalone (*Haliotis kamtschatkana* Jonas). *Tech. Rep. Can. Fish. Res. Board*, No. 279, 16 pp.

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

SANDERSON, C. J. & D. P. THOMAS, 1987. Macroalgal communities in the D'entrecasteaux Channel, Tasmania. *Aust. J. Ecol.*, Vol. 12, pp. 41–51.

SEBENS, K. P., 1983. The larval and juvenile ecology of the temperate octocoral *Alcyonium siderium* Verrill. I. Substratum selection by benthic larvae. *J. Exp. Mar. Biol. Ecol.*, Vol. 71, pp. 73–89.

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

SEKI, T. & H. KAN-NO, 1981b. Observations on the settlement and metamorphosis of the veliger of the Japanese abalone, *Haliotis discus hannai* Ino, Haliotidae, Gastropoda. *Bull. Tohoku Reg. Fish. Res. Lab.*, Vol. 42, pp. 31–39.

SHEPHERD, S. A., 1973. Studies on southern Australian abalone (genus *Haliotis*) I. Ecology of five sympatric species. *Aust. J. Mar. Freshwater Res.*, Vol. 24, pp. 217–257.

SHEPHERD, S. A. & H. M. LAWS, 1974. Studies on southern Australian abalone (genus *Haliotis*). II. Reproduction of five species. *Aust. J. Mar. Freshwater Res.*, Vol. 25, pp. 49–62.

SHEPHERD, S. A. & J. A. TURNER, 1985. Studies on southern Australian abalone (genus *Haliotis*). VI. Habitat preference, abundance and predators of juveniles. *J. Exp. Mar. Biol. Ecol.*, Vol. 93, pp. 285–298.

SHEPHERD, S. A., P. S. CLARKSON & J. A. TURNER, 1985. Studies on southern Australian abalone (genus *Haliotis*). V. Spawning, settlement and early growth of *H. scalaris*. *Trans. R. Soc. South Aust.*, Vol. 109, pp. 61–62.

SHUTO, T., 1983. Larval development and geographical distribution of the Indo-West Pacific *Murex*. *Bull. Mar. Sci.*, Vol. 33, pp. 536–544.

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

STRATHMANN, R. R., E. S. BRANSCOMB & K. VEDDER, 1981. Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. *Oecologia (Berlin)*, Vol. 48, pp. 13–18.

TANAKA, Y., 1978. Swimming behaviour of the abalone larvae, *Nordotis gigantea* (Gmelin), in an outdoor tank. *Bull. Tokai Reg. Fish. Res. Lab.*, Vol. 95, pp. 15–22.

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

THORSON, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.*, Vol. 25, pp. 1–45.

TOMITA, K., K. TAJIMA & K. KUDO, 1977. Morphological observations of the veliger and the creeping larvae of an abalone, *Haliotis discus hannai*, from Rebun Island in the North-Western Hokkaido. *Sci. Rep. Hokkaido Fish. Exp. Stn.*, No. 19, pp. 13–18.

UNDERWOOD, A. J., 1979. The ecology of intertidal gastropods. *Adv. Mar. Biol.*, Vol. 16, pp. 111–210.

VANDERMEULEN, H. & R. E. DEWREEDE, 1986. The phenology, mortality, dispersal and canopy species interaction of *Colpomenia peregrina* (Sauv.) Hamel in British Columbia. *J. Exp. Mar. Biol. Ecol.*, Vol. 99, pp. 31–47.

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

YANO, I. & T. OGAWA, 1977. Effects of light, temperature and hydrostatic pressure on vertical distribution of abalone larvae, *Haliotis gigantea*. *Bull. Tokai Reg. Fish. Res. Lab.*, Vol. 91, pp. 19–27.

YONGE, C. M., 1947. The pallial organs of aspidobranch Gastropoda and their evolution throughout the Mollusca. *Phil. Trans. R. Soc. Ser. B.*, Vol. 232, pp. 443–518.

YOUNG, C. M. & F.-S. CHIA, 1982. Factors controlling spatial distribution of the sea cucumber *Psolus chitonoides*: settling and post-settling behaviour. *Mar. Biol.*, Vol. 69, pp. 195–205.

A Method for Ageing the Abalone
Haliotis rubra (Mollusca : Gastropoda)

J. D. Prince[AB], *T. L. Sellers*[B], *W. B. Ford*[B] *and S. R. Talbot*[B]

[A] Zoology Department, University of Tasmania, G.P.O. Box 252C, Hobart, Tas. 7001.
Present address: P.O. Box 108, North Fremantle, W.A. 6159.
[B] Tasmanian Department of Sea Fisheries, Research Laboratory, Crayfish Point, Taroona, Tas. 7006.

Abstract

A technique for ageing *Haliotis rubra* is described. The spire of the shell is ground to create a polished disc of nacre in which rings are visible. The number of rings present in each shell is related to the size of the shell. The age at which each ring is deposited has been determined using an age-length key derived from length-frequency histograms and tag return data. For the population studied, three minor rings are deposited in the first 16 months of life and a major ring at an age of approximately 20 months. Subsequent rings are deposited at approximately annual intervals.

Introduction

The ability to age a species is an important tool in assessing the state of an exploited stock (Ricker 1977). Despite valuable fisheries for haliotids in many countries (Mottett 1978), no validated and reliable technique for ageing these commercially important species has been published (Ward 1986). Several studies have noted that in some populations external growth checks may be present on abalone shells, and in some studies these have been used to infer age (Forster 1967; Poore 1972; Kojima *et al.* 1977; Saito 1981). However, the presence of external growth checks is not universal (Muñoz-Lopez 1976; Mottett 1978) even within species (Poore 1972), or necessarily annual as often assumed (Shepherd and Hearn 1983). Cross sections of abalone shells have shown that interruptions also exist in the internal structure of the shell and may be associated with external checks (Sinclair 1963; Poore 1972; Munoz-Lopez 1976). Munoz-Lopez (1976) observed these interruptions in the Mexican abalone *Haliotis corrugata* and *H. fulgens* and suggested a method of sectioning the shell which allowed the interruptions to be viewed more easily as concentric circles. He noted that the number of rings observed in a shell increased with size and, after examining the structure of the shell, concluded that the rings were annual; however, this assumption was not verified with independent ageing data.

The importance of validating any ageing technique with independent length-frequency or mark-recapture data has been stressed by Beamish and McFarlane (1983). This paper describes the application of Munoz-Lopez's ageing technique to a Tasmanian population of *Haliotis rubra* (*H. ruber* Leach, emended Ludbrook 1984).

Materials and Methods

Sampling

Fieldwork was conducted at Blubber Head in Port Esperance, Tasmania (43°19′S.,147°04′E.). Between February 1984 and October 1985, the abalone population in this area was sampled at 4-monthly intervals. The anaesthetic sampling technique described by Prince and Ford (1985) was used to collect abalone at the site. The initial sampling (February 1984) of 16 m² at this site showed that the abalone were most abundant at depths <4 m, and that the size composition of the abalone population was

extremely variable over small distances (20–40 m). Because of this, in June 1984 sampling was confined to <4 m depth and the total area sampled was increased to 20 m². In October 1984 the area sampled was again increased, this time to 44 m², and sample sites were standardized. To achieve this, markers were placed on the shore-line at four points approximately 50 m apart; in front of each marker, an area totalling 11 m² was sampled by throwing a 1 m² quadrat from an anchored boat.

Analysis of Length-frequency Data

The 'Mix' program (Macdonald and Green 1985) was used to describe the length-frequency data. The program fits a series of normal distributions to a length-frequency histogram, estimating the mean and standard deviation of each distribution, and estimating the proportion of the histogram contained within each curve.

For this analysis, the data from the four standard sites were pooled. The February 1985 sample has not been analysed because of its small size. The low abundance of larger abalone in the samples prevented the 'Mix' model from converging on any unique description of the larger size classes. To enable the estimates of the model to converge, it was necessary to truncate the data sets and use only the more abundant smaller size classes. The June 1984 histogram has been truncated at 40 mm, because only 20 quadrats were sampled, resulting in a small sample size. The other samples have been truncated at 80 mm. Using truncated data sets, the 'Mix' model converged on a unique set of estimates for all the histograms excepting that of the October 1984 sample. For the October 1984 sample no unique solution could be found, so trial and error was used to obtain the best fit for the data. The estimated parameters for each distribution were used to provide age–length data for the analysis of growth parameters.

Table 1. Estimates, and their standard errors, of the means (mm), proportions (fraction of sample size) and standard errors (mm) of the size distributions contained in the 0–80 mm length-frequency histograms for *H. rubra*

The estimates were made using the 'Mix' model (Macdonald and Green 1985)

Sample analysed	Mean Estimate	s.e.	Proportion Estimate	s.e.	Standard deviation Estimate	s.e.	n	No. squares sampled	x^2 value	d.f.	P
June 1984	12·46	0·34	0·77	0·03	3·61	0·26	164	20	15·52	13	0·276
0–40 mm	29·71	0·63	0·23	0·03	3·40	0·51					
Oct. 1984	2·30	3·64	0·03	0·01	0·47	5·78					
0–80 mm	18·50	0·30	0·53	0·04	3·70	0·28	377	44	26·29	23	0·288[A]
	41·30	3·02	0·36	0·13	10·86	4·48					
	60·63	2·63	0·09	0·09	5·15	2·51					
Feb. 1985	4·81	0·08	0·62	0·02	1·55	0·06					
0–80 mm	26·60	0·92	0·25	0·02	6·46	0·73	688	44	38·99	27	0·064
	45·31	2·15	0·07	0·04	5·31	2·58					
	63·20	4·13	0·06	0·02	8·03	2·48					
June 1985	10·31	0·21	0·47	0·02	3·14	0·16					
0–80 mm	32·69	1·16	0·34	0·05	6·02	0·87	546	44	69·31	28	<0·001
	50·18	2·76	0·11	0·06	6·20	3·13					
	70·19	1·96	0·08	0·03	5·78	1·40					
Oct. 1985	3·84	0·58	0·24	0·03	3·41	0·63					
0–80 mm	16·04	0·39	0·42	0·03	3·34	0·36	393	44	33·14	28	0·231
	37·79	0·90	0·27	0·03	6·90	0·96					
	63·70	2·70	0·07	0·02	7·45	1·96					

[A] Estimates of parameter values did not converge.

Growth Studies

Between January 1983 and February 1985, 705 *H. rubra* individuals were tagged and released at the sample site. Two tagging techniques were used: small laminated tags glued to the shells with fast setting
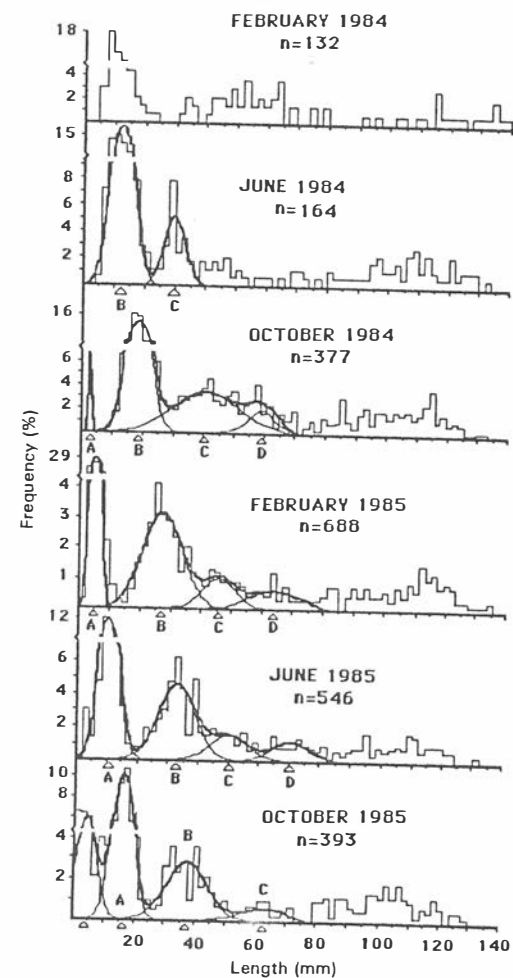
Fig. 1. Length-frequency histograms for *H. rubra* samples collected between February 1984 and October 1985, grouped in 2-mm size categories and showing the size distributions described using the 'Mix' model (Macdonald and Green 1985); capital letters identify modes described by the analysis (see text for details of the analysis).

glue, and disc tags riveted to a respiratory pore of the abalone. In total, 646 were tagged with the former technique and 59 with the latter. Animals representing the size range 34 to 126 mm were released. Recapture of released abalone took place during August and September 1986.

The methods of Fabens (1965) were used to analyse and describe the growth parameters of the abalone population. The Fabens method fits a von Bertalanffy growth curve to tag return data; by way of comparison, estimates of K and L_∞ were also obtained using the non-linear least-squares algorithm LMM1 modified by Dr A. J. Miller from Osborne (1976).

Growth Rings

Abalone from Blubber Head were sampled during August and October 1986 and the internal structure of their shells examined. The technique of Muñoz-Lopez (1976) was used to examine the internal structure of the abalone shells. The spire of each shell was ground flat until a small hole had been created through the spire. This process exposed a flat oval disc of nacre, up to 10-15 mm in diameter, and with an off-centre hole, where the spire had been. This disc of nacre was polished using emery paper.

The polished disc on each shell was examined with a dissecting microscope and direct lighting. The nacre was observed to contain a series of concentric translucent bands separated by narrower, more opaque, rings. The number of these rings was counted for each shell and the maximum shell length measured. Shells with spires damaged by boring organisms, or with discoloured bands of nacre indicating borer attack elsewhere in the shell, were discarded from this analysis.

Results

Analysis of Length-frequency Histograms

The size distributions described for the length-frequency histograms (Fig. 1) by the 'Mix' model for each sample are detailed in Table 1. Five major size classes were described with the Mix model. The smallest size class observed during the study began recruiting to the population in October 1984 and will be referred to as the A mode. Between October 1984 and February 1985, this size class increased in abundance, indicating that recruitment to the population continued during this period. The next-largest size class of animals observed (the B mode) was first observed in June 1984 at a mean size of $12 \cdot 5$ mm. This size class had increased in size to $37 \cdot 8$ mm by October 1985. The third size class (mode C) grew from $29 \cdot 7$ mm in June 1984 to a mean size of $63 \cdot 7$ mm in October 1985. The largest size class (mode D) described by the Mix model had a mean length of $60 \cdot 6$ mm in October 1984. This size class was observed until June 1985 when it had obtained a mean size of $70 \cdot 2$ mm.

Widespread spawning of H. rubra has been observed at a nearby site to begin during the last week of September (Prince et al. 1987). This timing is consistent with the observation that recruitment occurs between October and February. On this basis, October 1 has been assumed to be the 'date of birth' for this population. Using this date, modes A, B, C and D can be estimated to have been approximately 4, 16, 28 and 40 months old, respectively, in February 1985.

Growth

In all, 55 tagged abalone were recovered during the recapture searches with the time at liberty ranging from 490 to 1126 days. Nine of the abalone recaptured had been tagged with rivet tags. The tagged abalone were primarily from the larger size classes. Approximately 50% of those recovered had been released at a size >60 mm and over 85% of the animals recaptured were >90 mm when recovered. This was because of the difficulty of capturing, handling and tagging smaller abalone.

Analysis of the tag return data gave an estimate for K of $0 \cdot 024$ (s.e. $3 \cdot 10 \times 10^{-3}$) and an L_∞ of $139 \cdot 7$ mm (s.e. $7 \cdot 24$), when time was measured in months. These estimates were obtained with both the methods used. Shepherd and Hearn (1983) observed that the Fabens (1965) least-squares algorithm produces wider confidence intervals than the non-linear algorithm; however, the estimates and their standard errors obtained in this study using the two methods were consistent to the sixth and third decimal place, respectively.

A highly significant linear correlation ($P < 0 \cdot 001$; $r = 0 \cdot 991$; $n = 16$) exists between the means of the size classes (<80 mm), described by the 'Mix' model, and age. This relationship can best be described by the equation $A = 1 \cdot 41 + 0 \cdot 58\ L$, where A is the age in months and L is the length in millimetres. This equation implies that t_0 (the theoretical time when size is equal to zero) for this population is approximately $1 \cdot 4$ months. However, if a t_0 of $1 \cdot 4$ months is used with the parameters estimated for the von Bertalanffy curve, the curve greatly over-estimates the early growth described by the age–length data.

The growth of abalone in this population is best described by using both equations independently, describing the growth of <80-mm abalone in the area with a straight line and the growth of larger abalone with a von Bertalanffy curve. If 80 mm is accepted as the limit of both curves the straight-line equation can be used to estimate an age of $47 \cdot 8$ months for an 80-mm animal. Substituting these values into the von Bertalanffy equation, a t_0 of $12 \cdot 1$ months can be estimated for use with the von Bertalanffy section of the curve. It should be noted that this t_0 has no biological basis, but positions the von Bertalanffy section of the growth curve in relation to the linear growth phase. Using both these equations a growth curve and age-length key has been estimated (Fig. 2).
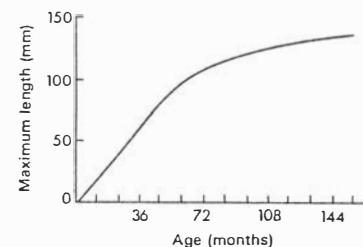

Fig. 2. Growth curve estimated for H. rubra at the Blubber Head study site. The curve uses age–length data derived from length-frequency histograms to describe the <80 mm section of the curve and von Bertalanffy parameters derived from tag return data to describe the curve >80 mm.

The accuracy of combining the two curves was checked using the tagged abalone released at sizes <80 mm and recaptured at >80 mm. Their age at time of release was estimated with the straight-line equation and, together with their time at liberty, used to calculate their age when recaptured. Using the estimated age of recapture, an expected size was calculated with the von Bertalanffy equation for comparison with their actual size of recapture. The hypothesis that actual sizes were different from expected sizes was tested with a paired t-test and rejected ($P > 0 \cdot 10$; $t = 0 \cdot 345$; d.f. $= 37$).

Growth Rings

Two types of ring structures were evident within the shells examined. The three outer-most rings were considerably finer than the inner rings. These minor rings were a uniform $0 \cdot 02$–$0 \cdot 05$ mm thick for the entire circumference of the shell section and were the first rings to be deposited, their deposition being complete before the abalone reached 30 mm (Fig. 3). In the larger shells (>90 mm) where a disc of 10-15 mm diameter had to be created to penetrate the shell, one or more of these minor rings were sometimes lost in the grinding process (Fig. 4). For this reason major and minor rings were counted separately. The major rings were distinguished from the minor rings by their greater width (generally $0 \cdot 05$–$0 \cdot 15$ mm), and by the fact that the width of individual rings varied around their circumference, with sections being up to $0 \cdot 3$ mm thick.

The number of rings present in the shells increased relatively smoothly with size (Fig. 3). Proportionately more of the larger shells were discarded because they showed evidence of having been affected by boring organisms and, because of this, the sample sizes declined.

Using the age-length key, it can be estimated that the three minor rings were deposited during the first 16 months of life (7·4, 11·4 and 15·7 months respectively). The first major ring was deposited during the second year of life (20·6 months) and a major ring was deposited during each subsequent year (32·7, 43·4, 59·2, 69·3, 79·8, 89·3 months
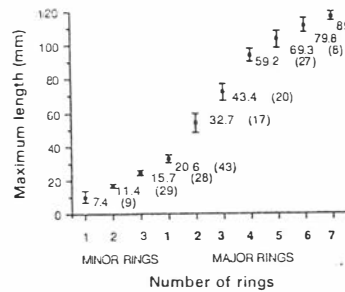

Fig. 3. Relationship between number of rings and length. Error bars indicate 95% confidence intervals; numerals outside parentheses indicate estimated age (months) when rings are formed; numerals inside parentheses indicate sample size (n).
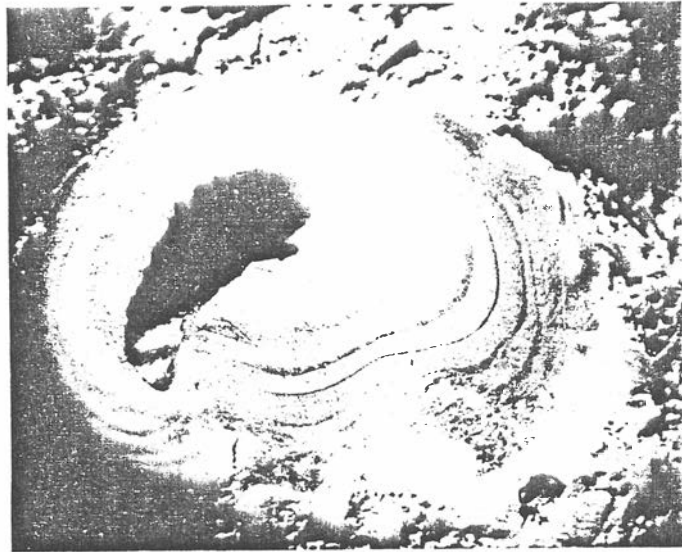

Fig. 4. Magnified section (c. 20×) of the polished nacre disk, created by grinding the spire of abalone shells, showing two minor rings (arrowed) outside six major rings.

respectively). This pattern indicates that the major rings are probably deposited during June–August of each year in 1+ abalone and older. This timing apparently coincides with the period of coldest water rather than with the September–November spawning period.

Discussion

The straight-line growth observed for the smaller size classes of abalone in this study has been observed or hypothesized for haliotids in a number of other studies (Forster 1967; Newman 1968; Poore 1972; Koike 1978; Hayashi 1980; Saito 1981). Several other studies have observed the early growth of haliotids to be non-linear, although the departure from linear in these studies has often been slight and in some studies appears to be more assumed than observed (Shepherd and Hearn 1983; Shepherd et al. 1985; Clavier and Richard 1986). A number of authors have also experienced difficulty matching the growth of juvenile and adult abalone using a von Bertalanffy curve (Poore 1972; Sainsbury 1982). Poore (1972) used a von Bertalanffy curve in the same way as it has been used in this study to describe only the upper portion of the growth curve. Yamaguchi (1975) discussed the limitations imposed by using von Bertalanffy curves to describe invertebrate growth more generally, but particularly when extrapolating curves, based on tagged adults, to describe juvenile growth. Yamaguchi found that if juvenile growth was not studied independently there was a serious risk of overestimating juvenile growth; a conclusion that is entirely consistent with the findings of this study.

The growth rates found by this study, particularly for the younger age classes, are lower than those documented by Harrison and Grant (1971) or Shepherd and Hearn (1983) who studied H. rubra in Tasmania and South Australia respectively. This could be explained by the known intra-specific variability of haliotid growth rates (Leighton and Boolootian 1963; Forster 1967; Harrison and Grant 1971; Shepherd and Laws 1974; Sainsbury 1982) and the emphasis these studies placed upon tagging data. In most of the earlier studies, t_0 was assumed to have a value of approximately zero. If this assumption had been made in the current study and used with the mark-recapture data, the age of an abalone at any given length could have been underestimated by up to 17 months.

It is evident that the major growth rings observed in this study are deposited during the winter months and probably represent winter growth checks rather than spawning checks. Such an interpretation is consistent with the fact that breeding in this population does not generally commence until a size of approximately 90 mm has been attained (Prince, unpublished data), indicating that growth checking is occurring in both breeding and non-breeding abalone. This interpretation of the rings is similar to that of Muñoz-Lopez (1976) who, without independent verification, inferred that the rings found in Mexican abalone were formed in winter.

The deposition of the minor rings at 7·4, 11·4 and 15·7 months of age can not be explained by winter temperatures or spawning. Larval haliotids settle on the surfaces of coralline algae on which they feed during the first phase of their juvenile life (Shepherd and Turner 1985); the older juveniles and adults live in crevices and eat macroalgae (Shepherd 1973). It can be expected that juvenile abalone move through a number of microhabitats during their first 12–18 months of life before adopting more adult-like habitats and feeding patterns; possibly the minor rings reflect a checking of growth during these changes. However, the precise explanation for the growth-checking that undoubtedly causes these structures to be formed will not be forthcoming until the biology and ecology of juvenile abalone are more clearly understood.

Samples of H. rubra shells from Port Phillip Bay in Victoria, from near Sydney in New South Wales, and elsewhere in Tasmania were examined at the end of this study. Using the growth parameters for the populations from which the samples were taken (R. Day and A. Leorke, unpublished data; G. Hamer, unpublished data; Prince, unpublished data) it appears that the interpretation of these structures, derived from this study, is valid for the Victorian and Tasmanian samples. It may not be applicable to the sample from New South Wales; here, the shells examined appeared to have a larger number of minor rings and no major rings. Moreover, these rings did not appear to have been laid down during each winter. It is possible that growth checking does not occur in New South Wales during

winter because of warmer water temperatures. Clearly this method of ageing should be used cautiously with stocks or species of abalone for which it has not been validated. However, as the major commercial stocks of abalone tend to be in cooler temperate waters with pronounced winter cooling (Mottet 1978) and these ring structures have also been detected in several Mexican species of haliotid (Muñoz-Lopez 1976), the general technique, as distinct from the interpretation, is likely to be applicable to most commercial haliotid species.

During this study, abalone shells affected by boring organisms were discarded from the analysis. A proportionately greater number of the larger shells were affected by these organisms and this could potentially limit the usefulness of the technique. In this context, the following observations regarding the effect of borers on the shells are relevant. Shells attacked by borers did not always show evidence of that attack throughout the shell; it appeared that in many cases the animal had been able to respond to the borer attack with a limited deposition of nacre that did not affect shell deposition in the spire. The rings in these shells could be counted in the normal manner. Where the boring organism had affected the area closer to the spire, the effect of the attack was evidenced by one or more thick discoloured layers of nacre within the spire. If these discoloured rings were not counted, the number of rings seemed to be consistent with other shells of similar size. In a third class of affected shells, the top of the spire had been completely eroded away removing an unknown number of layers and these shells were completely useless. From these observations it is apparent that the usefulness of the technique may be extended by using the first two categories of shells affected by boring organisms.

This study documents a technique for ageing a Tasmanian population of *H. rubra*. It is likely that this technique could be applied to a wide range of commercial haliotid species. A widely applicable ageing technique such as this has the potential to facilitate biological studies of these species, benefiting the management of existing haliotid fisheries (Ward 1986).

Acknowledgments

References

Beamish, R. J., and McFarlane, G. A. (1983). The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* **112**, 735–43.

Clavier, J., and Richard, O. (1986). Growth of juvenile *Haliotis tuberculata* (Mollusca : Gastropoda) in their natural environment. *J. Mar. Biol. Assoc. U.K.* **66**, 497–503.

Fabens, A. J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth* **29**, 265–89.

Forster, G. R. (1967). The growth of *Haliotis tuberculata*: results of tagging experiment in Guernsey 1963–65. *J. Mar. Biol. Assoc. U.K.* **47**, 287–300.

Harrison, A. J., and Grant, J. F. (1971). Progress in abalone research. *Tasmanian Fish. Res.* **5**, 1–10.

Hayashi, I. (1980). Structure and growth of a shore population of the ormer, *Haliotis tuberculata*. *J. Mar. Biol. Assoc. U.K.* **60**, 431–7.

Koike, Y. (1978). Biological and ecological studies on the propagation of the ormer, *Haliotis tuberculata* Linnaeus 1. Larval development and growth of juveniles. *Mer (Tokyo)* **16**, 124–36.

Kojima, H., Nakahisa, Y., Tanimoto, H., and Isibasi, K. (1977). A study on the stock of Japanese black abalone, *Haliotis discus discus* in Tokushima Prefecture 1. Growth of shells. *Bull. Tokai Reg. Fish. Res. Lab.* **90**, 25–37.

Leighton, D. L., and Boolootian, R. A. (1963). Diet and growth in the black abalone, *Haliotis cracherodii*. *Ecology* **44**, 227–38.

Ludbrook, N. H. (1984). Quaternary molluscs of South Australia. Handb. South Aust. Dep. Mines Energy No. 9.

Macdonald, P. D. M., and Green, P. E. J. (1985). 'Mix 2·2: An Interactive Program for Fitting Mixtures of Distributions.' (Icthus Data Systems: Hamilton, Ontario.)

Mottett, M. G. (1978). A review of the fishery biology of abalones. *Wash. Dep. Fish. Tech. Rep.* **37**, 1–78.

Muñoz-Lopez, T. (1976). Resultados preliminares de un método para determinar edad en abulones (*Haliotis* spp.) de Baja California. Memorias del Simposio sobre Recursos Pesqueros Masivos de México Ensenada, B.C., del 28 al 30 de Septiembre, 1976. pp. 281–301.

Newman, G. G. (1968). Growth of the South African abalone *Haliotis midae*. S. Afr. Div. Sea Fish. Invest. Rep. No. 67.

Osborne, M. R. (1976). Nonlinear least squares—the Levenberg algorithm revisited. *J. Aust. Math. Soc. Ser. B* **19**, 343–57.

Poore, G. C. B. (1972). Ecology of New Zealand abalones *Haliotis* species (Mollusca : Gastropoda). 3. Growth. *N.Z. J. Mar. Freshwater Res.* **6**, 534–59.

Prince, J. D., and Ford, W. B. (1985). Use of anaesthetic to standardize efficiency in sampling abalone populations (genus *Haliotis*; Mollusca : Gastropoda). *Aust. J. Mar. Freshwater Res.* **36**, 701–6.

Prince, J. D., Sellers, T. L., Ford, W. B., Talbot, S. R. (1987). Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*; Mollusca : Gastropoda). *J. Exp. Mar. Biol. Ecol.* **106**, 243–63.

Ricker, W. E. (1977). The historical development. In 'Fish Population Dynamics'. (Ed. J. A. Gulland.) pp. 1–12. (Wiley: New York.)

Sainsbury, K. J. (1982). Population dynamics and fishery management of the paua, *Haliotis iris* 1. Population structure, growth, reproduction, and mortality. *N.Z. J. Mar. Freshwater Res.* **16**, 147–61.

Saito, K. (1981). The appearance and growth of 0-year-old Ezo abalone. *Bull. Jpn Soc. Sci. Fish.* **47**, 1393–400.

Shepherd, S. A. (1973). Studies on southern Australian abalone (genus *Haliotis*) 1. Ecology of five sympatric species. *Aust. J. Mar. Freshwater Res.* **24**, 217–57.

Shepherd, S. A., Clarkson, P. S., and Turner, J. A. (1985). Studies on southern Australian abalone (genus *Haliotis*) V. Spawning, settlement and early growth of *H. scalaris*. *Trans. R. Soc. S. Aust.* **109**, 61–2.

Shepherd, S. A., and Hearn, W. S. (1983). Studies on southern Australian abalone (genus *Haliotis*). IV. Growth of *H. laevigata* and *H. ruber*. *Aust. J. Mar. Freshwater Res.* **34**, 461–75.

Shepherd, S. A., and Laws, H. M. (1974). Studies on southern Australian abalone (genus *Haliotis*) II. Reproduction of five species. *Aust. J. Mar. Freshwater Res.* **25**, 49–62.

Shepherd, S. A., and Turner, J. A. (1985). Studies on southern Australian abalone (genus *Haliotis*) VI. Habitat preference, abundance and predators of juveniles. *J. Exp. Mar. Biol. Ecol.* **93**, 285–98.

Sinclair, M. (1963). Studies on the paua, *Haliotis iris* Martyn in the Wellington district, 1945–46. Zool. Publ. Victoria Univ. Wellington No. 35.

Ward, T. J. (1986). Abalone biology and fisheries in Australia: a review of research. Australian Fisheries Service, Canberra, Aust. Fish. Pap. No. 86(12).

Yamaguchi, M. (1975). Estimating growth parameters from growth rate data. Problems with marine sedentary invertebrates. *Oecologia (Berl.)* **20**, 321–32.

Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca : Gastropoda)

J.D. Prince[1,2], T.L. Sellers[3], W.B. Ford[3] and S.R. Talbot[3]

[1]*North Fremantle, Western Australia;* [2]*Zoology Department, University of Tasmania, Hobart, Tasmania;* [3]*Tasmanian Department of Sea Fisheries, Research Laboratory, Taroona, Tasmania 7006, Australia*

Abstract: The hypothesis that for *Haliotis rubra* Leach the localized abundance of mature abalone determines the abundance of recruitment was tested with experimental reductions of breeding stock at four sites. At each site there was an experimental area 60 m in length, from which adult abalone were removed, and two control areas 60 m either side of the experimental area. The abundance of recruitment was found to vary significantly between the four sites and between control areas within three of the sites. Observations which are consistent with recruitment being highly localized. The overall density of recruitment to the experimental areas was significantly lower than in the control areas indicating that the abundance of breeding animals determines the abundance of recruitment. When these data were combined with data from the studies of Prince *et al.* (in press) for the same sites, a relationship between breeding stock and recruitment is clearly evident, confirming that the density of breeding stock was the major determinant of recruitment abundance. These results show that for this species, on a spatial scale measured in 10s of meters, the abundance of recruitment is directly related to the abundance of mature abalone.

Key words: Abalone; *Haliotis rubra*; Larval dispersal; Mollusca; Recruitment

INTRODUCTION

Haliotids have free-swimming lecithotrophic larvae which, in line with traditional marine biological perspectives (Knowlton & Keller, 1986), have been assumed to disperse relatively widely (Fedorenko & Sprout, 1982). A recent paper by Prince *et al.* (1987) described the results of an experiment which suggested that the recruitment patterns of the haliotid *Haliotis rubra* Leach were related to the immediate density of mature conspecifics. On this basis they hypothesized that the dispersal of larvae for this species is generally limited to a scale 0–50 m. Their experiment was extremely simple; a 90-m section of coastal reef was cleared of mature abalone and the resulting pattern of recruitment along the coast examined. The rationale for their experiment was that, if larval dispersal is limited, the removal of mature abalone from any area will reduce the abundance of recruitment. This article describes a more extensive experiment conducted to test the results of that earlier study.

Correspondence address: T.L. Sellers, Tasmanian Department of Sea Fisheries, Research Laboratory, Crayfish Point, Taroona, Tasmania 7006, Australia.

METHODS

The methods used in this study are based on those described in some detail by Prince *et al.* (1987) and the reader is directed to that work for a detailed description of the techniques and habitat used in this study. In this study four sites at the southern end of D'Entrecasteaux Channel in Tasmania, southern Australia ($43°19'S : 147°04'E$), were used: Ninepin Point, East Hope Is., North Hope Is., and Blubber Head (Fig. 1). The abalone-bearing habitat at each site was similar, with boulders extending from above the high water mark down to ≈ 10 m below the low water mark where it ran into sandy substratum.

At each site a 180-m stretch of abalone-bearing coastal reef was selected. The central 60-m section at each site was marked out as an experimental area from which adult abalone were removed. The shoreline at either end of the 180-m section of coastline served as control areas and the breeding stock in those areas was not disturbed (Fig. 1). Immediately prior to the removal of breeding stock from each experimental area, the original density of adult abalone within the experimental areas was measured. These measurements were performed by divers searching the substratum for abalone in 20×1-m^2 quadrats. The sampled areas were selected by throwing a quadrat from an anchored boat. Adult *H. rubra* live in noncryptic habitats and can be found relatively efficiently by searching divers (Prince *et al.*, in press) so that careful searching of small areas can be expected to measure adult density with a high degree of accuracy (Prince & Ford, 1985).

Because the abalone at the study sites breed during September–October of each year (Harrison & Grant, 1971; Prince *et al.*, 1987; Prince *et al.*, in press) breeding stock removals were conducted during July–August 1986. During this procedure a team of four divers searched each experimental area on four occasions. During the searches all abalone > 60 mm (maximum shell length) that could be taken without disturbing the substratum, were collected. Subsamples of these animals were used, together with the techniques outlined in Prince *et al.* (1987), to determine the size of first maturity at each site.

After the searches were completed the density of adult abalone remaining in each experimental area was measured. This was achieved by sampling a further 20 quadrats of 1 m^2 in each area. On this occasion the substratum in 10 of the quadrats was sampled by diver searching and the remaining 10 quadrats were sampled with the anaesthetic technique of Prince & Ford (1985). This latter technique samples abalone > 70 mm with the same efficiency as visual searching, however, it samples the smaller size classes more efficiently (Prince & Ford, 1985). This technique was used to adequately sample the immature size classes so that the size of the smallest size class present could be determined. It was not used throughout the study because it consumes more diving time than visual searching.

Between February and April 1987 after spawning and recruitment had occurred the abalone populations at each site were sampled a third time. During this postrecruitment

sampling the experimental area and the two control areas were sampled, at each of the four sites. A total of 20×1-m^2 quadrats were sampled in each area using the anaesthetic technique of Prince & Ford (1985).
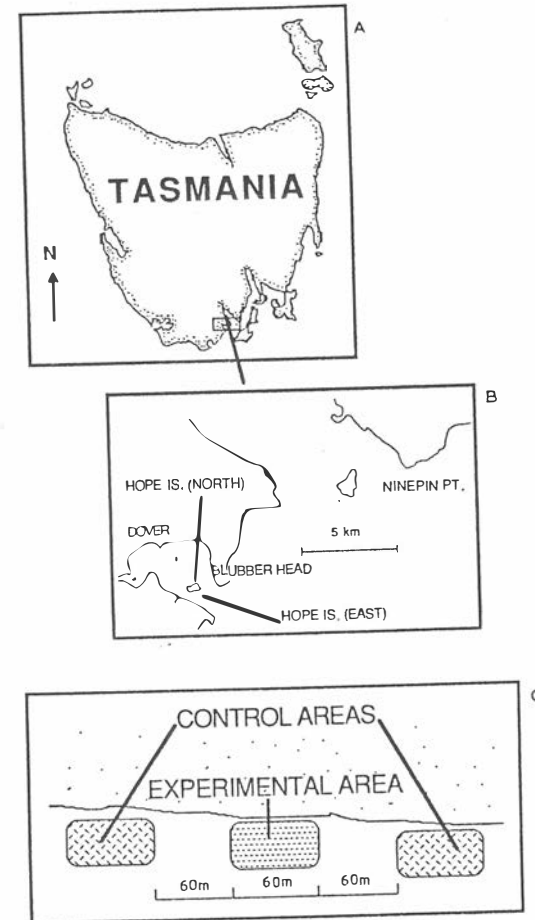

Fig. 1. A map of the of D'Entrecasteaux Channel in Tasmania, southern Australia showing the location of the study sites (A, B) and the design of the experiment (C).

The movement of adult *H. rubra* at the Blubber Head site, which is a similar habitat to the other sites, has been observed to be very limited, $10-20 \text{ m} \cdot \text{yr}^{-1}$, and without alongshore directionality (White & Whyte, pers. comm.). Mortality rates have also been observed to be relatively low in the adult population (Prince *et al.*, in press). For these reasons it can be assumed that the density of adult abalone measured at the control areas during the postrecruitment sampling, approximated the density present at these sites during the breeding period. Because of this and the prohibitive logistics of conducting this experiment, the actual density of breeding stock in the control areas was only measured as a part of the postrecruitment sampling. It is assumed that in these undisturbed control areas this density will approximate the density that was present during the time of spawning.

Because the measured densities of abalone were extremely low and in many quadrats there were no abalone, selected pairs of quadrats within each set of samples have been randomly pooled. Cochran's test for the heterogeneity of variances was used for all analyses (Winer, 1971).

A simple ANOVA was used to compare the densities of breeding stock within experimental areas before and after the removal of breeding stock. Nested ANOVAs were used to test between and within site variability of breeding stock and recruitment density. Where variables were used more than once, violating the assumption of independent variables, the Bonferri method was used to adjust the level of significance being tested (Day & Quinn, in prep.). Planned comparisons were used to test differences within individual sites (Winer, 1971).

ANOVAs were used to test the significance of different relationships between the density of breeding stock and recruitment.

RESULTS AND DISCUSSION

BREEDING STUDIES

The relationship between fecundity and maximum length at each site was adequately described by linear regressions (Table I). From these equations it can be estimated that the length at first maturity is ≈ 87, 81, 77, and 90 mm at Ninepin Point, North Hope

TABLE I

The relationship between fecundity (F, millions of ova) and maximum length (L, mm) at each site, together with the estimated size of first maturity ($F = 0$) at each site.

Site	Relationship	$F = 0$	r^2	df	P
Ninepin Pt.	$F = 0.026L - 2.219$	87	0.357	80	< 0.001
North Hope Is.	$F = 0.046L - 3.753$	81	0.342	53	< 0.001
East Hope Is.	$F = 0.012L - 0.930$	77	0.423	55	< 0.001
Blubber Hd.	$F = 0.026L - 2.339$	90	0.310	53	< 0.001

Is., East Hope Is., and Blubber Head, respectively. These sizes were consistent with the size of the smallest animals at each site found to have yolked ova in their gonads and with gonad index data collected at each site. These sizes have been used as cut-off points for estimating the density of breeding stock at each site.

BREEDING STOCK REMOVAL

The measured densities of breeding stock showed a tendency to be positively skewed about the mean and when the hypothesis that the variances of the breeding stock density measurements were unequal was tested it was accepted ($c = 0.282$, $k = 12$, $r = 9$, $P < 0.01$). Consequently these data were transformed using a $\log_e(x + 1)$ transformation. The hypothesis of unequal variances was rejected for the transformed data ($c = 0.149$, $k = 12$, $r = 9$, $P > 0.05$).

At each site the density of breeding stock tended to be higher at one control than the other, while the density in the experimental areas before the removal process, generally
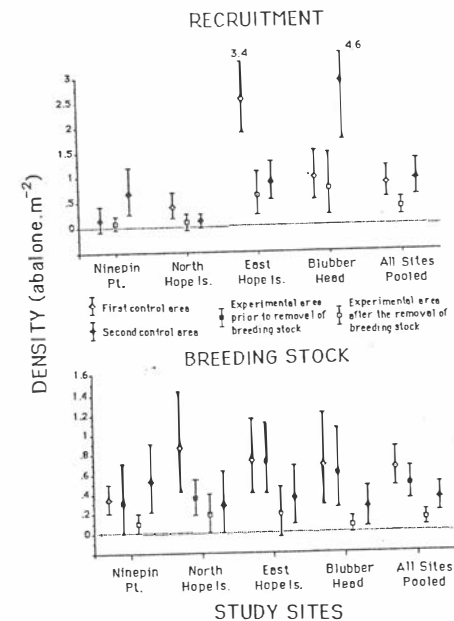

Fig. 2. Results of the experimental reduction of breeding stock at Ninepin Point, North Hope Is., East Hope Is., Blubber Head and for pooled data from all four sites (all sites); error bars denote 95% confidence intervals.

TABLE II

ANOVA table for two-factor ANOVA comparing the density of breeding stock in the experimental areas at the four sites, before and after the removal of breeding stock.

Source	df	Sum of squares	Mean square	F test	P value
Pre vs. postremoval (A)	1	1.766	1.766	18.91	< 0.001
Site (B)	3	0.518	0.173	1.85	> 0.10
AB	3	0.342	0.114	1.221	> 0.10
Error	72	6.723	0.093		

lay between those of the two controls (Fig. 2). After the removal of breeding stock the densities in the experimental areas at each site were lower than either corresponding control. ANOVA showed that the removal of mature abalone significantly reduced their density in the experimental areas and that between sites variability and interactions, between the removal process and sites were not significant (Table II). Planned comparisons showed that within individual sites the removal of breeding stock significantly decreased the density of adult abalone in the experimental area at East Hope Is. and Blubber Head but that the reduction of breeding stock was not significant at North Hope Is. or Ninepin Point (Table III).

Over all the sites there was no significant difference between the density of breeding stock measured in the control areas and that measured in the experimental areas prior to the removal of breeding stock (Table IV). However the density of breeding stock in the experimental areas after the removals was significantly lower than in the controls. The difference in density between the higher density controls at each site and the lower density controls was also significant. The differences between sites were not significant.

Planned comparisons showed that prior to the removal of breeding stock the only significant differences in density within sites were between; the higher density control

TABLE III

Planned comparisons testing the differences in breeding stock densities between areas within individual sites. Numbers indicate estimated F test values (df = 1,144). * denotes $P < 0.05$; ** denotes $P < 0.01$; *** denotes $P < 0.005$.

Tests	Ninepin Pt.	North Hope	East Hope	Blubber Hd.
Experimental areas before vs. after removal	0.585	0.776	6.430*	7.530**
High control vs. low control	0.710	6.643**	2.972	4.184*
Experimental area before removal vs. high control	1.092	4.778*	0.002	0.123
Experimental area before removal vs. low control	0.041	0.153	2.820	2.873
Experimental area after removal vs. high control	4.920*	9.410***	6.660**	9.576***
Experimental area after removal vs. low control	1.892	0.239	0.734	1.101

TABLE IV

ANOVA table for an ANOVA comparing the density of breeding stock within and between each of the four sites.

	df	Mean square	F test	P
A: Sites	3	0.103	0.93	> 0.10
B: Comparisons				
Experimental areas prior to the removal of breeding stock vs. control areas	1	4.0E−5	6.15E−4	> 0.10
Experimental areas after the removal of breeding stock vs. control areas	1	2.036	31.3	< 0.005
High density controls vs. low density controls	1	1.421	21.8	< 0.005
AB interaction	9	0.065	0.59	> 0.10
Error	144	0.110		

of North Hope Is. and the experimental and lower density control areas, and between the higher and lower density control areas at Blubber Head (Table III). Following the removal of breeding stock significant differences in density existed between the experimental area and higher density control of every site.

These tests showed that the control and experimental areas generally had similar levels of breeding stock prior to the removal of adult abalone, but that the experimental treatment significantly reduced the overall density of breeding stock in the experimental areas. The removal of breeding stock reduced the density of mature abalone in each experimental area to below that of the corresponding controls, however, within particular sites this reduction was only significant when compared with the higher density control of each site.

POPULATION STRUCTURE

Sampling of the juvenile population immediately after the removal of breeding stock (August–September 1986) and prior to commencement of the breeding period showed that the smallest size group of abalone present at the four sites were generally 8–20 mm in length with a modal length of ≈ 11–15 mm (Fig. 3).

SAMPLING OF RECRUITMENT

Sampling at the four sites in February–March 1987 showed that a new size group of abalone had been recruited to the population in each location. The newly recruited size class were 2–18 mm and had a modal length ranging from 4–12 mm between the sites (Fig. 3). The lengths of the newly recruited class did not overlap to any great extent with the larger size class at any location and it was possible to use 19–20 mm as a cut-off

point between the newly recruited animals and the older abalone, at all sites. These cut-off points may have caused a few animals to be wrongly classified as new or old recruits but because the cut-off points were applied uniformly within sites it is unlikely that any bias has resulted.
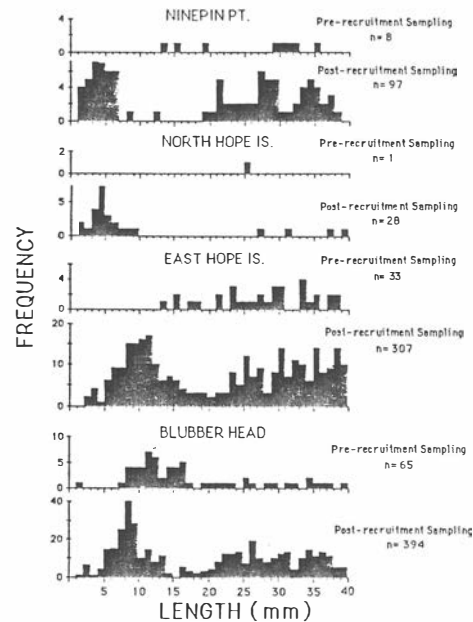

Fig. 3. Length frequency histograms showing 0–40-mm abalone sampled prior to recruitment (August–September 1986) and after recruitment (February–March 1987) at the four sites.

As with the density of breeding stock the measured densities of recruitment showed a tendency to be positively skewed about the mean and when the hypothesis that the variances of the recruitment density measurements were unequal was tested it was accepted ($c = 0.517$, $k = 12$, $r = 9$, $P < 0.01$). Consequently these data were also transformed using a $\log_e(x + 1)$ transformation. Using the transformed data the hypothesis of heterogeneous variances was rejected ($c = 0.194$, $k = 12$, $r = 9$, $P > 0.05$).

At each site the density of new recruits was lower within the experimental area than in either of the control areas (Fig. 2) and ANOVA showed that this difference was significant (Table V). With the exception of the Blubber Head site, within each site the

control area with the highest level of breeding stock also had the highest level of recruitment. ANOVA showed that unlike the density of breeding stock the density of recruitment varied significantly between sites. This contrast is probably because recruitment densities were higher than breeding stock densities while the error structure of both types of measurements were similar (Tables IV–V). Significant differences also existed between the controls with the highest density of recruitment at each site and those with

TABLE V

ANOVA table for an ANOVA comparing the density of recruitment within and between the four sites.

	df	Mean square	F test	P
A: Sites	3	3.866	35.1	<0.001
B: Comparisons				
Control areas				
vs.	1	4.671	22.7	<0.001
experimental areas				
High density controls				
vs.	1	2.884	14.0	<0.001
low density controls				
AB interaction	6	0.206	1.87	>0.10
Error	108	0.110		

the lower densities (Table V). Planned comparisons showed that within the individual sites significant variations in recruitment occurred at Ninepin Pt., East Hope Is. and Blubber Head (Table VI). At these sites the control area with the highest level of recruitment had significantly higher levels of recruitment than both the experimental and lower density controls.

These results show that recruitment was highly localized, with significantly different levels of recruitment occurring in some areas only 60 m apart. The fact that recruitment in the experimental areas was significantly lower than recruitment in the control areas demonstrates that the abundance of recruitment was influenced by the abundance of breeding stock. A conclusion which supports the findings of Prince *et al.* (1987). This relationship can be clearly demonstrated (Fig. 4) if these data are combined with those

TABLE VI

Planned comparisons of recruitment density between the areas within each site. Numbers show estimated F test values (df = 1,108). * denotes $P < 0.05$; ** denotes $P < 0.01$; *** denotes $P < 0.005$.

Tests	Ninepin Pt.	North Hope	East Hope	Blubber Hd.
High control vs. low control	7.72**	2.49	18.27***	21.52***
Experimental area				
vs. high control	8.68**	2.88	28.08***	29.60***
Experimental area				
vs. low control	0.16	0.02	1.05	0.64

from Prince *et al*. (1987), for the Ninepin Pt. site, and those from a related study of Blubber Head (Prince *et al.*, in press). These supplementary data were gathered using the same techniques as this study and provide 9 extra regression points for Ninepin Pt. from the 1985–86 recruitment period, and 10 extra points for Blubber Head from the period 1983–84 to 1985–86.
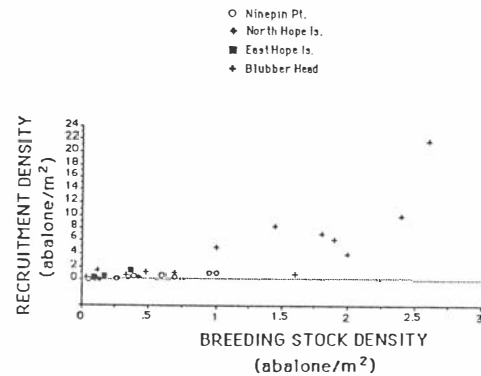

Fig. 4. The density of recruitment plotted against the density of breeding stock for the four study sites. The displayed data for Ninepin Pt. is collected from the present study and Prince *et al*. (1987), while the displayed data for Blubber Head is gathered from the present study and Prince *et al*. (in press).

Ninepin Pt. Data: Prince *et al*. (1987) – 9 × 1985/86; this study – 3 × 1986/87.

TABLE VIIa

Linear regression statistics for the relationship between breeding stock (*x*) and recruitment density (*y*) at Ninepin Pt.

Parameter	Value	SE	Standard value	*t* value	*P*
Intercept	0.036				
Slope	0.668	0.134	0.845	4.992	5.0000E–4

df	*r*	*r*²	Adj. *r*²	SE	
11	0.845	0.714	0.685	0.15	

ANOVA table

Source	df	Sum squares	Mean square	*F* test
Regression	1	0.564	0.564	24.922
Residual	10	0.226	0.023	*P* = 5.0000E–4
Total	11	0.79		

With the exception of East Hope Is. the relationship between breeding stock and recruitment was significant for each of the four individual sites (Table VIIa–d). In the case of East Hope Is. it is evident that the small number of regression points mitigated against a significant relationship being observed. These relationships suggest that ≈ 60–70% of the variation observed in recruitment density can be explained on the basis of the variability of breeding stock density. When the data for all four sites were

North Hope Is. Data: This study – 3 × 1986/87.

TABLE VIIb

Linear regression statistics for the relationship between breeding stock (*x*) and recruitment density (*y*) at North Hope Is.

Parameter	Value	SE	Standard value	*t* value	*P*
Intercept	–1.420E–3				
Slope	0.473	0.031	0.998	15.454	0.0411

df	*r*	*r*²	Adj. *r*²	SE	
2	0.998	0.996	0.992	8.018E–3	

ANOVA table

Source	df	Sum squares	Mean square	*F* test
Regression	1	0.015	0.015	238.831
Residual	1	6.4281E–5	6.4281E–5	*P* = 0.0411
Total	2	0.015		

East Hope Is. Data: This study – 3 × 1986/87.

TABLE VIIc

Linear regression statistics for the relationship between breeding stock (*x*) and recruitment density (*y*) at East Hope Is.

Parameter	Value	SE	Standard value	*t* value	*P*
Intercept	–0.089				
Slope	3.653	0.585	0.987	6.245	0.1011

df	*r*	*r*²	Adj. *r*²	SE	
2	0.987	0.975	0.95	0.117	

ANOVA table

Source	df	Sum squares	Mean square	*F* test
Regression	1	0.538	0.538	38.994
Residual	1	0.014	0.014	*P* = 0.1011
Total	2	0.552		

Blubber Head. Data: Prince *et al.* (in press) − 2 × 1983/84, 4 × 1984/85. 4 × 1985/86; this study − 3 × 1986/87.

TABLE VIId

Linear regression statistics for the relationship between breeding stock (x) and recruitment density (y) at Blubber Head.

Parameter	Value	SE	Standard value	t value	P
Intercept	−1.42				
Slope	5.22	1.333	0.763	3.917	0.0024

df	r	r^2	Adj.r^2	SE	
12	0.763	0.582	0.544	4.026	

ANOVA table

Source	df	Sum squares	Mean square	F test
Regression	1	248.615	248.615	15.341
Residual	11	178.268	16.206	$P = 0.0024$
Total	12	426.883		

All sites combined.

TABLE VIIe

Linear regression statistics for the relationship between breeding stock (x) and recruitment density (y) when the data for all sites are combined.

Parameter	Value	SE	Standard value	t value	P
Intercept	−1.134				
Slope	4.82	0.648	0.81	7.436	1.0000E−4

df	r	r^2	Adj. r^2	SE	
30	0.81	0.656	0.644	2.681	

ANOVA table

Source	df	Sum squares	Mean square	F test
Regression	1	397.541	397.541	55.295
Residual	29	208.495	7.189	$P = 1.0000E−4$
Total	30	606.036		

pooled a highly significant relationship between breeding stock and recruitment density was still evident (Table VIIe), despite the intersite variability which may have been introduced by pooling the data.

To the knowledge of the authors these data are the first estimates of a relationship between breeding stock and recruitment in haliotids to be published. Linear regressions

have been fitted to this relationship simply to demonstrate that a relationship exists and should not be taken to imply that we believe this accurately represents the true nature of the relationship. With the limitations of our data. in terms of measurement precision and restricted range of adult densities, we believe there is little to be gained by trying to fit more complex models to this relationship.

Prince *et al.* (1987) argued in some detail that this localized relationship could only be explained by two hypotheses; either by the effect of adult conspecifics in promoting gregarious settlement, or restricted larval dispersal. The latter hypothesis was considered the most plausible explanation.

The review of the literature on haliotids by Prince *et al.* (1987) suggests that the assumption of widespread larval dispersal in these species is based mainly on the larval capacity for free swimming; an assumption which dominates the study of larval biology in marine invertebrates. Knowlton & Keller (1986) demonstrated that the recruitment of a tropical alpheid shrimp was highly localized despite the fact that the larvae are free-swimming for at least 7 days, and suggested that the assumption of dispersed recruitment for marine invertebrates with free swimming larvae, should not be made too readily.

Knowlton & Keller (1986) were able to distinguish between the effect of the physical and reproductive presence of the adults by using sterilized adult shrimp. Before the role of these differing factors can be determined absolutely for haliotids it will be necessary to develop a similar capability with these species. To the knowledge of the authors no technique for sterilizing adult abalone exists, but in this respect the study of Tong *et al.* (1987) has considerable potential. Tong *et al.* (1987) produced competent haliotid veligers in a hatchery and introduced them directly into the natural environment. This suggests the possibility of using eggs fertilized in the hatchery to manipulate the breeding potential of abalone independently of the density of mature abalone. Such techniques may make possible an experiment capable of determining whether the relationship between breeding stock and recruitment is due to gregarious recruitment around conspecific adults or to localized larval dispersal.

Whichever underlying cause results in the relationship between breeding stock and recruitment, the fact that the relationship exists is of relevance to the managers of haliotid fisheries. These results clearly show that abalone populations will be extremely prone to the concentration of fishing pressure within specific areas, as this could cause localized recruitment overfishing. These results also show that the spatial scale on which this could occur could be as small as 10–100 m. To counter this possibility, management strategies should be developed to disperse fishing effort evenly over a fishery. In this respect the imposition of conservative minimum size limits would apparently offer the most promise; forcing people to leave some breeding stock in all locations. These results also indicate the feasibility of using the relationship between stock and recruitment to develop and implement fishery management strategies which monitor and maintain sufficient breeding stock to ensure the long term viability of abalone fisheries.

Acknowledgements

References

DAY, R.W. & G.P. QUINN, in prep. Comparison of means after an ANOVA. *Ecol. Monogr.*

FEDORENKO, A.Y. & P.E. SPROUT, 1982. Abalone biology, fishery regulations, commercial catch (1952–1980), and current state of resource in British Columbia. *Can. Man. Rep. Fish. Aquat. Sci.*, No. 1658, pp. 1–74.

HARRISON, A.J. & J.F. GRANT, 1971. Progress in abalone research. *Tasmanian Fish. Res.*, Vol. 5, pp. 1–10.

KNOWLTON, N. & B.D. KELLER, 1986. Larvae which fall short of their potential: highly localized recruitment in an alpheid shrimp with extended larval development. *Bull. Mar. Sci.*, Vol. 39, pp. 213–223.

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

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

PRINCE, J.D., T.L. SELLERS, W.B. FORD & S.R. TALBOT, in press. Recruitment, growth mortality and population structure in a southern Australian population of *Haliotis rubra* (genus *Haliotis*; Mollusca : Gastropoda). *Mar. Biol.*

TONG, L.J., G.A. MOSS & J. ILLINGWORTH, 1987. Enhancement of a natural population of the abalone, *Haliotis iris*, using cultured larvae. *Aquacult.*, Vol. 62, pp. 67–72.

WINER, B.J., 1971. *Statistical principles in experimental design.* McGraw-Hill Kogakusha. Tokyo, 907 pp.

Recruitment, growth, mortality and population structure in a southern Australian population of *Haliotis rubra* (Mollusca: Gastropoda)*

J. D. Prince[1,2], T. L. Sellers[3], W. B. Ford[3] and S. R. Talbot[3]

[1] P.O. Box 108, North Fremantle, Western Australia 6159, Australia
[2] Zoology Department, University of Tasmania, G.P.O. Box 252C, Hobart, Tasmania 7001, Australia
[3] Tasmanian Department of Sea Fisheries, Research Laboratory, Crayfish Point, Taroona, Tasmania 7053, Australia

Abstract

A population of *Haliotis rubra* Leach at Blubber Head in south-eastern Tasmania, Australia (43°19'S; 147°04'E) was sampled between February 1984 and October 1985. Relatively large numbers of 30 to 45 d-old new recruits were observed entering the population between October and February of each year. The annual instantaneous rate of natural mortality, Z, was 0.70 during the second year of life. The rate of natural mortality declined with age. The onset of sexual maturity began at 4 to 5 yr of age or an approximate maximum length of 90 mm, and most abalone in the population were mature at 6 to 7 yr of age or at lengths > 110 mm. The onset of sexual maturity coincided with a decline in growth rates and the emergence of abalone from the sub-boulder habitat. These observations are discussed in the light of previous observations of population structure in haliotid populations.

Introduction

In common with other marine molluscan species, the biology of juvenile abalone (genus *Haliotis*), in the natural environment has been little studied (Yamaguchi 1977, Jensen 1981). Abalone larvae settle preferentially onto the surfaces of encrusting coralline algae (Shepherd and Turner 1985), where they feed on the algal cuticle and bacterial biota (Garland et al. 1985). Juvenile abalone are cryptically coloured and, after moving off the coralline surfaces, continue living beneath the boulder substratum. Abalone become less cryptic as they increase in size (Shepherd 1973). The preference of small abalone for cryptic habitats makes them extremely difficult to sample, a characteristic shared by many species of marine invertebrates (Sarver 1979), and at least partly responsible for the lack of research into this facet of haliotid biology.

The aim of the current study was to use recently developed sampling techniques (Prince and Ford 1985) to study the population structure of a southern Australian population of *Haliotis rubra* Leach.

Materials and methods

Sampling

The study area at Blubber Head in Port Esperance, Tasmania (43°19'S; 147°04'E) is a uniform section of rocky coastline extending approximately 70 m from high water mark to a depth of 11 m. The bottom is principally composed of three layers of boulders resting on silt, although in some areas the underlying substratum is solid rock. The boulders are of irregular shape and are mostly 30 to 40 cm in length and 10 to 20 cm in depth and breadth.

The macroalgal community of the area is typical of a fucoid association indicative of slight to moderate wave action (Sanderson and Thomas 1987). Some compression of the floral zones is evident at the site which is probably caused by tannin-stained freshwater influence from the nearby Esperance River reducing light levels (Sanderson personal communication). The shallow region (0 to 5 m) is dominated by *Durvillaea potatorum* (Labill.) Aresch. and *Xiphophora* sp., particularly down to 1 m. Below 1 m, the algal assemblage is more heterogeneous and principally includes *Phyllospora* ap., *Acrocarpia paniculata* (Turn.) Aresch., and *Cystophora moniliformis* (Esper) Wom. and Niz. The alga *Sargassum bracteolosum* (Mertens) C. Agardh., *Lessonia corrugata* Lucas, *Perithalia* sp., and *Macrocystis pyrifera* (L.) C. Agardh are also present, but they are less abundant. The algal assemblage below 5 m is depauperate with $< 20\%$ algal cover. The main macroalgal species in this region are *A. paniculata*, and species of *Ecklonia*, *Phyllospora*, *Thamnoclonium*, *Peyssonnelia*, *Zonaria* and encrusting coralline algae.

Initial surveys of the site (February 1984 and June 1984) revealed that *Haliotis rubra* each were most abundant at

---

* Please address all requests for reprints to T.L. Sellers at the Tasmanian Department of Fisheries

depths <4 m and that the size composition of the abalone population was extremely variable over small distances (20 to 40 m). After these initial surveys, the abalone were sampled at 4-monthly intervals, commencing in October 1984. Sampling took place at four points approximately 50 m apart along the shoreline; these points were marked to ensure consistency. A 1 m² quadrat was thrown from a boat anchored directly in front of each marker in order to select 11 quadrats for sampling at each point. If the quadrat landed on an area where the boulders were too large to collect, or the substratum was entirely sand and silt, or if the square landed in more than 4 m depth, the square was retrieved and re-thrown. From each selected area, a diver collected all the substratum material possibly suitable for abalone, principally boulders and kelp. The few boulders too large to lift to the surface were searched underwater and all abalone collected.

The substratum material was placed in bins and bathed in a 1% solution of ethanol in sea water for a minimum of 10 min. This material was then brushed with a soft brush before being removed from the solution. After all the boulders removed from a square had been soaked, the contents of the bins were drained through 15 mm and 0.5 mm sieves. Abalone retained by the coarser sieve were collected, and the sample held by the smaller sieve was returned to the laboratory for examination. These samples were washed through sieves of 9, 4, 2 and 1 mm aperture and the abalone were preserved. Maximum shell length of all abalone collected was measured to the nearest milimetre.

Analysis of length-frequency data

The Mix program (Macdonald and Green 1985) was used to decompose the length-frequency data. The program fits a series of normal curves to a multimodal length-frequency distribution, estimating the mean and standard deviation of each component distribution and the proportion of the sample represented by each component curve.

For this analysis, the data from the four sampled points were pooled. The February 1984 sample was not analysed because of its small size. The low abundance of larger abalone in the samples prevented the Mix model from converging on any unique description of the larger size classes. To enable the estimates of the model to converge, it was necessary to truncate the data sets and use only the more abundant smaller size classes. The samples were truncated at 80 mm except for the June 1984 histogram, which was truncated at 40 mm because only 20 quadrats were sampled. Using the truncated data sets, the Mix model converged on a unique set of estimates for all data sets excepting the October 1984 sample. For this sample no unique solution could be found, so trial and error was used to obtain the best fit for the data.

Growth

Growth in abalone <80 mm was examined by following the progression of the modes described with the Mix model

within the truncated length-frequency data. The growth of larger individuals was examined using growth-increment data collected from a tagging program. This facet of the study has been detailed by Prince et al. (1988).

Mortality

The length-frequency histograms were re-analysed with the Mix model. In this second analysis the mean lengths and standard deviations estimated using the Mix model and the truncated data sets were held fixed. The growth patterns described by the growth study were used to estimate the mean size of the >80 mm age classes present in the population and a fixed standard deviation for these distributions was estimated on the the basis of the preliminary analysis. These parameters were then held fixed while the Mix model was allowed to converge on new estimates of the proportion of abalone in each size class. The results of this analysis were used to estimate the density of the year classes. The initial sample collected in February 1984 has been excluded, as depths >4 m were sampled on that occasion.

Estimates of the instantaneous rate of total mortality (Z) were made by regressing the natural logarithm of density against age (Beverton and Holt 1957).

Breeding

Samples of approximately 20 abalone from each 10 mm size class >60 mm were collected for breeding studies in July 1986. After fixation in 10% formalin, the visceral mass was sectioned beneath the visceral coil and the cross section placed against clear plastic and drawn. The relative areas of gonad and digestive gland in the cross section were calculated by weighing the plastic outlines. A gonad index was calculated as the proportion of the area of the cross section made up by the gonad multiplied by ten. The gonads were also examined to ascertain whether yolked eggs were present. After the cross sections had been drawn, the gonads of the female abalone were dissected from the digestive gland and gently teased apart into 50 to 250 ml of water. The water was agitated until all the eggs were free and evenly dispersed; two or three 0.5 to 1.0 ml samples were then taken and examined for the presence of yolked eggs.

Size at emergence

The size of abalone that had emerged from the sub-boulder habitat and were living on top of the boulder substratum in non-cryptic habitats (emergent abalone), and their relationship to the rest of the population, were examined in July 1986. A 60 m-long section of shoreline was marked out by research divers and the density of abalone in the area was measured by randomly selecting and sampling a total of 20 × 1 m² quadrats. Research divers then spent a total of 46 diving-hours collecting all the abalone that could be found

in the 60 m section of shoreline without disturbing the substratum. All abalone collected were measured to the nearest millimetre. After removing the emergent abalone, a further $20 \times 1 m^2$ was sampled in order to measure the remaining density of abalone. Sampling was conducted using the anaesthetic technique described in "Sampling" subsection.

Results

Recruitment

The smallest individuals of *Haliotis rubra* sampled were 1 to 2 mm in maximum length, at which size they were in the process of forming, or had just completed forming, their first respiratory pore. The results of laboratory studies of larval and early juvenile growth in *H. rubra* suggest that this

size is reached at approximately 30 to 45 d post-fertilization (J. F. Grant personal communication).

Large numbers of new recruits were found to have entered the population in October 1984 and 1985 (Fig. 1). In October 1984 the newly recruited class was detected at densities of 0.3 abalone m^{-2}; by February 1985 this age class had increased in abundance to 9.7 abalone m^{-2}, indicating that recruitment to the population had continued during this period. A total of 130 abalone in the 3 to 4 mm size class were found in February 1985 along with only 18 abalone in the 1 to 2 mm size class, indicating that the major period of recruitment occurred before February. However the fact that eight abalone <4 mm were also found in June 1985 indicates that some minor spawning and recruitment is possible at other times of the year.

The rate of recruitment over the two years of the study was relatively constant, with the density of new recruits
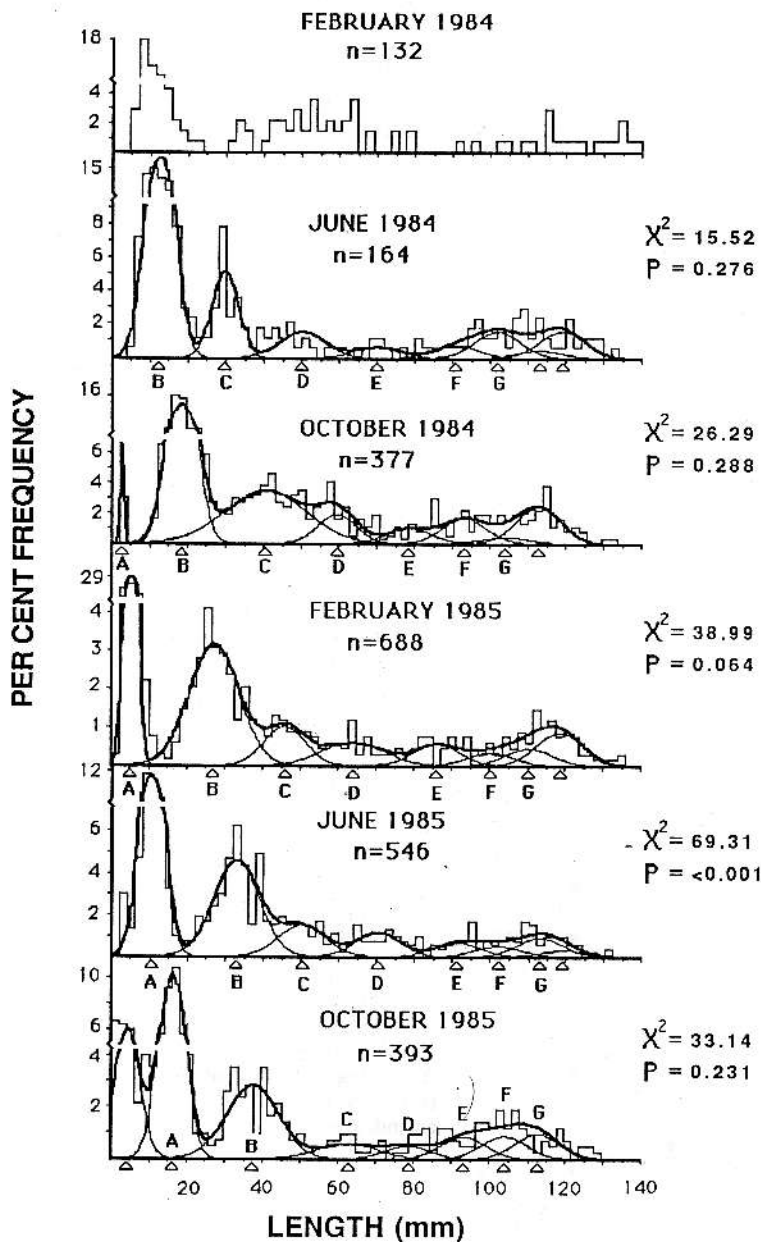

Fig. 1. *Haliotis rubra.* Length-frequency histograms for abalone sampled at Blubber Head between February 1984 and October 1985; curves fitted using Mix model. Values of χ^2 and P refer to Mix analysis of <80 mm histograms. Thin lines: component distributions described by Mix; thick lines: shape of component curves pooled. A−G: Individual year-classes identified by analysis (see "Results − Natural mortality" for definitions)

measured in June 1984 approximating that measured in June 1985.

Growth

The growth of abalone in this population (Fig. 2) is best described by using two separate equations (Prince et al. 1988). Growth of <80 mm abalone follows the linear equation

$$L = 20.83 \, A - 2.46,$$

where A is age in years and L is length in mm. The growth of >80 mm abalone is described by the von Bertalanffy parameters: $K = 0.288$, $L_\infty = 139.7$ mm and $t_0 = 1.01$ yr, where K is the rate at which the size of an individual approaches the asymptotic size for the species, L_∞, and t_0 is the age at which the size of an individual would be zero if growth followed the curve throughout life.

Natural mortality

Using the age-length key described by the analysis of growth, the length-frequency histograms were re-analysed.

The age-length key was used to estimate the mean length of the size classes >80 mm and a standard deviation of 6 mm was assumed for these larger distributions, this being the approximate standard deviation estimated for the smaller size classes.

With these values, Mix was used to estimate the proportion of each sample represented by each of the youngest eight age classes. These year-classes have been nominated as follows: Mode A began recruiting in October 1984, while it is assumed that Mode B began recruiting in October 1983 and Mode C in the previous year. The largest size class fitted by Mix in the October 1984 sample was Mode G (Fig. 1), which it is assumed began recruiting in 1978. The error associated with the estimated proportions indicated that the quality of these estimates declined for the size classes >80 mm. This prevented the analysis from being extended beyond the youngest eight year-classes.

The estimated proportions were used to estimate the density of each year-class in each sample. If the estimated densities of each mode ($\log_e$-transformed) are regressed against age, the instantaneous rate of total mortality can be estimated (Fig. 3). The estimated density of Mode A in October 1984 was omitted from this analysis, as this year-class
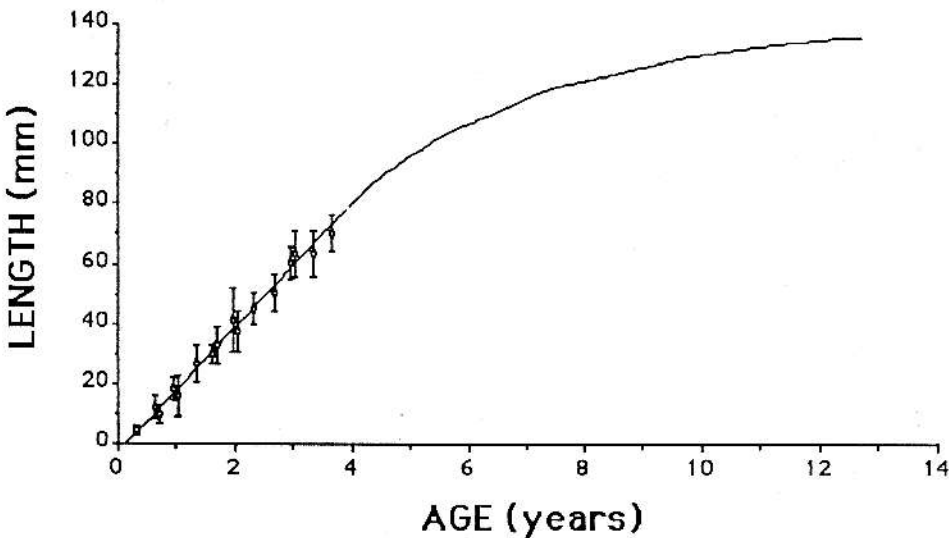

Fig. 2. *Haliotis rubra*. Growth curve estimated for abalone at study site. Curve uses length at age data derived from length-frequency histograms in Fig. 1 to describe <80 mm section of the curve, and von Bertalanffy parameters derived from tag-return data to describe the >80 mm section. (From Prince et al. 1988). Mean lengths at age ± standard deviation of distribution are shown
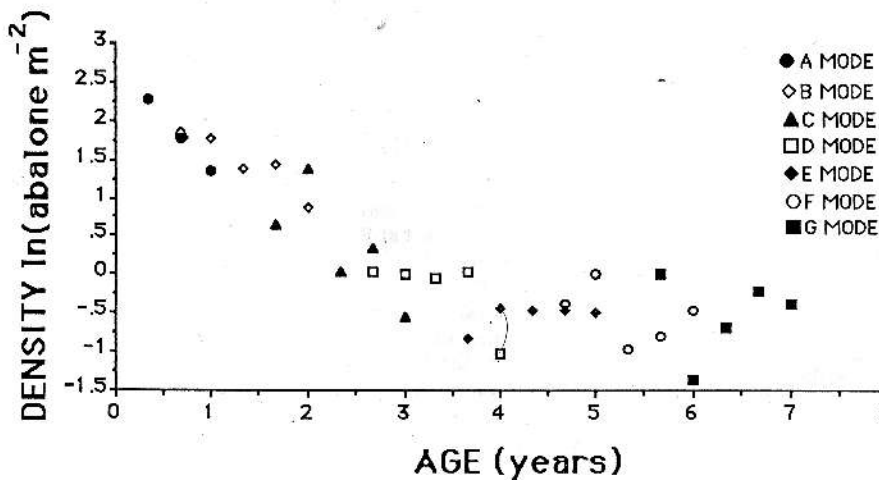

Fig. 3. *Haliotis rubra*. Density of Modes A–G ($\log_e$-transformed) plotted against age (yr). Density of Mode A in October 1984 excluded, since year-class not then fully recruited
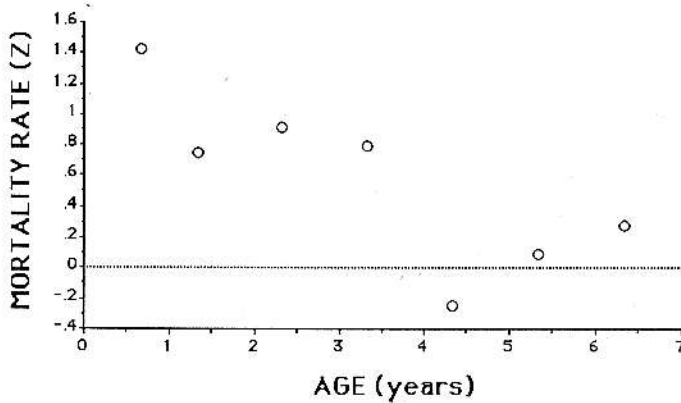
Fig. 4. *Haliotis rubra.* Mortality rates, Z, of Modes A−G plotted against mean age (yr) of each mode. Dotted line: $Z = 0$
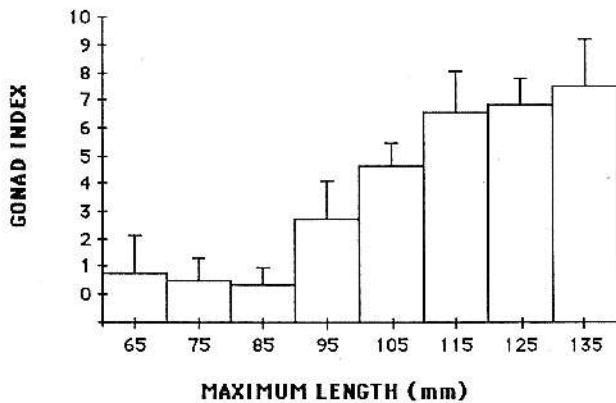

Fig. 5. *Haliotis rubra.* Relationship between size and gonad index (proportion of visceral mass cross-section made up by gonad × 10) of abalone collected during July 1986; bars indicate 95% confidence intervals (approximately 20 individuals per 10 mm length class)
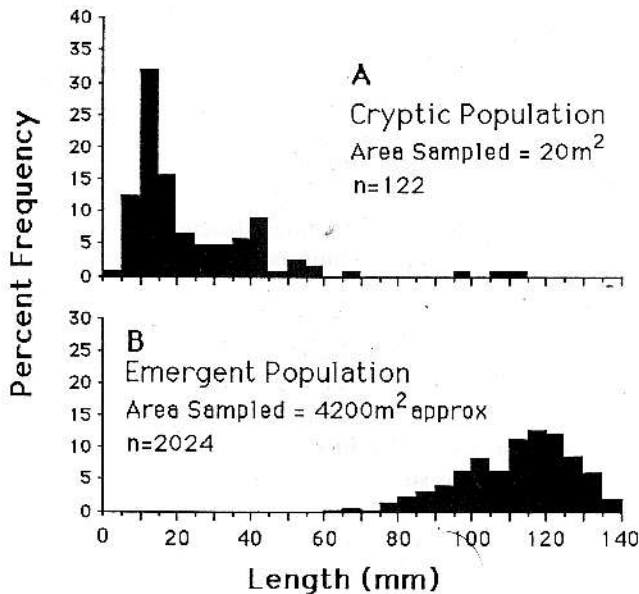

Fig. 6. *Haliotis rubra.* Length-frequency histograms of cryptic population remaining after removal of emergent individuals (A), and of emergent individuals collected (B); July 1986

was clearly not fully recruited at that time. When the individual year-classes were analysed separately only the regression for Mode B was significant ($r = 0.94$, Student's t-test $= 4.71$, df $= 4$, $p = 0.018$), suggesting an instantaneous mortality rate of 0.698. The lack of significant relationships can be attributed to the small number of points being regressed and the error associated with the initial density estimates.

Despite the limitations of this analysis, it is evident that the density pattern observed does not show the simple log-linear decline that would be expected if a constant mortality rate was responsible for the declining density of successive modes. Crude estimates of the instantaneous mortality rates can be derived for each mode by subtracting the initial and final density measured for each mode and dividing by the time between measurements. When these estimates are plotted against the mean age of each mode (Fig. 4), a significant relationship is revealed between mortality rate and age ($r = 0.80$, $t = 2.95$, df $= 6$, $p = 0.032$). This level of significance is increased if the mean size of each mode is used instead of the age ($r = 0.83$, $t = 3.37$, df $= 6$, $p = 0.020$).

Breeding

The smallest abalone observed to have free eggs within its gonads had a maximum length of 91 mm and the gonad indices of the abalone increased markedly at a size > 85 mm (Fig. 5). These two observations suggest that some individuals in the population mature at approximately 90 mm. The fact that the gonad index reaches maximal values at > 110 mm indicates that by this size most abalone in the population are mature.

Emergence

The modal length of abalone collected by divers from the non-cryptic habitat was 110 to 115 mm and 80% of the sample were greater than 90 mm (Fig. 6B). These data, when considered with the reproductive data, suggest that primarily mature abalone emerge from the cryptic habitat. The measured density of abalone > 90 mm in maximum length prior to the collection of emergent abalone was 0.71 abalone m^{-2}, and 0.07 abalone m^{-2} after the collection. This suggests that almost all mature abalone in this population are non-cryptic in nature.

Discussion

Recruitment

The length-frequency histograms of *Haliotis rubra* from February 1984, February 1985, October 1985, and subsequent sampling in 1987 (Prince et al. in press) suggest that the protracted period of recruitment during October−February of each year is a relatively stable feature of this popu-

lation. As the recruitment observed by this study was of 30 to 45 d-old individuals, a spawning season of August – January is suggested. This is consistent with the results of other studies of this species conducted in the general area (Harrison and Grant 1971, Prince et al. 1987).

Growth

The nature of growth in this population has been discussed in some detail by Prince et al. (1988), who noted that the straight-line growth observed for the smaller size classes of abalone in this population has been observed or hypothesized for haliotids in a number of other studies (Forster 1967, Newman 1968, Poore 1972, Koike 1978, Hayashi 1980, Saito 1981). For this reason some previous studies, like the present one, have only used von Bertalanffy parameters to describe the growth of the larger abalone in the population (Poore 1972, Sainsbury 1982). This is in contrast to several other studies which have assumed that a single set of von Bertalanffy parameters can be used to model abalone growth throughout life (e.g. Harrison and Grant 1971, Shepherd and Hearn 1983, Shepherd et al. 1985, Clavier and Richard 1986).

The growth rates in our study, particularly for the younger age classes, are lower than those documented by Harrison and Grant (1971) or Shepherd and Hearn (1983) who studied *Haliotis rubra* in Tasmania and South Australia, respectively. Yamaguchi (1975) found that the von Bertalanffy parameters that modelled adult growth in marine invertebrates were likely to seriously overestimate juvenile growth. Prince et al. (1988) have suggested that this together with the known intra-specific variability of haliotid growth rates (Leighton and Boolootian 1963, Forster 1967, Harrison and Grant 1971, Shepherd and Laws 1974, Sainsbury 1982) explains the differences observed between this and previous studies.

Mortality

The instantaneous rate of mortality estimated by this study for 1 + abalone (i.e., in their second year of life) is approximately 0.70 per annum (50% survival per annum) but declines with age or size. During this study, the population above a legal minimum size limit of 127 mm was vulnerable to fishing pressure. All the size classes under study were below this legal minimum size limit, rendering them invulnerable to legal fishing. In addition, the majority of the age classes under study were also living in the sub-boulder population and thus unlikely to be prone to illegal fishing pressure. For these reasons it is exceedingly unlikely that any form of fishing mortality had affected the observed mortality rates. Consequently, it can be assumed that the mortality rates observed in this study are natural rates of mortality.

Because mortality declines with age, a concave downward or Type III survivorship schedule (Deevey 1947) is apparently applicable for *Haliotis rubra*. This contrasts with the study of Shepherd et al. (1982), who found that mortality acted at a constant rate over time and proposed a log-linear or Type II survival curve for abalone. However, the study of Shepherd et al. concentrated on the older age classes, which on the basis of our results can be expected to experience relatively low and stable rates of mortality.

There is considerable circumstantial evidence in the literature to suggest that a concave downward survival curve applies generally to abalone populations. Tegner and Butler (1985) cite several Japanese studies documenting between 21 and 37% survival per annum for juvenile abalone released into the environment during reseeding trials; these rates increase if the size of release is increased. In their own study, Tegner and Butler recorded a survival rate of between 8 and 65% for released juvenile hatchery abalone and approximately 12% for natural abalone. These studies are almost exclusively based on hatchery-produced abalone released into the natural environment and, because of this, are not strictly comparable with studies of wild populations. However, the consistency of their results with those of the current study is of considerable interest. A low survival rate for juvenile wild populations is also suggested by Hines and Pearse (1982), who postulated that high mortality rates must exist after observing a turnover rate of 92% per annum in a stable abalone population which was heavily predated by sea otters.

In contrast to the poorly detailed survival of juvenile abalone, survival rates of mature haliotids have been well documented (Doi et al. 1977, Beinssen and Powell 1979, Sainsbury 1982, Shepherd et al. 1982, Fournier and Breen 1983) as being high (65 to 90% survival per annum). Acceptance that the mortality rate of abalone declines with age or size reconciles the high survival rates observed in adult haliotid populations with the relatively low juvenile survival rates observed in this study. This form of survivorship has been documented in other studies of molluscan species (e.g. by Creese 1981, Vincent et al. 1981, Seager 1982, Berg and Alatalo 1985), and perhaps should be expected for abalone if predation is considered likely to constitute the major cause of natural mortality. This is because smaller abalone with weaker shells and weaker powers of attachment to the substratum are probably more prone to predation.

The technique used to sample abalone in this study increases and standardizes searching efficiency compared to the techniques of visual searching used in most other studies, although it is still unlikely to be sampling the youngest age classes with absolute efficiency (Prince and Ford 1985). However, Powell et al. (1984) found that even with a technique that is 100% efficient, the temporal resolution of the sampling regime can cause recruitment density to be underestimated by at least a factor of ten, since the life span of many new recruits is so short that they live and die between samples and thus are not detected as being part of the population. Consequently, the estimated rate of natural mortality for 0 + to 1 + abalone (i.e., in their first two years of life) is undoubtedly an underestimate, and it is likely that an accurate measurement would further accentuate the fact that mortality rates decline with age.

Reproduction and emergence

Haliotis rubra at Blubber Head begins maturing at approximately 90 mm or at about 4 to 5 yr of age. Shepherd and Laws (1974) studied this species in South Australia and observed maturity at 3 to 4 yr of age. Harrison and Grant (1971) found that the size of first maturity in a Tasmanian population of *H. rubra* could be as low as 70 mm and that all individuals were mature by 95 mm. From their growth data this would indicate 2 to 4 yr as the age of first maturity. However, as discussed by Prince et al. (1988), it is possible that the estimated ages of maturity in these earlier studies are based on overestimated growth rates and this may explain the slightly older age of first maturity documented by the present study. The fact that the gonad index for the population does not reach maximal values until >110 mm suggests that many individuals do not mature until 6 to 7 yr of age.

The age at first maturity coincides with the end of the linear growth phase. This is as expected, as abalone have been observed to transfer energy from somatic growth into egg production at this stage of their life (Peck et al. 1987). This age and size also coincided with the movement of abalone from a cryptic to a non-cryptic habitat.

Shepherd (1973) and Witherspoon (1976) noted that *Haliotis rubra* and other species of abalone became less cryptic with increasing size, although they did not attempt to correlate this with any biological change. Shepherd hypothesized that juvenile abalone remain cryptic to avoid predators, leaving the cryptic habitat when they reach a size that is less prone to predation. Our data offer the interesting suggestion that the onset of maturity is also associated with this change in micro-habitat. The data presented here is not sufficient for us to argue conclusively that this is the sole, or even one, of several possible factors affecting the emergence of *H. rubra* from cryptic habitats. However, aggregation (Shepherd 1986) and movement of abalone to local elevations (Breen and Adkins 1980) during the breeding season have been documented for other species of abalone. If *H. rubra* exhibits these behaviour patterns they could provide the mechanism linking emergence with the onset of sexual maturity in this species.

Population structure

The size structure of the abalone population evident in the length-frequency histograms remained relatively stable over the time span of this study. The smallest length intervals (0 to 50 mm) were the most numerically abundant, the middle length intervals (50 to 90 mm) least abundant, and the largest size intervals (>90 mm) moderately abundant. This structure is apparently maintained by the effects of growth and mortality. The juvenile year-classes (<90 mm; <4+) grow rapidly and remain relatively distinct in the length-frequency histograms so that the effect of high mortality rates can be clearly observed in the declining numerical abundance of abalone in the 0 to 90 mm length intervals.

Growth and mortality rates decline in the mature year-classes (>90 mm; >4+) so that the modes of older year-classes coalesce. This causes the apparently anomalous situation where abalone in length intervals >90 mm are numerically more abundant than those in the 50 to 90 mm length intervals.

In several other studies, the low numerical abundance of the mid-sized length intervals compared to that of the largest size intervals, has been observed and used to infer recruitment failure (Forster et al. 1982, Sainsbury 1982). However, from the present study it would appear possible that those results may have been based on an artifact of length-frequency histograms which would not have been apparent had it been possible to accurately age the abalone. It seems possible that undetected size- or age-dependent mortality within those populations, rather than recruitment failure, may have been the cause of the population structure observed by those studies.

Most studies of abalone have not observed significant numbers of juveniles and have concluded that abalone populations are dominated by accumulations of mature abalone. This has led to the assumption that abalone populations are relatively static and non-productive (Tegner in press). This does not satisfactorily describe the abalone population we observed. We observed that juveniles were abundant, and that the juvenile phase was characterized by a dynamic population structure with high levels of recruitment, growth and mortality. The adult phase of the population conformed to the observations made in other studies, being stable and relatively static; this part of the population is more easily collected than the cryptic juvenile population.

Our conclusion is that the population structure of *Haliotis rubra* that we have observed at this and other sites (Prince et al. 1987) may not be unique, but that some previous studies may have failed to detect juvenile abalone in their true abundance. Similar circumstances may also explain some of the apparently adult-dominated populations observed for other gastropod species (Yamaguchi 1977).

Literature cited

Beinssen, K., Powell, D. (1979). Measurement of natural mortality in a population of blacklip abalone, *Notohaliotis ruber*. Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer 175: 23–26

Berg, C. J. Jr., Alatalo, P. (1985). Biology of the tropical bivalve *Asaphis deflorata* (Linne, 1758). Bull. mar. Sci. 37: 827–838

Beverton, R. J. H., Holt, S. J. (1957). On the dynamics of exploited fish populations. Fishery Invest., Lond. (Ser. 2) 19: 1–5333

Breen, P. A., Adkins, B. E. (1980). Spawning in a British Columbia population of northern abalone, *Haliotis kamtschatkana*. Veliger 23: 177–179

Clavier, J., Richard, O. (1986). Growth of juvenile *Haliotis tuberculata* (Mollusca: Gastropoda) in their natural environment. J. mar. biol. Ass. U.K. 66: 497–503

Creese, R. G. (1981). Patterns of growth, longevity and recruitment of intertidal limpets in New South Wales. J. exp. mar. Biol. Ecol. 51: 145–171

Deevey, E. S., Jr. (1947). Life tables for natural populations of animals. Q. Rev. Biol. 22: 283–314

Doi, T. S., Guzmán del Próo, S. A. Marín, V., Ortíz, M. Q. Camacho, J. A., Temístocles Muñoz, T. (1977). Analisis de la problación y diagnóstico de la pesqueria de abulon amarillo (*Haliotis corrugata*) en el área de Punta Abreojos e Isla Cedros, B.C. Série cient. Dir. gen. Inst. nac. Pesca, Méx: 18

Forster, G. R. (1967). The growth of *Haliotis tuberculata:* results of tagging experiment in Guernsey 1963–65. J. mar. biol. Ass. U.K. 47: 287–300

Forster, G. R., Potts, G. W., Swinfen, R. (1982). Changes in the ormer populations of Guernsey and Jersey. J. mar. biol. Ass. U.K. 62: 717–727

Fournier, D. A., Breen, P. A. (1983). Estimation of abalone mortality rates with growth analysis. Trans. Am. Fish. Soc. 112: 403–411

Garland, C. D., Cooke, S. L., Grant, J. F., McMeekin, T. A. (1985). Ingestion of the bacteria on the cuticle of crustose (nonarticulated) coralline algae by post-larval and juvenile abalone (*Haliotis ruber* Leach) from Tasmanian waters. J. exp. mar. Biol. Ecol. 91: 137–149

Harrison, A. J., Grant, J. F. (1971). Progress in abalone research. Tasm. Fish. Res. 5: 1–10

Hayashi, I. (1980). Structure and growth of a shore population of the ormer, *Haliotis tuberculata*. J. mar. biol. Ass. U.K. 60: 431–437

Hines, A. H., Pearse, J. S. (1982). Abalones, shells, and sea otters: dynamics of prey populations in central California. Ecology 63: 1547–1560

Jensen, J. T. (1981). Distribution, activity, and food habits of juvenile *Tegula funebralis* and *Littorana scutulata* (Gastropoda: Prosobranchia) as they relate to resource partitioning. Veliger 23: 333–338

Koike, Y. (1978) Biological and ecological studies on the propagation of the ormer, *Haliotis tuberculata* Linnaeus 1. Larval development and growth of juveniles. La Mer (Bull. Soc. franco-jap. Océanogr., Tokyo) 16: 124–136

Leighton, D. L., Boolootian, R. A. (1963). Diet and growth in the black abalone *Haliotis cracherodii*. Ecology 44: 227–238

Macdonald, P. D. M., Green, P. E. J. (1985). Mix 2.2: an interactive program for fitting mixtures of distributions. Icthus Data Systems, Hamilton, Ontario

Newman, G. G. (1968). Growth of the South African abalone *Haliotis midae*. Investl Rep. Div. Sea Fish. S. Afr. 67: 1–24

Peck, L. S., Culley, M. B., Helm, M. M. (1987). A laboratory energy budget for the ormer *Haliotis tuberculata* L. J. exp. mar. Biol. Ecol. 106: 103–124

Poore, G. C. B. (1972). Ecology of New Zealand abalones, *Haliotis* species (Mollusca: Gastropoda). 3. Growth. N.Z. Jl mar. Freshwat. Res. 6: 534–559

Powell, E. N., Cummins, H., Stanton, R. J. Jr., Staff, G. (1984) Estimation of the size of molluscan settlement using the death assemblage. Estuar. cstl Shelf Sci. 18: 367–384

Prince, J. D., Ford, W. B. (1985). Use of anaesthetic to standardize efficiency in sampling abalone populations (genus *Haliotis*; Mollusca: Gastropoda). Aust. J. mar. Freshwat. Res. 36: 701–706

Prince, J. D., Sellers, T. L., Ford, W. B., Talbot, S. R. (1987). Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*; Mollusca: Gastropoda). J. exp. mar. Biol. Ecol. 106: 243–263

Prince, J. D., Sellers, T. L., Ford, W. B., Talbot, S. R. (1988). A method for ageing the abalone *Haliotis rubra* (Mollusca: Gastropoda). Aust. J. mar. Freshwat. Res. 39: 167–175

Prince, J. D., Sellers, T. L., Ford, W. B., Talbot, S. R. (in press). Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca: Gastropoda). J. exp. mar. Biol. Ecol.

Sainsbury, K. J. (1982). Population dynamics and fishery management of the paua, *Haliotis iris*. I. Population structure, growth, reproduction, and mortality. N.Z. Jl mar. Freshwat Res. 16: 147–161

Saito, K. (1981). The appearance and growth of 0-year-old Ezo abalone. Bull. Jap. Soc. scient. Fish. 47: 1393–1400

Sanderson, J. C., Thomas, D. P. (1987). Subtidal macroalgal communities in the D'Entrecasteaux Channel, Tasmania. Aust. J. Ecol. 12: 41–51

Sarver, D. J. (1979). Recruitment and juvenile survival in the sea hare *Aplysia juliana* (Gastropoda: Opisthobranchia). Mar. Biol. 54: 353–361

Seager, J. R. (1982). Population dynamics of the antarctic opisthobranch *Philine gibba* Strebel. J. exp. mar. Biol. Ecol. 60: 163–179

Shepherd, S. A. (1973). Studies on southern Australian abalone (genus *Haliotis*). I. Ecology of five sympatric species. Aust. J. mar. Freshwat. Res. 24: 217–257

Shepherd, S. A. (1986). Studies on southern Australian abalone (genus *Haliotis*). VII. Aggregative behaviour of *H. laevigata* in relation to spawning. Mar. Biol. 90: 231–236

Shepherd, S. A., Clarkson, P. S., Turner, J. A. (1985). Studies on southern Australian abalone (genus *Haliotis*). V. Spawning, settlement and early growth of *H. scalaris*. Trans. R. Soc. Aust. 109: 61–62

Shepherd, S. A., Hearn, W. S. (1983). Studies on southern Australian abalone (genus *Haliotis*). IV. Growth of *H. laevigata* and *H. ruber*. Aust. J. mar. Freshwat. Res. 34: 461–475

Shepherd, S. A., Kirkwood, G. P., Sandland, R. L. (1982). Studies on Southern Australian abalone (genus *Haliotis*). III. Mortality of two exploited species. Aust. J. mar. Freshwat. Res. 33: 265–272

Shepherd, S. A., Laws, H. M. (1974). Studies on southern Australian abalone (genus *Haliotis*). II. Reproduction of five species. Aust. J. mar. Freshwat. Res. 25: 49–62

Shepherd, S. A., Turner, J. A. (1985). Studies on southern Australian abalone (genus *Haliotis*). VI. Habitat preference, abundance and predators of juveniles. J. exp. mar. Biol. Ecol. 93: 285–298

Tegner, M. J. (In press). the California abalone fishery: production, ecological interactions, and prospects for the future. In: Caddy, J. F. (ed.) Scientific approaches to the management of invertebrate stocks. John Wiley & Sons, London

Tegner, M. J., Butler, R. A. (1985). The survival and mortality of seeded and native red abalones, *Haliotis rufescens*, on the Palos Verdes Peninsula. Calif. Fish Game 71: 150–163

Vincent, B., Vaillancourt, G., LaFontaine, N. (1981). Cycle de développement, croissance et production de *Pisidium amnicum* (Mollusca: Bivalvia) dans le Saint-Laurent (Québec). Can. J. Zool. 59: 2350–2359

Witherspoon, N. B. (1976). Sizes in the Tasmanian commercial catch of black-lip abalone (*Haliotis ruber*) – possible effects of changing habitat during growth. Tasm. Fish. Res. 9: 15–22

Yamaguchi, M. (1975). Estimating growth parameters from growth rate data. Problems with marine sedentary invertebrates. Oecologia 20: 321–332

Yamaguchi, M. (1977). Shell growth and mortality rates in the coral reef gastropod *Cerithium nodulosum* in Pago Bay, Guam, Mariana Islands. Mar. Biol. 44: 249–263

DSF study throws new light on abalone

A DSF experiment indicates that abalone have little ability to resettle areas from which all breeding stock has been removed.

If the results are confirmed they point to a need to leave every area of reef with its own resident population of breeding abalone, or risk an industry collapse.

The FIRTA-funded study, designed to find out how far abalone larvae can move after hatching, was made at Ninepin point in D'Entrecasteaux channel.

Abalone produce millions of eggs each breeding season which hatch into larvae capable of swimming for up to 5-6 days. Scientists around the world have believed that abalone larvae may move up to 100km during this short period of their lives and resettle outlying reefs which may have been overfished. However a study previously completed at Blubber Head in Port Esperance suggested to

● Jeremy Prince

DSF scientists that the accepted international beliefs may in fact be incorrect.

To test this theory, between August and September 1985, DSF staff, Jeremy Prince, Tracy Sellers, Wesley Ford and Simon Talbot set about removing as many abalone as possible from a section of shoreline at Ninepin point.

Over a total of 85 diver hours they collected about 3,500 abalone from a 90m section of shoreline. They even spent six nights in the water between midnight and dawn in the hope that more abalone would be active at that time of the night. During this process they calculate that they collected more than 90 per cent of the mature abalone.

The idea behind the experiment was that, if abalone larvae do not normally swim long distances then removing mature abalone from an area should decrease the amount of abalone settling on the bottom. However if the larvae normally swim long distances, the number of larvae settling in an area should not be affected by the removal of mature abalone. Between March and April this year, following the breeding of abalone in the Ninepin point area, the number of newly settled abalone in and outside the area from which adults had been removed was measured. It was found that very few abalone had settled in the area from which the mature abalone had been taken.

While the DSF intends to repeat this experiment to confirm this finding, the present results lead DSF scientists to believe that abalone larvae generally may not move more than 10m-20m from their parents.

This finding has very important implications for the abalone fishery, which is currently Tasmania's most valuable fishery.

The result suggests that abalone have very little ability to resettle areas from which all breeding stock has been removed. If this is true then each area of reef needs to be left with its own breeding population. In fact the consequence of removing all the broodstock from a patch, less than 100m from other abalone, may be that the abalone production from that patch is lost to Tasmania for decades.

These results may explain why so many overseas abalone fisheries have collapsed. Obviously if larval dispersal is restricted, small patches within the fishery can easily be destroyed by overfishing.

The collapse of successive patches would decrease the overall productivity of the fishery and concentrate the efforts of the industry on fewer and fewer areas, making each one more prone to collapse. In fisheries where the size limits are too small or not strictly enforced, or where too many divers are allowed to catch too much, the collapse of small areas could quickly snowball — destroying the productivity of the entire fishery. — *Jeremy Prince, DSF marine biologist.*□

Dr June Olley's merit award

JUNE OLLEY, head of the seafood technology section of the CSIRO Fisheries Research Division, has won the annual award of merit from the Australian Institute of Food Science and Technology.

Dr Olley joined the CSIRO regional laboratory in Hobart in 1967.

The award of merit, the institute's top citation, is in recognition of a lifetime of service to the food industry.

Besides the direct help he has received, Les Dick has been heartened by the enthusiasm of the northern community, particularly the old and the very young.

The classes of schoolchildren inspecting the old ketch have, he says, been enthralled.

The Defender will, it seems, have an army of admirers when she feels the thrust of the wind once again.

For Les Dick the five year project is proof that with the right support nothing is impossible.

"All you need", he says "is a strong arm and a big heart". □

DSF finds a way to age abalone

A THORN in the side of fisheries biologists studying abalone stocks around the world has been their inability to determine the age of abalone.

Ageing techniques are extremely important to scientists trying to measure rates of growth and mortality and the extent of fishing pressure. These techniques had been denied to scientists studying abalone because of their inability to age this species.

Because of this, when the Fishing Industry Research Committee, the body controlling the Fishing Industry Research Trust Account (FIRTA), commissioned a review of abalone research last year, the finding concluded that one of the four highest priorities should be to develop an ageing technique.

Previously, considerable work had been done in Japan and in the USA sectioning and fracturing shells attempting to discover a satisfactory method of ageing. This work had found some evidence of age-related structures in abalone shells but had not managed to devise consistent methods for observing shell structure. Nor had it proved the relationship between age and the structures.

Recently DSF staff Jeremy Prince, Tracy Brothers, Wesley Ford and Simon Talbot have found a technique that allows the age of abalone to be easily determined. With this method the spire of the abalone shell is ground flat until a small hole is made through the centre of the shell. This creates a disc of nacre, also

● Closeup of the ring structures found by DSF researchers in abalone shells.

known as mother of pearl, which is polished and then viewed under a microscope. When this is done growth rings similar to those found in trees can be seen.

The study has shown that three fine rings are formed during the first 14 months of an abalone's life and one thick ring at 18 months. After this a single ring is formed each year, apparently coinciding with winter.

These findings are already being used by scientists in Victoria working with abalone and are likely to prove useful to many other abalone researchers as well. — *Jeremy Prince, DSF abalone research officer.*

49