FINAL REPORT TO FIRDC

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Settlement and recruitment in abalone: their use in predicting stock abundance

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ADELAIDE

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FINAL REPORT TO FIRDC

SETTLEMENT AND RECRUITMENT IN ABALONE: THEIR USE IN PREDICTING STOCK ABUNDANCE.

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INTRODUCTION

The purpose of the grant was to develop a method of measuring density of settlement of the abalone Haliotis laevigata in relation to spawning stock size and the subsequent catch in the fishery. It was hoped that settlement strength, if it was controlled by oceanographic conditions, would be a useful index of subsequent abalone abundance, and so would provide a method of predicting abalone catches.

RESULTS

The results of the various studies were prepared as draft papers and are included as appendices of this report. Studies on settlement of abalone gave inconclusive results (Appendix 1) and it became clear that the original objectives of the study were not achievable. Accordingly, the direction of the study was changed. Instead of pursuing simple settlement studies, an experiment was set up to measure by experimental manipulation the relation between local stock size and abundance of settling abalone. As it transpired valuable information was also obtained on topographic and other features which influence settlement strength and the dispersal of larvae. (Appendix 4).

Other studies on growth, fecundity and spawning were continued and (except that on spawning which is unfinished), are included in Appendices 2 and 3. Late in the study, shell collections from some of the study sites were examined for growth rings and the result of the analysis, which included other historical data from other sites, are given in Appendix 5.

Overall the study was highly productive in terms of data. However, the changes in staff during the study and early termination of the grant caused delays in analysis of the data and presentation of the results.

IMPLICATIONS OF THE RESEARCH FOR MANAGEMENT

Discussion of ways to manage abalone fisheries at the La Paz, Mexico conference in November 1989 led to consensus among abalone biologists that, in the absence of knowledge of the stock/recruitment relation, egg-per-recruit (EPR) analyses were likely to offer the best tool for biologists to assess size limits and more generally to make a prognosis of abalone stocks. Although minimum egg production levels are not known, the analysis of many stocks, including declining ones, will provide a better basis on which judgements about minimum necessary egg production levels can be made.

This study has given a valuable impetus to achieving the goal of a corpus of EPR analyses for many sub-stock of greenlip abalone on Eyre Peninsula. EPR analyses require (inter alia) good data on growth and fecundity and some understanding of the size of a stock. There is now sufficient data for EPR analyses for some 6 substocks on Eyre Peninsula.

The study of growth rings, which conceptually show great promise, discloses the limitations of the technique and calls for caution in its use. Nevertheless the method may be useful to further define growth and mortality for a few carefully chosen sites.

Perhaps the most interesting result of the study is that relating to larval dispersal. The finding that abalone larvae are likely to be dispersed over hundreds of metres, contrary to earlier studies, has important implications for identification of stocks. These are likely to cover areas of 10-100km^2, at least for H. laevigata.

It is doubtful whether measurement of settlement strength of this abalone, as a means of measuring recruitment, is worth pursuing in future studies. Efforts should be devoted to studies of the ecology of recruitment and determination of the factors that influence its variability. Recruitment studies as a means of monitoring the stocks are best carried out on abalone that are 2-3 years of age and are non-cryptic and so more easily accessible by a diver. The density of this cohort of emergent abalone has been shown to be a good index of recruitment at West Island. This needs to be validated for other sites. The relation between this index and later recruitment to the fishery is still unknown, and needs elucidation. At present, the consensus of abalone biologists is that monitoring of emergent abalone at specific sites is still the best way of obtaining independent and direct information on the abundance of abalone.

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Settlement and recruitment in abalone: their use in predicting stock abundance
Grant 86/61

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6 March 1991

LIST OF APPENDICES

APPENDIX 1.

RECRUITMENT STUDIES

Initially McShane's method of vacuum sampling the substratum was tried at a number of sites to measure abundance of juveniles 1-5mm shell length (SL). The problem was that the habitat of juvenile greenlip is on reef of low relief and very large quantities of sediment are entrained with juvenile abalone. About 8-10 microscope hours per sample were required to thoroughly search for juveniles. The result of sampling with the vacuum sampler are given in Table 1. Densities of abalone found were very low. Further sampling with the vacuum sampler was discontinued after November 1987. Due to the very high demands of laboratory time to sort samples, a back log of samples rapidly accumulated.

However, the effectiveness of sampling depends on knowing promptly whether newly settled abalone were present in the habitat sampled. The inability to obtain a rapid feed-back of information from the sampling and the extreme demands of laboratory time caused us to abandon vacuum sampling in favour of direct sampling the substratum with an underwater magnifier as developed by Shepherd.

The results using this technique are summarised in Table 2, except those at Taylor Island which are analysed separately. Densities of newly settled greenlip averaged about 1 per square metre (ie about one per hour searching time) and were too low to determine significant differences between sites.

TABLE 1 Summary of results of sampling with vacuum suction sampler at various sites.

Date	Site	Area sampled (m^2)	Mean juvenile abalone density (Nos m^{-2})
12.8.87	McLaren Pt	7	0.14 (*H. scalaris*)
13.8.87	Taylor Is	2	0
25.8.87	Anxious Bay	3	0
2.9.87	Sceale Bay	3	0
16.9.87	Taylor Is	4	0
7.10.87	Cape Blanche	4	0
25.10.87	Taylor Is	4	0.25 (*H.rubra*)
27.10.87	"	3	0.3 (*H.rubra*)
29.10.87	Waterloo Bay	6	0
7.11.87	Sceale Bay	3	0.3 (*H.rubra*)

TABLE 2 Summary of results of sampling with underwater magnifier at various sites

Date	Site	Area sampled (m^2)	Mean juvenile abalone density (Nos m^{-2})
Oct - Jan 1988	McLaren Pt	7	1.25
Oct - Jan 1989	"	14	0.59
Oct - Dec 1988	Yanerbie	4	1.25
Oct - Dec 1988	Sceale Bay	4	1.00

APPENDIX 2

Studies on southern Australian abalone (genus Haliotis)

XII. Fecundity of H. laevigata

by S A Shepherd[1], Cecilia Godoy[1,2], and S M Clarke[1]

SUMMARY

Fecundity and length-weight relations were determined for 6 populations of the greenlip abalone *Haliotis laevigata* on the coast of Eyre Peninsula.

The relation between length and fecundity was non-linear with power coefficients of length ranging from 3.7 to over 7 for different sites. Length-weight relations showed minor differences between sites, and power co-efficients of length ranged from 2.8 to 3.2. The between-site variation in fecundity is attributed to differences in food supply, water movement and habitat, although genetic effects cannot be excluded.

Key words: abalone, fecundity, *Haliotis*, morphometry.

INTRODUCTION

The fecundity of abalone is a life history trait that is important for modelling exploited stocks (Sluczanowski 1984) and for artificial spawning and mariculture.

The greenlip abalone *Haliotis laevigata* Donovan is the basis of an important fishery in South Australia and of increasing interest for culture. In this paper we describe the fecundity of populations of *H. laevigata* at a number of sites on the coast of Eyre Peninsula, where the principal fishery is based (Fig. 1).

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MATERIALS AND METHODS

H. laevigata spawns synchronously from October to March at West Island (Shepherd & Laws 1974) and during November and December on southern Eyre Peninsula (unpublished data). Three pairs of study sites (the sites within each pair being about 5km apart) were selected in the southern, central and northern part of the west coast of Eyre Peninsula. Samples were collected at each site in September 1987 before the commencement of spawning and when ova are large and rounded. Samples were taken over the full available size range of sexually mature individuals.

Shell length was recorded for each female and the ovary and visceral mass excised and preserved in 10% formalin and sea water until firm.

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

Subsequently, in further sampling at each site in December 1987, shell length (in mm) and total weight (in g) of samples of H. laevigata were recorded in order to calculate the relation between length and total weight.

Linear regressions of log fecundity (number of eggs) on log length were fitted to the data sets using the regression option of the computer package Lotus 123. Analysis of covariance was performed to compare fecundity between different populations.

RESULTS

Log-log regressions gave satisfactory fits to the fecundity data (Table 1). Plots of the data are shown in Figure 2 and the fitted regression equations are shown in Figure 3. Analysis of covariance of the regressions for each population showed that the fecundity relationships differed significantly between populations (d.f. 6, 89; F=2.59 $P<0.05$).

The results of linear regressions of log total weight on log length are given in Table 2 and shown in Figure 4. Coefficients of determination indicate satisfactory goodness of fit of linear regression models to the data. Analysis of covariance showed significant differences between populations ($F = 17.9$; $P<0.05$). We did not further analyse those differences because the samples were taken from the various sites over a period of a month (see Table 2) during the peak of spawning season, when marked changes in the length-weight relation are expected within a population as gametes are released (McShane et al. 1988). In fact when the date of sampling and the regression constant b in Table 2 are ranked, and the Spearman rank correlation co-efficient calculated the correlation is significant ($r_s = 0.93$; $P< 0.05$).

DISCUSSION

In these populations the relation between fecundity and length is non-linear with power coefficients ranging from 3.7 to over 7 (Table 1). A power of 3 suggests a linear relation with weight and for 3 of the 6 populations the power and its 95% confidence interval includes 3. The fecundity of the remaining populations appears to be non-linear with weight. Ault (1985) reviewed the fecundity of abalone and noted that a linear relation with weight is found for many species. This is expected because proliferation of oocytes, strictly a surface phenomenon, should be related to gonad volume. However, if the germinal epithelium becomes highly convoluted then a significant increase in fecundity becomes possible, giving rise to non-linearity.

The fecundity of abalone is known to vary between individuals, between populations and even between years (Tutschulte & Connell 1981, Ault 1985, McShane et al. 1986). This study shows similar individual and population variability in H. laevigata but in general sample sizes are too small to characterise accurately the differences, and too little is known to allow speculation on the cause.

Variability in fecundity arises from differences in food availability (Tutschulte & Connell 1981), and Shepherd (1987) showed that abalone transplanted to sites with better or worse food supplies showed corresponding increases or decreases in fecundity. The food availability at the sites studied in this paper will not be known until growth studies are complete. Shepherd (1987) also suggested that fecundity might vary between populations due to differences in strategies of energy allocation between populations. This hypothesis needs experimental testing by transplant experiments.

The relationship between length and total weight also shows some variation between populations. This may be due to differences in the growth rate between sites or may simply reflect the expected decline in weight relative to length due to loss of gametes during spawning. McShane et al. (1988) showed that seasonal and inter-population differences occur in the morphometric relations of H. rubra. They attributed the differences to variation in growth patterns between populations; these in turn were probably due to differences in food availability. H. laevigata feeds mainly on drift algae, whose availability depends on water movement and frequency of storms (Shepherd 1973). Thus between-site habitat differences and water movement variability must play an important role in morphometric and fecundity differences between populations of this abalone species.

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Table 1

Constants of regression equations relating fecundity (F) in millions of eggs and length (L) in mm for H. laevigata at various sites. Equations are of the form $F = aL^b$. N is the sample size.

Site	N	a	b±s.e.	R^2
Cape Blanche (A)	17	6.19×10^{-10}	7.24±0.91	0.81
Yanabie (D)	14	0.011	3.87±0.65	0.75
Anxious Bay (E)	15	0.029	3.70±0.93	0.55
Waterloo Bay (F)	15	0.0064	3.85±0.91	0.57
Taylor I. (C)	15	7.55×10^{-6}	7.73±0.54	0.88
McLaren Point (B)	14	1.93×10^{-6}	5.61±0.42	0.94

Table 2

Constants of regression equations relating length (L) in mm and total weight (TW) in g for H. laevigata at various sites. Equations are of the form $TW = aL^b$. N is the sample size. Date is the date of collection.

Site	Date	N	a($\times 10^{-5}$)	b±s.e.	R^2
Cape Blanche (A)	30/12/87	47	39	2.77±0.21	0.76
Yanabie (D)	4/12/87	53	4.6	3.20±0.08	0.97
Anxious Bay (E)	15/12/87	46	10	3.07±0.07	0.98
Waterloo Bay (F)	14/12/87	57	20	2.92±0.06	0.98
Taylor I. (C)	10/12/87	45	4.7	3.16±0.06	0.98
McLaren Point (B)	10/12/87	47	5.8	3.12±0.05	0.99

CAPTIONS TO FIGURES

Fig. 1 Map of South Australia showing study sites.

Fig. 2 Plots of fecundity (number of eggs in millions) against length for *Haliotis laevigata* at 6 sites.

Fig. 3 Regression lines showing the relation between fecundity (number of eggs) and length for *Haliotis laevigata* at 6 sites. A = Cape Blanche; B = McLaren Point; C = Taylor I.; D = Yanabie; E = Anxious Bay; F = Waterloo Bay.

Fig. 4 Regressions of length vs total weight for 6 population samples of *Haliotis laevigata*. See Fig. 3 for key to sites.

FIG. 1

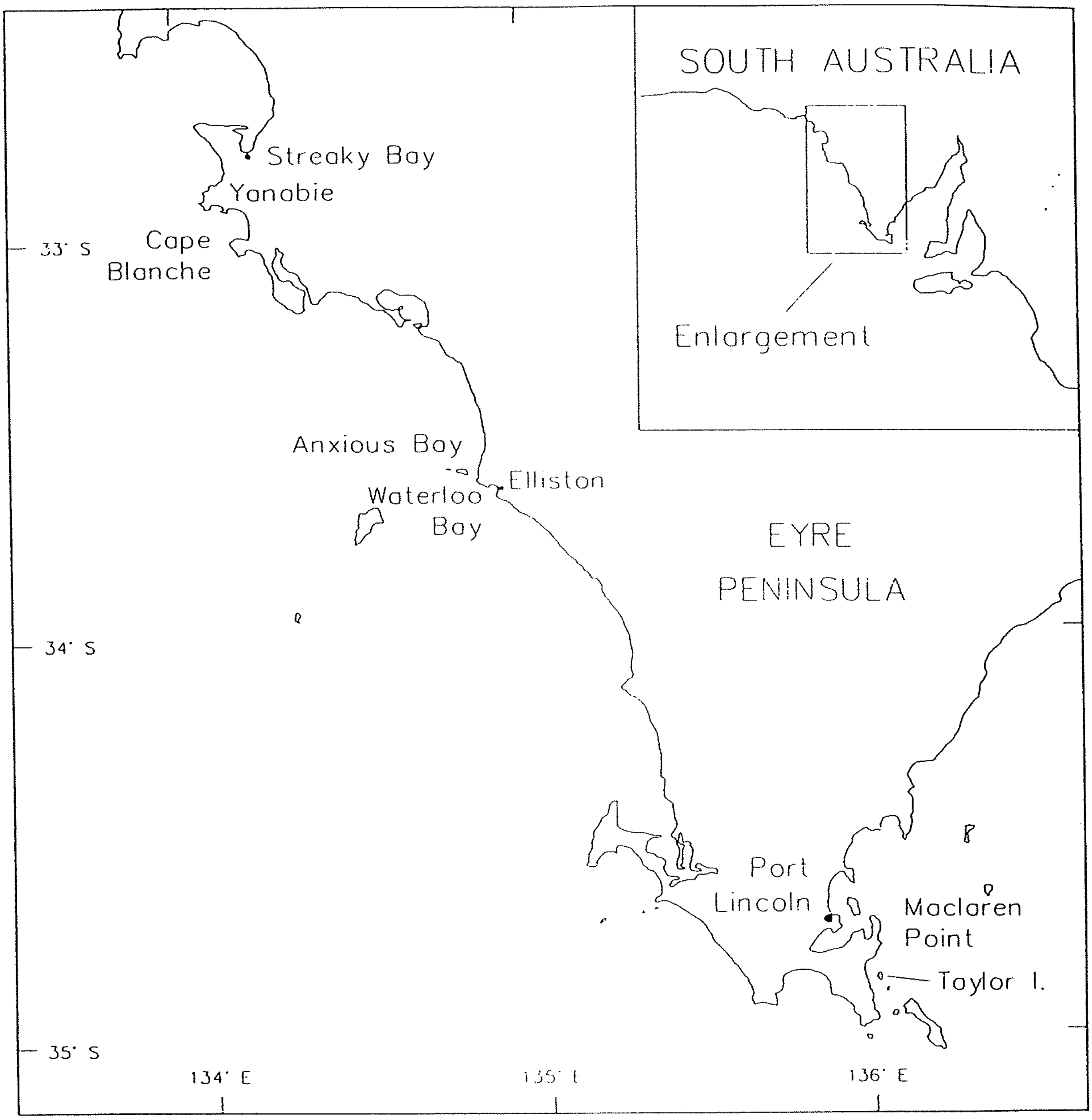

SOUTH AUSTRALIA
Enlargement
Streaky Bay
Yanobie
Cape Blanche
33° S
Anxious Bay
Elliston
Waterloo Bay
EYRE PENINSULA
34° S
Port Lincoln
Maclaren Point
Taylor I.
35° S
134° E
135° E
136° E

FIG 2

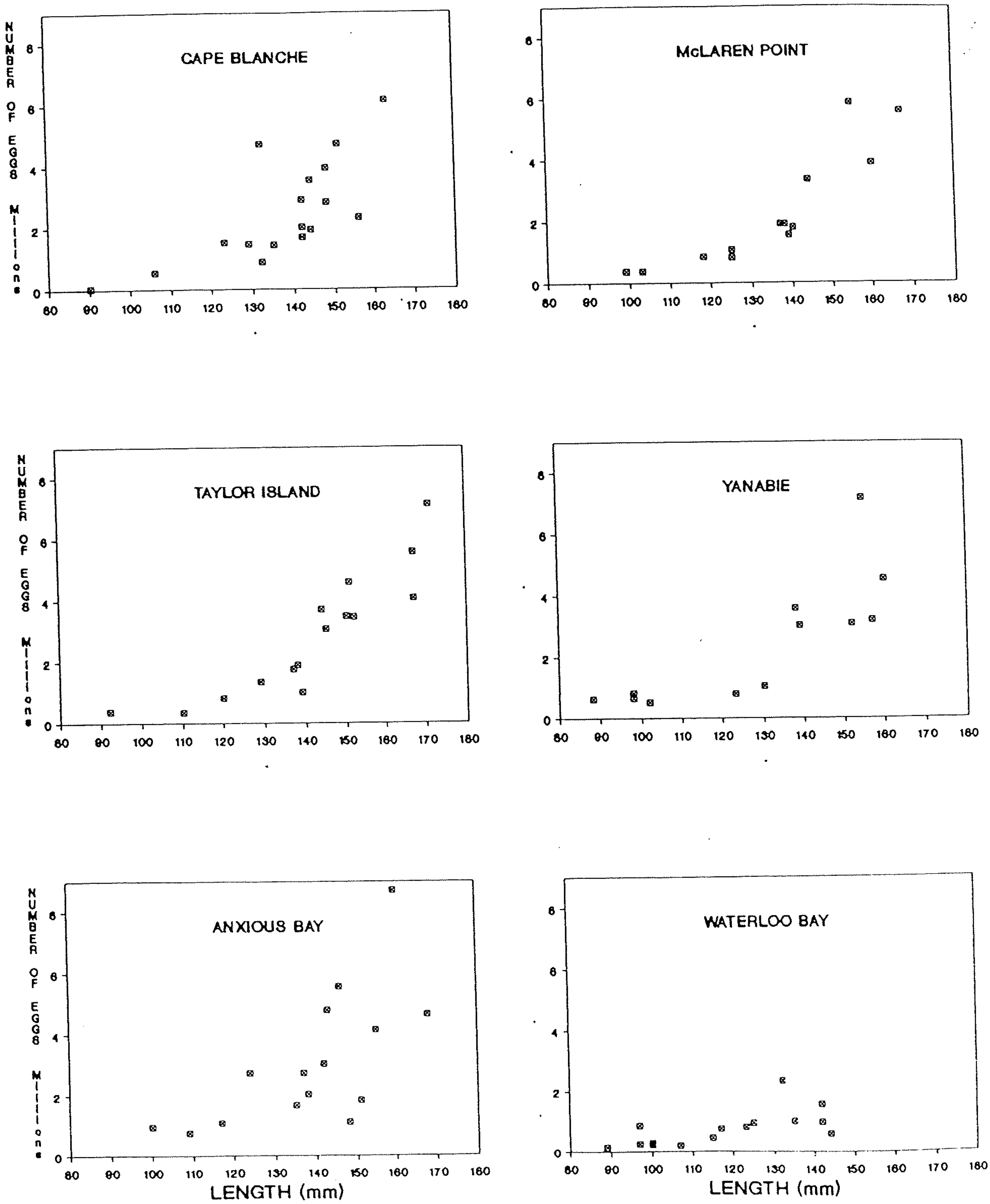
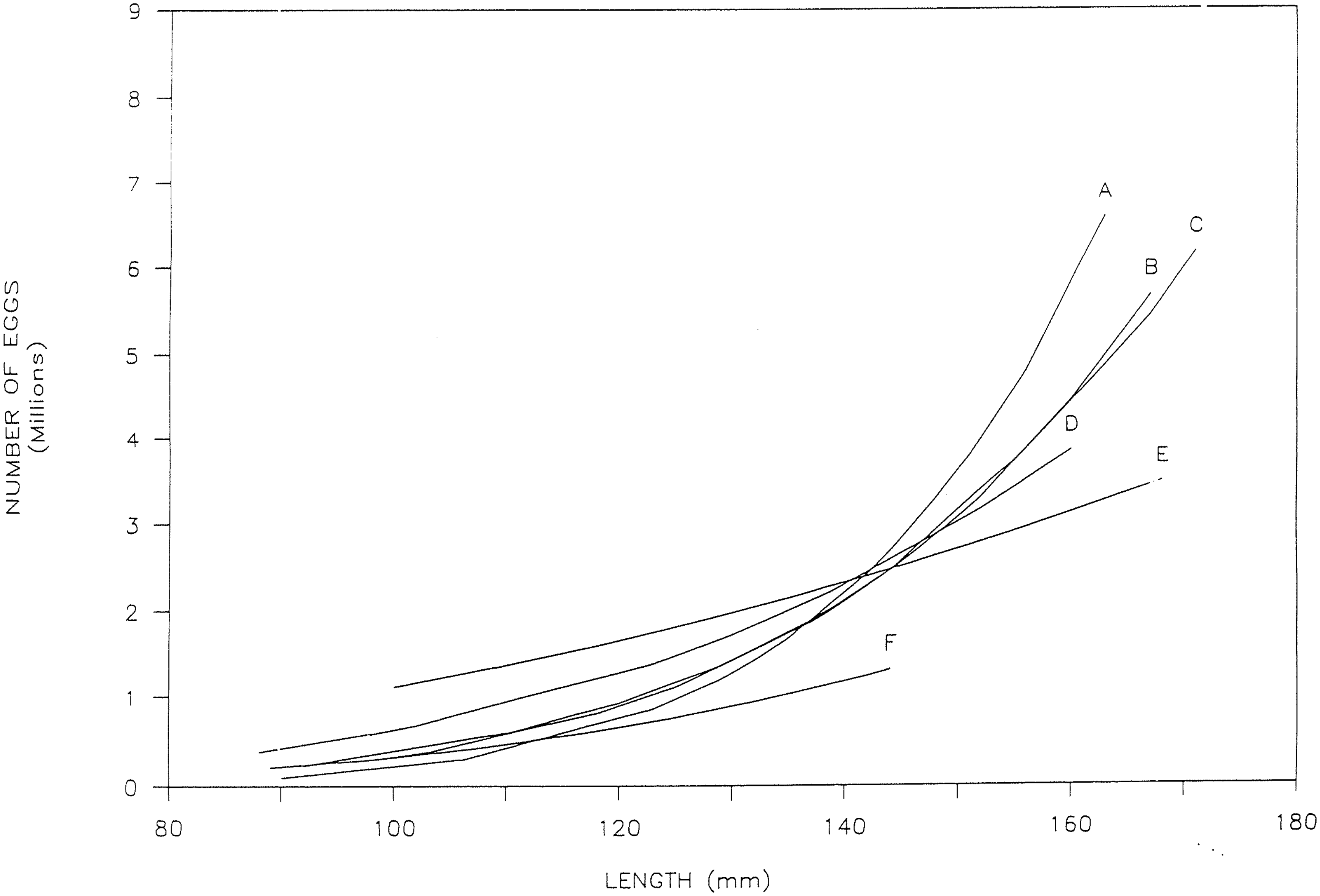

CAPE BLANCHE
McLAREN POINT
TAYLOR ISLAND
YANABIE
ANXIOUS BAY
WATERLOO BAY
NUMBER OF EGGS Millions
0
2
4
6
8
80
90
100
110
120
130
140
150
160
170
180
LENGTH (mm)

FIG 3


NUMBER OF EGGS
(Millions)
0
1
2
3
4
5
6
7
8
9
80
100
120
140
160
180
LENGTH (mm)
A
B
C
D
E
F

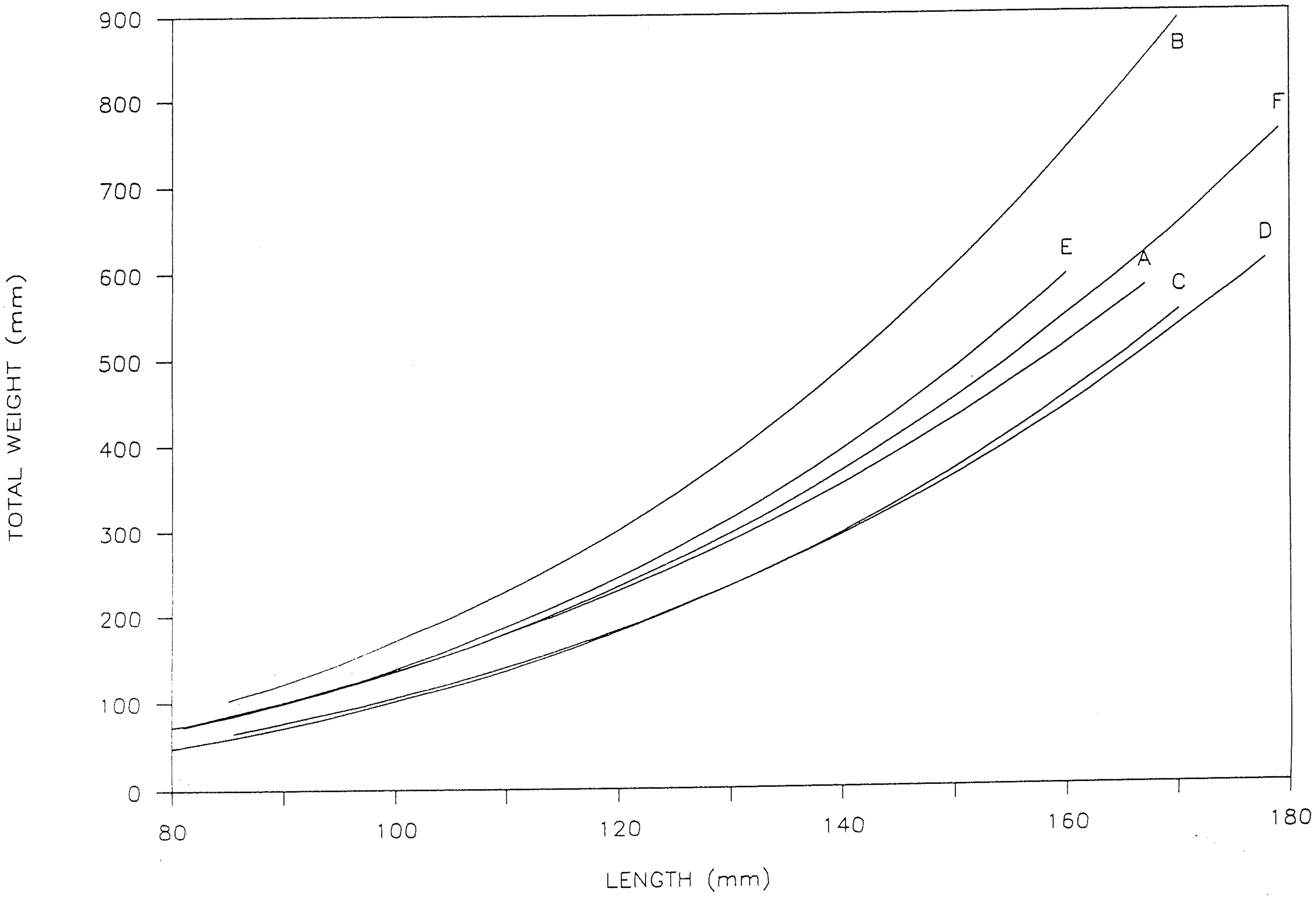

TOTAL WEIGHT (mm)
900
800
700
600
500
400
300
200
100
0
80
100
120
140
160
180
LENGTH (mm)
B
F
E
A
C
D

FIG 4

APPENDIX 3

Studies on southern Australian abalone (genus Haliotis) XIII. Growth of H. laevigata on Eyre Peninsula

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ABSTRACT

The growth rate of Haliotis laevigata Donovan was examined at 6 sites on Eyre Peninsula, South Australia, by mark-recapture experiments and by analysis of length-frequency distributions. Juvenile growth rates were linear at all sites except one, and in the range 20 - 40 mm y^{-1}, whereas growth of older individuals was satisfactorily described by the von Bertalanffy growth curve. The Brody growth coefficient, K, ranged from 0.19 to 0.55 y^{-1}, and L_{∞} from 119.5mm to 186.3mm according to site.

In general growth rates tended to decline with decreasing latitude.

INTRODUCTION

The management of exploited abalone resources requires a good understanding of growth for the purpose of modelling individual stocks and fixing appropriate size limits. Because the growth rate of abalone is often variable between sites it is necessary to measure growth at a number of sites to determine the extent of variability.

The greenlip abalone Haliotis laevigata Donovan is heavily exploited on the west and south coast of Eyre Peninsula. The growth of the species in this part of its range has previously been known only from Waterloo Bay. The purpose of this study was to examine the growth of H. laevigata at a number of sites on Eyre Peninsula, as part of a program to review the management of the fishery at a finer scale. We analysed length - frequency data to measure juvenile growth (Shepherd 1988) and data from mark-recapture experiments for older individuals (Shepherd and Hearn 1983). These methods have been found to be the most satisfactory for this species of abalone.

MATERIALS AND METHODS

The 6 sites (Fig. 1) were selected to span the geographic range of the principal exploited stocks off Eyre Peninsula. The two southern sites in Spencer Gulf are on granitic substratum with numerous rounded boulders to 30cm diameter at a depth of 5-10m.

The three northern sites are on an aeolianite substratum, eroded in part but with very few free slabs or boulders, at 5-7m depth. All sites are more or less sheltered from the prevailing swell, but the two northernmost sites are the least, and the two southernmost sites the most, sheltered.

Animals were marked by fixing a circular numbered plastic tag by a nylon rivet to the proximal pore-hole of the shell (Prince 1991). Marking was done in cool weather on the boat, or underwater, to minimise marking mortality. On subsequent visits to each site 9 - 18 months after marking, marked individuals were re-measured in situ. Unmarked populations of H. laevigata were also measured in situ to provide data for the preparation of length-frequency distributions. Except at Taylor I, where specific studies were made on cryptic juveniles, the smallest size classes (< 50mm shell length (SL)) were absent or poorly represented in the sampling.

Data Analysis

The von Bertalanffy growth equation has been widely used to describe the growth of abalone (Day and Fleming 1991). Estimates of the growth parameters, K and L_{oo}, and standard errors were obtained by fitting the von Bertalanffy equation, using the Fabens (1965) least squares algorithm (see Shepherd & Hearn 1983). To minimise possible seasonal effects we selected data for which the periods of freedom were not less than 270 days. Where multiple recaptures occurred, the final recovery was used, giving one data triplet (L_1, t, L) per animal. T_o was calculated from the youngest age-group to which the von Bertalanffy equation was fitted (Gulland 1985).

The MIX computer program was used to fit and separate modes of length frequency distributions. The procedure fits Gaussian curves and uses maximum likelihood methods to separate them (MacDonald and Green 1985). Probability values >0.05 indicate statistically satisfactory fits.

RESULTS

Taylor I

A plot of the annual length increment data vs initial length is given in Fig. 2. The mean annual growth rate of the putative 1+ age class (30-50mm SL) was 43.4 mm (s.e. 2.2mm) and that of the putative 2+ age class (65-99mm SL) was 38.7mm (s.e. 1.7mm) which are not significantly different from each other (t test with pooled variance; t_{32}=1.1, $P > 0.1$). Hence the von Bertalanffy growth model, which requires a growth rate that declines by a constant amount as L approaches L_{oo}, does not adequately describe the whole data set. For this reason we excluded the 5 data points of the putative 1+ age class and fitted the von Bertalanffy curve to the remaining data points (Table 1).

A length-frequency distribution from Taylor I (see Shepherd and Lowe in prep) obtained in March 1988 with fitted modes is shown in Fig. 3. The modal means were then plotted against age (Fig. 4) assuming a birth date on December 1 and that the modes represent successive cohorts (Shepherd and Lowe in prep). The growth rate of the 1+ and 2+ age classes from the mark-recapture data (see above) are plotted for comparison (Fig. 4) and show good agreement with the growth rate inferred from the modes of the length-frequency distribution. We conclude that the first four modes represent annual age classes; however the 5th and 6th modes are not well defined and probably include a mixture of age classes.

The 2nd to 5th modes inclusive are very nearly linear with age ($R^2 = 0.999$) and are described by the linear regression:

$L = 39.6A - 24.1$

where L is the length in mm and A is the age in years.

McLaren Point

A plot of the annual increment data vs initial length (Fig. 5) suggested that, as for Taylor I., the von Bertalanffy equation might not adequately describe growth over the whole size range. So we excluded the putative 1+ age class (30 - 70mm SL) and fitted the equation to the remaining data. Results are given in Table 1 and plotted in Fig. 7.

Length-frequency data taken at the site in August 1987, with fitted modes, are shown in Fig. 6. In contrast to Taylor I., searching was not conducted in cryptic habitat, so the smallest (0+) age class is missing. The modal means were plotted against age, assuming the 1st mode was the 1+ age class and the birth date 1 December. A linear regression fitted to the modal means (Fig. 7) provides a satisfactory fit to the data ($R^2 = 0.99$). The mean growth rate from the modal data is 23.6mm/year which is in close agreement with the growth rate of marked individuals in the 1+ age class (26.3mm/year; s.e. 2.9mm). We conclude that at least the first 3 modes represent annual age classes. The later modes are less certain and probably contain a mixture of age classes.

Ward I

A plot of annual increment data vs initial length (Fig. 8) shows that the von Bertalanffy equation provides a reasonable fit to the data. The parameters of the fitted equation are given in Table 1.

Juveniles were rarely found, because cryptic habitat could not be sampled adequately. Hence the juvenile growth rate must be inferred from the modes of a length frequency distribution (Fig. 9). The 0+ age class is presumed to be missing, and those larger ones < 140mm SL are probably annual cohorts. A linear regression fitted to the modal means (assuming a birth date on 1 December) provides a satisfactory fit to the data ($R^2 = 0.99$) and gives a mean juvenile growth rate of 25.7mm $year^{-1}$. A plot of the combined growth curves for juveniles and adults is given in Fig. 10.

Anxious Bay.

A plot of annual increment data vs initial length (Fig. 11) shows that a von Bertalanffy equation provides a satisfactory fit to all data. The parameters of the fitted equation are given in Table 1.

Length-frequency data were obtained on two occasions. Cryptic habitat could not be sampled adequately, so it was not possible to determine the growth rate of juveniles. Modes were fitted to the length-frequency data (Fig. 12) and those modal means <100mm SL, which are assumed to be annual, are plotted together with the fitted growth curve in Fig. 13. We assume a mean length of 50mm SL at age 2.5 years for the purpose of fitting the growth curve to maximise agreement with the position of the modal means. The growth curve is tentative until more data are available.

Yanerbie and Sceale Bay

A plot of the annual increment data vs initial length (Fig. 14) indicates that the von Bertalanffy equation will satisfactorily fit the data.

We analysed the growth data in the same way as for Anxious Bay. Juveniles were rarely found because we could not search cryptic habitat, so we could not characterise the juvenile growth rate. Only at Yanerbie were juveniles 10 - 20 mm SL found (putatively 1 year old) and these supported the postulated juvenile growth rate. Length frequency distributions and fitted modes are given in Fig. 15. Growth curves for the two sites derived from interpretation of modal means and from growth data are given in Fig. 16. Values for T_o (Table 1) were calculated on the basis that the mean size of a 3-year-old is 60mm SL at Yanerbie, and that of a 2.9-year-old is 70mm at Sceale Bay.

DISCUSSION

An assumption of using tagging data to measure growth is that the tags do not affect the growth rate (Day and Fleming 1991). The rivet tag of Prince (1991) which we used has not been tested to determine whether it affects the growth rate. However we have observed that a layer of nacre is laid over the intrusive nylon part of the tag within 4 - 8 weeks, suggesting that interruption to growth (if any) is temporary.

The results show a general trend of declining growth rate, as indicated by declining K values and slower linear juvenile growth rates, from south to north. Values for L_{oo} are variable, but, as pointed out by Day and Fleming (1991), its value is dependent on the length range of the recapture data. In theory it is the maximum length to which individuals can attain, but, in practice, few large individuals are ever found in fished populations, so a lower value than the theoretical one usually results. In Anxious Bay small abalone predominated in inshore areas where marking was done, and large ones in off-shore areas. We observed a general movement of marked individuals off-shore with increasing size. Hence the growth curve describes the growth only of the inshore population. This explains the low L_{oo} of 119.5mm compared with the maximum observed size of 170mm SL in the length-frequency data which included individuals further off-shore.

The growth rate of abalone has often been linked to the quality and availability of algal food; others have speculated that exposure to wave action plays a role (reviewed by Day and Fleming 1991). Our results agree qualitatively with the food supply hypothesis, although we have not attempted to quantify food availability. Algal drift is conspicuously abundant at Taylor I. and McLaren Point all year round, and often in banks up to 1m high which inhibit searching. At Yanerbie algal drift is scarce and the site was selected because the abalone there are notoriously stunted. At the other sites algal drift is variable in abundance.

The growth rate data show no obvious relation with exposure to wave action. The two northernmost sites and Waterloo Bay have the highest exposure to wave action but with very different growth rates. The causes of the different growth rates observed can only be determined after much more careful studies of the habitat, which was beyond the purpose of this study.

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TABLE 1

Summary of growth parameters, T_o, K and L_∞, of the von Bertalanffy growth equation at different sites for H. laevigata. Sites are ranked from south to north, and data for Waterloo Bay (from Shepherd and Hearn 1983) are included for comparison. Juvenile growth rates given in mm $year^{-1}$; an asterisk indicates estimated rate. n.a. = not available. Standard errors in brackets.

Site	N	Juvenile Growth rate	T_o	K y^{-1} (s.e.)	L_∞ (mm) (s.e.)	r
Taylor I	41	20-39.6+	1.34	0.552 (0.087)	180.4 (10.3)	0.713
McLaren Point	35	23.6	1.65	0.368 (0.102)	178.3 (7.7)	0.534
Waterloo Bay	126	20-25*	n.a.	0.595 (0.036)	147.8 (1.8)	0.921
Ward I.	36	25.7	1.77	0.413 (0.053)	167.2 (5.2)	0.810
Anxious Bay	26	20*	1.11	0.385 (0.069)	119.5 (5.3)	0.744
Yanerbie	19	20*	0.94	0.268 (0.076)	140.4 (8.6)	0.642
Sceale Bay	9	23.6*	0.42	0.186 (0.042)	186.3 (28.2)	0.856

+ growth rate about 20mm in first year and 39.6mm in second year.

Captions of Figures

Fig. 1. Map of Eyre Peninsula showing study sites.

Fig. 2. Plot of annual increment vs initial length for mark-recapture data at Taylor I.

Fig. 3. Length-frequency distribution, with fitted modes, for *H. laevigata* from Taylor I. obtained in March 1988.

Fig. 4. Plot of modal means (with standard errors) of length-frequency data (Fig. 3) against age. Plots of mean growth rate of 1+ and 2+ aged groups of marked individuals are shown for comparison. The true growth rate is shown by a curve fitted by eye.

Fig. 5. Plot of annual increment data vs initial length for mark-recapture data from McLaren Point.

Fig. 6. Length-frequency distribution, with fitted modes, for *H. laevigata* from McLaren Point obtained in August 1987.

Fig. 7. Plot of modal means with standard errors of length frequency distribution (Fig. 6) against age, with fitted liner regression equation for McLaren Point. Growth of 1+ age class and growth of older age classes with fitted von Bertalanffy equation are plotted separately. The von Bertalanffy growth curve is displaced to the left slightly for clarity.

Fig. 8. Plot of annual increment data vs initial length for mark-recapture data from Ward I.

Fig. 9. Length-frequency distribution, with fitted modes, for *H. laevigata* at Ward I.

Fig. 10. Plot of modal means (with standard errors) of length-frequency distribution (Fig. 9) against age, and fitted von Bertalanffy equation for *H. laevigata* from Ward I.

Fig. 11. Plot of annual increment data vs initial length for mark-recapture data from Anxious Bay.

Fig. 12. Length-frequency distributions with fitted modes for H. laevigata from Anxious Bay.

Fig. 13. Plot of modal means with standards errors, of length-frequency distributions (Fig. 12) against age for Anxious Bay, with the fitted von Bertalanffy equation for mark-recapture data.

Fig. 14. Plot of annual increment data vs initial length for mark-recapture data from Yanerbie and Sceale Bay for H. laevigata.

Fig. 15. Length-frequency distributions with fitted modes, for H. laevigata from Yanerbie (4.12.87) and Sceale Bay.

Fig. 16. Plots of modal means, with standard errors, of length-frequency distributions (Fig. 15) and fitted von Bertalanffy equations for H. laevigata from Yanerbie and Sceale Bay.

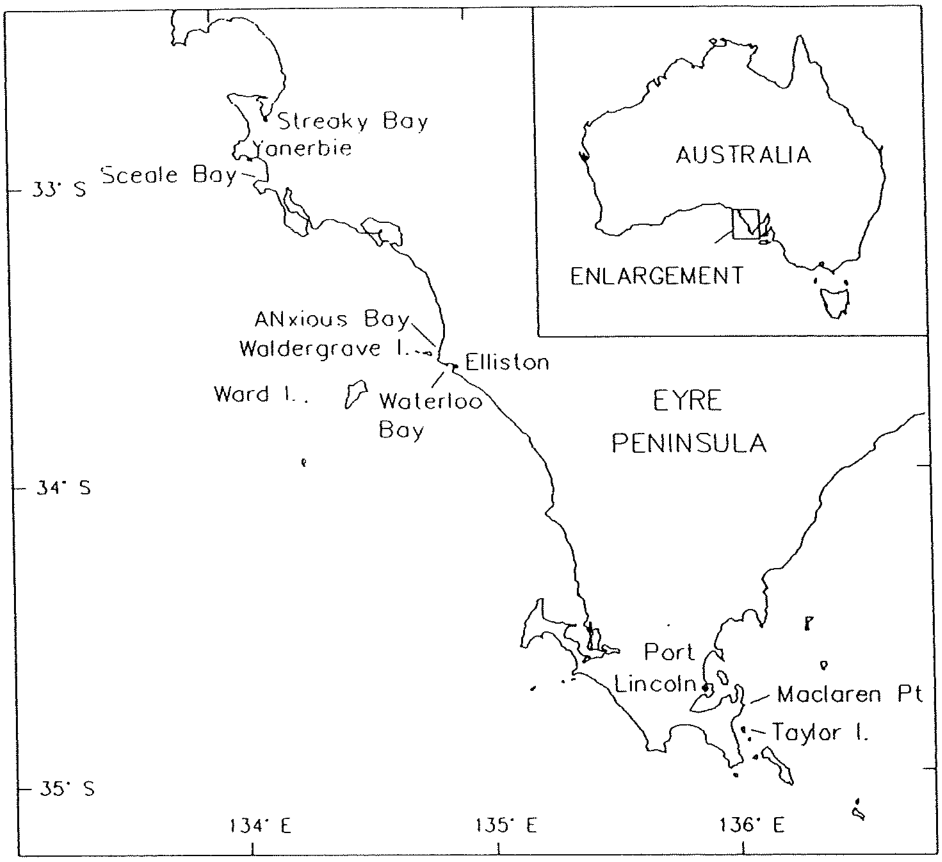
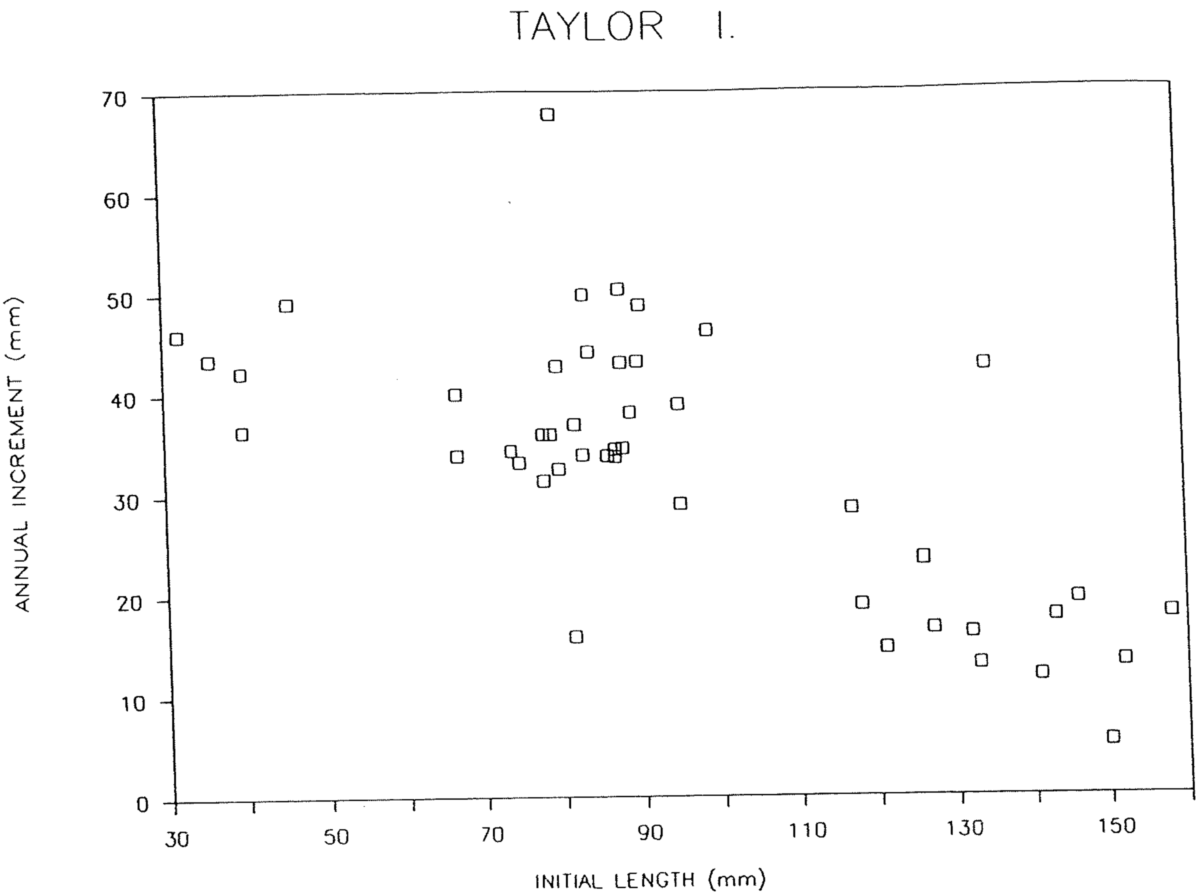
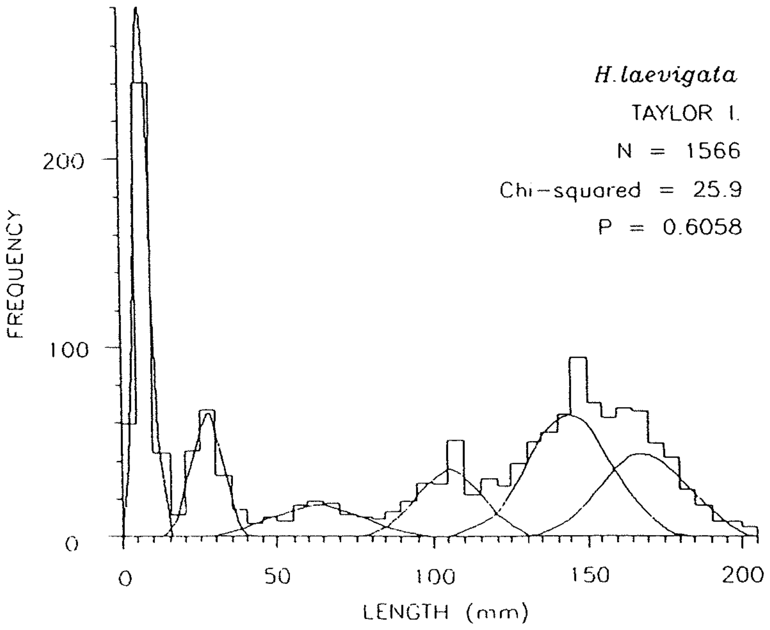

Streaky Bay
Yanerbie
Sceale Bay
33° S
ANxious Bay
Waldergrave I.
Elliston
Ward I.
Waterloo Bay
34° S
EYRE PENINSULA
Port Lincoln
Maclaren Pt
Taylor I.
35° S
134° E
135° E
136° E
AUSTRALIA
ENLARGEMENT

FIG. 1

Fig 2


TAYLOR I.
ANNUAL INCREMENT (mm)
0
10
20
30
40
50
60
70
30
50
70
90
110
130
150
INITIAL LENGTH (mm)

ig 3


H. laevigata
TAYLOR I.
N = 1566
Chi-squared = 25.9
P = 0.6058
FREQUENCY
0
100
200
0
50
100
150
200
LENGTH (mm)

ig 4

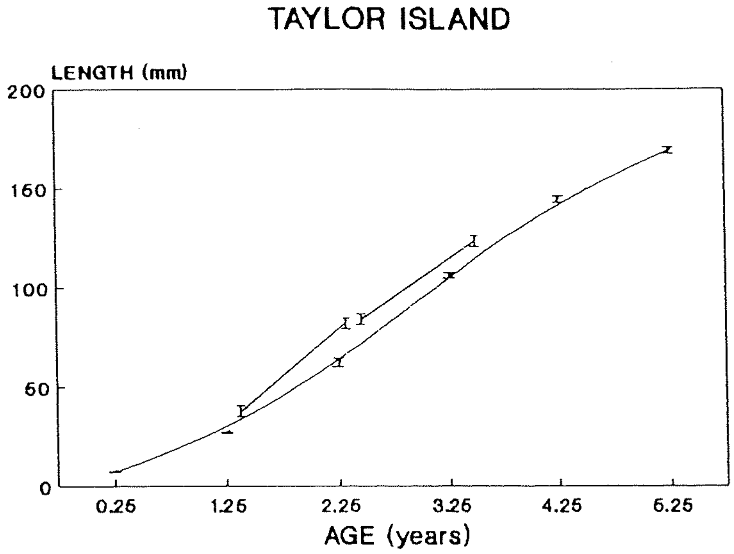

TAYLOR ISLAND
LENGTH (mm)
200
160
100
60
0
0.25
1.25
2.25
3.25
4.25
6.25
AGE (years)

Fig. 5

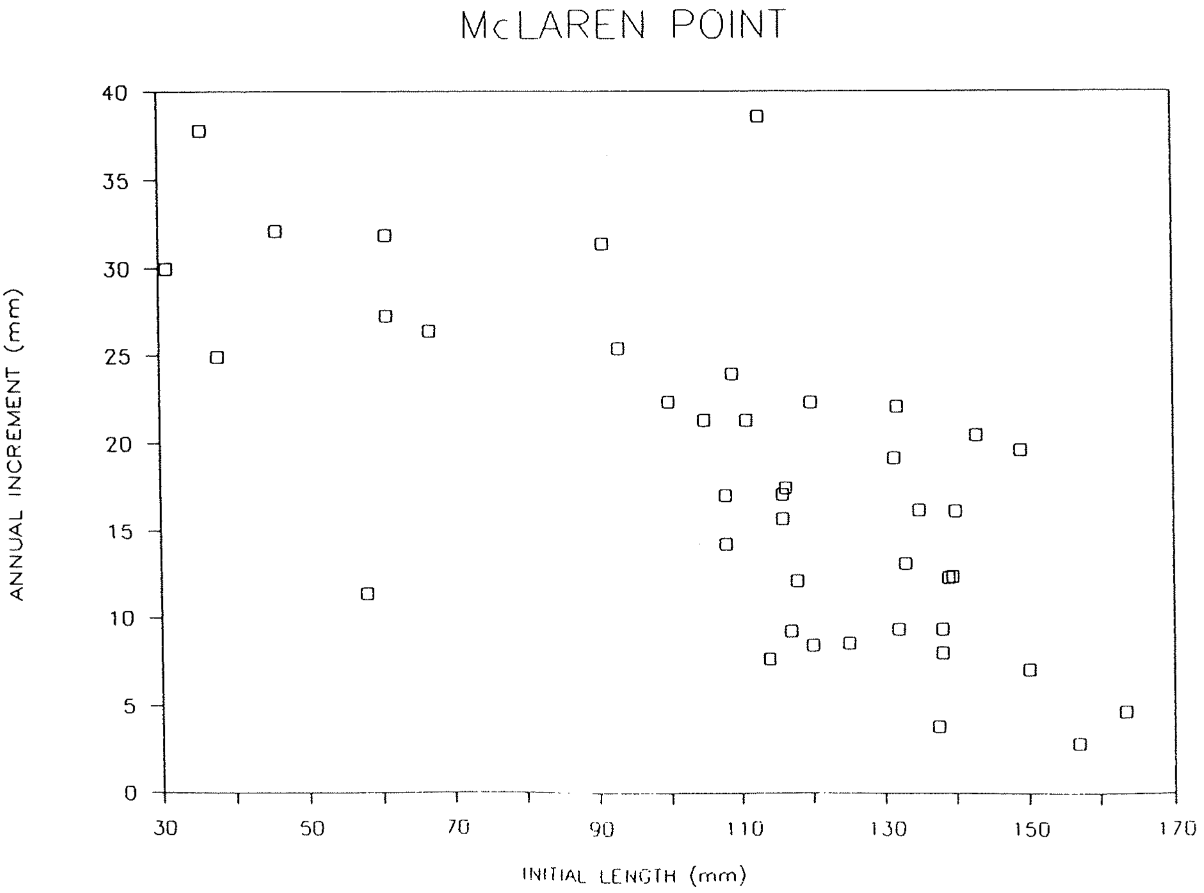

McLAREN POINT
40
35
30
25
20
15
10
5
0
ANNUAL INCREMENT (mm)
30
50
70
90
110
130
150
170
INITIAL LENGTH (mm)

Fig 6

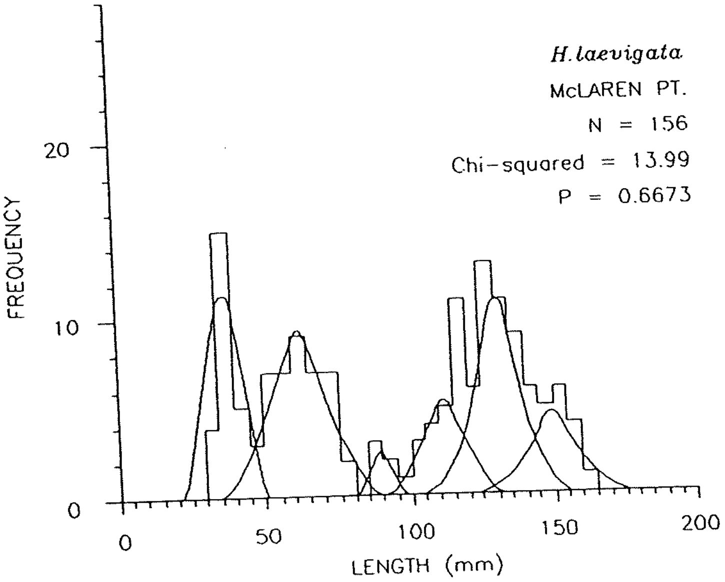

H.laevigata
McLAREN PT.
N = 156
Chi-squared = 13.99
P = 0.6673
FREQUENCY
0
10
20
0
50
100
150
200
LENGTH (mm)

Fig 7

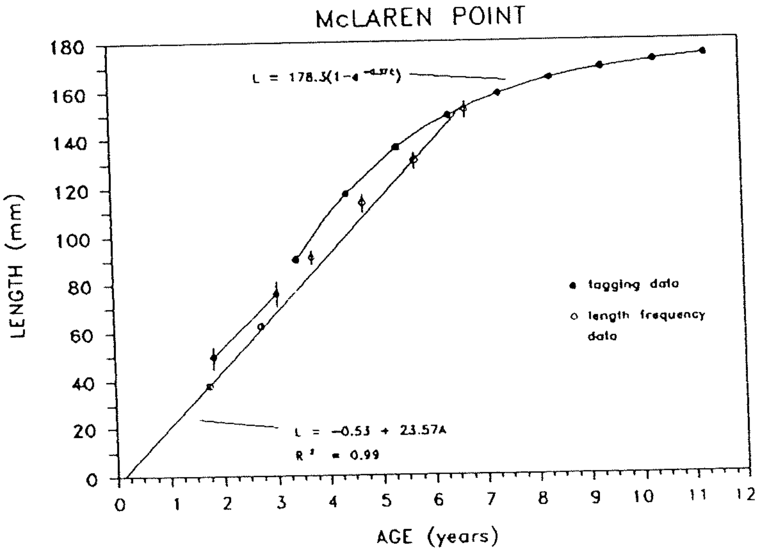

McLAREN POINT
L = 178.3(1-e^-0.37t)
L = -0.53 + 23.57A
R² = 0.99
● tagging data
○ length frequency data
LENGTH (mm)
0
20
40
60
80
100
120
140
160
180
0
1
2
3
4
5
6
7
8
9
10
11
12
AGE (years)

Fig. 8

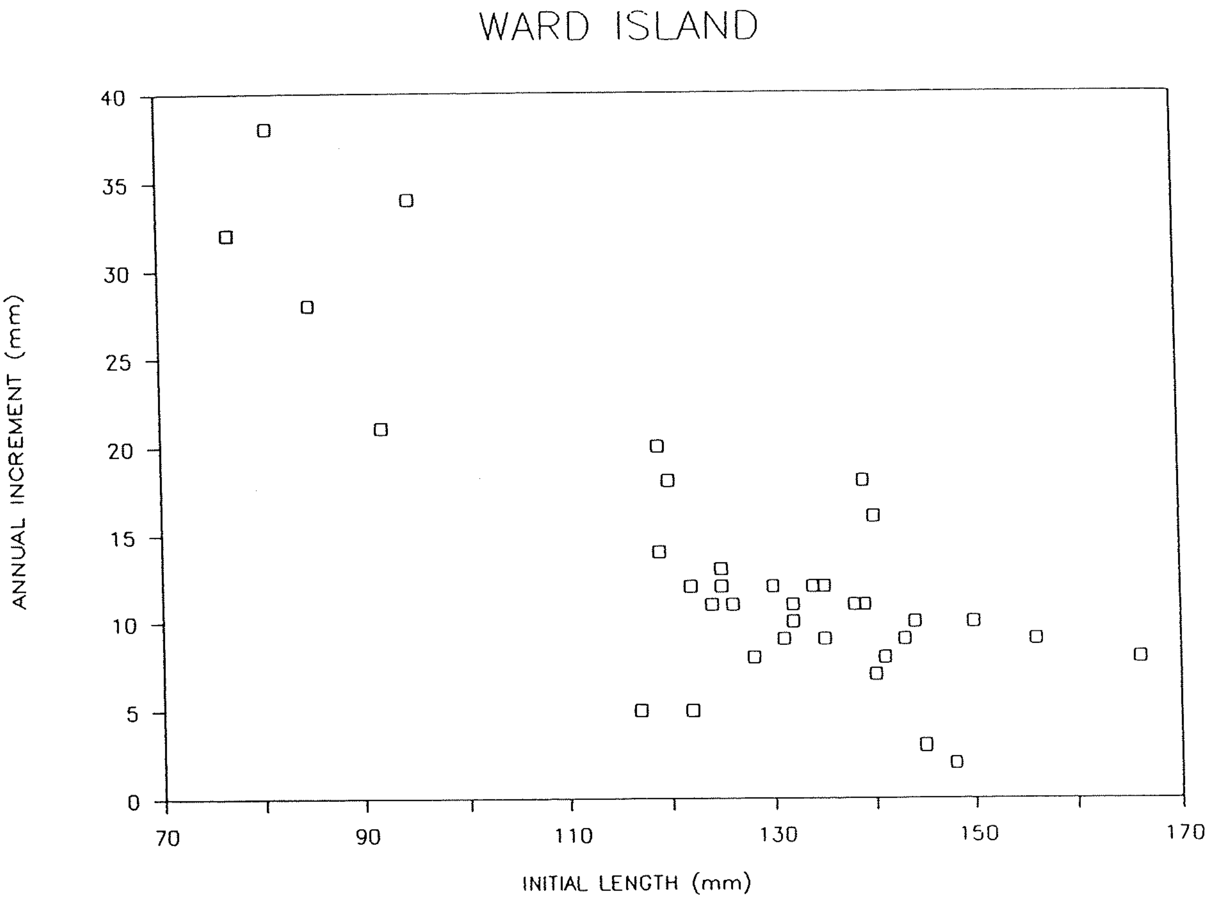

WARD ISLAND
ANNUAL INCREMENT (mm)
INITIAL LENGTH (mm)
0
5
10
15
20
25
30
35
40
70
90
110
130
150
170

FIG 9

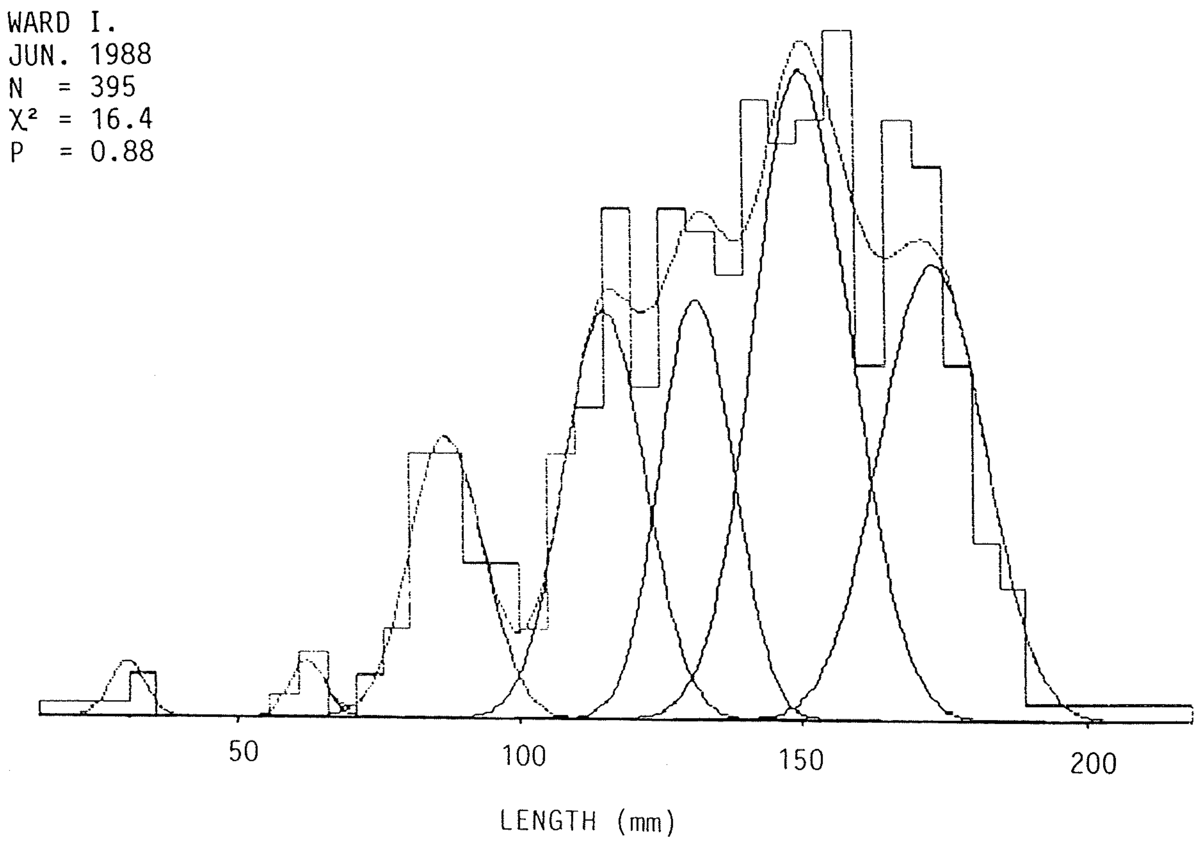


Fig 10

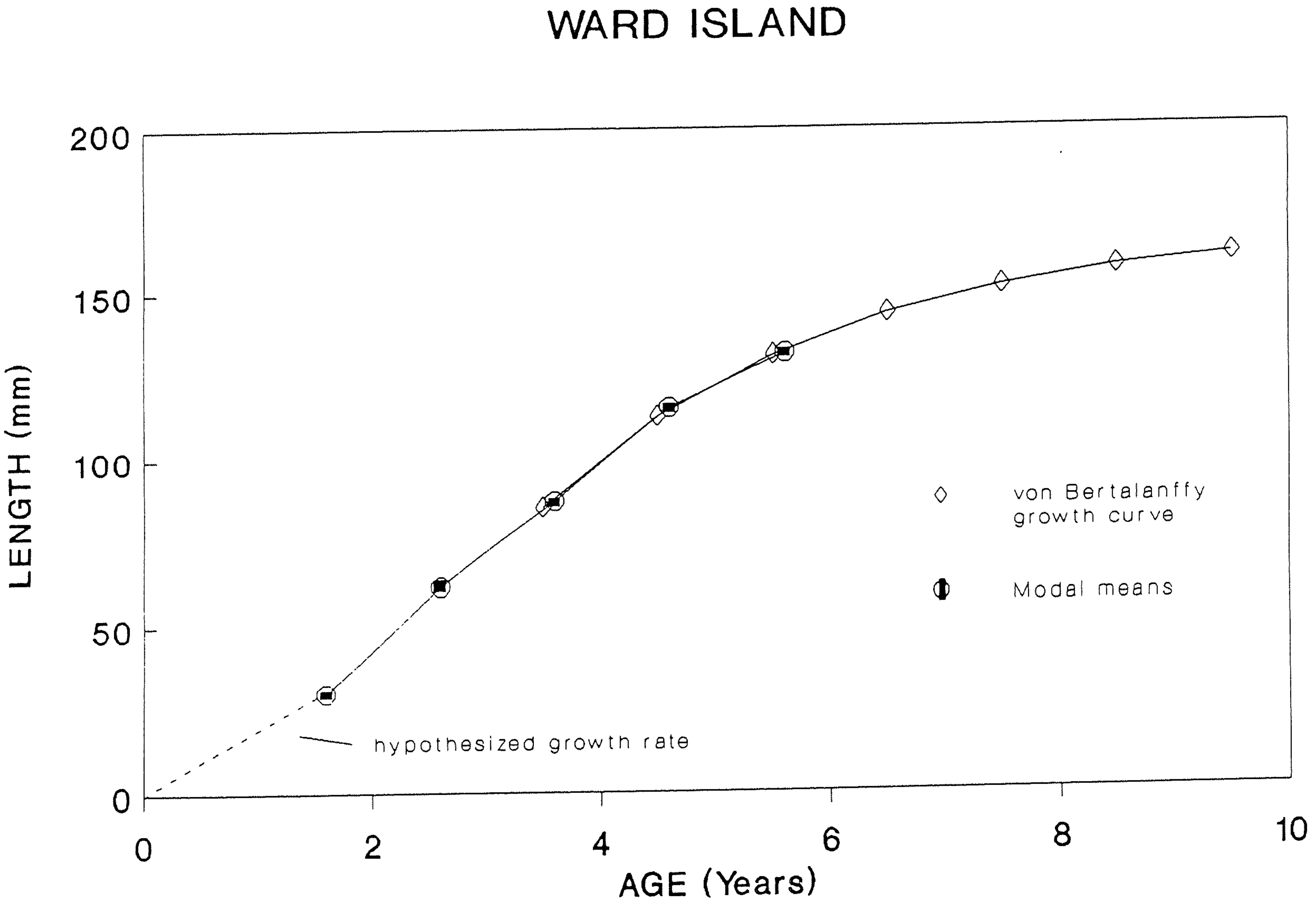

WARD ISLAND
LENGTH (mm)
0
50
100
150
200
AGE (Years)
0
2
4
6
8
10
von Bertalanffy growth curve
Modal means
hypothesized growth rate

Fig. 11

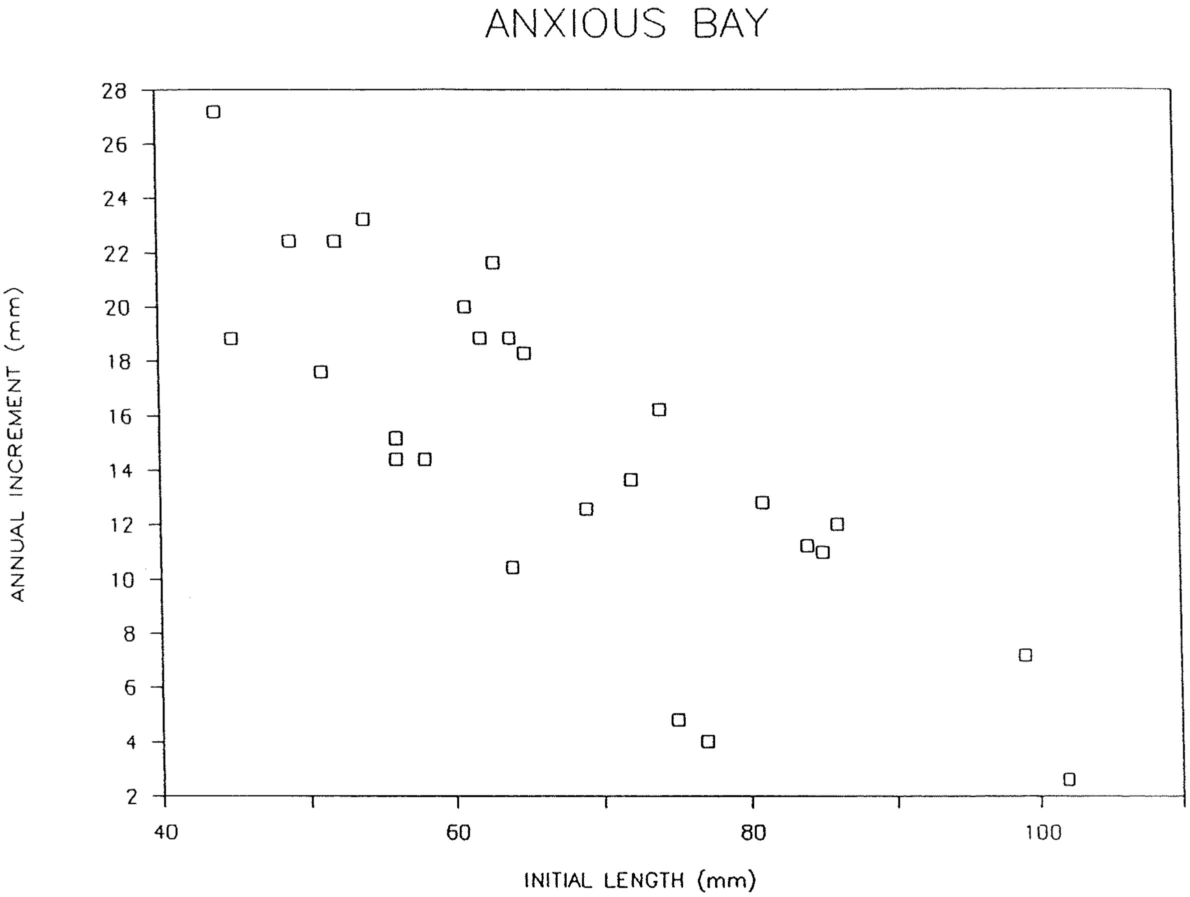
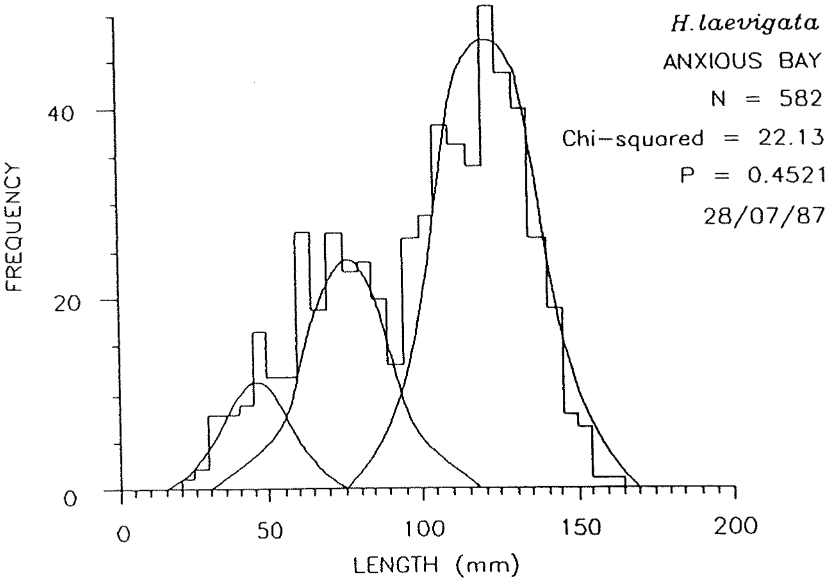
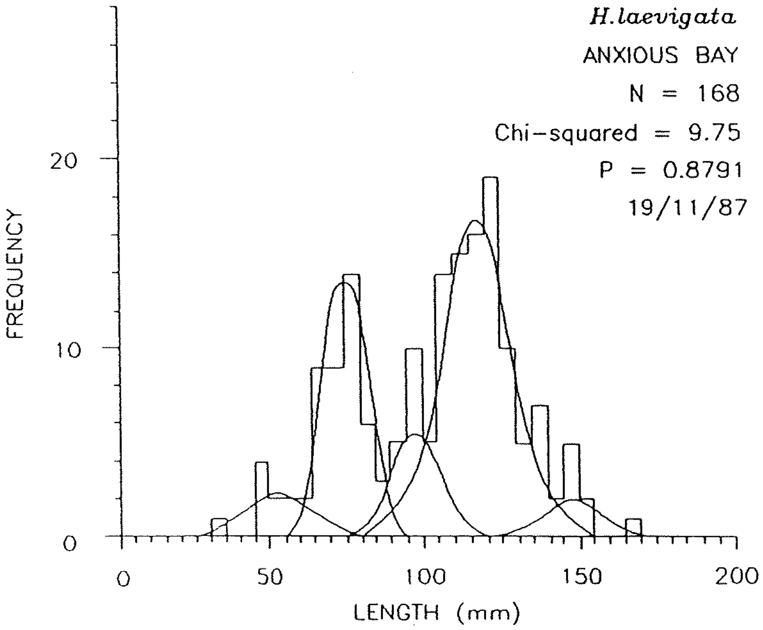

ANXIOUS BAY
ANNUAL INCREMENT (mm)
28
26
24
22
20
18
16
14
12
10
8
6
4
2
40
60
80
100
INITIAL LENGTH (mm)

FIG 12



H. laevigata
ANXIOUS BAY
N = 582
Chi-squared = 22.13
P = 0.4521
28/07/87
FREQUENCY
0
20
40
0
50
100
150
200
LENGTH (mm)



H. laevigata
ANXIOUS BAY
N = 168
Chi-squared = 9.75
P = 0.8791
19/11/87
FREQUENCY
0
10
20
0
50
100
150
200
LENGTH (mm)

Fig 13

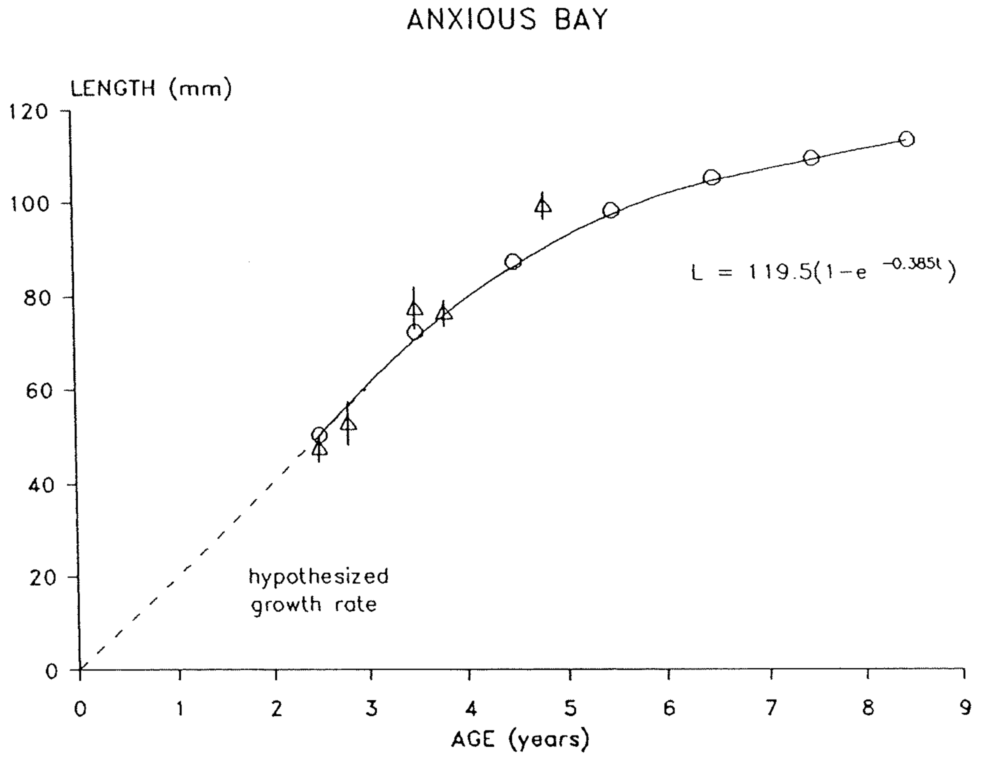
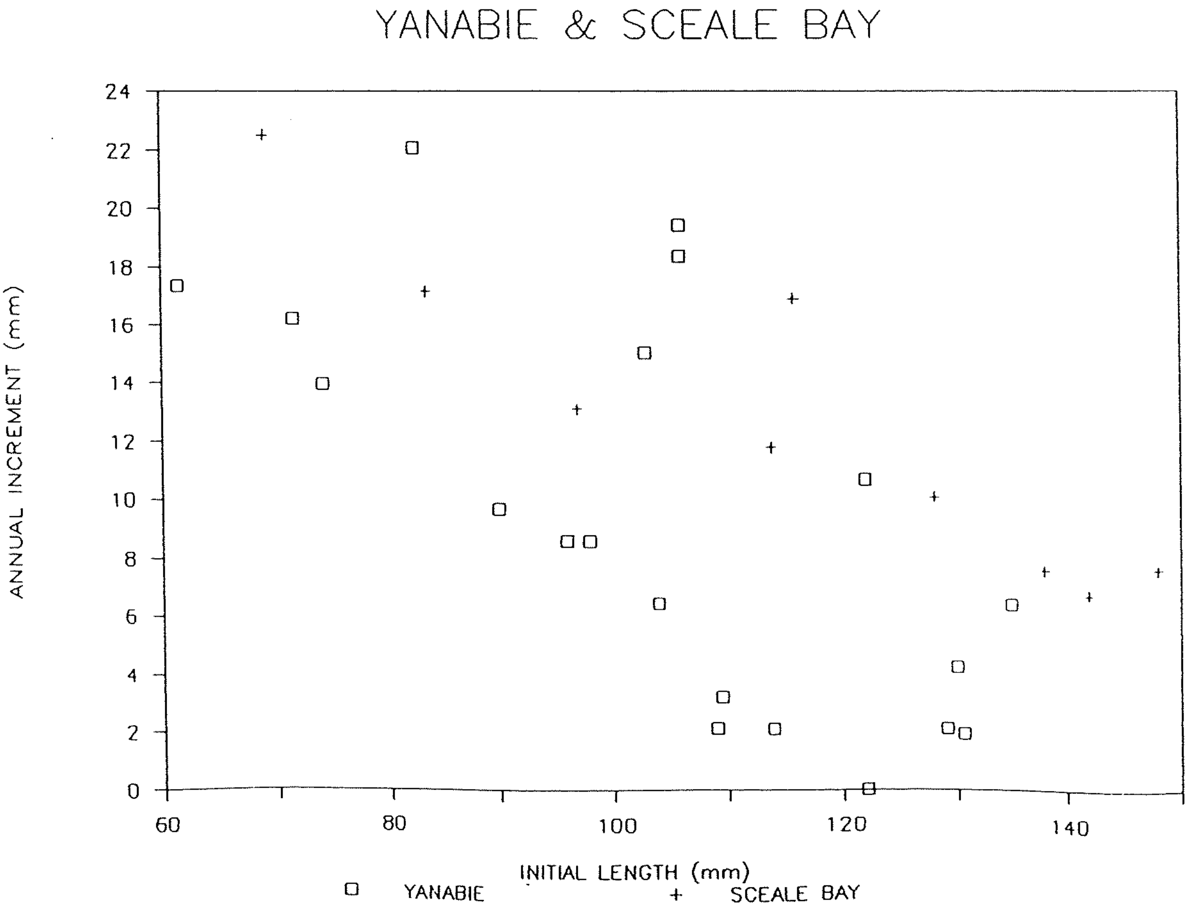
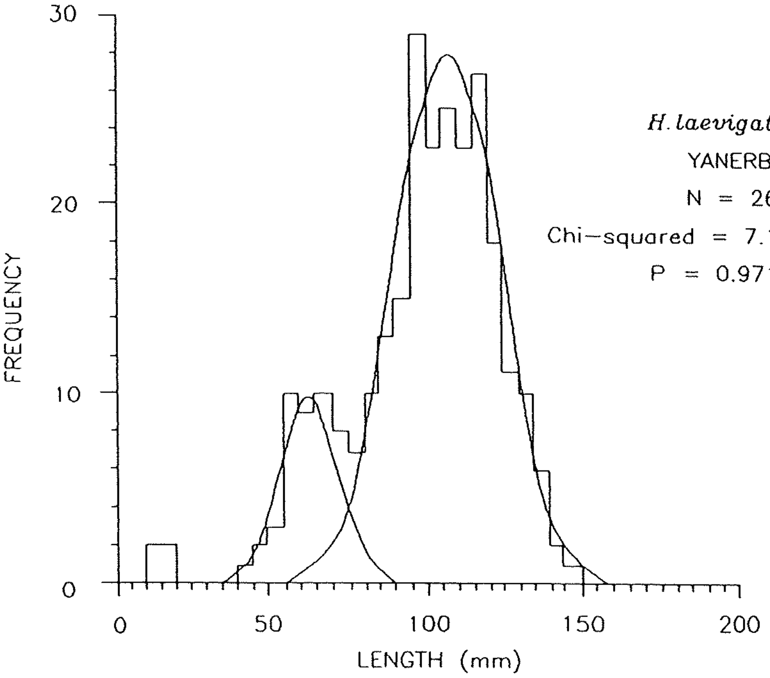
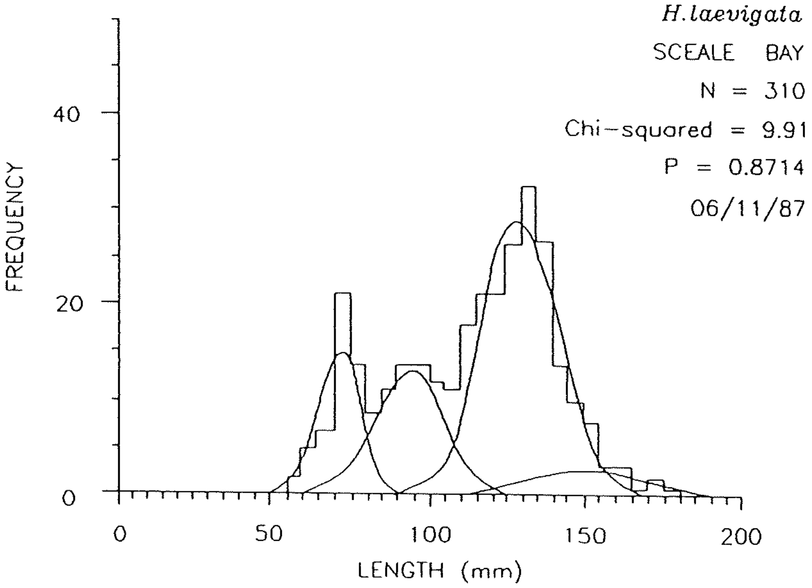

ANXIOUS BAY
LENGTH (mm)
120
100
80
60
40
20
0
L = 119.5(1-e -0.385t)
hypothesized
growth rate
0
1
2
3
4
5
6
7
8
9
AGE (years)

Fig. 14


YANABIE & SCEALE BAY
24
22
20
18
16
14
12
10
8
6
4
2
0
ANNUAL INCREMENT (mm)
60
80
100
120
140
INITIAL LENGTH (mm)
□ YANABIE
+ SCEALE BAY


H. laevigata
YANERBIE
N = 263
Chi-squared = 7.10
P = 0.9713
FREQUENCY
0
10
20
30
0
50
100
150
200
LENGTH (mm)


H. laevigata
SCEALE BAY
N = 310
Chi-squared = 9.91
P = 0.8714
06/11/87
FREQUENCY
0
20
40
0
50
100
150
200
LENGTH (mm)

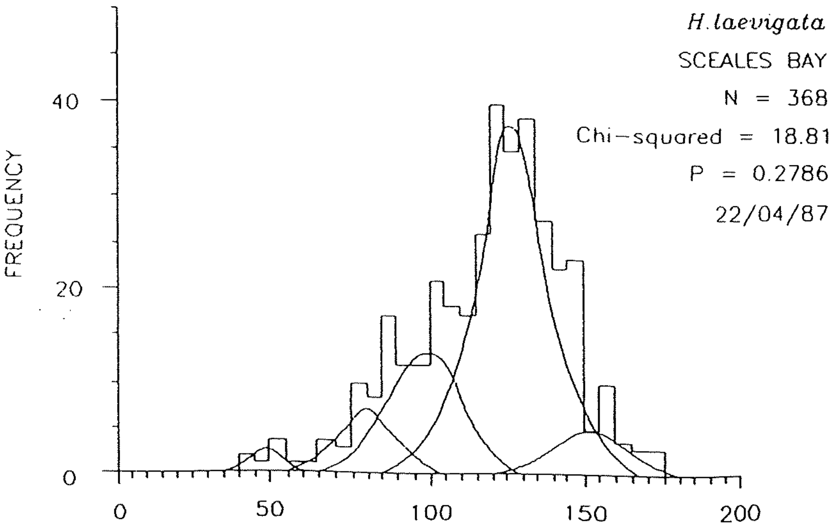
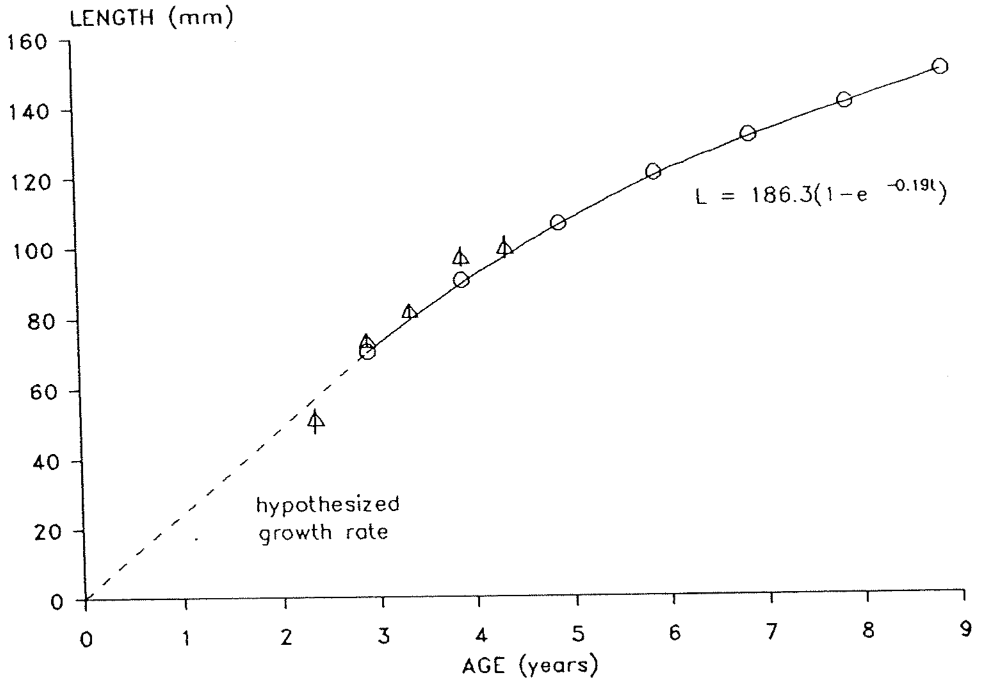
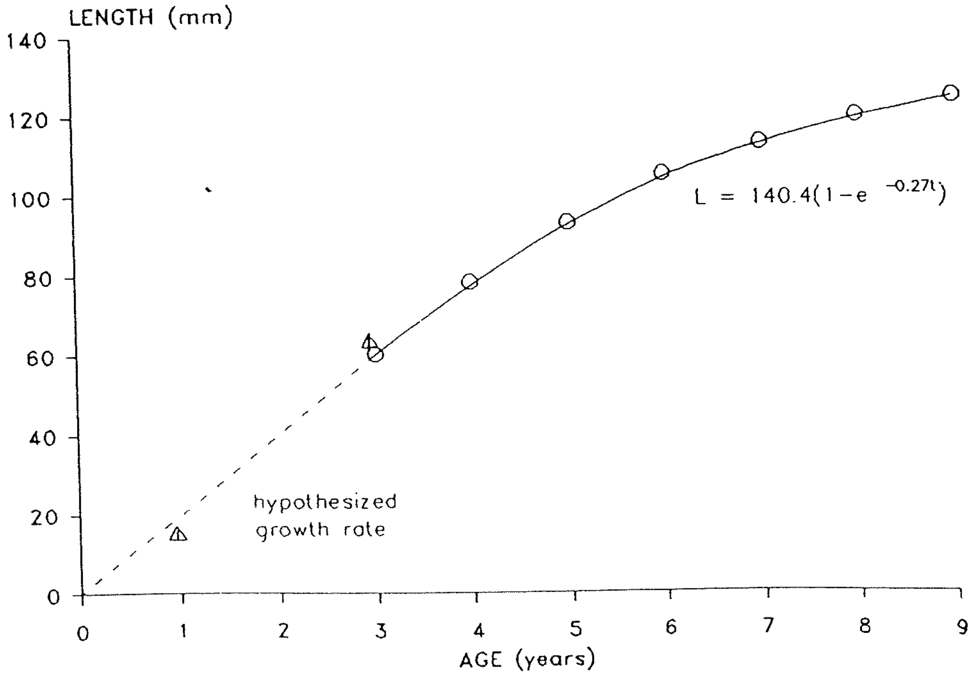

H. laevigata
SCEALES BAY
N = 368
Chi-squared = 18.81
P = 0.2786
22/04/87
FREQUENCY
0
20
40
0
50
100
150
200

Fig. 15

SCEALE BAY



YANERBIE



APPENDIX 4

STUDIES ON SOUTHERN AUSTRALIAN ABALONE (Genus *Haliotis*) XIII*

Larval dispersal and recruitment

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RUNNING TITLE: Larval dispersal and recruitment

Key words: Abalone, *Haliotis*, recruitment, larval dispersal

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ABSTRACT

Adult densities of the greenlip abalone, Haliotis laevigata Donovan were manipulated in 24 100 m segments of coastline over a distance of 2.4 km. Recruitment at an age of about 3 months from spawning of the manipulated population was measured in each segment, by using a direct searching technique with an underwater magnifier.

Recruitment strength was independent of adult density within 100 m segments, but varied according to features of coastal topography. Recruitment was highest in inlets and in the lee of submerged pinnacles and lowest on points or headlands. It is hypothesised that abalone larvae are transported in near-bottom tidal currents for distances of hundreds of metres to kilometres, and are concentrated in places where the bottom and shore topography cause eddies and stagnation zones.

INTRODUCTION

An understanding of the relationship between stock size and recruitment is critical for the management of fisheries, and especially so for those on abalone. In these fisheries the diver removes the abalone by hand and can take practically the whole of the parent stock from local areas. Hence it is important to know what constitutes a stock for a given area in order to avoid recruitment overfishing. This requires a knowledge of the extent of larval dispersal of abalone.

Abalone have lecithotrophic larvae with a larval life of several days for all known species (reviewed by McShane 1991) and have the potential for dispersal from their source of the order of kilometres. The possibility that abalone larvae might settle close to their parents had not been tested until the recent studies of Prince et al (1987, 1988) and McShane et al (1988). These authors provided evidence that the larvae of Haliotis rubra were likely to settle successfully only within the same reef as the parents and that dispersal of larvae was of the order of 0 - 50 metres. If this proves to be general then the stock - recruitment problem referred to above could be examined experimentally at the scale of a local reef.

In this paper we describe an experimental manipulation of adult densities of the greenlip abalone, Haliotis laevigata Donovan. We wished to test the hypothesis that larval recruitment strength is dependent on the local density of parental abalone. We chose a section of coast 2.4 km long in which to do the experiment because we wished to measure the dispersal of larvae at the largest scale possible, namely hundreds of metres. If larval dispersal were less than this scale we would expect larval recruitment to depend upon and show some relationship with the number of adults in the vicinity.

MATERIALS AND METHODS

Study Site

The site of the study was a nearly uniform section of coast along Taylor I. and Owen I., South Australia (Fig. 1). The islands are granite and generally the rock falls steeply to meet the sand at a depth of 7-10 m. Small boulders up to 50 cm diameter are scattered at the junction of rock and sand.

The tidal pattern is semi-diurnal and tidal flow is north and south. Currents at the sea surface some 50 m off-shore may reach maximum values of 50 cm sec^{-1} but close in-shore, or near the sea-bed they are not perceptible and < 5 cm sec^{-1}.

At the southern end of Taylor I algal communities are dominated by Ecklonia radiata, Cystophora monilifera and Seirococcus axillaris. Going from south to the northern end of Owen I. there is a gradual transition of dominants to C. monilifera, and C. subfarcinata, Scaberia agardhii and Sargassum spp., suggesting a weak gradient of decreasing water movement from south to north (see Shepherd and Womersley 1981). This is consistent with the direction of approaching swell from the south. Sandy bottom adjacent to the islands is colonised by Posidonia spp.

H. laevigata occurs in a narrow band 1 - 7 m wide (according to site) where rock is buried by sand.

The area was closed to commercial divers for a year from March 1987 during the experiment. Before the closure the area had been intensely fished by divers and density was generally low and usually less than 0.5 m^{-2}.

Manipulation of breeding stock

The purpose of the manipulations was to create areas of high density of adult abalone interspersed with areas of low or background density. Some areas of naturally high density were fished down to as low a density as possible by removing all visible abalone > 100 mm long on at least 2 occasions and transplanting them into areas of low density. In addition about 1500 individuals were transplanted from the western side of Taylor I to further increase the density in the high density segments. In all, densities were increased in 5 segments, decreased in 8 segments, and left unchanged in 11 segments (see Fig. 1 and Table 1 for details). The manipulations were done between May and July 1987 well before the spawning season of H. laevigata.

After the manipulations censuses of abalone were carried out by two divers swimming together the length of each segment, and measuring on an underwater measuring gauge (Shepherd 1985) all visible, emergent greenlip abalone (ie those over about 50 mm shell length). From these data the number of adults (those > 100 mm SL) per segment was derived. The diver also estimated the number of aggregated adults per segment by excluding adults which were > 1 m from their nearest neighbour. In practice it was found that in segments with few abalone, few or none were aggregated, whereas at higher densities the opposite was true. Mean abalone habitat width in each segment was crudely estimated by averaging 2 - 4 measurements of the width of the band of rocky bottom occupied by emergent abalone. This distance of each segment from the southern boundary of the study site was estimated from the map of the region.

In order to crudely measure the effect of coastal topography on recruitment, an inlet value, IV, taking an integer value from 0 to 2, was allotted to each segment. The value allotted was: zero where abalone habitat in the segment was predominantly within an inlet or where the coastline receded from the long-shore current; 1 where the coastline was linear; and 2 where the coastline projected into the long-shore current, as at a point.

Lastly we derived an index of larval abundance, L, under the hypothesis that abalone larvae are more widely dispersed away from the parents in accordance with a simple diffusion model. We supposed larvae to be carried north and south and to be normally distributed about the centre of each segment, with a standard deviation of 200 m. We used the total number of aggregated abalone per segment as a crude index of larval production. We did not test other models of diffusion or use different values for the standard deviation because it became evident in the analysis that this was an improbable source of variation.

Recruitment surveys

Pilot studies at Taylor I in the previous year had established that juvenile H. laevigata settled on rocky bottom of low relief where rock meets sand at a depth of 7-10 m. Divers used the underwater magnifier (x3) described by Mladenov and Powell (1986) which is optically superior to that described by Shepherd and Turner (1985) to search for juvenile abalone.

Searching was standardised in the under-boulder habitat in the following way. In each segment the diver selected randomly 12 - 17 sites where boulders were present, stratified throughout the segment and at each site searched 5 boulders, each with an average area of planar projection of about 0.2 m^2. The diver recorded in situ the length of juvenile H. laevigata found, the presence of adults nearby, and topographic features. Recruitment surveys commenced in March 1988 and were completed within a month.

Validation of searching technique

In order to validate the visual searching technique we compared the results obtained by that method with those obtained by the anaesthetic technique of Prince and Ford (1985). We carried out 3 experiments (Mar. 1987, Apr. 1988 and Jan. 1990) at West Island where a similar boulder habitat occurs. Divers searched 20-30 boulders for small abalone with a magnifier, and recorded the length and species of each individual in situ. Each boulder immediately after being searched was placed in a numbered plastic bag, which was sealed and taken to the laboratory on shore nearby. Each boulder was washed in dilute formalin and seawater and its surface carefully brushed. The epibiota retained by a 0.5 mm sieve was sorted under a dissecting microscope, and the length and species of abalone recorded.

The resultant data were analysed as a mark-recapture experiment (Bailey 1951), in which the abalone identified and measured in situ were treated as marked individuals and those subsequently found in the laboratory as recaptures. The total number (N) of abalone on the boulders in any one experiment is given by:

$$N = T.\ n/m$$

where T is the number of abalone recorded by the diver in situ, n is the number recorded in the laboratory, of which m is the smaller number also recorded in situ (ie co-incident in length and species).

The standard error of N is :

$$\text{s.e.}(N) = (T^2 n(n-m)\ /m^3)^{1/2}$$

The efficiency of the searching technique is given by T/N and that of the anaesthetic technique by n/N.

Efficiency values, with standard errors were calculated for each of 4 size classes (1 - 5, 6 - 10, 11 - 15, 16 - 20 mm SL for the two species combined (H. laevigata and H. scalaris) for each experiment.

An assumption of the method is that individual abalone recorded in situ cannot be confused with ones later recorded in the laboratory. This could occur if two conspecific individuals of the same length were on the same boulder. The chance of this happening was small because the maximum mean density of any 5 mm size class in any experiment was only 1.2 per boulder; only once in 70 boulders were 2 conspecific individuals of the same length recorded, giving a probability of that event of 0.012 per boulder.

Statistical analysis

Length-frequency data obtained by combining the recruitment survey data (March - April 1988), and data from censuses of the adult population during the same period (excluding segments where densities were experimentally increased), were analysed with the MIX interactive computer program (McDonald and Pitcher 1979), and modes fitted, with constraints imposed only on the two right hand modes.

Reproductive cycle

Concurrent studies on the reproductive cycle of H. laevigata at Taylor I and nearby sites (Shepherd and Lowe in prep) showed a peak in the gonad index in September to November 1987 and a sharp decline in December 1987 indicating the onset of epidemic spawning in that month at Taylor I and in adjoining areas to the north and south.

RESULTS

Searching efficiency

The mean efficiency of the searching technique as compared with the anaesthetic technique is shown in Fig. 2 for 4 size classes. Mean efficiencies of the two methods differed, but not significantly ($X^2=1.6$; $0.1<P<0.25$), for the smallest size class, and were nearly identifical for larger size classes. Thus the searching technique appears to be as efficient as the anaesthetic technique. Next we examined the data for changes in efficiency of the searching technique with density. Here we combined the two smallest size classes and compared the 3 experiments. The results (Table 1) showed differences in searching efficiency with density, but they were not significant ($X^2 = 2.0$; $0.1<P<0.25$ for March 1987 and April 1988 experiments). We conclude that searching efficiency is independent of density over the range examined (to 15 mm SL).

Recruitment

A composite length-frequency distribution with fitted modes, from under - and above - boulder surveys in March-April 1988, is given in Fig. 3. The left-hand mode is considered to represent the 0+ year class, following settlement from spawning in November - December 1987, and was absent in under - boulder searches conducted 5 months before. The succeeding 3 modes to the right are older year classes (unpublished data). Recruitment density (R) in this paper is the abundance of the putative 0+ year class. The area searched per segment and density values are given in Table 2.

The manipulative changes in numbers of adult abalone, the variables mean habitat width, H, Inlet Value, IV, distance from the southern boundary, D, total numbers of adults, N_1, numbers of aggregated adults, N_2, and an index of larval abundance, L, under a postulated dispersion model with a standard deviation of 200 m for each segment are given in Table 2.

The relation between mean recruitment strength per segment, R, and the variable IV was examined first by analysis of variance because values of the variable, IV, were not continuous but integers. The relationship between IV and R was significant ($F=5.27$; $P<0.05$).

Next, we examined by multiple regression analysis the relation between R and the variables H, IV, D, N_1, N_2 and L according to the model:

$$R = a_0 + a_1H + a_2D + a_3IV + a_4X$$

where N_1, N_2, $L = X$ were included seriatim in the analysis. N_1, N_2 and L were all found to be non-significant, but the variables, H, D and IV were significant.

The regression equation (with standard errors in brackets) is:

$$R = 0.54\ (0.17) + 0.22\ (0.05)\ H - 0.05\ (0.01)\ D$$
$$+ 0.33\ (0.17)\ IV_1 + 0.66\ (0.19)\ IV_2$$

However, H is correlated with D ($r = 0.55$; $P < 0.01$), N_1 ($r = 0.67$; $P < 0.01$), N_2 ($r = 0.61$; $P < 0.05$) and L ($r = 0.64$; $P < 0.01$); these correlations partially confound the conclusions that can be drawn.

We then repeated the regression analyses, inserting only one of the variables (H, D, IV, N_1, N_2, L) at a time. The only significant regressions were IV ($P < 0.05$) accounting for 27% of the variance, and D ($P < 0.05$) accounting for 19% of the variance.

Next we examined the effect of granite pinnacles on R. There were 4 large pinnacles up to 3 m high and 3 - 5 m basal diameter situated in abalone habitat in Segments 11, 13, 14 and 17. We compared the density of recruits in the lee of these pinnacles, by searching replicate samples of 2 m^2 on the north and south (lee) sides of each pinnacle and in the same segment away from the pinnacle. The mean density of recruits in the lee of the pinnacles was 4.7 m^{-2} (s.e.1.0) and away from the pinnacles was 1.3 (s.e.0.3). The difference was significant by parametric and non-parametric tests ($t_{23} = 3.7$, $P < 0.002$; Mann Whitney U test, $U = 16$, $P < 0.01$).

DISCUSSION

Searching efficiency

Three methods to measure the abundance of newly settled abalone are in use: the suction sampling technique of McShane and Smith (1988), the anaesthetic technique of Prince and Ford (1985) and the direct search technique of Shepherd and Turner (1985).

McShane and Smith (1988) compared the first two methods with each other and with visual searching without a magnifier. They found no significant difference between the suction and anaesthetic methods but not surprisingly, found that visual searching (without a magnifier) was inefficient compared to the other methods. This study shows that searching with a magnifier is equally efficient as the anaesthetic technique, but both are imperfect. In searching visually the diver must manipulate the boulder in one hand while holding the magnifier in the other. Very small abalone (<5 mm SL) could easily be missed because of the cryptic colour or location, whereas larger ones can crawl out of sight. With the anaesthetic technique the diver must lift the boulder and place it in a bag. During this process small abalone may fall off the boulder in an escape response similar to that of some chitons (eg Ludbrook and Growlett-Holmes 1989, p 513).
However, we should point out that the anaesthetic technique as used by Prince (1987, 1988) may be more efficient than as used by us, because in our experiments the boulders were first searched visually before being placed in plastic bags, thus allowing more time for small abalone to fall of.

The suction technique does not have these problems, but it has other limitations. It is best on reef of high relief (the habitat of H. rubra) but is less effective on reef of low relief (the habitat of H. laevigata), where large volumes of sediment are entrained. The sorting of samples is time consuming enough in a relatively sediment-free habitat (McShane and Smith

1988), but prohibitively so in habitat with abundant sediment, as we discovered in pilot experiments.

The visual searching technique is the best in the habitat of H. laevigata, but, nevertheless, has disadvantages. It is costly in terms of underwater time (40 - 60 minutes per m^2), and is probably of low efficiency for abalone 0.5 - 1 mm long (although only one in this size range was recorded in any of the 3 experiments). Lastly, it cannot be done effectively where there is much surge from prevailing swell.

Recruitment variability

Our measurements of recruitment strength were made 2 - 3 months after settlement, so it is possible that differential mortality between segments may contribute to recruitment variability. Shepherd (1987) examined the mortality of H. laevigata and H. scalaris at West Island and found in one year of strong settlement evidence of density-dependent mortality. However, the differences in recruitment strength between years at West Island were much greater than the between segment differences at this study site, so density-dependent mortality seems an unlikely explanation for the recruitment variability. It is also possible that there are differences in predator abundance between segments. However, the same under-boulder habitat was sampled throughout the study site so this explanation, too, seems unlikely.

This study found three significant sources of variation: habitat width, H, distance from the southern boundary, D, and topography (presence of inlets and pinnacles).

H is a crude measure of the extent of suitable habitat available for settlement. It was estimated on the visible extent of emergent abalone and might therefore be biased if juvenile migration occurred. However, earlier studies (Shepherd 1973, Shepherd and Turner 1985, unpublished data) have shown that juveniles are found in the same habitat (rocky bottom of low relief) where larval settlement occurs. Hence the presence of juveniles is a good indication of the areal extent of settlement habitat. The high proportion of the variance explained by this variable shows the importance of habitat (which may be a complex of factors) compared with others.

The second variable of major importance, D, indicates a gradient in recruitment throughout the length of the study site. We postulate several factors which may be involved:

(a) the environmental gradient (possibly water movement) suggested by the algal community changes may in some way influence recruitment strength;

(b) populations of H. laevigata on this coast gradually decline from south to north. A major fishery occurs from the southern end of Taylor Island for a further 8 - 10 km south. North of Taylor Island abalone abundance declines rapidly, so that 15 km north of Owen Island populations are sparse and unexploited. One explanation of this pattern of distribution is that there is a strong gradient in recruitment strength from south to north throughout the region. The southerly populations may be a major source of recruits for more northerly populations, in accordance with the prevailing northerly current flow in western Spencer Gulf (Bye and Whitehead 1975).

Two aspects of topography, inlets (IV) and the presence of pinnacles, shown to be important influences on recruitment strength, suggest that abalone larvae are transported passively by coastal currents. It is known that bays, inlets and small islands generate sheer zones, eddy systems with counter-currents, and stagnation zones in the presence of currents (Hamner and Hauri 1977 and reference cited) (Fig 4). Empirical studies confirm that these anomalies concentrate plankton to many times background levels (Alldredge and Hamner 1980, Tanaka et al 1986). The mechanism by which larvae are concentrated is still unclear. Alldredge and Hamner (1980) argued that reverse currents have downward vertical components and that photopositive larvae, by swimming upward, will become more concentrated at the surface and will disperse into the quiet region. Black (1988) modelled the diffusion of neutrally buoyant larvae as a random walk with diffusion coefficients set to simulate the processes of vertical sheer and random diffusion. He concluded that these physical processes alone can explain the concentration of larvae (up to 5 times) in eddies. If bottom boundary layers were taken into account larval residence times in eddies would be further increased. Thus hydrodynamic processes alone or combined with simple larval behavioural patterns can explain an increased settlement of larvae in quiet waters.

McShane (1991) reviewed the behaviour and dispersal of abalone larvae. He showed that for morphological reasons the larva has little capacity for directional movement, and is transported passively by coastal currents.

In places of low wave and current energy dispersal of abalone larvae can be very localised (Prince et al. 1987, 1988) but even in places of high wave energy larval dispersal may be localised due to attenuation of currents by algal forests, reef topography and swell (Black and McShane 1990, McShane 1991).

This study does not provide any direct evidence on the extent of larval dispersal of H. laevigata. However, if dispersal were very localised and less than the 100 m scale of manipulations of adult densities, then it might be expected that density of recruits would vary in accordance with the abundance of local spawning adults. This did not happen. Nor was there any detected effect assuming that larvae are dispersed at a larger scale of about 200 m. We cannot conclude that the local abundance of spawning adults was not important, but only that the immigration of larvae from a greater distance than the scale of the experiment was sufficient to mask any local stock - recruitment relationship. The results contrast with those of Prince et al. (1987, 1988) who found a significant relation between local stock and recruitment for H. rubra.

The habitats of H. laevigata and H. rubra are quite different (Shepherd 1973) so it would be surprising if different mechanisms for dispersal did not evolve for each species. The capability of abalone larvae for dispersal will not be understood until studies of larval behaviour have been undertaken. This remains a principal challenge in abalone biology.

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TABLE 1. Searching efficiency for the size range 1-10 mm of *H. laevigata* for 3 experiments at different densities of the size class. Standard errors in brackets.

DATE	**SEARCHING EFFICIENCY**	**DENSITY (Nos. per boulder)**
March 1987	0.86 (0.07)	1.29
April 1988	0.64 (0.13)	0.81
January 1990	0.78 (0.09)	1.46

TABLE 2. Abundance and recruitment of *H. laevigata* per segment at Taylor and Owen Islands, with data on the variables, mean habitat width, H, distance from southern boundary of study site, D, (in hundreds of metres), Inlet Value Index, IV, number of spawning adults, N_1, number of aggregated adults, N_2, and index of larval abundance, L.

Manipulations of abundance per segment, M, are shown as net increase (+) or a net decrease (-) in numbers or as no change (0). Recruitment data given are area searched, A, in metres, and density of recruits (in numbers, m^{-2}) with standard errors in brackets.

								RECRUITMENT		
Segment Number	H (m)	D	IV	N_1	M	N_2	L	Area (m^2)	Density	(s.e.)
1	1	0	1	23	-40	0	100	12	1.0	(0.3)
2	1	1	0	15	-20	0	143	12	0.9	(0.4)
3	3	2	2	162	+90	152	162	12	1.3	(0.5)
4	3	3	2	21	-180	3	152	12	2.2	(0.5)
5	3	5	2	78	0	9	121	7	1.3	(0.6)
6	2	6	1	34	0	2	143	13	1.0	(0.3)
7	2	7	0	78	0	76	202	12	0.4	(0.2)
8	2	8	0	94	0	90	282	16	0.4	(0.2)
9	3	9	2	57	-180	6	412	14	1.7	(0.4)
10	4	10	1	112	0	20	583	13	1.2	(0.4)
11	3	11	1	174	0	168	722	14	0.9	(0.2)
12	5	12	1	575	+450	575	741	14	1.9	(0.4)
13	5	13	1	230	0	210	636	12	1.3	(0.3)
14	5	14	1	70	-200	15	480	13	1.3	(0.3)
15	5	15	1	120	0	25	392	15	0.8	(0.3)
16	5	16	1	15	-100	0	433	14	1.1	(0.3)
17	5	17	0	55	-50	0	537	13	0.9	(0.2)
18	7	18	2	581	+420	581	581	15	1.7	(0.7)
19	7	19	2	728	+560	728	514	12	1.7	(0.4)
20	4	20	1	172	0	158	514	16	0.8	(0.2)
21	5	21	1	75	0	0	186	15	0.5	(0.3)
22	3	26	1	27	-60	0	213	16	0.3	(0.1)
23	3	27	1	36	0	0	308	15	0.07	(0.06)
24	4	28	2	348	+180	348	350	16	0.6	(0.2)

TABLE 3. Multiple regression analyses; (1), (2) and (3) include step wise the variables N_1, N_2 and L and (4) excludes these variables.

(1) $R^2 = 0.74$

Source	d.f.	SSQ	MSQ	V.R.
H	1	0.890	0.890	11.60 **
D	1	2.707	2.707	35.27 ***
IV	2	0.857	0.429	5.58 *
N_1	1	0.040	0.040	0.52 NS
Residual	18	1.381	0.077	

(2) $R^2 = 0.74$

Source	d.f.	SSQ	MSQ	V.R.
H	1	0.990	0.990	13.04 **
D	1	2.727	2.727	35.93 ***
IV	2	0.859	0.430	5.66 *
L	1	0.055	0.055	0.72 NS
Residual	18	1.366	0.076	

(3) $R^2 = 0.78$

Source	d.f.	SSQ	MSQ	V.R.
H	1	0.460	0.460	7.22 **
D	1	2.513	2.513	39.46 ***
IV	2	1.237	0.619	9.71 *
N_1	1	0.275	0.275	4.32 NS
Residual	18	1.146	0.064	

(4) $R^2 = 0.74$

Source	d.f.	SSQ	MSQ	V.R.
H	1	1.762	1.762	23.54 ***
D	1	2.747	2.747	36.71 ***
IV	2	0.994	0.497	6.64 **
Residual	18	1.422	0.075	

CAPTIONS TO FIGURES

Fig. 1 Taylor Island, showing 24 segments in which densities of *H. laevigata* were manipulated.

Fig. 2 Comparison of the mean efficiencies of the searching technique and the anaesthetic technique for four size classes. Bars represent standard errors.

Fig. 3. Length-frequency data for under- and above-boulder surveys of *H. laevigata*, with fitted modes.

Fig. 4. Eddies generated in an inlet and behind a pinnacle in the presence of coastal currents.

Fig. 1

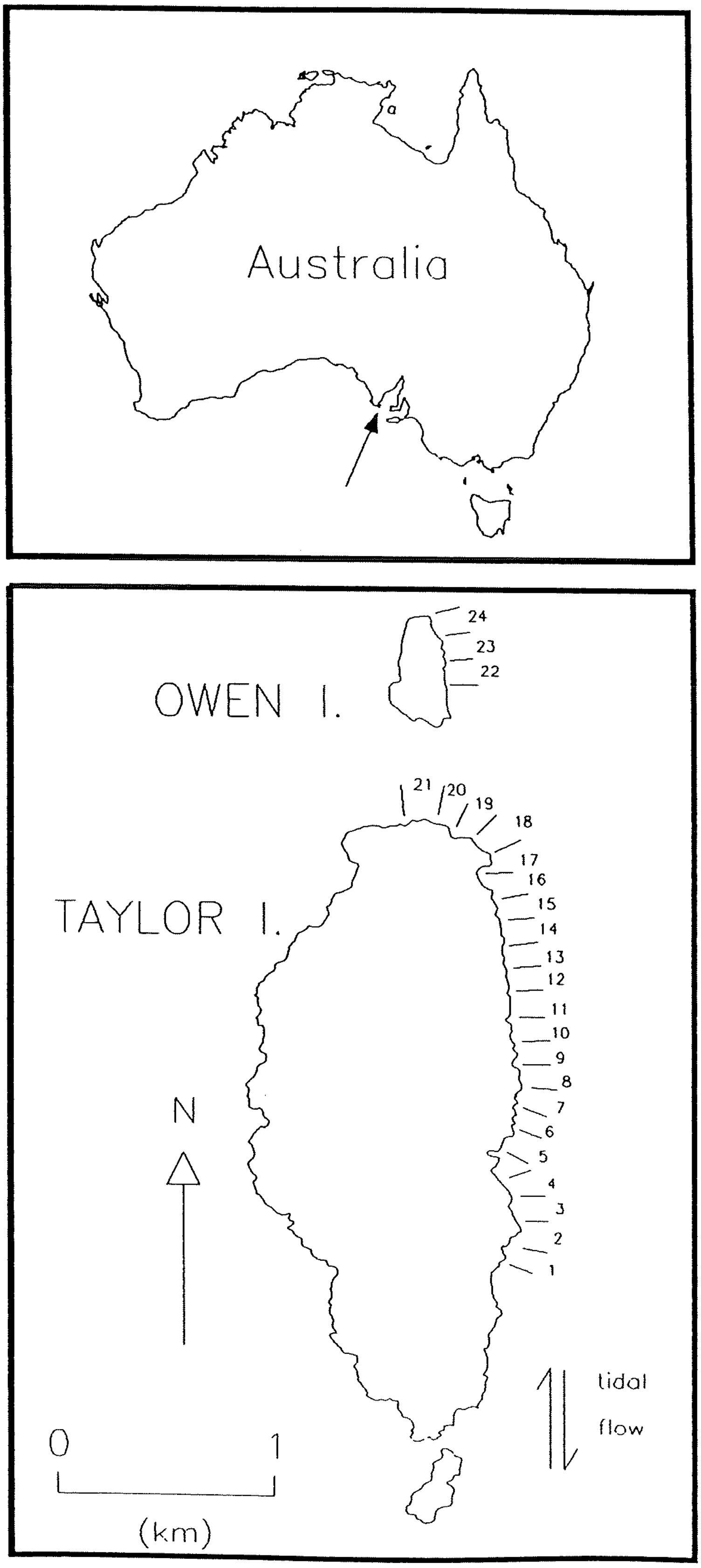

Australia
OWEN I.
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
TAYLOR I.
N
0
1
(km)
tidal
flow

Fig. 2

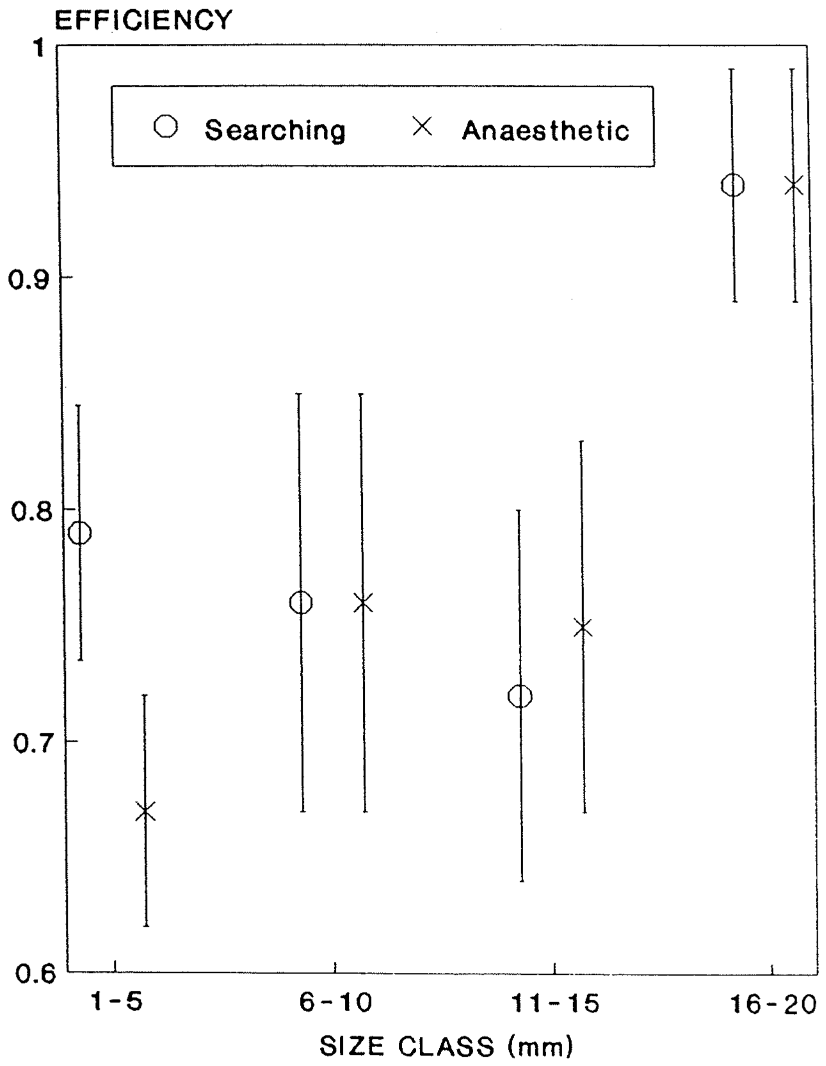

EFFICIENCY
1
0.9
0.8
0.7
0.6
○ Searching
× Anaesthetic
1-5
6-10
11-15
16-20
SIZE CLASS (mm)

Fig. 3.

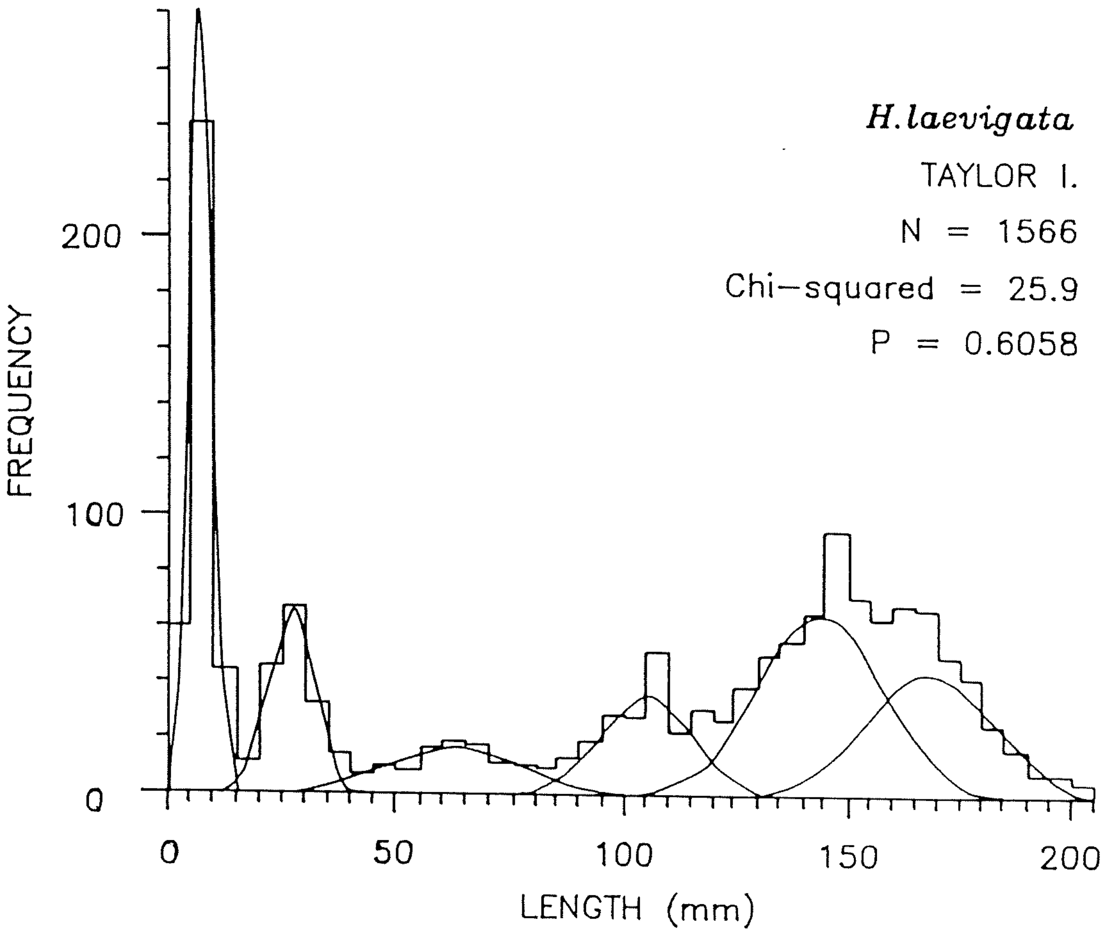
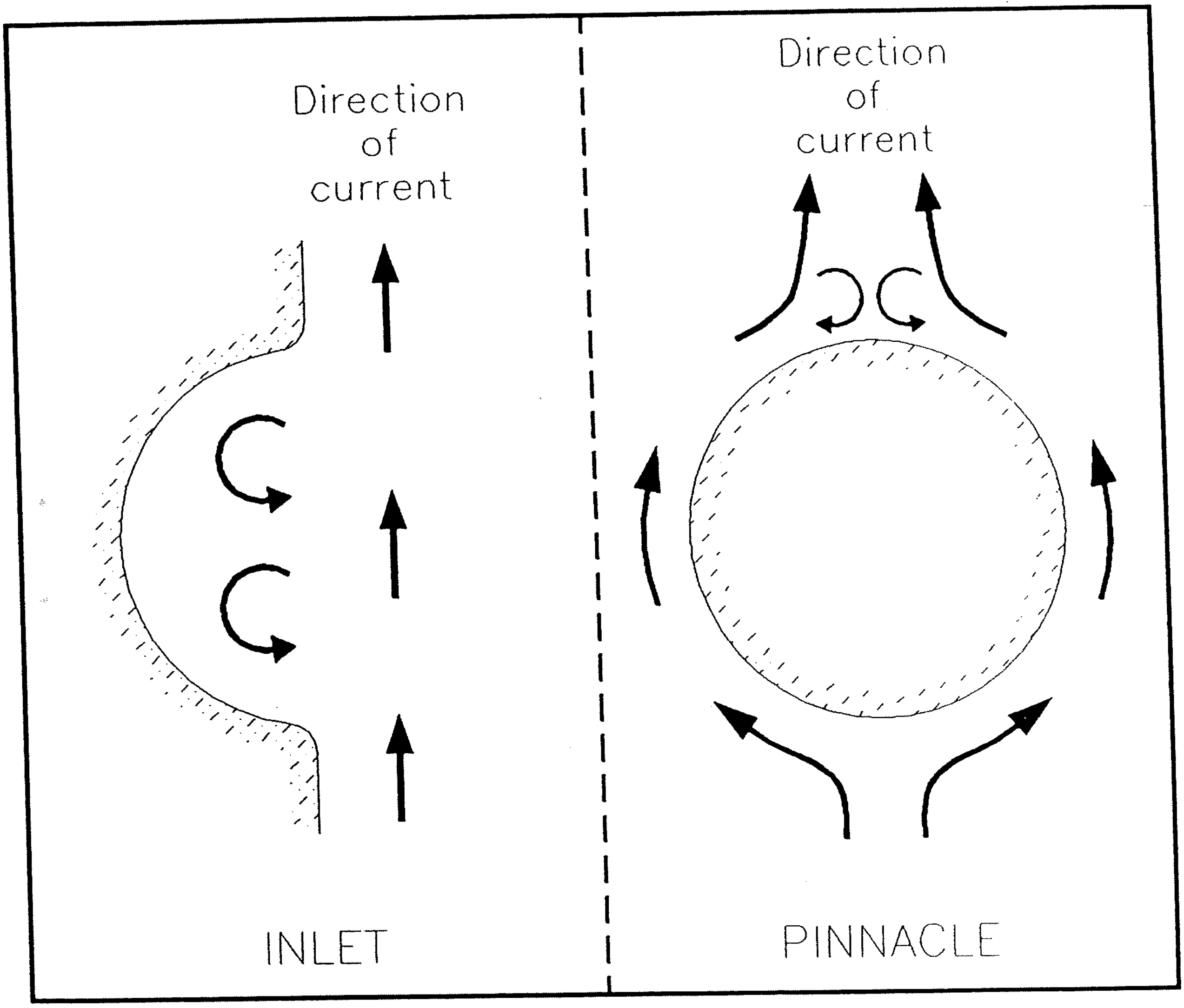

H.laevigata
TAYLOR I.
N = 1566
Chi-squared = 25.9
P = 0.6058
FREQUENCY
0
100
200
0
50
100
150
200
LENGTH (mm)

Fig. 4



APPENDIX 5

STUDIES ON SOUTHERN AUSTRALIAN ABALONE

(genus Haliotis) 14.

INTERPRETING NACRE LAYERS IN H. LAEVIGATA

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ABSTRACT

Rasping the spire of the greenlip abalone, Haliotis laevigata, discloses the presence of layers of nacre (rings) which increase in number with the size of the shell. On average 2 rings are laid down each year in the shell, but examination of shells of known age shows high individual variability in the number of rings accumulated over time due to sand abrasion, boring organisms and other causes. Although growth rates derived from length-at-age data (reading the rings) and length-increment data (from tagging experiments) show little agreement, the ageing technique may have merit where systematic biases can be overcome.

INTRODUCTION

The ability to age an exploited species provides a powerful tool for stock assessment. If, for example, annual rings are laid down in the hard parts of the animal, information on longevity, mortality, growth rate and relations with environmental and biotic factors can be assessed.

Muñoz-Lopez (1976) first suggested the use of layers of nacre to age abalone. Prince (1988) and Nash (1991) applied the method to the blacklip abalone H. rubra in Tasmania. Day and Fleming (1991) reviewed this and other methods used to age abalone and emphasised the need to verify the method used for each area studied.

In this paper the application of the Muñoz-Lopez technique to ageing the greenlip abalone Haliotis laevigata Donovan is examined in four populations in South Australia. The purpose was to discover if nacre layers provide a practical tool for ageing this abalone species. We used shells of known age to validate the technique. We then examined samples of shells from four sites where the growth rate of H laevigata was known from length-increment tagging data, and derived length-at-age data. We compared the growth rates obtained by the 2 different methods and evaluated the ageing technique in the light of the findings.

MATERIALS AND METHODS

Shell samples of H. laevigata were taken from 4 study sites where the growth rate of this abalone had been previously studied (Shepherd and Hearn 1983, Shepherd 1988, Shepherd et al. 1991). These were supplemented with marked shells of known age from earlier mark-recapture experiments and with juvenile unmarked shells, whose ages were inferred by identifying cohorts in length-frequency distributions. The spire of each shell was ground flat with emery paper until a minute hole appeared. The nacre layers so exposed were polished with fine emery paper and etched with Hcl (Prince 1988). The nacre was examined under a dissecting microscope and the number of layers counted. The layers are of conchiolin and alternate with aragonite nacre (Day and Fleming 1991), producing fine discontinuities between layers, which we call rings.

Layers were difficult to detect in small abalone (<30mm shell length (SL)) and were visible, if at all, as very fine rings. With increasing size the rings became more conspicuous, but there was no sharp transition from the fine, minor rings to the thicker, major rings produced later as found by Prince (1988). Attempts to so categorise them found no agreement between independent workers and were abandoned. Only the total number of rings was therefore recorded.

Two workers independently counted the rings and if they disagreed, re-examined the shell. Often further fine polishing and etching improved the legibility of the shells and produced agreement.

The juvenile growth rate of <u>H laevigata</u> has not been previously described for Tiparra Reef, so a length frequency distribution was decomposed into component modes by using the MIX computer package (see Shepherd 1988). Age cohorts were identified from the modes and the juvenile growth rate inferred.

RESULTS

Relation between nacre layers (rings) and age

A plot of the number of rings vs age for untagged and tagged individuals of known age is given in Fig. 1. The diagonal line represents the regression where 2 rings are laid down each year. Points lying above the line represent fewer, and points below the line more than 2 rings on average a year. The tagging history of marked individuals is summarised in Table 1.

At West I there are on average only 2 rings at age 2, with a variable number (2-6) added in the following year. Subsequently an average of 2 rings a year are accumulated. The 2 oldest marked individuals (7 and 19 years) had 2 fewer rings than expected for their age whereas the two 4 year olds had more. The data from Taylor I show that on average 2 rings a year are accumulated from birth.

The two shells aged 11 years from Waterloo Bay (Table 1) were at a site (A1) where considerable sand abrasion occurs (Shepherd 1986). One of the shells (No. 92) was overgrown dorsally with brown algal crusts of *Archaeolithoderma* sp which appeared to protect the shell from sand abrasion, whereas the other (No. 80) was unprotected in this way and was obviously worn. The latter had 6 fewer rings than expected for its age, assuming 2 rings a year are laid down. Presumably outer rings were lost through sand abrasion.

Of interest is the tagged individual No. 3026 (Fig 1. Table 1) which had 5-7 fewer rings than expected. Marked at 2 years of age this abalone grew only 2mm in 2 years, probably because the nylon rivet protruded into the shell and interrupted growth. Apparently no rings were laid down after marking during the 2 years at liberty.

Juvenile growth is less well known at Anxious Bay and Tiparra Reef so we have less confidence in predicting age of juveniles from length. Nevertheless the data (see below) suggest that at Tiparra Reef juveniles have only 3 rings at 3 years of age and, thereafter, accumulate 2 rings a year, whereas at Anxious Bay they have 6 rings on average at 3 years of age and accumulate 2 rings a year.

Relation between nacre layers and length

Plots of mean length, with standard errors, vs number of nacre layers are shown for each site and are superimposed on the growth curve for the respective site (Figs 2-5). Parameters of the von Bertalanffy growth curve calculated from the length-at-age data are given in Table 2.

Within site comparisons show little concordance between K and L_∞ values derived by the two methods. However, in most cases the respective standard errors overlap indicating that differences between values are not significant.

The standard errors of K and L_∞ from length-at-age data are wide and reflect the relatively small sample sizes from which they were derived.

At Anxious Bay most length-at-age data points lie above the growth curve derived from tagging data, suggesting that the extant number of rings are fewer than predicted under the hypothesis of two rings being produced a year. As the site is subject to severe sand abrasion, rings are likely to be lost as the surface of the shell is eroded away.

Analysis of the length-frequency distribution for Tiparra Reef showed distinct modes which were inferred to be age cohorts (Fig. 5). From these data, and the known growth rate of larger individuals (Shepherd and Hearn 1983) a composite growth curve was constructed, consisting of a linear phase (to age 4) and a declining exponential phase for older age classes. Best agreement between this composite growth curve and the ring data occurs under the assumption that 3 rings are extant at age 3 and thereafter 2 rings a year are added.

DISCUSSION

Although studies of molluscan growth patterns have a long history (reviewed by Lutz and Rhoads 1980) little attention has been given to haliotids. Growth checks have been found in a few species of abalone (reviewed by Day and Fleming 1991), and Hayashi (1955) and Muñoz-López 1976) described the presence of nacre layers in the region of the spire which were later used to age abalone (Prince 1988, Nash 1991, Turrubiates and Castro 1991). These authors assumed or concluded from available evidence that one ring was laid down each year.

This study at 4 sites shows that, on average, 2 rings are laid down each year, but there is wide individual variation in the number of rings for a given age (Fig 1). The number of rings in a 4 or 5 year old abalone, for example, can vary between 3 and 11. It appears that the number of extant rings in the shell depends on (a) the number of rings produced as a juvenile, (b) the occurrence of interruptions to growth and (c) the loss of the oldest rings through sand abrasion. In addition, the presence of boring organisms can further confound the results, by making the shell unreadable, or possibly causing more rings to be laid down (Prince 1988, unpublished data).

The deposition of 2 rings a year in the shell is not new among gastropods (reviewed by Bretos 1980, and see Bretos 1982, Harrington 1989). They are believed to coincide in some cases with summer maximum and winter minimum sea temperatures which interrupt the seasonal growth pattern.

The diffuse relation between the number of rings and age as demonstrated in this study emphasises the need for rigorous validation of the ageing technique for all age classes at every site (see Day and Fleming 1991). Validation can be achieved by the use of vital markers (eg Sire 1984, Kobayashi and Taki 1969) to determine the number of layers deposited in a known time interval, or by mark-recapture experiments. The latter will take many years if validation for older age classes is to be achieved.

The failure of the two methods of estimating the von Bertalanffy growth parameters to produce agreement does not per se invalidate the ageing technique. Day and Fleming (1991) reviewed the estimation of growth parameters in abalone and showed that biases in estimating K and L_∞ occur both with length-at-age data and length-increment data, but that the bias is greater with the latter kind of data. Hearn (1986) showed that where length-increment data are for 1-2 year periods only, K is always under-estimated and L_∞ over-estimated. The growth parameters for Taylor I. and Anxious Bay were derived from limited tagging data for 1-2 year periods (Shepherd et al 1991) so are unlikely to be accurate. The length-at-age data for all sites suffered from limitations in sample sizes and numbers of shells over a wide range of ages. Larger sample sizes may produce more precise estimates of growth parameters, but will not reduce biases produced, for example, by boring organisms or sand abrasion.

But there is one more serious problem with the aging technique. Since the whole purpose of ageing is to obtain population parameters for management purposes without long and costly field experiments, the requirement for validation at every site raises doubts about the wide usefulness of the technique, except in a limited number of situations such as those described by Prince (1988) and Nash (1991) where biases can be confidently excluded. Even in these situations, however, we need better understanding of the nature of shell deposition in the abalone, of the processes that cause rings to appear, of the variability that exists, and of the environmental correlates of such variability. Only then will it be possible to confidently translate the cryptic record written in the shell.

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TABLE 1. Mark-recapture data, age and number of rings of tagged H. laevigata at various sites. Birthdate (1 JAN of year given) is inferred from length at tagging date. WI = West I.; T.I. = Taylor I.; Anx. = Anxious Bay.; W.B. = Waterloo Bay; L_1 = Length at tagging; L_2 = length at recapture.

No.	Place	Birthdate	Tagging Date	L_1 (mm)	L_2 (mm)	Age (yrs)	No. of rings
113	W.I.	1965	23.3.69	87	122	19.5	36
990	W.I.	1966	10.12.69	75	132	7.3	13
B66	W.I.	1973	3.11.70	73	110	4.2	9
A74	W.I.	1968	12.6.70	48	117	5.0	6
3517	W.I.	1983	13.6.86	65	78	4.3	11
3026	W.I.	1985	5.3.87	50	52	5.1	3
4727	W.I.	1986	1.10.87	36	56	3.8	3
3514	T.I.	1985	11.6.87	55	159	5.9	
3762	T.I.	1985	11.6.87	80	158	5.4	9
4117	T.I.	1986	16.9.87	31	97	3.2	8
2691	Anx	1985	29.1.87	45	85	4.5	8
92	W.B.	1980	30.9.82	81	124	11.0	20
80	W.B.	1980	30.9.82	86	131	11.0	16

TABLE 2. Parameters of von Bertalanffy growth curves derived from length-at-age data and length-increment data for H laevigata at 4 sites. Standard errors are in brackets. K and L_∞ values from tagging data are derived from Shepherd and Hearn (1983) for West I., and Tiparra Reef, and from Shepherd et al (1991) for Taylor I. and Anxious Bay.

	Length-at-age			Length-increment	
	to(y)	Ky^{-1}	L_∞(mm)	Ky^{-1}	L_∞(mm)
West I	1.18 (0.48)	0.364 (0.11)	133.2 (10.2)	0.479 (0.029)	137.9 (1.9)
Taylor I	1.30 (0.11)	0.877 (0.207)	149.3 (8.5)	0.552 (0.087)	180.4 (10.3)
Anxious Bay	0.14 (0.56)	0.214 (0.084)	146.1 (11.5)	0.385 (0.069)	119.5 (5.3)
Tiparra Reef	2.10 (0.37)	0.403 (0.078)	145.7 (6.4)	0.406 (0.047)	130.8 (2.5)

CAPTIONS TO FIGURES

Fig. 1 Plot of age vs number of rings for tagged individuals of known age and untagged individuals whose age was estimated by cohort analysis.

Fig. 2 Plots of (1) mean length vs number of rings (standard errors in brackets) and (2) von Bertalanffy growth curve derived from tagging data for H laevigata at West Island.

Fig. 3 Plots of (1) mean length vs number of rings (standard errors in brackets), and (2) modal means of length frequency distribution, and (3) von Bertalanffy growth curve from tagging data for H laevigata at Taylor Island.

Fig. 4 Plots of (1) mean length vs number of rings (standard errors in brackets) and (2) von Bertalanffy growth curve from tagging data for H. laevigata in Anxious Bay.

Fig. 5 Length-frequency distribution for H laevigata at Tiparra Reef decomposed into component normal distributions.

Fig. 6 Plots of (1) mean length vs number of rings (standard errors in brackets), (2) modal means of length frequency distribution and (3) von Bertalanffy growth curve from tagging data for H laevigata at Tiparra Reef.

Fig. 1

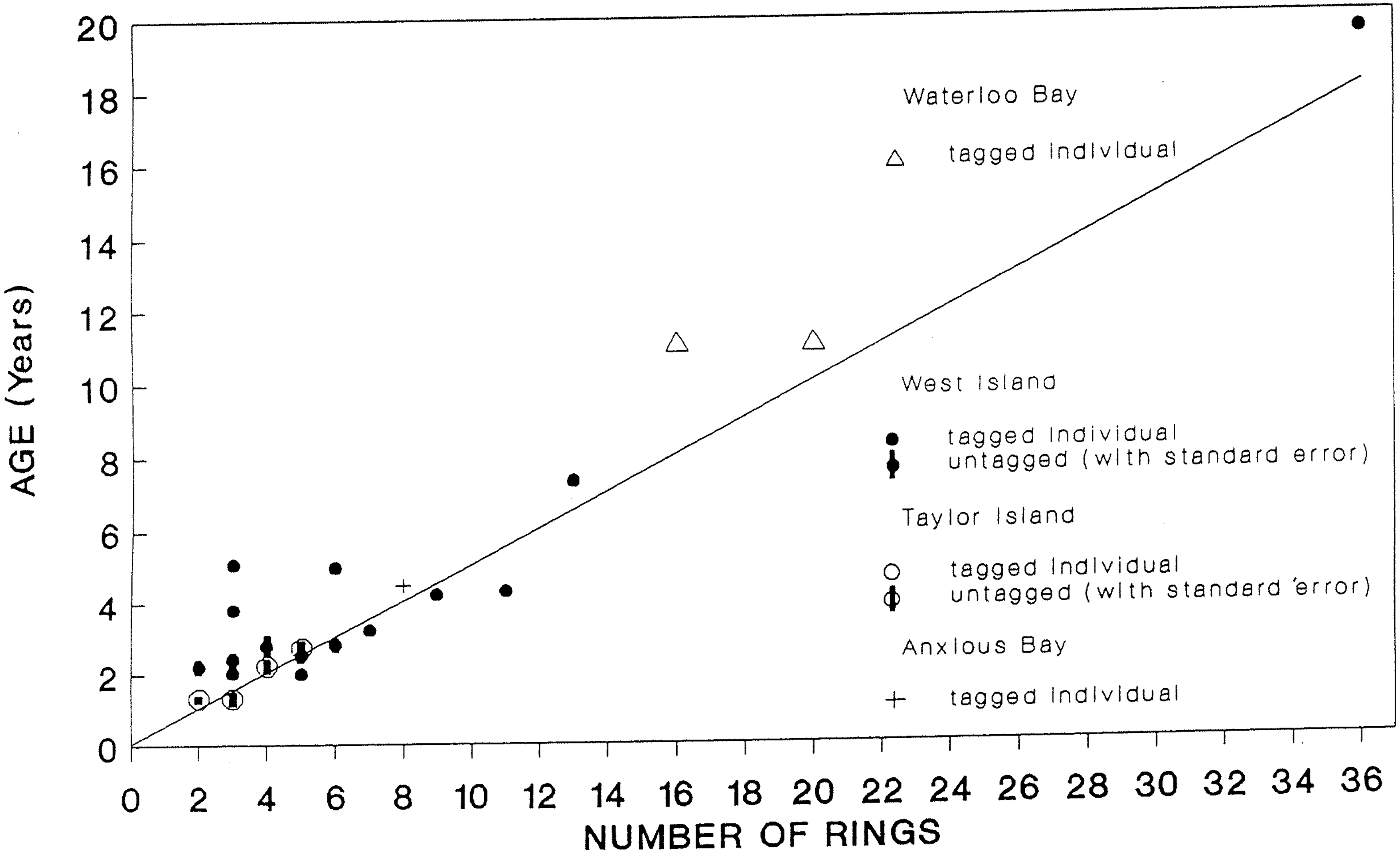
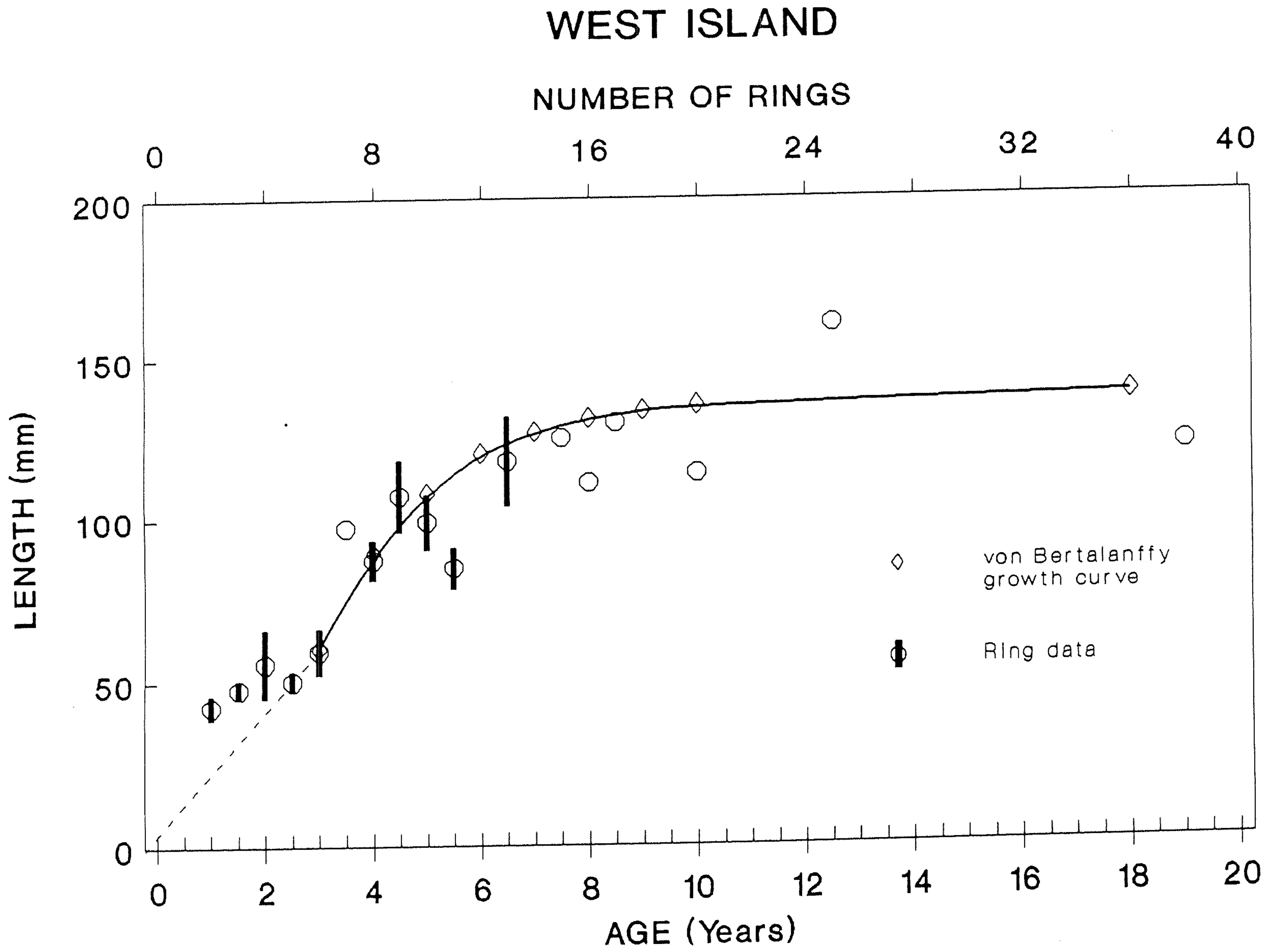

AGE (Years)
0
2
4
6
8
10
12
14
16
18
20
NUMBER OF RINGS
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
32
34
36
Waterloo Bay
△ tagged individual
West Island
● tagged individual
untagged (with standard error)
Taylor Island
○ tagged individual
untagged (with standard error)
Anxious Bay
+ tagged individual

Fig. 2


WEST ISLAND
NUMBER OF RINGS
0
8
16
24
32
40
200
150
100
50
0
LENGTH (mm)
0
2
4
6
8
10
12
14
16
18
20
AGE (Years)
von Bertalanffy growth curve
Ring data

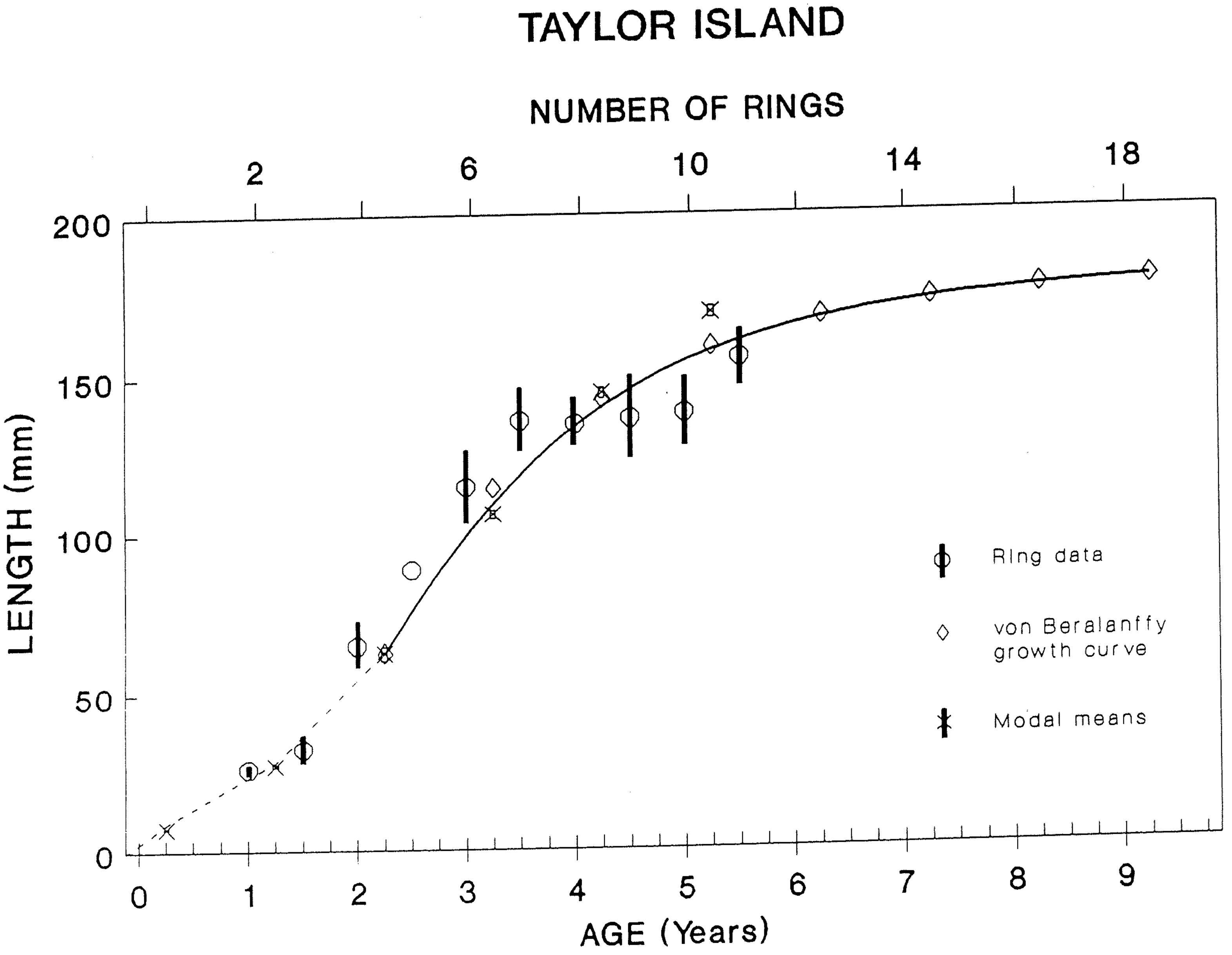

TAYLOR ISLAND
NUMBER OF RINGS
2
6
10
14
18
LENGTH (mm)
200
150
100
50
0
0
1
2
3
4
5
6
7
8
9
AGE (Years)
Ring data
von Beralanffy growth curve
Modal means

Fig. 3

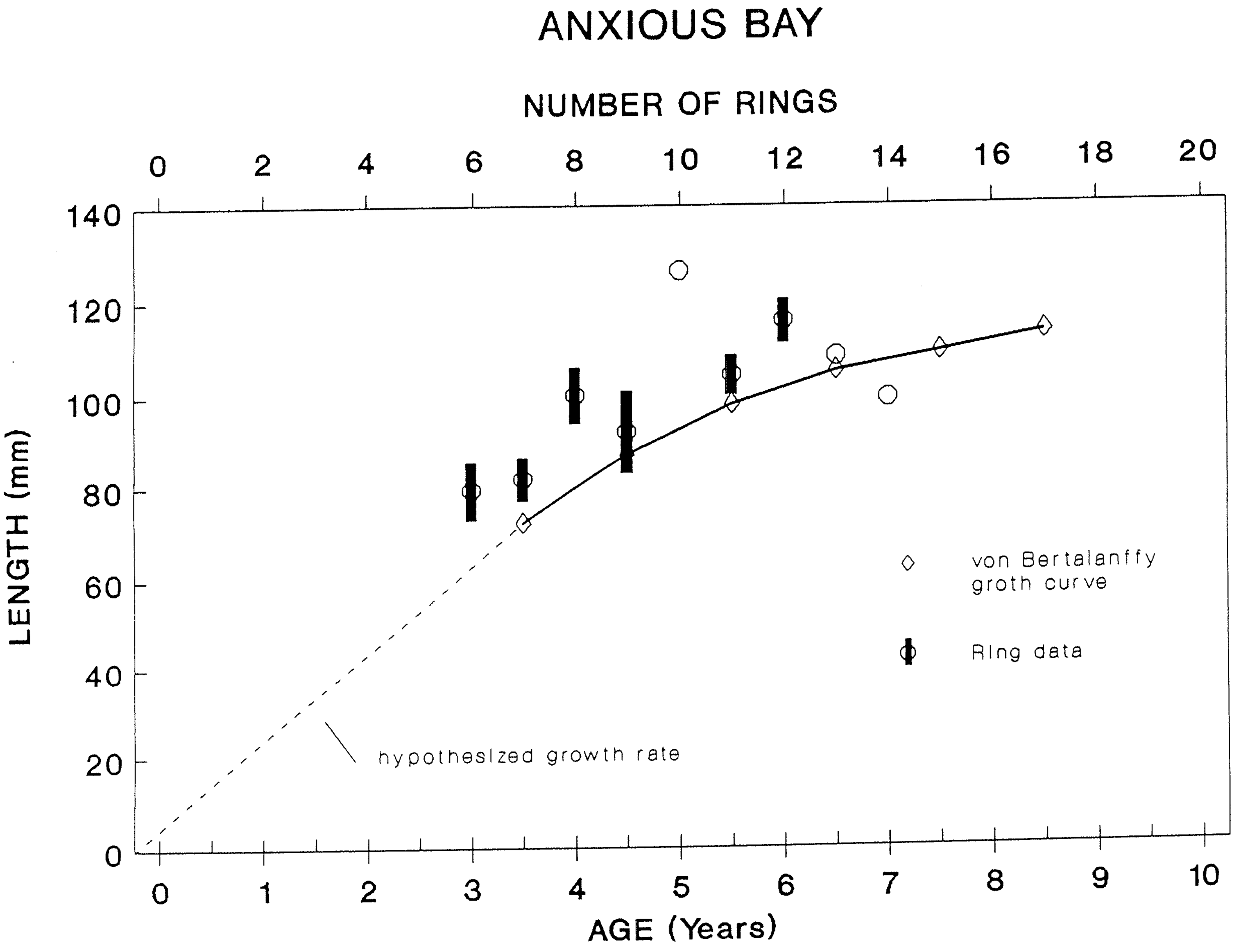

ANXIOUS BAY
NUMBER OF RINGS
0
2
4
6
8
10
12
14
16
18
20
LENGTH (mm)
140
120
100
80
60
40
20
0
AGE (Years)
0
1
2
3
4
5
6
7
8
9
10
von Bertalanffy groth curve
Ring data
hypothesized growth rate

Fig. 4

FIG. 5

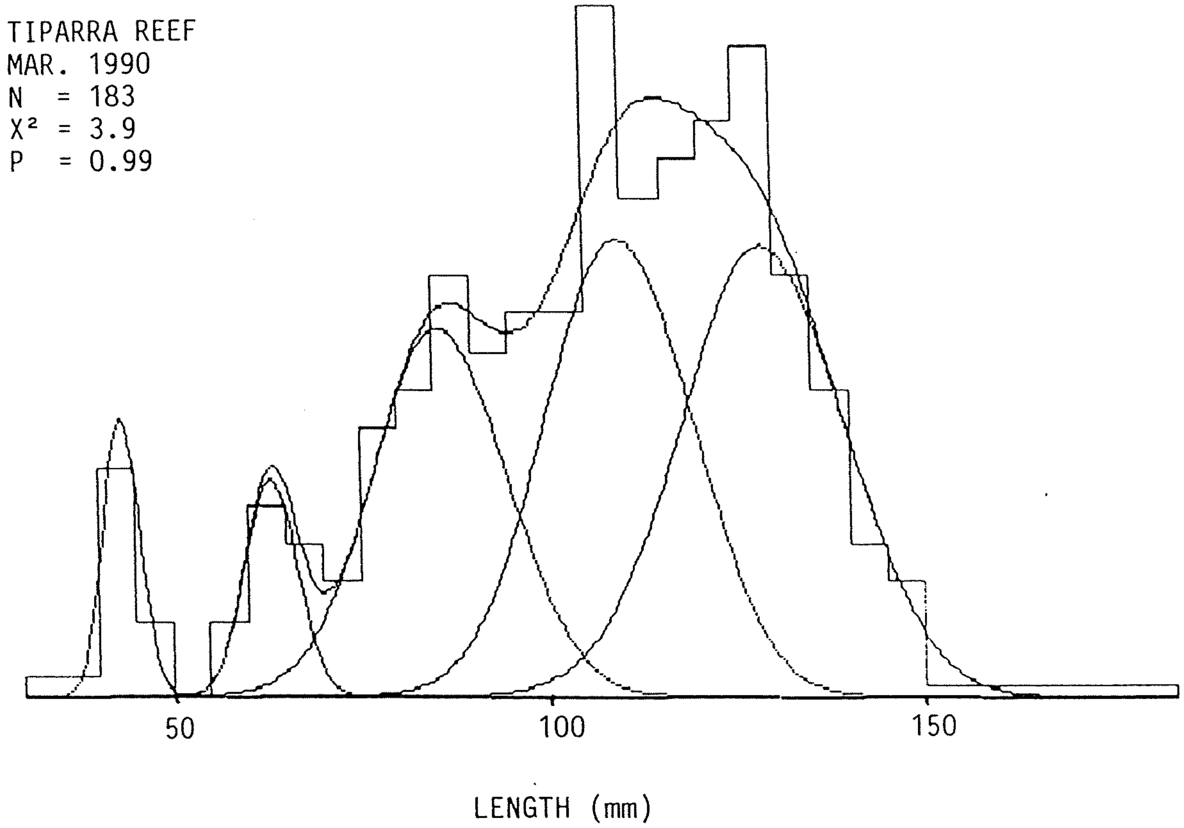
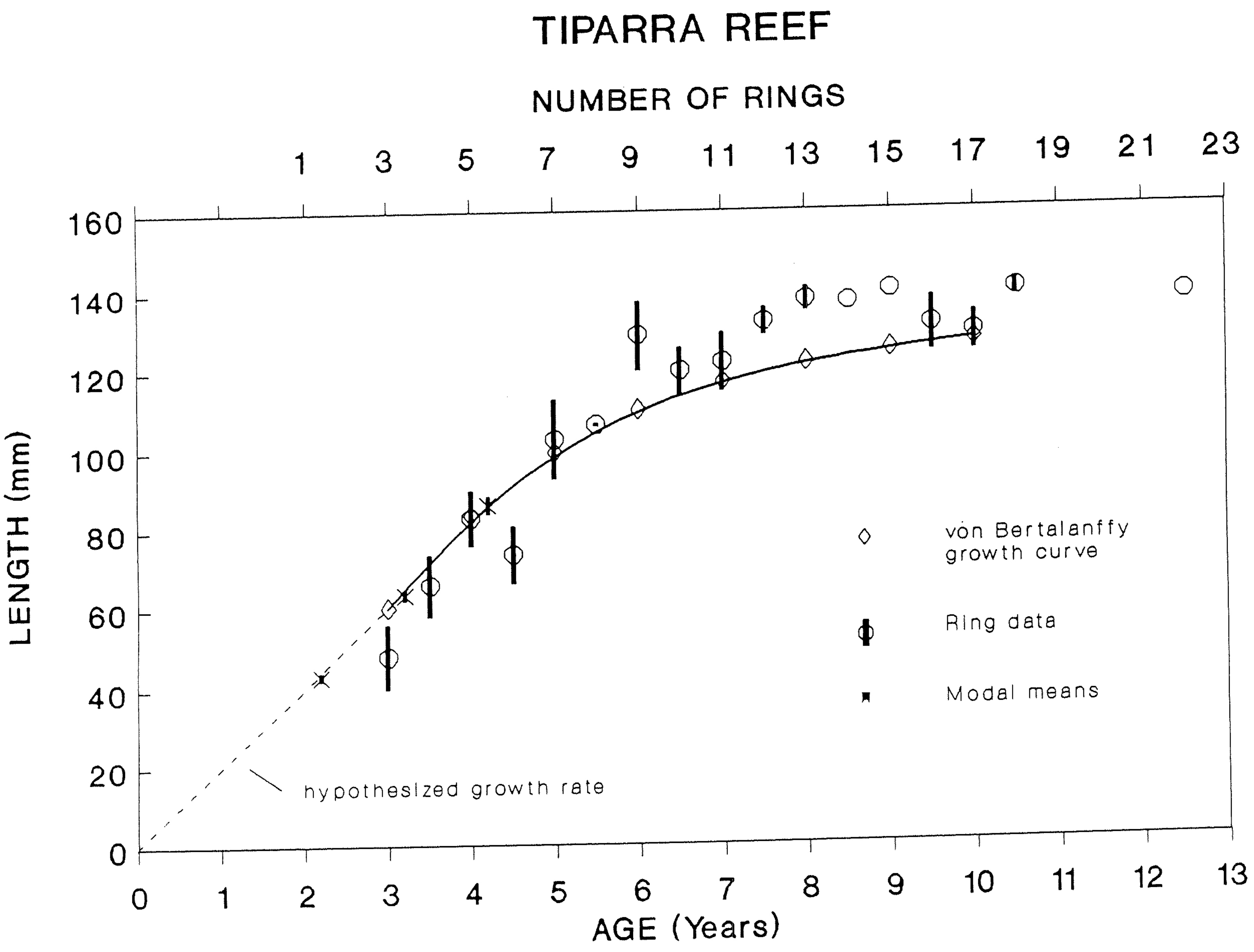


Fig. 6


TIPARRA REEF
NUMBER OF RINGS
1
3
5
7
9
11
13
15
17
19
21
23
160
140
120
100
80
60
40
20
0
LENGTH (mm)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
AGE (Years)
von Bertalanffy growth curve
Ring data
Modal means
hypothesized growth rate