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SIZE LIMITS FOR GREENLIP ABALONE IN TASMANIA

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Tasmanian Aquaculture
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Summary

This study aimed to minimise the possibility of recruitment overfishing of Tasmanian greenlip abalone by suggesting minimum size limits that would maintain sufficient egg production. The data for the analyses required was collected in late 1998 from abalone sampled at thirty-eight sites in the Furneaux Group, at King Island, the North west, North east and at the mouth of the Tamar River.

Analysis of growth ring deposition in abalone of known age allowed estimates of age to be verified. Sexual maturation was first found in abalone of about three years of age, and 100% maturity was achieved by about five years of age. The size at which abalone would have two years to reproduce was estimated to be 130 mm in the Furneaux Group and at the Tamar mouth, 145 mm at King Island, 132 mm in the North east and 131 mm in the North west. These size limits are likely to be insufficient for the maintenance of egg production because of the probability that recruitment is sporadic. Additional breeding seasons should be allowed if applying this method of establishing size limits for greenlip abalone.

Information on the morphology, age, growth, mortality, sexual maturation, fecundity and sex ratios of these greenlip populations was used in per-recruit analyses which suggest the sizes at which yield may be optimised whilst ensuring conservation of sufficient egg production. The egg-per-recruit analyses were found to be particularly sensitive to changes in natural mortality and maximum age. Unfortunately these two parameters are poorly defined. Therefore, the analyses were constructed conservatively and their results should be interpreted cautiously. Egg conservation estimates at various size limits were compared against thresholds established in other greenlip abalone fisheries, that is 40 to 50 % of virgin levels. Interim size limits were found to be within an appropriate range in the North east and North west. Even at high levels of fishing mortality the 50 % threshold was exceeded in the Furneaux Group and at the Tamar mouth at the current interim size limit of 150 mm. This suggests that the size limits could be lowered in these areas. The interim size limit of 150 mm at King Island was found to be insufficient to maintain more than 40 % of virgin egg production at moderate levels of fishing mortality. An increase in the minimum size limit in this region is therefore recommended.

Despite the conservative approach taken in these analyses, it is suggested that establishing size limits entirely on this basis may not be sensible. This is because of the incapacity of egg-per-recruit analyses to accommodate the probability of variable recruitment success. Gamete production may be very low if adult densities have been so reduced by fishing that physical separation of adults denies successful fertilisation. Inability to find a mate of the opposite sex may also be exacerbated by the uneven sex ratios found in this study.

The size limits suggested will provide differing levels of protection to abalone populations at different localities but will not overcome the uneven distribution of diver effort which may be occurring in the greenlip fishery. Another mechanism proposed to enhance local egg production and recruitment is the establishment of closed areas. Abalone within a closed area may grow to a larger size where fecundity is maximal and they can aggregate into very large clusters where fertilisation success is high. Larvae could be transported to downstream populations where they may enhance recruitment. Industry perceptions of the status of populations are also ignored by per-recruit analyses. It is suggested that interim size limits be set at conservative levels that allow extra capacity for the rebuilding of populations where concern over serious depletion exists.

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1. Introduction

Two methods are used in the Tasmanian abalone fishery to protect stocks from overfishing: a legal minimum size limit and a total allowable catch (TAC). The rationale behind the minimum size limit is that it ensures sufficient egg production occurs in the fraction of the population smaller than the size limit to maintain the population at a relatively high level, even when fishing is reasonably intense. Fishing intensity, in turn, is controlled by the size of the TAC. Whilst size limits are set separately for blacklip abalone, *Haliotis rubra*, and greenlip abalone, *H. laevigata*, the TAC is set for both species combined. Therefore, whilst the greenlip catch may be relatively small in comparison to the blacklip catch, a transfer of even a small amount of effort from blacklip to greenlip abalone stocks can substantially increase the fishing pressure on greenlip abalone.

The status of stocks of the greenlip abalone in the north of Tasmania has become a matter of increasing concern. This concern has arisen from a preliminary analysis of catch-effort data (Officer, 1997; Officer, 1999) and from anecdotal information provided by abalone divers. The catch-effort data for the Furneaux Group show that, despite a substantial reduction in the total catch of greenlip abalone from this region since 1984, there has been little change in catch rates (Officer, 1999). If stocks were healthy, and if catch rates were a useful index of abundance, then the decline in catches should have been accompanied by an increase in catch rates. The observed stability in catch rates suggests that the abundance of legal-size greenlip abalone has not increased over this period or that catch rate information is not a useful indicator of abalone abundance.

This stability in catch rates may be partly explained by divers increasingly targeting larger greenlip abalone for the live greenlip abalone market and thus reducing the proportion of the population that is being targeted. However, this is unlikely to have significantly affected the early catch rates because selective targeting did not commence until about 1992; and between 1984 and 1992 the large reduction in catch was not associated with a noticeable increase in catch rate. Therefore, it seems likely that the abundance of legal-size greenlip abalone in the Furneaux Group has remained static or possibly declined since the mid-1980s. In light of these concerns, the Fisheries Department, the Tasmanian Abalone Council and the Abalone Fishery Advisory Committee held discussions about possible management options and the Fisheries Department implemented several management strategies to control the greenlip catch.

The management plan for the abalone fishery (Anonymous, 1997) established strategies to:

- sub-divide the state-wide greenlip abalone fishery into two regions (the Furneaux Group and all the other greenlip-producing areas),
- set a monthly catch limit for the Furneaux Group
- close the fishery for greenlip abalone in the Furneaux Group for the remainder of the month when the limit was reached or exceeded,
- set daily catch limits for abalone divers operating in the Furneaux Group,

- set possession limits for abalone divers operating in the Furneaux Group,
- set a trigger point for the annual greenlip catch for the rest of Tasmania
- consider closing the entire fishery if the trigger point were reached or appeared likely to be reached.

More recently, a review of the management arrangements for the greenlip abalone fishery (Anonymous, 1998) established increased interim size limits for greenlip abalone. This was done to minimise the chances of recruitment overfishing occurring whilst the size limits for greenlip abalone were re-evaluated. The research described in this study was undertaken to provide this evaluation.

The study was conducted for the entire Tasmanian greenlip abalone fishery and therefore included sites in the main greenlip abalone-producing regions. The study did not set out to establish an appropriate total allowable catch (TAC) for greenlip abalone stocks. Such an assessment would require information on the abundance of abalone, reliable estimates of which are extremely difficult to obtain. The objectives of the study were to:

- Measure the size composition of greenlip populations in several regions,
- Determine the size and age at which onset of sexual maturity occurs,
- Measure rates of growth and mortality,
- Determine the relationship between fecundity and size.

The ultimate aim of these analyses was to suggest appropriate legal minimum size limits for greenlip abalone that would ensure the maintenance of sufficient egg production to minimise the possibility of recruitment overfishing occurring. Where evidence already exists for recruitment overfishing additional means of rebuilding the stock are discussed.

2. Methods

2.1 Field Procedures

Surveys of greenlip abalone producing areas were undertaken over two months, from September 22nd, to November 19th, 1998. Sampling was scheduled in this period as it precedes the main spawning period of late spring/early summer. The gonads of abalone sampled at this time would therefore be most likely to be ripening. This was most important as an estimation of fecundity was a major aim of the study.

Abalone populations were surveyed in five regions: the Furneaux Group, King Island, North East, North West and Tamar River mouth (Fig. 1).

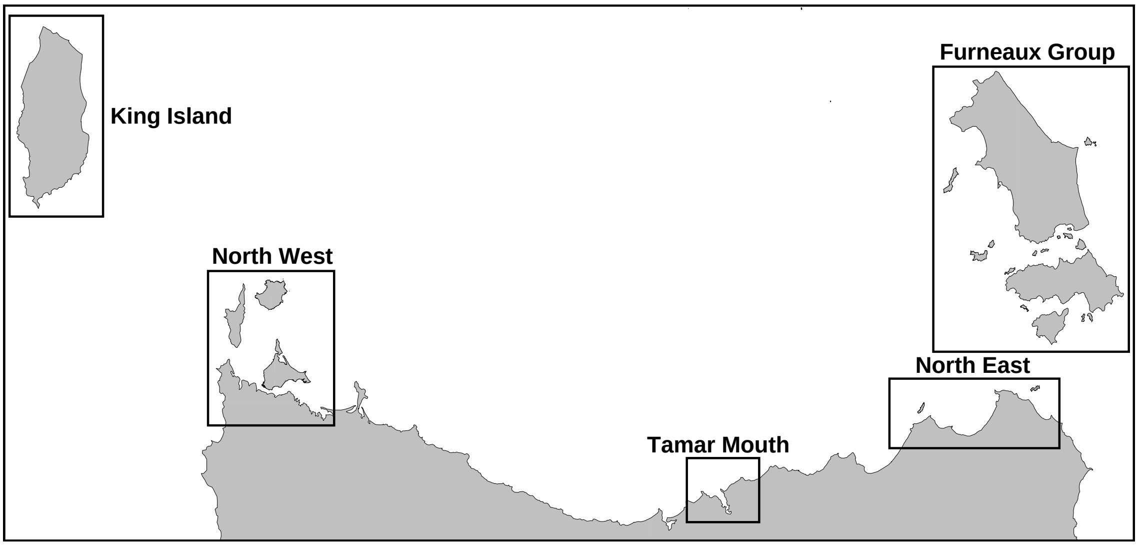

Fig. 1. Map of Northern Tasmania showing the five regions where sampling was undertaken in 1998.

Thirty-eight sites were surveyed (Fig. 2). Because the survey was of greenlip abalone, only greenlip habitat was visited. Surveys in the Furneaux Group and at King Island were conducted from the dinghy *Allopidae*, launched from the 20 m vessel *Challenger* (which was used as a mother-ship). In the North west and North east the surveys were conducted from the dinghies *Lowinna* and *Poolta*. Surveys at the Tamar mouth sites were conducted under permit by Mr Warwick Nash of the Australian Maritime College, Beauty Point.

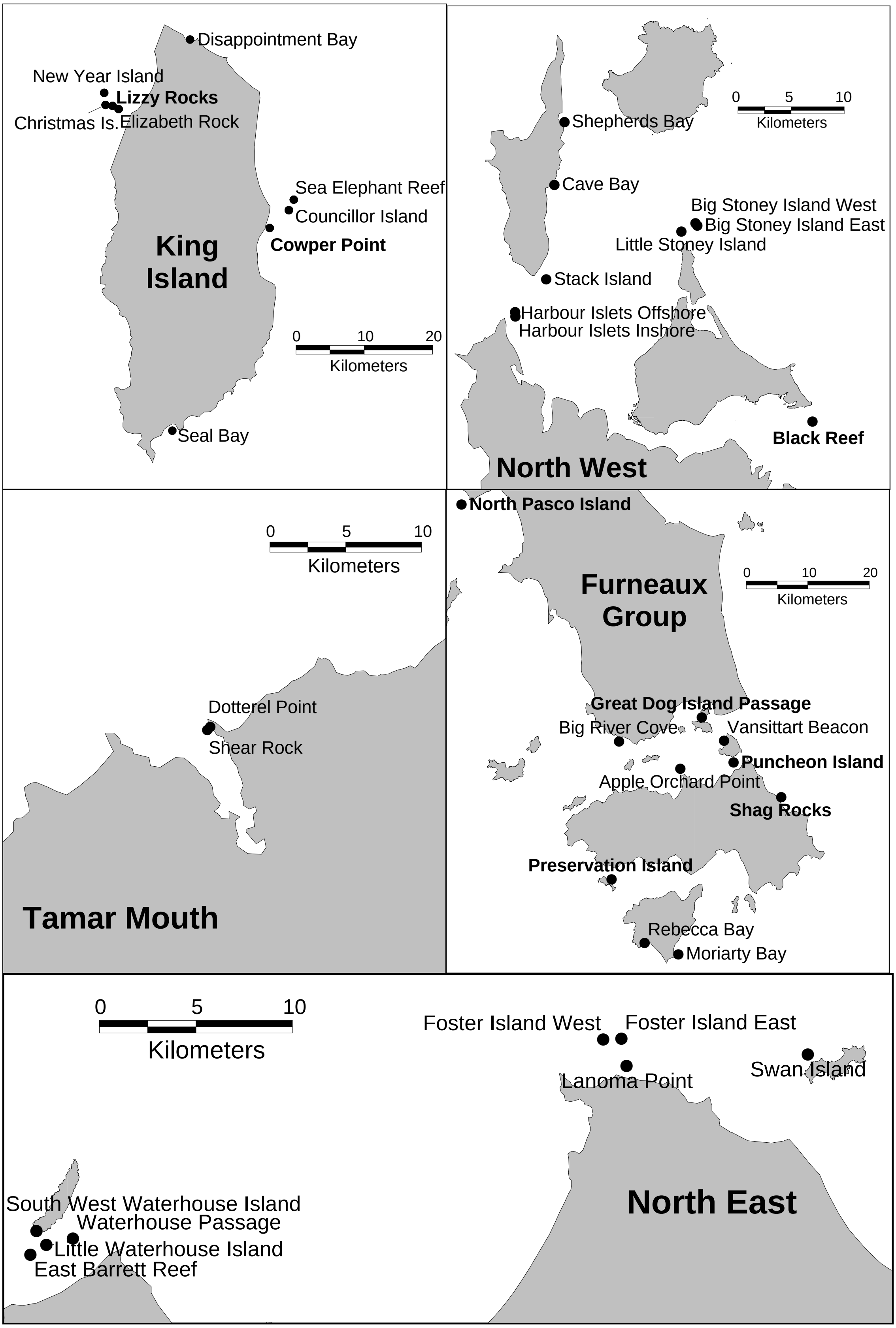

Fig. 2. Survey sites sampled in each region. Abalone were tagged at sites shown in bold type. At Lizzy Rocks off King Island a sample was only taken for tagging.

Both fished and unfished populations of greenlip abalone were sampled. At each site the sampling procedure involved divers collecting all greenlip abalone, regardless of size, that could be found in exposed positions. A sample of at least 200 animals, encompassing the entire size range, was taken to establish the age-length relationship. Samples of this size were required because of the large variation in growth rates between individual abalone, and also because it was expected that a proportion of the abalone would be impossible to age because of damage to the shell by boring sponges.

All abalone collected were either taken to the mother-ship or the nearest abalone processing facility, where they were kept frozen until their return to Hobart. At the Taroona laboratories the abalone were stored at -30 °C until they were processed.

2.2 Laboratory and Analytical Procedures

2.2.1 Morphometry

The following morphological data were recorded for each abalone:

- whole weight
- shucked meat weight
- dry shell weight
- shell length
- shell width, and,
- vertical shell height.

Weight and length data were fitted to the power equation:

$$\text{whole weight} = a.\text{length}^{b}$$

Equation 1

where a and b are parameters of the power relationship.

2.2.2 Age and Growth Estimation

Age estimation

With the exception of samples from the Tamar mouth, shells from abalone sampled in this study were transferred to the South Australian Research and Development Institute (SARDI) Aquatic Sciences Centre for age estimation. Age estimates from shells from the Tamar mouth were determined by students of the Australian Maritime College, Beauty Point. Shells from the Tamar mouth were sectioned through the spire of the shell and stained to reveal growth rings. For all other regions the spire of the shells was ground down and polished to reveal growth rings. The count of the rings was used to estimate age.

The relationship between age and number of growth rings in the spire of the shell determines the value of growth parameters and total mortality (when derived by catch curve analysis), which in turn affects the results of other analyses, including yield- and egg-per-recruit. Age (in years) has been calculated as the number of major growth rings divided by two (i.e. two growth rings per year). The deposition of two growth rings per year has been verified from a sample of greenlip abalone from Flinders Island. In late 1988 / early 1989 abalone born in December 1988 at the Tasmanian Univalve hatchery from Flinders Island brood-stock were tagged and placed out in the lease area of Furneaux Aquaculture Pty Ltd on concrete blocks at a depth of about 5 m in a tide race. The abalone were left to grow under wild conditions and then recaptured in February 1998 at an age of about 9.2 years. Their shells were retained for age estimation. The results from this study are presented below in Section 3.2.

The age-length data couplets were fitted by non-linear least squares estimation to the von Bertalanffy growth function:

$$L_t = L_\infty . \left[1 - e^{-K(t-t_0)}\right]$$

Equation 2

where L_t is the length at time t, L_∞ is the theoretical maximum (asymptotic) length that the species would reach if it lived indefinitely, K is a growth coefficient measuring the rate at which maximum size is reached, and t_0 is the theoretical age at zero length.

These estimations yield positive values of t_0, the theoretical age at which length equals zero if the animals had grown according to the von Bertalanffy growth function since birth. This is because the growth of abalone is sigmoidal: the rate of growth of abalone increases from birth to a maximum at the age corresponding to an inflection point on the growth curve. The rate of growth then declines asymptotically to zero at L_∞. The von Bertalanffy growth function describes growth which declines monotonically from birth and therefore can only properly describe the part of a sigmoid growth curve to the right of the inflection point.

Growth estimation from tagged abalone

To determine rates of growth by mark-recapture methods abalone were tagged at 8 selected sites (shown in bold type in Fig. 2). The abalone collected for tagging off Cowper Point, King Island were returned to the seabed at Councillor Island. These abalone were relocated to a well defined site off Councillor Island to improve the chances of their recapture. At each tagging site at least 200 abalone were collected in the same fashion as those retained for biological analysis. The tags used were perforated discs made by Floy Tag, Seattle, USA. Each disc was uniquely marked and fastened to the abalone using plastic rivets attached through open respiratory pores. The abalone were brought to the surface for measurement and tagging. Each was marked with two tags prior to being returned to the bottom. The first and third pores were the preferred sites for tag attachment. This tagging procedure generally follows that described by Prince (1991).

The lengths of these abalone were included in analyses of length frequency distributions in each of the regions. Surveys were conducted approximately one year after tagging with the aim of recovering tagged abalone. Abalone divers and processors have also been notified that greenlip abalone have been tagged and returned to the sea. Divers were requested not to disturb the tagged abalone until a year had passed since the abalone were released. Efforts could then be made to recover the tagged abalone.

Tagging sites were revisited as close as possible to one year after the date of tagging to simplify the analysis and interpretation of growth increments. Recaptured tagged abalone were measured and removed from the site. Growth increments were analysed using a non-linear regression of the Fabens (1965) re-parameterisation of the von Bertalanffy growth function:

$$\Delta L_i = (L_\infty - L_i)(1 - e^{-Kt_i})$$

Equation 3

where ΔL_i is the growth increment, L_∞ is asymptotic or average maximum length, L_i the release length, K the coefficient of growth and t_i the time at liberty of individual abalone.

In February 1998 Dr Scoresby Shepherd (SARDI) marked 40 greenlip abalone and placed these on a natural reef close to the lease area of Furneaux Aquaculture Pty Ltd, Flinders Island. These abalone will be also examined in the future for further validation of the rate of ring deposition.

2.2.3 Sexual Maturation, Fecundity and Sex ratio

Sexual maturation

Sexual condition (whether male, female or immature) was determined for each abalone by visual inspection of the intact gonad. If gonad (either testis or ovary) could be discerned abalone were considered to be sexually differentiated. Rates of maturation by size and by age were determined by fitting the maturation data to the logistic equation:

$$p = \frac{e^{c+d.x}}{1 + e^{c+d.x}}$$

Equation 4

where p is proportion mature, x is length (or age), and c and d are parameters of the logistic function.

Fecundity estimation

Gonads from female abalone sampled in all regions but the Tamar mouth were retained for analysis. Whilst the ideal measure of fecundity is the number of eggs spawned per individual female per year, this is generally impossible to measure. Fecundity is therefore usually measured as the number of ripe eggs in the gonad, the weight of the gonad (either fresh or the ash-free dry weight), or as gonad volume. Although gonad volume does not allow the determination of egg numbers spawned, it does allow the relationship between abalone size and potential fecundity, or abalone age and potential fecundity, to be determined. For the purposes of egg-per-recruit analyses, the relative fecundity between size or age classes is more important than the absolute fecundity.

The cross-sectional area of the gonad taken at the base of the conical appendage (Fig. 3) was used as an index of gonad volume because measuring gonad volume directly is very time-consuming. The validity of this approach has been established by Nash et al. (1994) who demonstrated that gonad area is closely and linearly related to gonad volume in blacklip abalone. Following fixation of the conical appendage in 70 % alcohol, the cut surface of the conical appendix was pressed lightly against an acetate sheet, and the outlines of the gonad and digestive gland were traced onto the sheet. The tracings of the cross-sections of the conical appendages were scanned onto a computer, and the cross-sectional areas of gonad and digestive gland measured in mm^2 using an image analysis program.

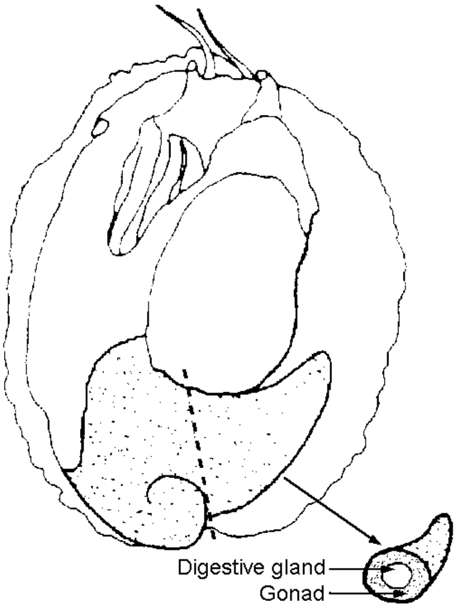

Fig. 3. Diagram of the dorsal surface of an abalone with the shell removed, showing the gonad (stippled) and the plane of sectioning for gonad analysis (dotted line). Modified after Nash (1994).

Relationships between length and fecundity were fitted to the equation:

$$\text{Fecundity} = x.(\text{Length})^{y}$$

Equation 5

where x and y are parameters of the power relationship.

Sex ratio

The ratio of males to females was compared at each site and for each region. Chi-squared analysis was used to test sex ratios for significant departure from a one to one relationship.

2.2.4 Mortality Estimation

Instantaneous total mortality (Z) was measured by catch curve analysis: the number of abalone in each age class ($\log_e(x+1)$ transformed) was plotted against age. The slope of the regression line fitted to those age classes that are fully represented in the sample is equal to the instantaneous rate of total mortality (Z) of that population (with the sign of the slope changed). This is strictly correct only in a population with stable age structure (constant rates of recruitment through time) and constant age-specific mortality rates. The extent to which these conditions may be violated, and the effects such violations have on total mortality determination, are discussed in Section 4.4 below.

Pauly (1990) proposed that the regression line be fitted to those points to the right of the highest point (P_{max}) on the catch curve; P_{max} should be excluded because of incomplete recruitment effects. This procedure was adopted unless P_{max} lay above the leftward projection of the regression line that did not include P_{max} because this indicates that recruitment is complete (Pauly, 1990).

In an unfished population fishing mortality (*F*) is zero and the total mortality therefore equals the natural mortality (*M*). Some of the sites chosen were areas where fishing pressure is very low, and from which estimates of natural mortality could therefore be obtained. These areas included Puncheon Island and the Tamar River mouth, where the growth rates and maximum sizes are much lower than in other parts of Tasmania. In these areas, greenlip abalone hardly reach the minimum legal length. Hence, the fishing mortality of these abalone is very low, and all mortality may therefore be considered to be natural. Estimates of natural mortality from such sites are very important to per-recruit and other analyses.

Estimates of the natural mortality rate, *M*, from fished areas are more difficult to obtain, but an idea of the likely value of *M* can be derived from the survival of known age abalone recovered from the wild. Estimates of *M* were calculated from abalone recovered from those placed out on concrete blocks in the sea by Furneaux Aquaculture Pty Ltd.

Estimates of *Z* were also obtained using the Sparre et al. (1989) approximation:

$$Z_{A99\%} = \log_e 100 / A_{max}$$

Equation 6

where A_{max} is the maximum age reached by approximately 1 % of the population. In this study the 99th percentile of the age distribution was used to estimate this age. At sites where fishing mortality is low this approximation of *Z* would be close to *M*.

2.2.5 Per-recruit Analyses

Yield-per-recruit

To assess the potential effect on yield of varying minimum size limits, yield-per-recruit (YPR) analyses were conducted at different combinations of fishing mortality (*F*) and minimum size limit (l_c). The data required for the YPR analyses are the constants *a* and *b* from the length-weight relationship (Equation 1), the von Bertalanffy growth parameters (L_∞, *K* and t_0, Equation 2), the constants *c* and *d* from the logistic maturation curve (Equation 4), the instantaneous natural mortality coefficient (*M*), and the maximum age (A_{max}, Equation 6). Yield-per-recruit was expressed as a percentage of the maximum biomass potentially attained by a cohort. To conduct the YPR analyses, both *F* and the size limit were varied in incremental steps.

Egg-per-recruit

Egg-per-recruit (EPR) analyses were conducted to estimate the proportion of egg production conserved, relative to that of the unfished stock, at different levels of fishing mortality (F) and minimum size limit (l_c). The data parameters required for these analyses were the same as those used for YPR, plus the constants x and y from the length-fecundity relationship (Equation 5). It was assumed that spawning occurs once per year and that all eggs are released. EPR was calculated as a percentage of the egg production in the absence of fishing.

3. Results

Management arrangements for greenlip abalone are likely to operate on a regional basis. Therefore survey data from each dive site sampled were pooled for each of the five regions sampled. This approach ignores within-area variation which can be significant. Such variation is therefore described and discussed where appropriate.

3.1 Morphometry

Length frequency distributions are given for each region in Fig. 4. These data include the lengths of those abalone tagged and returned to the bottom. The modal size class was above the old size-limit of 140 mm in all areas but the Tamar mouth. In the North east and at King Island the proportion of abalone in the 150 to 155 mm size class appeared to be have been reduced.

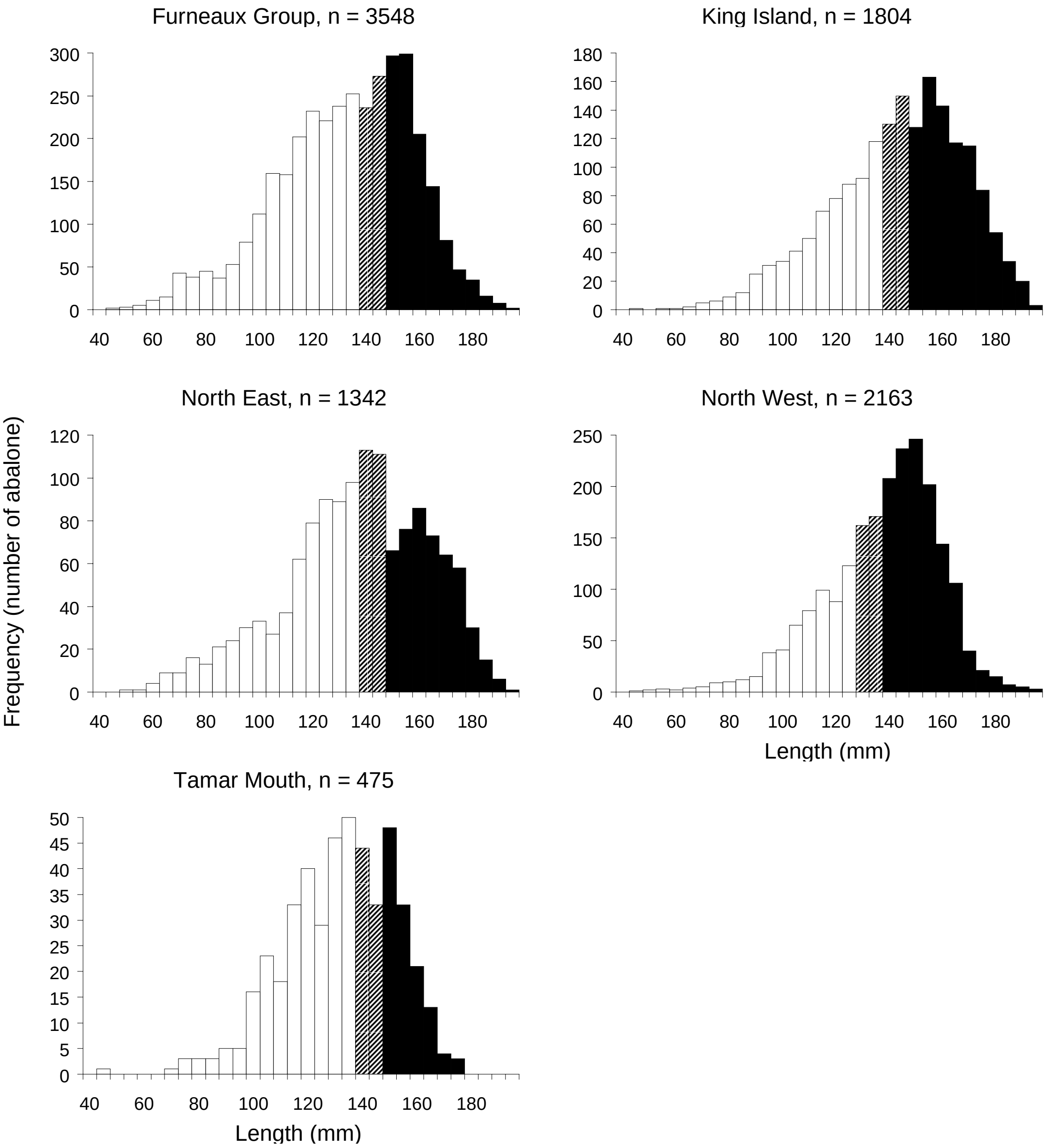

Fig. 4. Length frequency distributions of abalone caught in each region. The lengths of abalone tagged and returned to the water are included in these samples. Filled bars indicate abalone larger than the interim size limits introduced on January 1, 1999. Dashed bars indicate abalone between the old and interim size limits. (In the North West the old limit was 132 mm. The dashed area in the North West graph includes abalone from 130 mm and hence slightly overestimates the proportion of the population between the old and interim size limits.)

The relationship between shell length and whole weight at each of the regions is shown in Table 1 and Fig. 5. The relationship between shell length and meat weight of abalone is shown in Table 1 and Fig. 6. These relationships were close to a cubic relationship in all regions.

Table 1. Relationship between shell length and whole weight for *Haliotis laevigata* at each of the regions. a and b are constants in the equation whole weight = a.(shell length)^b. r^2 = coefficient of determination, n = sample size.

Region	*a*	*b*	r^2	*n*
Whole weight				
Furneaux Group	0.0000368	3.245	0.961	2225
King Island	0.0000452	3.226	0.958	1416
North East	0.0000110	3.495	0.966	1342
North West	0.0000604	3.146	0.941	1942
Tamar Mouth	0.0000302	3.313	0.945	475
Meat weight				
Furneaux Group	0.0000123	3.273	0.926	2225
King Island	0.0000182	3.203	0.923	1416
North East	0.0000019	3.654	0.953	1342
North West	0.0000246	3.141	0.916	1942
Tamar Mouth	0.0000088	3.358	0.929	475

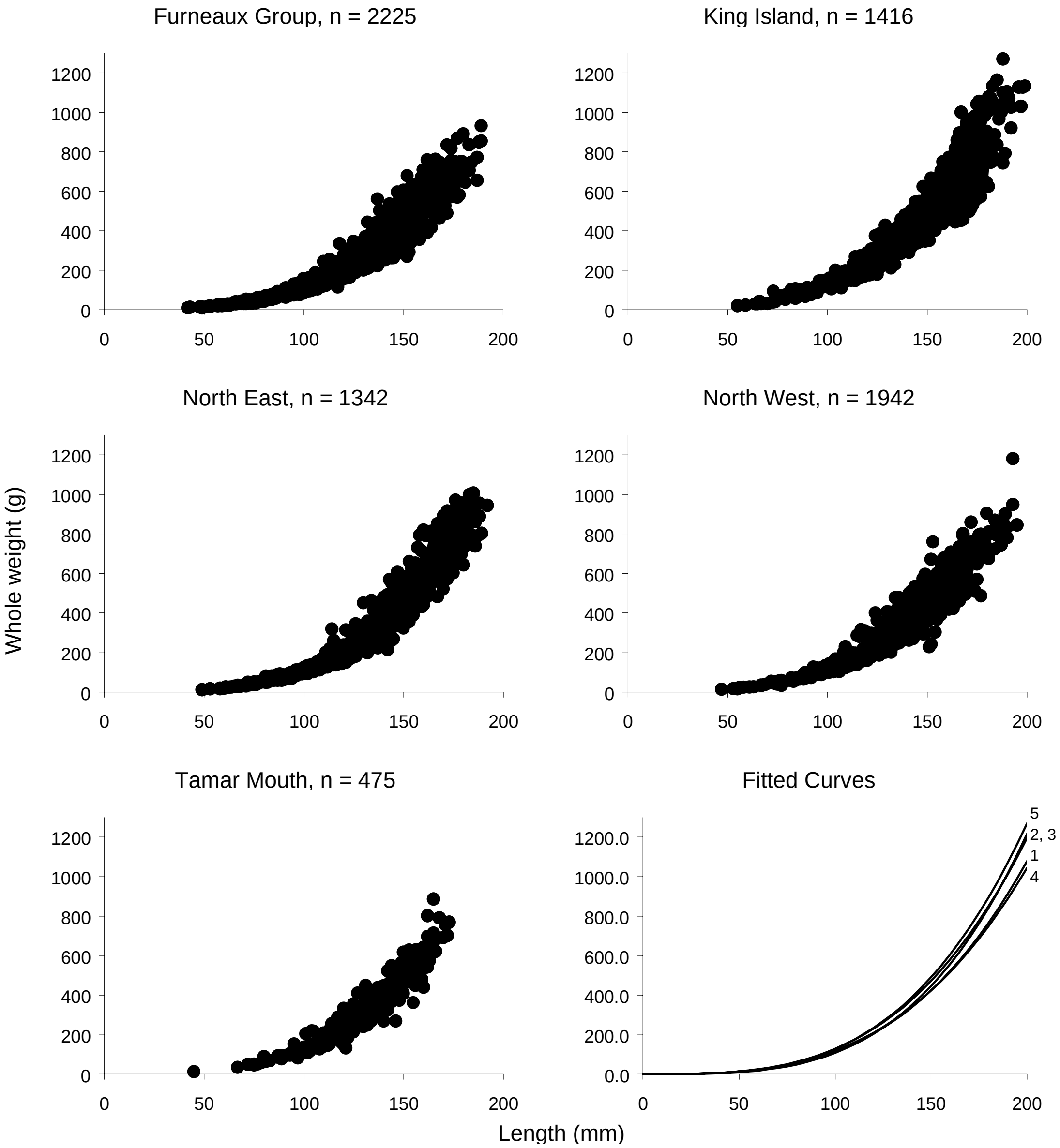

Fig. 5. Relationship between shell length and whole weight for *Haliotis laevigata* at each of the regions. n is the number of abalone measured. The bottom right graph illustrates the fitted curves for each region (1: Furneaux Group, 2: King Island, 3: North East, 4: North West, and 5: Tamar Mouth).

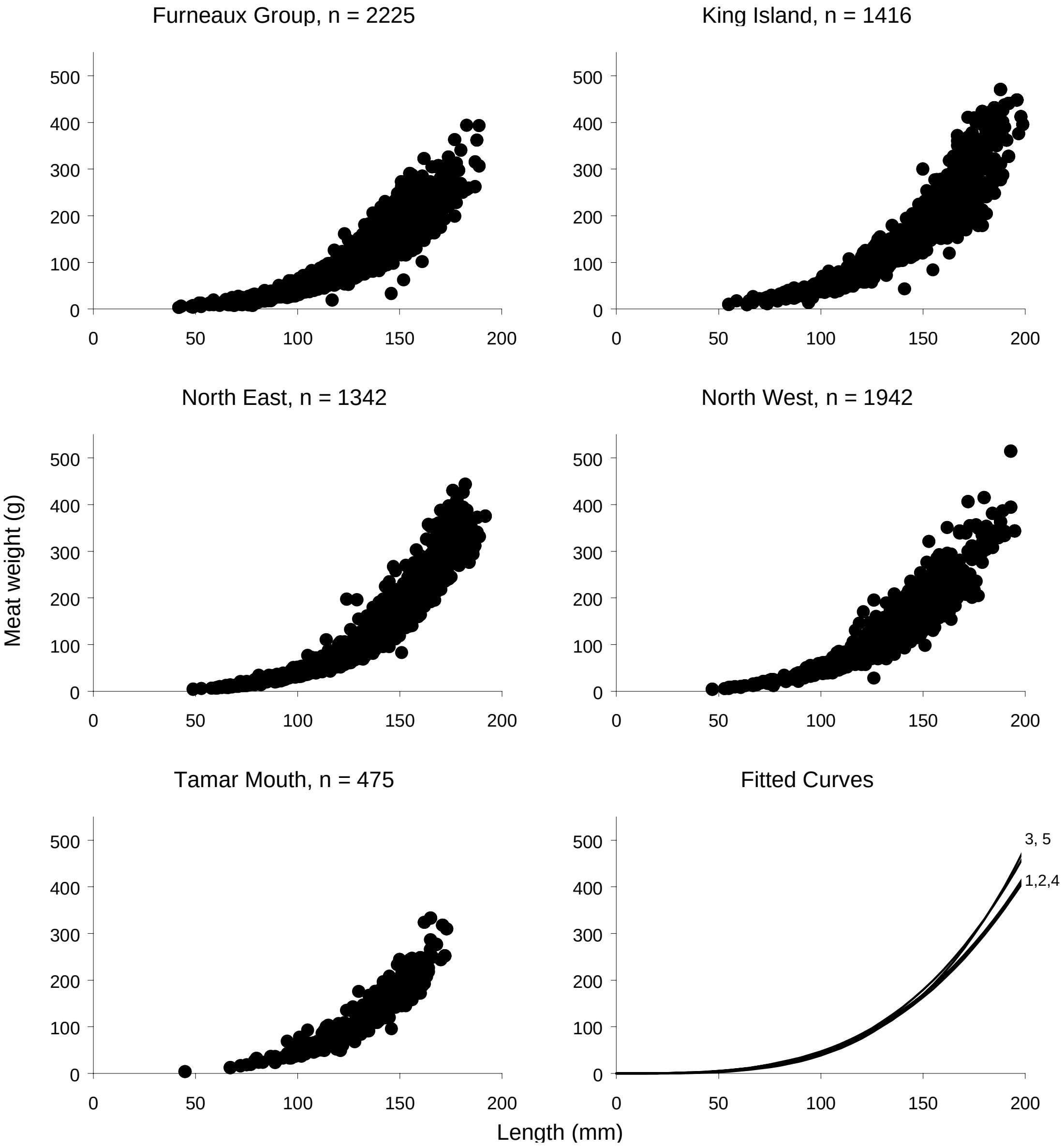

Fig. 6. Relationship between shell length and meat weight for *Haliotis laevigata* at each of the regions. n is the number of abalone measured. The bottom right graph illustrates the fitted curves for each region (1: Furneaux Group, 2: King Island, 3: North East, 4: North West, and 5: Tamar Mouth).

3.2 Age and Growth Estimation

3.2.1 Age estimation

Counts of rings in shells of known age show that on average 1.8 to 2.0 rings per year were laid down (Table 2). This does not differ significantly from two rings per year for each age group. For this analysis brown rings were excluded from the count. Shepherd and Triantafillos (1997) found that brown rings are adventitious and occur as a response to boring. Of the 17 nine year-old shells recovered six had no brown rings, six had one brown ring and five shells had two or more brown rings. The mean number of rings for shells without brown rings was 17.2 (s.e. 0.5), for shells with one brown ring 18.3 (s.e. 0.3), and for shells with two or more brown rings 19.0 (s.e. 0.3).

Table 2. Number of rings found in the shells of hatchery-produced greenlip abalone of known age. Abalone aged 1, 3 and 4 years were grown on shore or in mesh bags at sea, and those aged 9 years were placed on concrete blocks in the sea at age one year. (s.e.; standard error).

Age (years)	No. of shells examined	Average length (mm) (s.e.)	Average no. of rings (s.e.)	Equivalent no. of rings/year
1	11	11.4 (0.4)	1.9 (0.2)	1.9
3	20	42.2 (0.6)	5.8 (0.2)	1.9
4	7	55.6 (3.5)	7.3 (0.4)	1.8
9	17	149.4 (2.8)	18.2 (0.3)	2.0

The proportion of abalone in each sample that could be aged (i.e., for which growth rings could be counted clearly) ranged from 57 percent for the Tamar mouth sample to 99 percent at King Island (Table 3). The size composition of the readable and unreadable fractions of the population are shown in Fig. 7. Inability to age a shell was because of either physical abrasion of the spire, extensive boring of the shell by polychaetes or sponges, or other physical damage to the shell. The shells from the Tamar mouth were most difficult to read with 43 % of samples rejected. Readability was generally high for abalone sampled in the four main fishing regions. Where estimates of readability were lowest in these regions this was due to poor readability at a few sites (eg. Foster Island East and Swan Island in the North east, Table 3).

Table 3. The number and proportion of shells from each region and site that were readable.

Region and site	Number of shells where: Ageing was attempted	Number of shells where: Shell was readable	% of shells that were readable
Furneaux Group (all sites)	**2408**	**2237**	**93%**
Apple Orchard Point	204	201	99%
Big River Cove	228	224	98%
Great Dog Island Passage	245	242	99%
Moriarty Bay	391	331	85%
North Pascoe Island	194	175	90%
Preservation Island	221	221	100%
Puncheon Island	257	240	93%
Rebecca Bay	240	225	94%
Shag Rocks	208	178	86%
Vansittart Beacon	220	200	91%
King Island (all sites)	**1390**	**1374**	**99%**
Christmas Island	191	191	100%
Councillor Island	196	195	99%
Cowper Point	197	193	98%
Disappointment Bay	191	188	98%
Elizabeth Rock	204	203	100%
New Year Island	94	94	100%
Sea Elephant Reef	199	195	98%
Seal Bay	118	115	97%
North East (all sites)	**1313**	**1153**	**88%**
East Barrett Reef	88	86	98%
Foster Island East	167	112	67%
Foster Island West	247	229	93%
Lanoma Point	157	123	78%
Little Waterhouse Island	184	182	99%
South West Waterhouse Island	157	156	99%
Swan Island	160	121	76%
Waterhouse Passage	153	144	94%
North West (all sites)	**1878**	**1835**	**98%**
Big Stoney Island East	174	173	99%
Big Stoney Island West	204	203	100%
Black Reef	240	235	98%
Cave Bay	214	208	97%
Harbour Islets Inshore	197	194	98%
Harbour Islets Offshore	219	210	96%
Little Stoney Island	187	186	99%
Shepherds Bay	238	231	97%
Stack Island	205	195	95%
Tamar mouth (all sites)	**475**	**270**	**57%**
Dotterel Point	250	155	62%
Shear Rock	225	115	51%

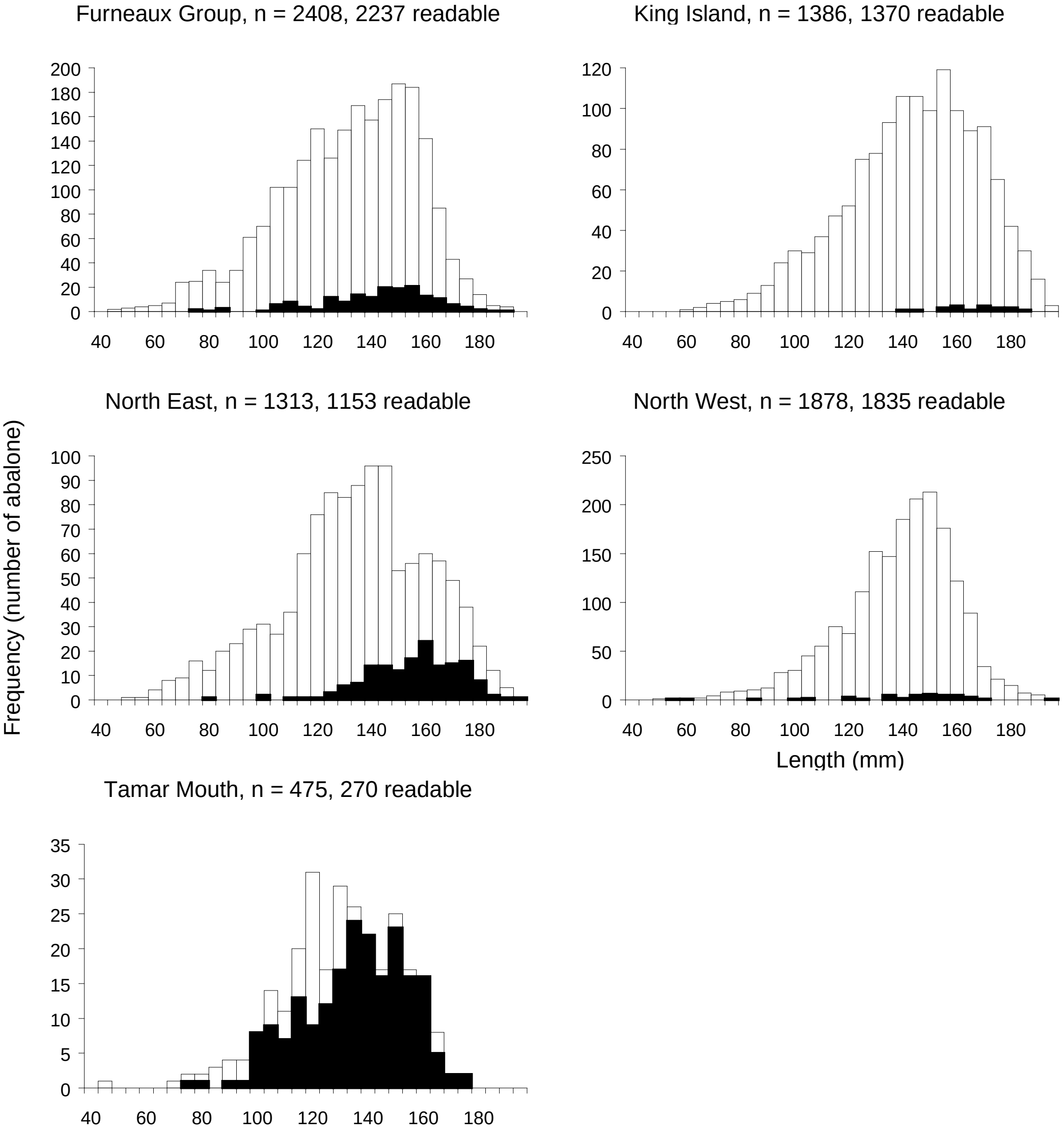

Fig. 7. Length composition of the readable (unfilled bars) and un-readable (black bars) fractions of the population sample at each region. n equals the number of shells on which age estimation was attempted.

The relationship between shell length and age is shown for each region in Fig. 8. The wide variation in length-at-age that is characteristic of abalone populations was found in all regions. The length and age compositions of each population are shown in Fig. 4 and Fig. 9 respectively.

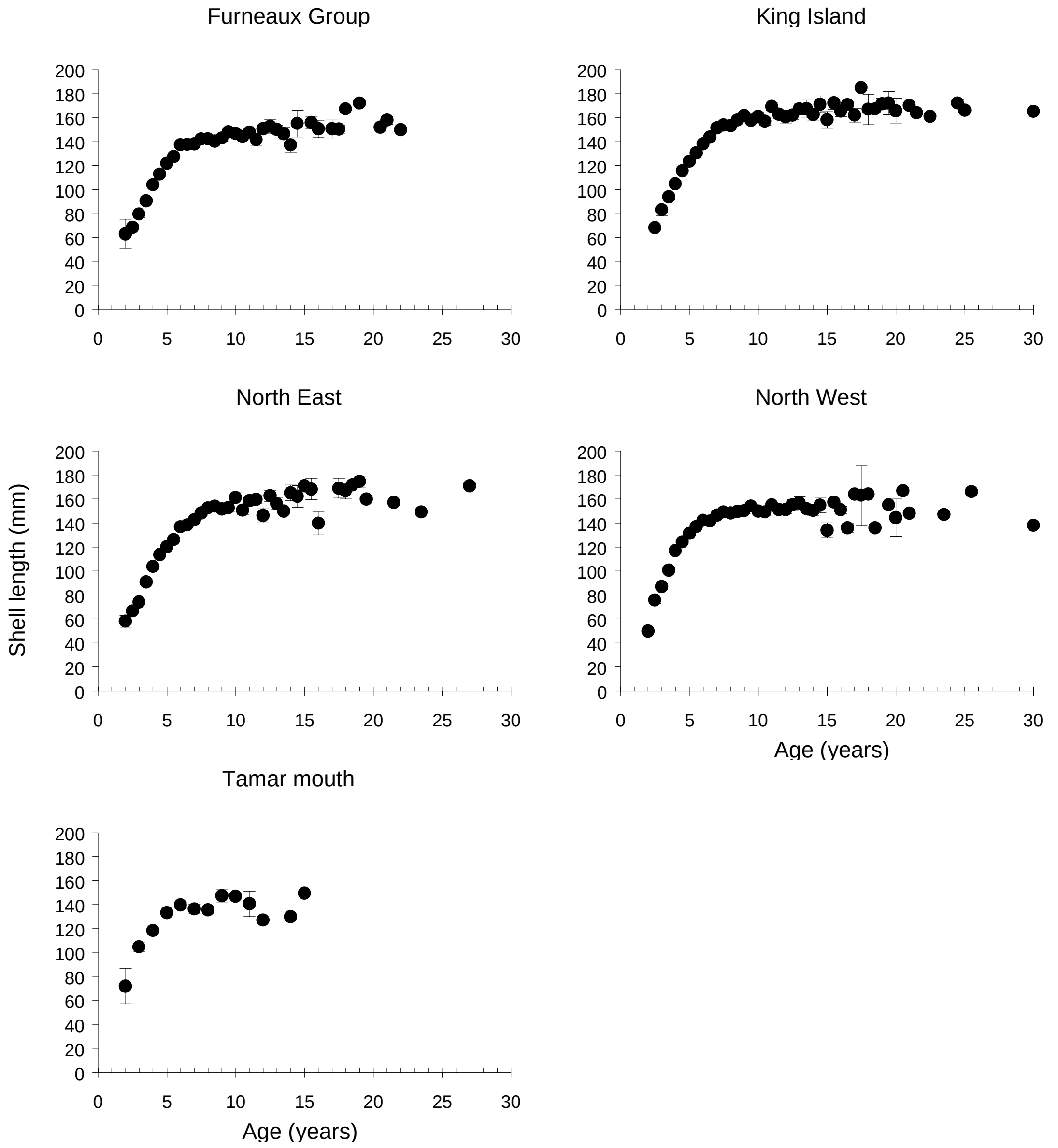

Fig. 8. Relationships between average age and shell length at each of the five regions. Error bars indicate the standard error about the average length-at-age.

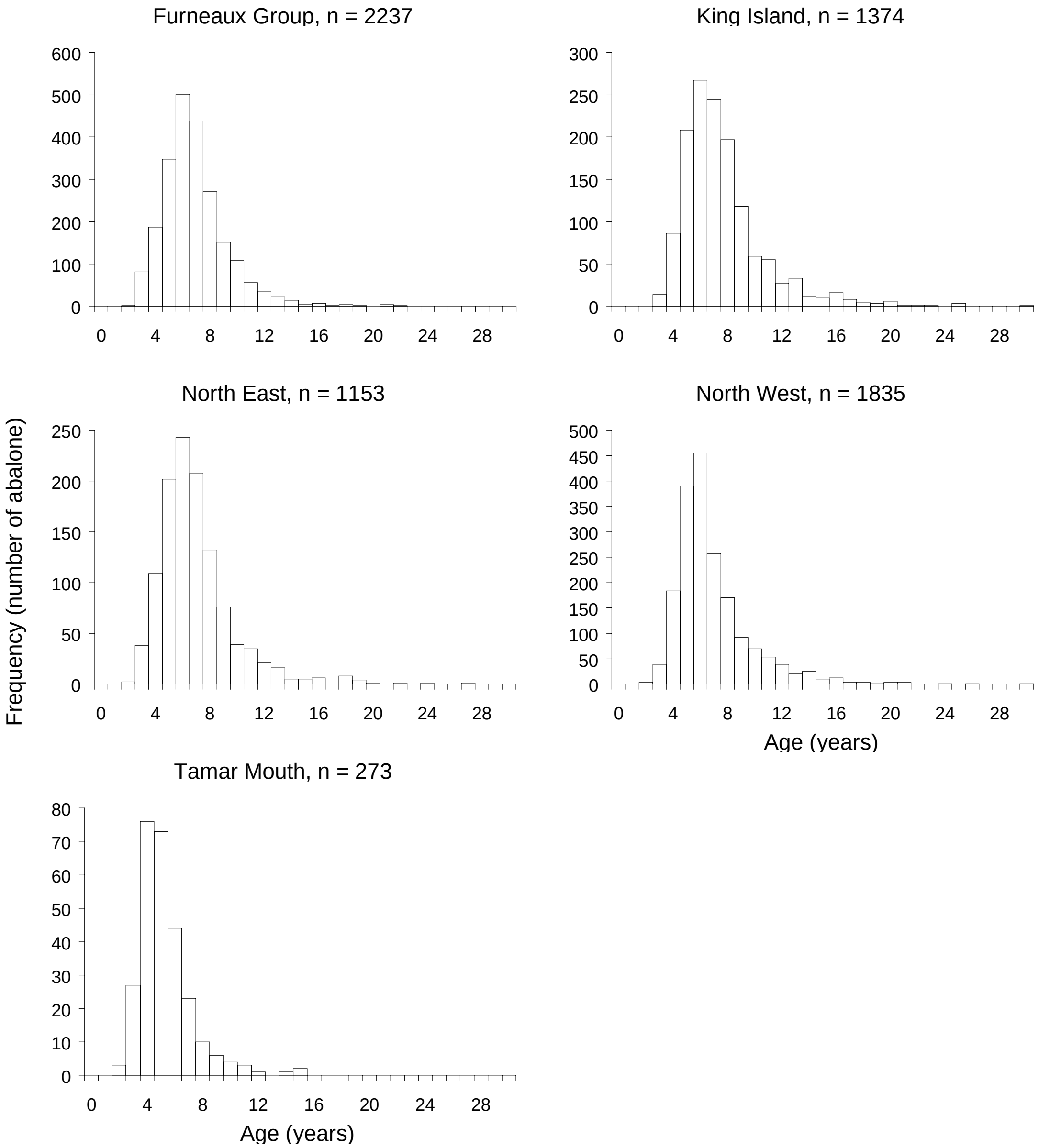

Fig. 9. Age composition of *Haliotis laevigata* at each of the five regions. n is the number of abalone measured.

3.2.2 Growth estimation from aged shells

Values of the von Bertalanffy growth parameters are shown in Table 4, derived using a shell layer deposition rate of two growth rings per year. By region, L_∞ ranged from 143.9 mm at the Tamar mouth to 169.0 mm at King Island, and by site it ranged from 116.1 mm at Puncheon Island (Furneaux Group) to 184.4 mm at Elizabeth Rock (King Island). There was considerable variability between estimates of growth parameters within regions, particularly within the Furneaux Group and the North East.

Table 4. Parameters of the von Bertalanffy growth function (Equation 2) estimated for each region and site. 95 % confidence intervals allow parameter estimates for each site to be compared with the overall estimate for the region. Where these differ significantly an arrow indicates if the site estimate is greater than (↑) or less than (↓) the regional estimate. *n* equals the sample size.

		Estimated values of growth parameters (± 95 % confidence intervals)		
Region and site	n	L_∞	K	t_0
Furneaux Group (all sites)	**2237**	**150.1 ± 2.2**	**0.455 ± 0.041**	**1.324 ± 0.18**
Apple Orchard Point	201	133.8 ± 4.5 ↓	0.555 ± 0.162	1.130 ± 0.648
Big River Cove	224	152.6 ± 3.7	0.620 ± 0.1 ↑	1.966 ± 0.228 ↑
Great Dog Island Passage	242	166.7 ± 6.6 ↑	0.446 ± 0.106	1.067 ± 0.436
Moriarty Bay	331	146.6 ± 5.2	0.384 ± 0.083	1.270 ± 0.512
North Pascoe Island	175	140.6 ± 7.1 ↓	0.419 ± 0.116	1.430 ± 0.523
Preservation Island	221	158.7 ± 4.8 ↑	0.478 ± 0.08	1.373 ± 0.264
Puncheon Island	240	116.1 ± 2.4 ↓	0.700 ± 0.157 ↑	1.552 ± 0.382
Rebecca Bay	225	161.1 ± 5.9 ↑	0.370 ± 0.067	1.326 ± 0.37
Shag Rocks	178	165.2 ± 8.2 ↑	0.417 ± 0.148	1.480 ± 0.892
Vansittart Beacon	200	150.9 ± 3.9	0.650 ± 0.202	1.301 ± 0.673
King Island (all sites)	**1374**	**169.0 ± 2.7**	**0.367 ± 0.036**	**1.336 ± 0.255**
Christmas Island	191	173.5 ± 8.3	0.382 ± 0.093	1.623 ± 0.485
Councillor Island	195	165.6 ± 7.9	0.376 ± 0.103	0.880 ± 0.67
Cowper Point	193	179.0 ± 5 ↑	0.475 ± 0.104 ↑	2.122 ± 0.507 ↑
Disappointment Bay	188	168.6 ± 6.9	0.287 ± 0.067	1.092 ± 0.696
Elizabeth Rock	203	184.4 ± 22	0.253 ± 0.112	0.758 ± 1.008
New Year Island	94	177.6 ± 4.7 ↑	0.422 ± 0.078	2.751 ± 0.405 ↑
Sea Elephant Reef	195	148.1 ± 2.8 ↓	0.559 ± 0.13 ↑	1.761 ± 0.584
Seal Bay	115	176.1 ± 9.1	0.348 ± 0.114	1.335 ± 0.944
North East (all sites)	**1153**	**163.6 ± 3.4**	**0.357 ± 0.037**	**1.203 ± 0.23**
East Barrett Reef	86	142.6 ± 12.4 ↓	0.489 ± 0.207	1.720 ± 0.648
Foster Island East	112	164.2 ± 6	0.394 ± 0.114	1.581 ± 0.732
Foster Island West	229	144.2 ± 4.2 ↓	0.513 ± 0.09 ↑	1.579 ± 0.293 ↑
Lanoma Point	123	173.6 ± 3.7 ↑	0.524 ± 0.104 ↑	1.840 ± 0.397 ↑
Little Waterhouse Island	182	155.0 ± 15.7	0.324 ± 0.115	0.921 ± 0.562
South West Waterhouse Island	156	138.3 ± 6.3 ↓	0.535 ± 0.131 ↑	1.608 ± 0.36 ↑
Swan Island	121	156.9 ± 6.1	0.399 ± 0.116	1.331 ± 0.743
Waterhouse Passage	144	165.5 ± 3.4	0.765 ± 0.144 ↑	1.826 ± 0.241 ↑
North West (all sites)	**1835**	**154.4 ± 1.7**	**0.492 ± 0.042**	**1.169 ± 0.197**
Big Stoney Island East	173	155.5 ± 4.5	0.771 ± 0.247 ↑	2.369 ± 0.5 ↑
Big Stoney Island West	203	150.1 ± 6.6	0.471 ± 0.153	1.280 ± 0.782
Black Reef	235	160.1 ± 5.9	0.335 ± 0.082 ↓	0.356 ± 0.753
Cave Bay	208	155.6 ± 4.8	0.778 ± 0.372	1.410 ± 1.041
Harbour Islets Inshore	194	146.5 ± 5.9 ↓	0.527 ± 0.114	1.423 ± 0.334
Harbour Islets Offshore	210	152.5 ± 4.6	0.479 ± 0.096	1.240 ± 0.4
Little Stoney Island	186	143.2 ± 2.4 ↓	0.925 ± 0.221 ↑	1.819 ± 0.35 ↑
Shepherds Bay	231	150.7 ± 4.1	0.612 ± 0.166	1.424 ± 0.588
Stack Island	195	156.4 ± 3.1	0.583 ± 0.114	1.661 ± 0.365 ↑
Tamar mouth (all sites)	**270**	**143.9 ± 5.7**	**0.583 ± 0.18**	**0.846 ± 0.602**
Dotterel Point	155	141.6 ± 5.9	0.744 ± 0.254	1.196 ± 0.526
Shear Rock	115	147.9 ± 13	0.425 ± 0.254	0.303 ± 1.452

3.2.3 Growth estimation from recaptured tagged shells

To date, tagged abalone have been recovered by research divers from six of the eight tagging sites. A summary of the recoveries is given in Table 5. At Shag Rocks inclement weather prevented a thorough search of the tagging site by research divers. Two days were spent searching for tagged abalone at Black Reef but none were recovered. At sites where tagged abalone were recaptured the percentage recovered ranged from 9 % at Puncheon Island to 54 % at Preservation Island. The poor recovery rate at Puncheon Island was largely due to a high rate of tag loss from the brittle shells characteristic of this site. Only three of the 22 tagged shells recovered from the site retained both tags. At Puncheon Island research divers found numerous loose tags on the seabed and recovered many abalone that had been previously tagged but had lost both tags (evident as widened respiratory pores). At New Year Island recovery rates were low due to logistical difficulties limiting the period of time available for searching. Periods at liberty ranged from 359 days (Great Dog Island Passage) to 365 days (Puncheon Island).

Table 5. The number of greenlip abalone tagged and recovered from each of the eight tagging sites.

	Number of abalone:			
Region and site	Tagged	Recaptured	% recaptured	Days at liberty
Furneaux Group				
Great Dog Island Passage	210	59	28%	359
North Pasco Island	207	67	32%	364
Preservation Island	207	111	54%	364
Puncheon Island	238	22	9%	365
Shag Rocks	212	0	0%	n/a
King Island				
Cowper Point	200	93	47%	364
Lizzy Rocks	191	25	13%	363
North West				
Black Reef	221	0	0%	n/a

Measurements from dead shells and from abalone that had negative length increments were excluded from growth increment analyses reported here (Fig. 10 and Table 6). Whilst preliminary analyses of the data suggested that inclusion of negative growth increments would have little impact on the values of growth parameters derived from the analysis, negative growth increments were excluded because they do not make sense biologically. Negative increments generally appeared to be the result of measurement error (95 % of negative increments represented length reductions of four mm or less).

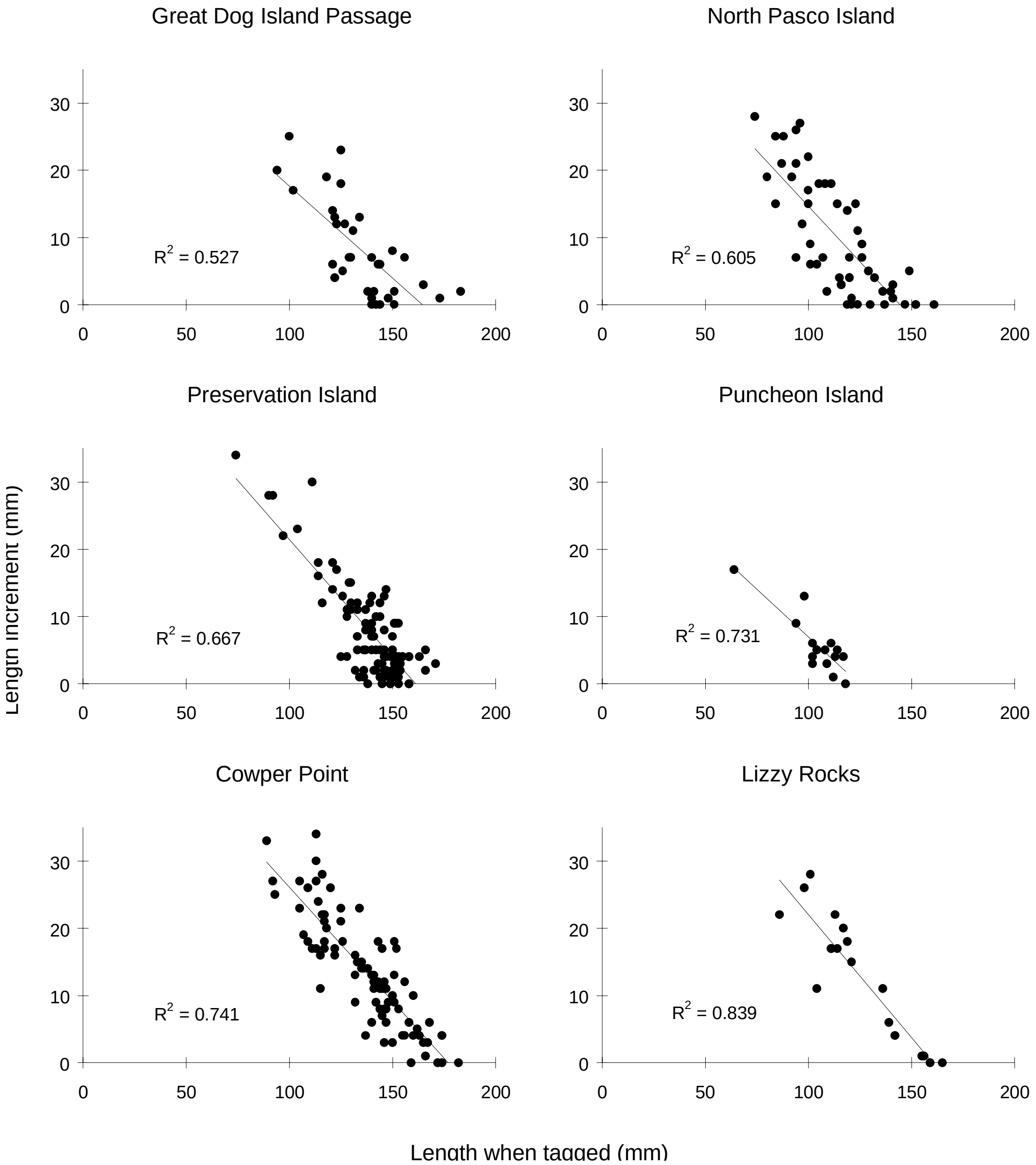

Fig. 10. Regressions of length increment versus length at date of tagging for tagged greenlip abalone recovered from six sites in Tasmania. R^2 is the coefficient of determination.

Abalone were recaptured across a broad range of sizes and length increments at most sites (Fig. 10). This meant that regressions of length increment versus length at tagging produced reasonably close relationships for most sites.

Table 6. Comparison of von Bertalanffy growth parameters derived from the Tag-recapture and Age-length analyses of growth. Significantly different values are shown in bold type. Proper estimation of t_0 by the tag-recapture method requires animals of known age. Where known age animals are not available a t_0 of 0 is assumed. *n* equals the sample size (for the tag-recapture method this is the number of recaptured live abalone with positive growth increments).

		Estimated values of growth parameters (± 95 % confidence intervals)			
Region and site	Method	L_∞	K	t_0	n
Furneaux Group					
Great Dog Island Passage	Tag-recapture	164.5 ± 11.6	0.325 ± 0.128	0	35
	Age-length	166.7 ± 6.6	0.446 ± 0.106	1.067 ± 0.436	242
North Pasco Island	Tag-recapture	144.3 ± 8.1	0.401 ± 0.113	0	52
	Age-length	140.6 ± 7.1	0.419 ± 0.116	1.430 ± 0.523	175
Preservation Island	Tag-recapture	161.2 ± 3.7	0.432 ± 0.076	0	99
	Age-length	158.7 ± 4.8	0.478 ± 0.081	1.373 ± 0.264	221
Puncheon Island	Tag-recapture	124.4 ± 8.5	**0.336** ± 0.143	0	15
	Age-length	116.1 ± 2.4	**0.700** ± 0.157	1.552 ± 0.382	240
King Island					
Cowper Point	Tag-recapture	177.1 ± 5.7	0.416 ± 0.066	0	86
	Age-length	179.0 ± 5.0	0.475 ± 0.104	2.122 ± 0.507	193
Lizzy Rocks	Tag-recapture	160.2 ± 9.1	0.459 ± 0.129	0	19
Christmas Island	Age-length	173.5 ± 8.3	0.382 ± 0.093	1.623 ± 0.485	191

The growth parameters L_∞ and K derived from the tag-recapture estimation methods were remarkably similar to the age-length based estimates for each site (Table 6). The only significant difference occurred at Puncheon Island between the coefficient of growth rate (K) (Table 6). Few tagged abalone were recaptured at Puncheon Island (22), and only 15 of these had positive length increments. Only one of these abalone had a length less than 90 mm at the time of tagging. The data from this abalone therefore has a strong influence on the relationship calculated for this site (Fig. 10).

The general similarity between parameter estimates from each method held across the range of sites despite there being very different growth characteristics between sites (Table 4). The comparison at the Lizzy Rocks site was complicated by the fact that the tag-recapture sample was taken at Lizzy Rocks but the population sample used for ageing was taken at Christmas Island, about 600 m from the tagging site. Despite this separation no significant differences in the growth parameters L_∞ and K was found between the sites (Table 6).

3.3 Sexual Maturation, Fecundity and Sex ratio

3.3.1 Onset of Sexual Maturity

The process of sexual maturation with size varied considerably between regions. Length at 50 % maturity ranged from 71.7 mm in the North-west to 95.5 mm at King Island (Table 7). Confidence limits about these estimates were reasonably tight at the four main fishing regions. However, at the Tamar mouth immature abalone were particularly poorly represented in the sample. This substantially decreases the confidence in the estimate of length at 50 % maturity calculated for this region.

Full sexual maturity was achieved at about 100 mm (most regions) through to about 120 mm (King Island) (Fig. 11). For the four main fishing regions rates of transition from immature to mature (measured by the parameter *d* of the logistic equation) were highest in the North East (*d* = 0.183) and lowest at King Island (*d* = 0.122).

Table 7. Rates of onset of sexual maturity by length and by age of *Haliotis laevigata* at each of five regions in Tasmania. *c* and *d* are parameters of the logistic function given in Equation 4. $L_{50\%}$ and $A_{50\%}$ are the length and age, respectively, at 50 % sexual maturity.

	Length					Age				
				95% Confidence Limits ($L_{50\%}$)					95% Confidence Limits ($A_{50\%}$)	
Region	*a*	*b*	$L_{50\%}$	Lower	Upper	*a*	*b*	$A_{50\%}$	Lower	Upper
Furneaux Group	-11.54	0.143	80.9	78.7	82.9	-4.60	1.546	3.0	2.7	3.2
King Island	-11.67	0.122	95.5	92.2	98.2	-4.49	1.306	3.4	3.1	3.7
North East	-14.38	0.183	78.5	75.5	81.0	-7.52	2.414	3.1	2.9	3.3
North West	-11.51	0.161	71.7	65.9	75.8	-5.15	2.247	2.3	1.7	2.6
Tamar mouth	-6.23	0.085	73.6	55.4	83.2	-1.15	0.992	1.2	-3.8	2.3

The process of sexual maturation with age followed a similar pattern in the four main fishing regions: at these regions onset of maturity began in abalone aged between about 2.5 and 3.5 years, with an increasing proportion of successively older year classes being mature (Fig. 12). At the Tamar mouth immature abalone were poorly represented in the sample and the confidence in the estimate of age at 50 % maturity is therefore poor.

Maturation of each population occurred over a relatively short period of years, so by five years of age almost all animals were sexually mature at each region. For the four main fishing regions age at 50 percent maturity ranged from 2.3 to 3.4 years (Table 7). For these regions rates of transition from immature to mature were similar to those calculated for length at maturity being highest in the North East (*d* = 2.414) and lowest at King Island (*d* = 1.306). For the main fishing regions reasonable agreement was found between estimated lengths at 50 % maturity and the lengths-at-age calculated using the von Bertalanffy growth function from the age at 50 % maturity. In all cases the calculated length-at-age (± confidence limits) fell between the confidence limits for estimated length at 50 % maturity.

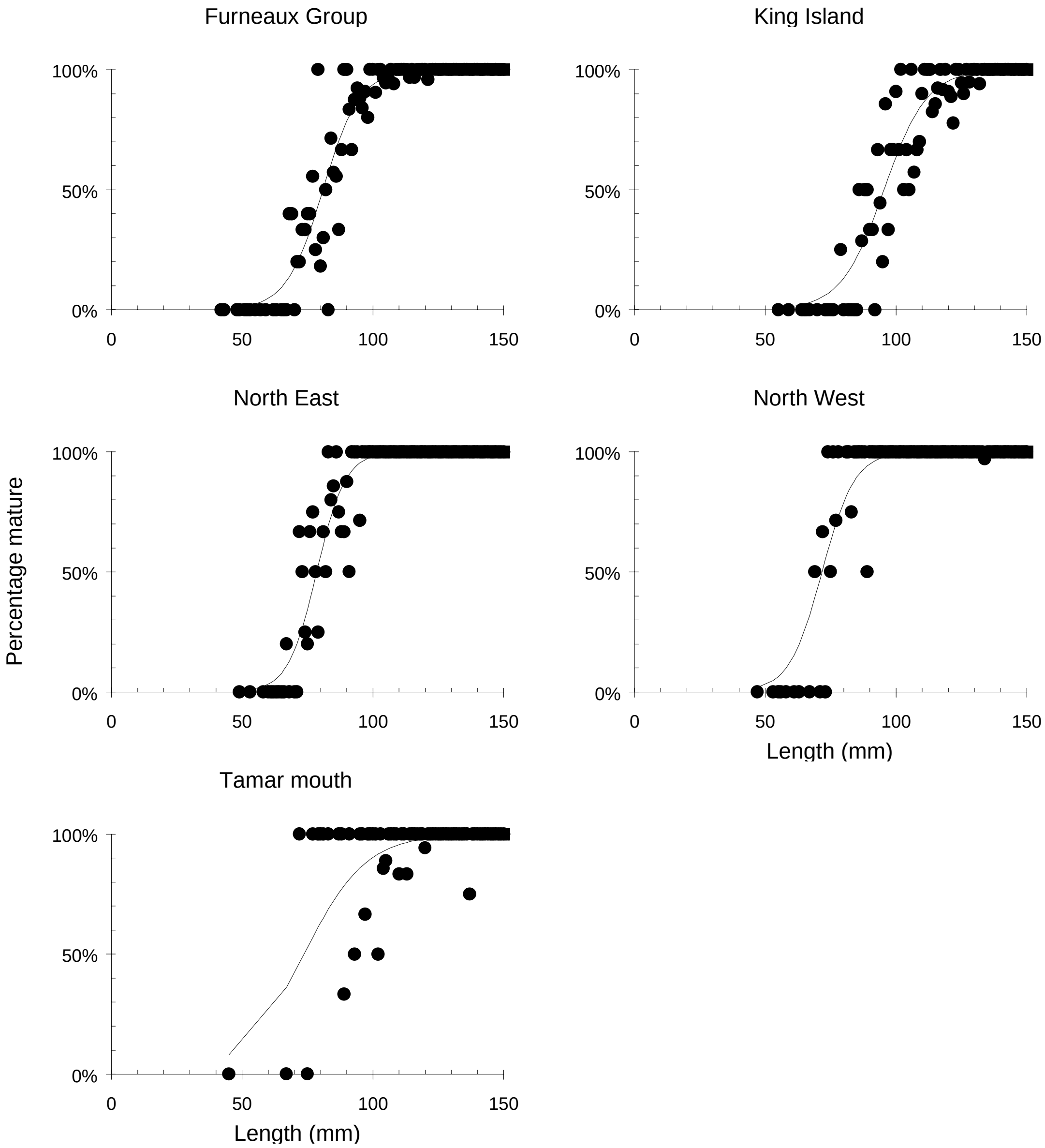

Fig. 11. Rates of maturation by length for *Haliotis laevigata* from the five regions of Tasmania. The solid line shows the fit of the maturation data to the logistic function described in Equation 4.

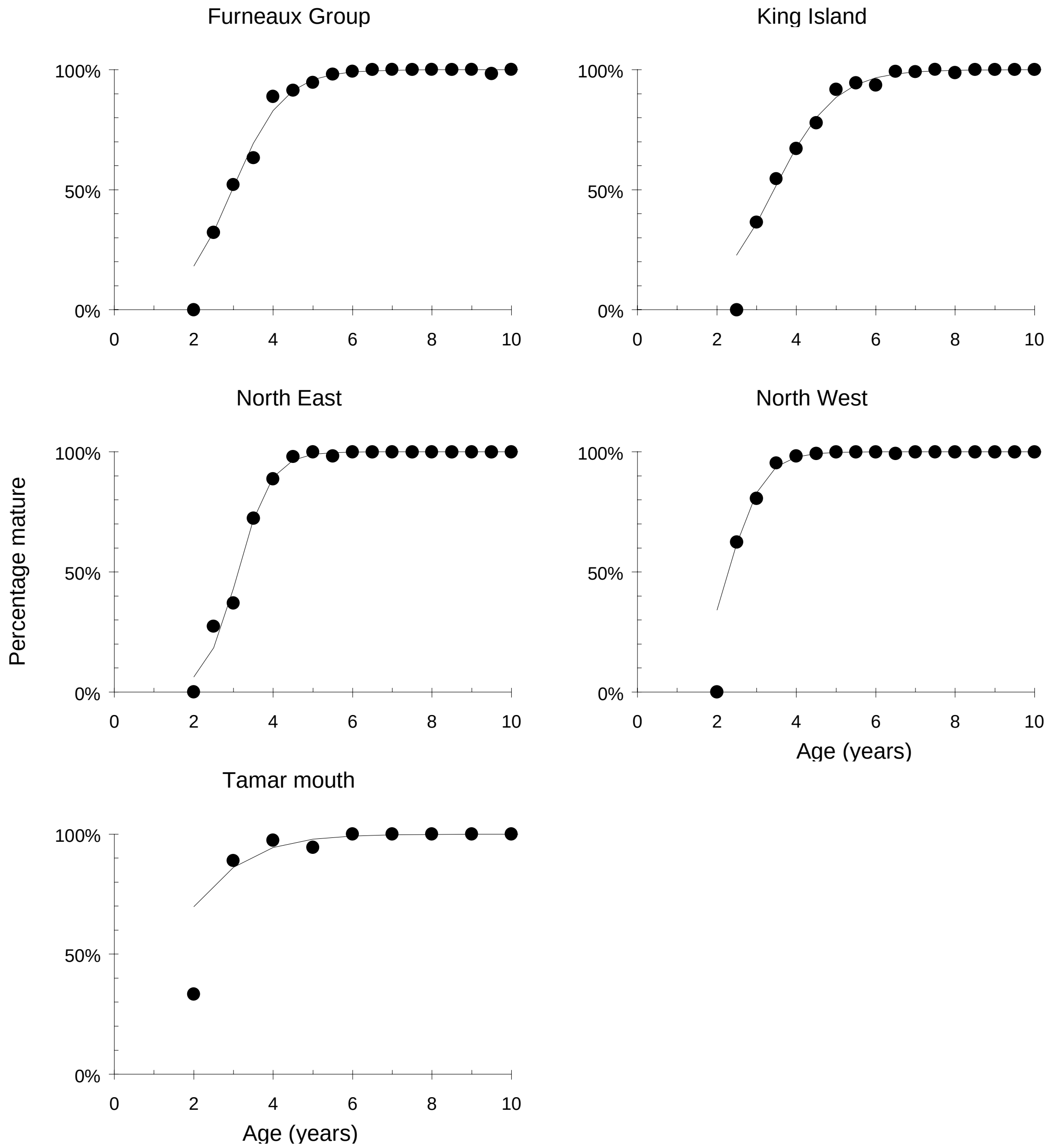

Fig. 12. Rates of maturation by age for *Haliotis laevigata* from the five regions of Tasmania. The solid line shows the fit of the maturation data to the logistic function described in Equation 4.

The approximate length at full maturity in each region was used as the basis for the estimation of the lengths attained by abalone after one to four subsequent breeding seasons. The age at approximate length at full maturity was estimated using the von Bertalanffy growth parameters, lengths were then calculated at this age plus one to four years. The results of these calculations are given in Table 8.

Table 8. Estimated lengths at which abalone achieve between one to four breeding seasons after full maturity. The von Bertalanffy growth parameters given in Table 4 were used to calculate these lengths for each region.

Region	Approximate length (mm) at 100% maturity	Estimated length (mm) after:			
		1 breeding season	2 breeding seasons	3 breeding seasons	4 breeding seasons
Furneaux Group	100	118	130	137	142
King Island	120	135	145	153	158
North East	100	119	132	142	148
North West	90	115	131	140	145
Tamar mouth	100	119	130	136	140

3.3.2 Fecundity

Previous studies have shown that the relationship between age and fecundity (measured as gonad cross-sectional area) is poor (Nash *et al.*, 1994). Relationships calculated between length and fecundity determined in this study were closer (Fig. 13) and show that fecundity increases exponentially with length (Table 9). The rate of increase of fecundity with length was strongly allometric ($y > 3$) at King Island.

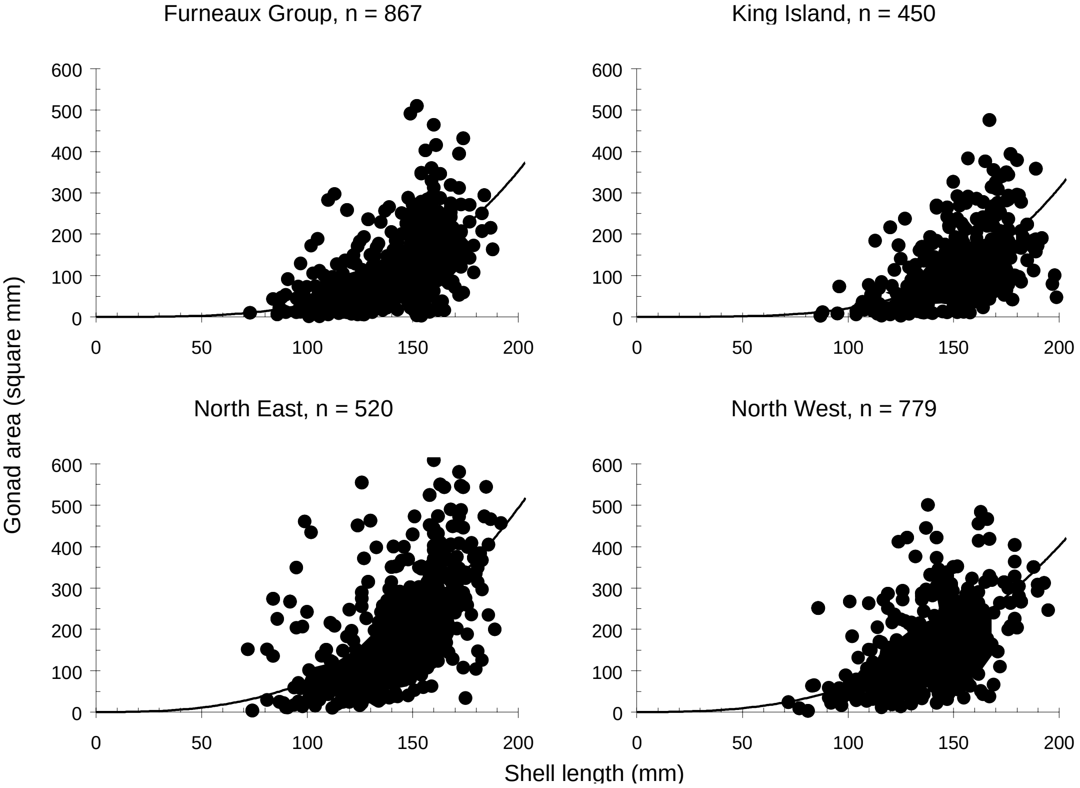

Fig. 13. Relationship between length and fecundity of *Haliotis laevigata* collected from four regions. Parameter values for the fitted power curves are given in Table 9. n is the number of abalone measured.

Table 9. Relationship between length and fecundity of *Haliotis laevigata* collected from four regions. x and y are constants in the function: Fecundity = $x.(\text{Length})^y$. r^2 is the coefficient of determination and n equals the sample size.

Region	x	y	r^2	n
All sites	0.0000589	2.914	0.283	2616
Furneaux Group	0.0000138	3.169	0.340	867
King Island	0.0000002	3.976	0.365	450
North West	0.0013619	2.322	0.270	779
North East	0.0000624	2.974	0.367	520

At some sites in the North west and at several sites in the North east some abalone had begun spawning at the time of sampling. The power relationship could not be fitted at these sites. A general relationship between fecundity and length for all sites was therefore calculated (Table 9). This relationship was assumed in subsequent egg-per-recruit analyses for the Tamar mouth (where gonads were not sampled) and at sites where the power relationship could not be fitted.

3.3.3 Sex ratio

The ratio of males to females differed significantly from a one to one relationship at several sites and in all five regions. In all cases where differences in sex ratio were significant there were more males than females.

Table 10. Regions and sites where the sex ratio differed significantly from a one to one relationship. χ^2: the Chi-squared statistic, P: Probability of the difference occurring by chance.

	Number of:			
Region and site	Males	Females	χ^2 statistic	P
Furneaux Group (all sites)	**1266**	**1065**	**17.2**	**< 0.01**
Moriarty Bay	214	143	13.7	< 0.01
Puncheon Island	148	113	4.4	0.035
King Island (all sites)	**727**	**596**	**12.8**	**< 0.01**
Disappointment Bay	95	67	4.5	0.034
North East (all sites)	**708**	**578**	**12.9**	**< 0.01**
East Barrett Reef	53	26	8.6	< 0.01
Lanoma Point	94	67	4.2	0.040
Little Waterhouse Island	104	63	9.6	< 0.01
Waterhouse Passage	91	60	6.0	0.015
North West (all sites)	**1044**	**876**	**14.5**	**< 0.01**
Little Stoney Island	114	83	4.6	0.033
Tamar mouth (all sites)	**266**	**198**	**9.7**	**< 0.01**
Shear Rock	128	90	6.3	0.012

3.4 Mortality Estimation

The catch curves used to calculate instantaneous total mortality (*Z*) for each of the five regions are shown in Fig. 14. By region the estimated rates of instantaneous total mortality ranged from 0.300 (26 % per annum) at King Island to 0.506 (40 % per annum) at the Tamar mouth (Table 11). Mortality rates were much more variable by site and ranged from 0.189 (17 % per annum) at Disappointment Bay, King Island to 1.301 (73 % per annum) at South-west Waterhouse Island in the North-east.

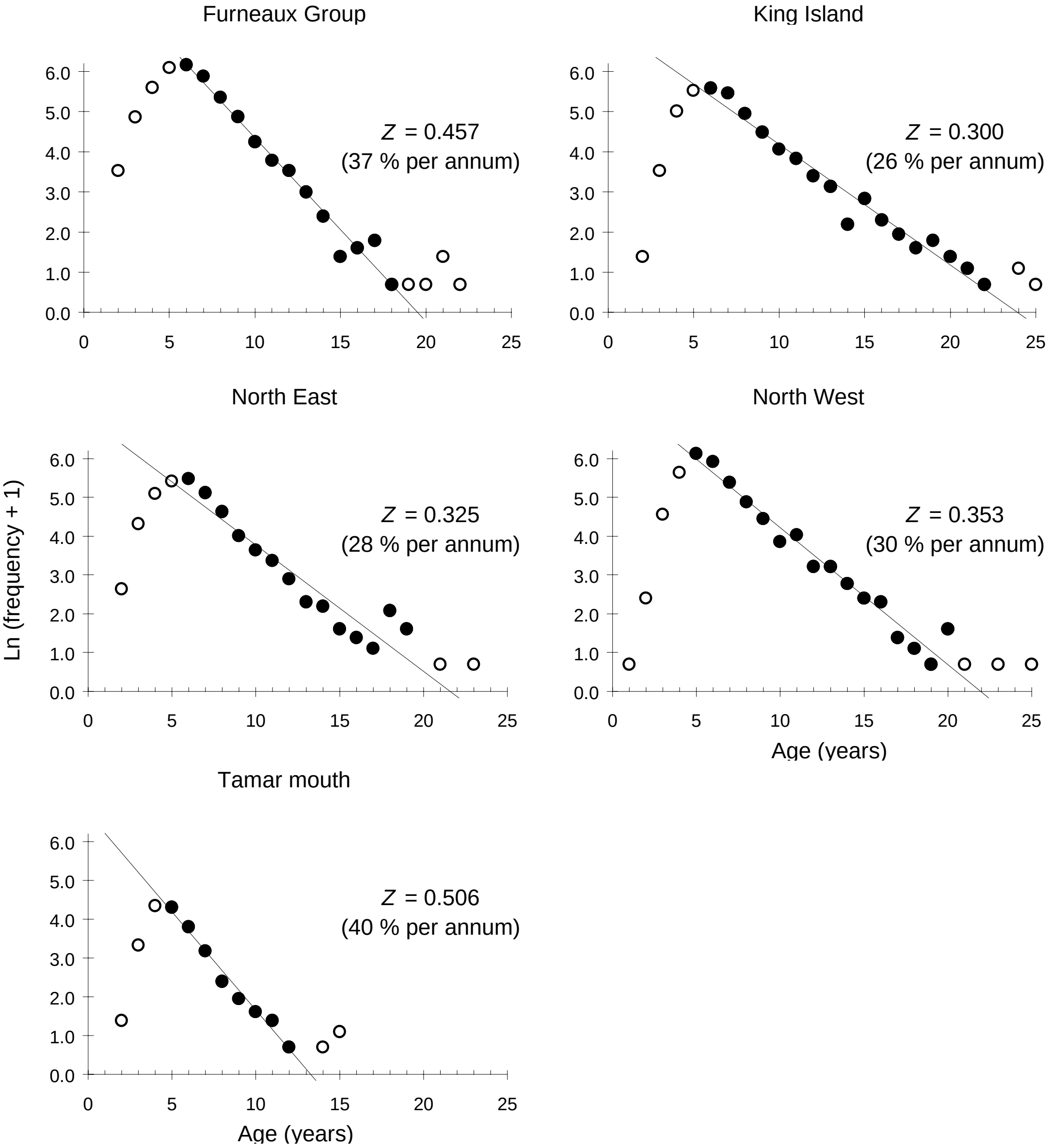

Fig. 14. Total mortality estimates of *Haliotis laevigata* collected from five regions. The total instantaneous mortality (*Z*) is calculated as the negative slope of the regression line fitted to the filled data points (●).

Table 11. Instantaneous mortality estimates (*Z*), annual mortality (=1-e^{-Z}) and survival rates (=e^{-Z}) of *Haliotis laevigata* collected from five regions and estimated by catch curve analysis. *n* is the number sampled, r^2 is the coefficient of determination. At sites where fishing mortality was thought to be low approximations are also given of the instantaneous rate of mortality ($Z_{A99\%}$) calculated from the maximum age ($A_{99\%}$) (Equation 6).

		Annual rate of:					
Region and site	*Z*	Mortality	Survival	*n*	r^2	$A_{99\%}$	$Z_{A99\%}$
Furneaux Group (all sites)	**0.457**	**37%**	**63%**	**2237**	**0.976**	**14**	
Apple Orchard Point	0.552	42%	58%	201	0.888	11	
Big River Cove	0.363	30%	70%	224	0.902	17	
Great Dog Island Passage	0.765	53%	47%	242	0.964	12	
Moriarty Bay	0.291	25%	75%	331	0.900	17	0.276
North Pascoe Island	0.292	25%	75%	175	0.865	16	0.291
Preservation Island	0.506	40%	60%	221	0.870	12	
Puncheon Island	0.477	38%	62%	240	0.953	11	0.419
Rebecca Bay	0.305	26%	74%	225	0.943	18	0.252
Shag Rocks	0.340	29%	71%	178	0.920	12	
Vansittart Beacon	0.435	35%	65%	200	0.929	13	
King Island (all sites)	**0.300**	**26%**	**74%**	**1374**	**0.969**	**19**	
Christmas Island	0.568	43%	57%	191	0.943	11	
Councillor Island	0.566	43%	57%	195	0.925	16	
Cowper Point	0.301	26%	74%	193	0.828	17	
Disappointment Bay	0.189	17%	83%	188	0.914	21	0.218
Elizabeth Rock	0.529	41%	59%	203	0.940	11	
Sea Elephant Reef	0.276	24%	76%	195	0.914	17	
Seal Bay	0.422	34%	66%	115	0.878	20	0.232
North East (all sites)	**0.325**	**28%**	**72%**	**1153**	**0.896**	**18**	
East Barrett Reef	0.430	35%	65%	86	0.945	9	
Foster Island East	0.239	21%	79%	112	0.938	19	
Foster Island West	0.429	35%	65%	229	0.952	12	
Lanoma Point	0.269	24%	76%	123	0.876	19	
Little Waterhouse Island	1.063	65%	35%	182	0.992	8	
South West Waterhouse Island	1.301	73%	27%	156	1.000	8	
Swan Island	0.251	22%	78%	121	0.858	20	
Waterhouse Passage	0.508	40%	60%	144	0.847	13	
North West (all sites)	**0.353**	**30%**	**70%**	**1835**	**0.963**	**16**	
Big Stoney Island East	0.323	28%	72%	173	0.803	21	0.221
Big Stoney Island West	0.562	43%	57%	203	0.970	11	
Black Reef	0.248	22%	78%	235	0.901	20	
Cave Bay	0.599	45%	55%	208	0.943	10	
Harbour Islets Inshore	0.566	43%	57%	194	0.934	11	
Harbour Islets Offshore	0.311	27%	73%	210	0.813	16	
Little Stoney Island	0.593	45%	55%	186	0.957	15	
Shepherds Bay	0.361	30%	70%	231	0.891	14	
Stack Island	0.228	20%	80%	195	0.961	16	
Tamar mouth (all sites)	**0.506**	**40%**	**60%**	**273**	**0.981**	**13**	**0.367**
Dotterel Point	0.443	36%	64%	158	0.885	13	0.347
Shear Rock	0.457	37%	63%	115	0.990	11	0.424

Fortunately the ageable and non-ageable fractions of each population had similar length compositions for those lengths which correspond to the age classes used to estimate Z (Fig. 7). Z is therefore likely to be accurate and it was not necessary to estimate the age composition of the entire population sample, including un-ageable animals, using the relationship between age and length, derived from ageable animals (i.e.; by using age-length keys).

Size-related crypsis and size-related ageability of abalone shells both act to underestimate Z for other species of abalone (Nash *et al.*, 1994). However, these factors do not appear to be as important for greenlip abalone and therefore the confidence in our estimates of Z calculated by catch-curve analysis is increased.

Estimates of the natural mortality rate, M, were derived from the abalone placed out on concrete blocks in the sea by Furneaux Aquaculture Pty Ltd. Of the 40 greenlip abalone aged one year old placed out, 17 survivors were found 8 years later. From the equation given by Seber (1982), M is therefore calculated at about 0.11 (10 % per annum).

Approximations of the total mortality rate based on the longevity of the abalone (Equation 6) were only calculated for sites with apparently little fishing mortality. These estimates yielded higher estimates of Z at stunted sites (Table 11). By site $Z_{A99\%}$ ranged from 0.218 (20 %) at Disappointment Bay, King Island to 0.424 (34%) at Shear Rock at the Tamar mouth.

3.5 Yield Optimisation

The values of the various parameters required for the yield-per-recruit (YPR) analyses are given in Table 12. Instantaneous rates of natural mortality (M) of 0.1 and 0.2 were used in the analyses. YPR relationships at the five regions are shown graphically at various levels of fishing mortality (F) and size-limit in Fig. 15 at M = 0.1, and in Fig. 16 at M = 0.2.

Table 12. Values of the parameters used in the calculation of yield-per-recruit and egg-per-recruit for greenlip abalone in the five regions. $A_{99\%}$ is the theoretical maximum age (as defined in Equation 6), L_∞, K and t_0: von Bertalanffy growth parameters (Equation 2); a, b: parameters of the length-whole weight equation (Equation 1); c, d: parameters of the logistic maturation-by-length equation (Equation 4); x, y: parameters of the length-fecundity equation (Equation 5).

		von Bertalanffy growth			Length-weight		Maturation-by-length		Length-fecundity	
Region	$A_{99\%}$	L_∞	K	t_0	a	b	c	d	x	y
Furneaux Group	14	150.12	0.455	1.32	0.0000367	3.242	-11.54	0.143	0.0000138	3.169
King Island	19	169.02	0.367	1.34	0.0000348	3.280	-11.67	0.122	0.0000002	3.976
North East	18	163.59	0.357	1.20	0.0000102	3.509	-14.38	0.183	0.0000624	2.974
North West	16	154.41	0.492	1.17	0.0000675	3.121	-11.51	0.161	0.0013619	2.322
Tamar mouth	13	143.86	0.583	0.85	0.0000230	3.344	-6.23	0.085	0.0000589	2.914

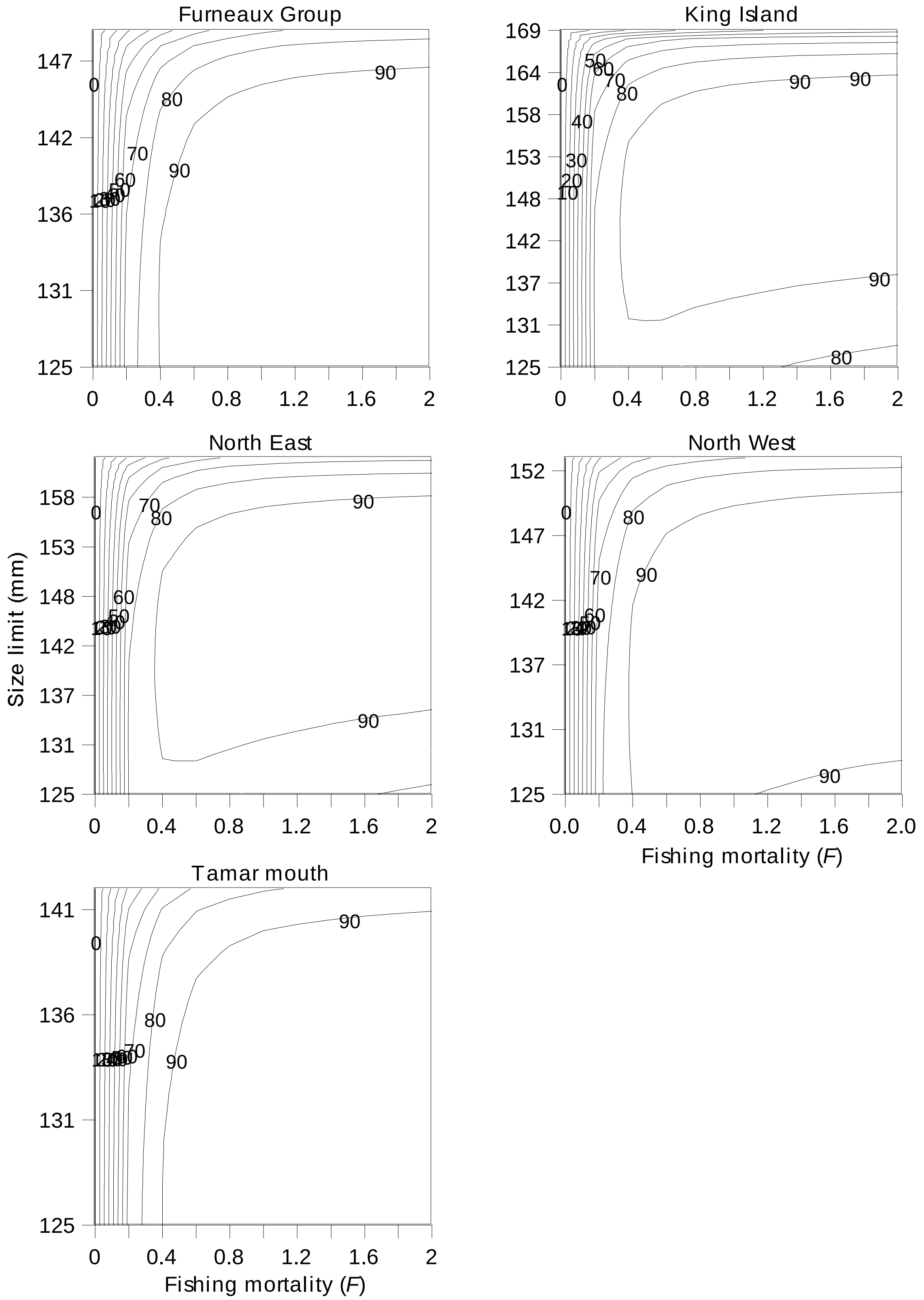

Fig. 15. Yield-per-recruit contour diagrams for *Haliotis laevigata* from the five regions estimated with an instantaneous rate of natural mortality (*M*) of 0.1. Isopleths indicate the percentage of the maximum potential biomass obtained at various size limits and levels of fishing mortality (*F*).

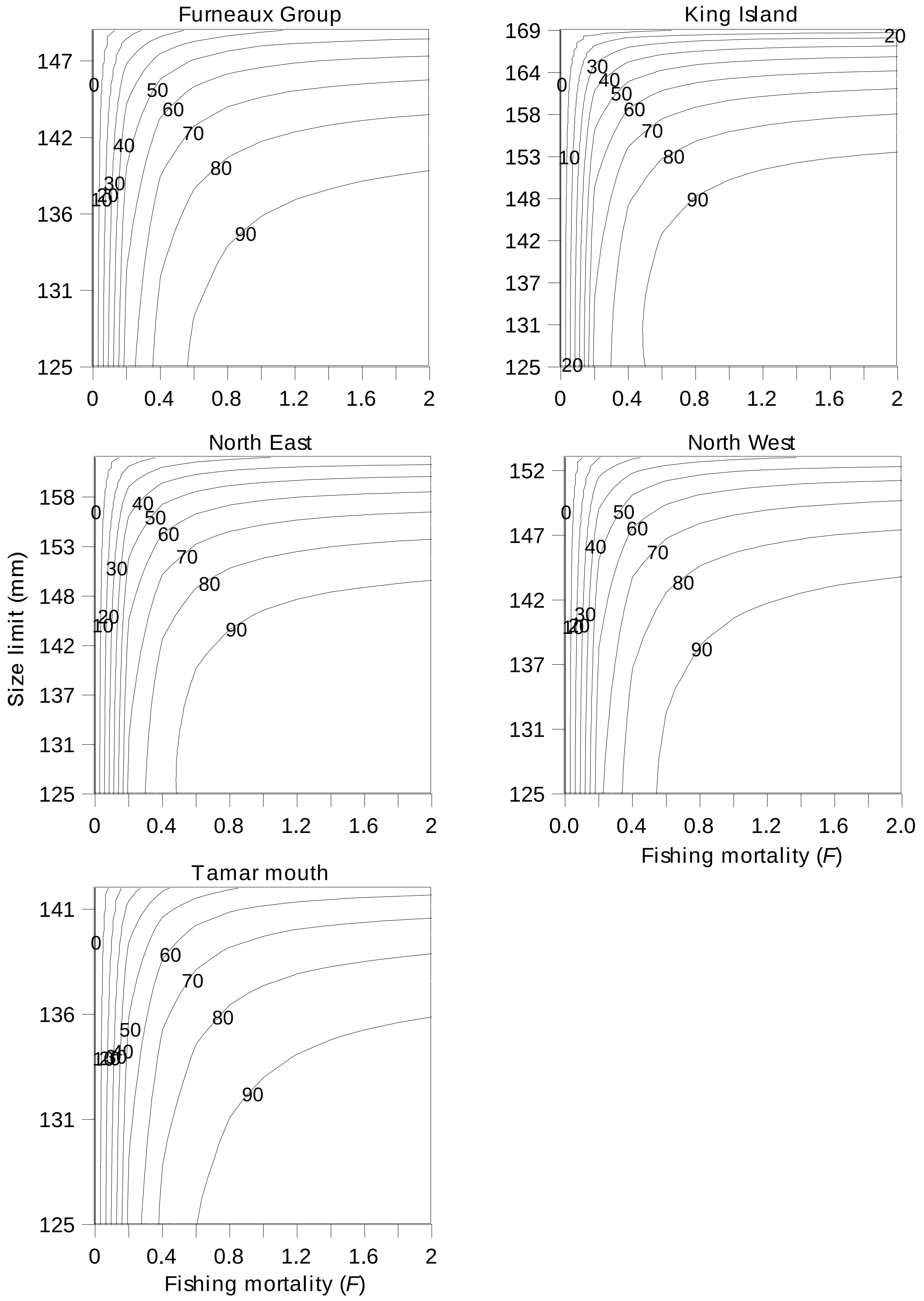

Fig. 16. Yield-per-recruit contour diagrams for *Haliotis laevigata* from the five regions estimated with an instantaneous rate of natural mortality (*M*) of 0.2. Isopleths indicate the percentage of the maximum potential biomass obtained at various size limits and levels of fishing mortality (*F*).

The sizes at which YPR is greatest for a range of *F* values are shown in Table 13. YPR analyses are sensitive to the rate of natural mortality (*M*). In these models a reduction in *M* increased the size at which the maximum yield would be obtained.

Table 13. Size (mm) at which yield-per-recruit is greatest at a range of values of natural mortality (*M*) and fishing mortality (*F*).

	Fishing mortality (*F*)				
Region	0.4	0.8	1.2	1.6	2.0
M = 0.1					
Furneaux Group	130	135	137	137	138
King Island	146	150	152	153	153
North East	141	147	148	149	150
North West	134	140	141	142	143
Tamar mouth	126	132	133	134	134
M = 0.2					
Furneaux Group	125	125	126	127	127
King Island	128	136	138	139	139
North East	126	133	134	135	137
North West	125	127	130	132	133
Tamar mouth	125	125	125	126	126

At relatively modest levels of *F* (0.4) and conservative levels of *M* (0.1) the size limit at which the yield is greatest is less than the interim size limits in all regions.

3.6 Egg Conservation

The values of the various parameters required for the egg-per-recruit (EPR) analyses are shown in Table 12. EPR relationships at the five regions were calculated at two levels of *M* (0.1 and 0.2). The results of these analyses are shown graphically at various levels of *F* and size limit in Fig. 17 (*M* = 0.1) and in Fig. 18 (*M* = 0.1).

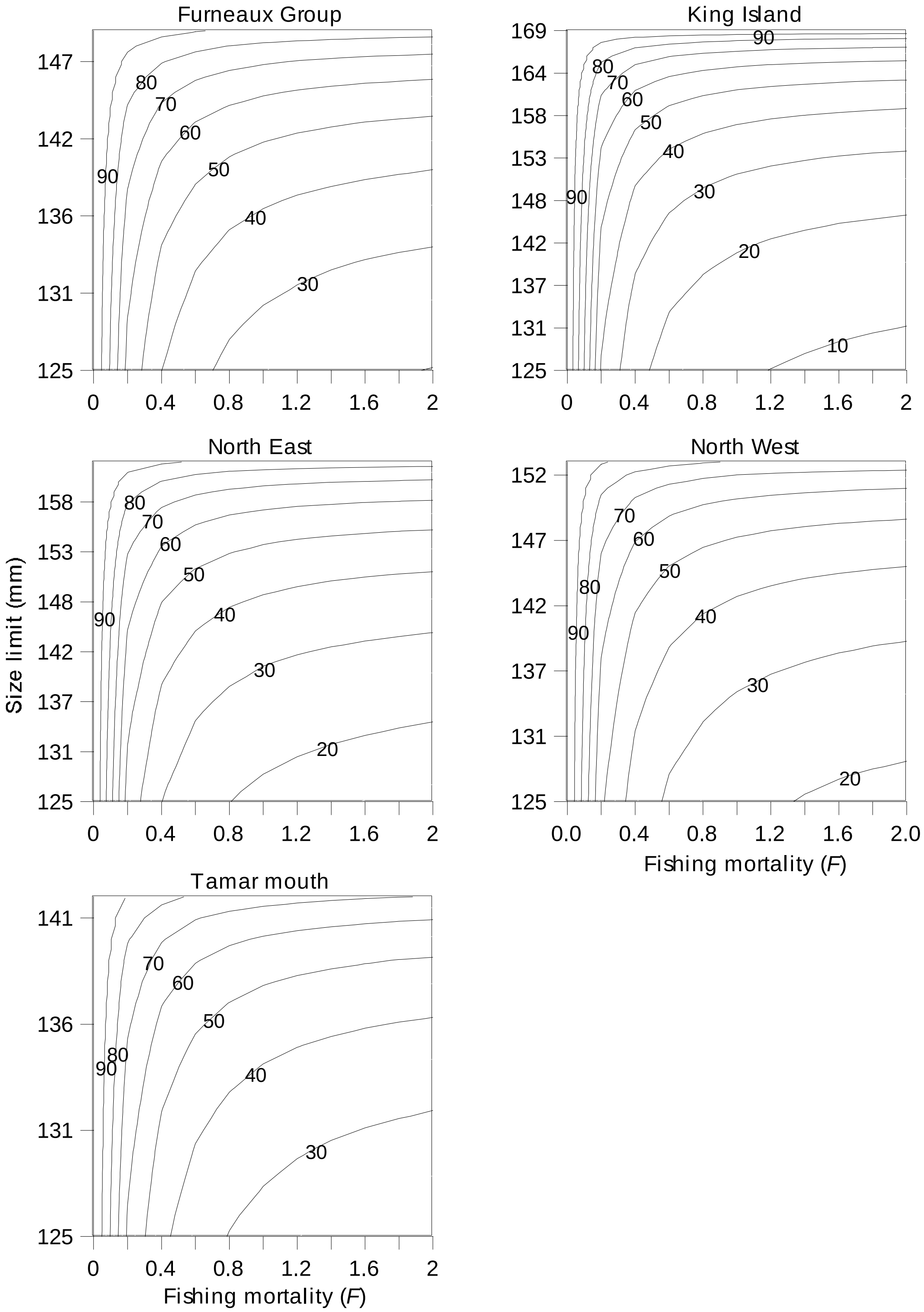

Fig. 17. Egg-per-recruit contour diagrams for *Haliotis laevigata* from the five regions. The value used of the instantaneous rate of natural mortality (*M*) was 0.1. Isopleths indicate the percentage of the virgin egg production conserved at different combinations of size limit and fishing mortality (*F*).

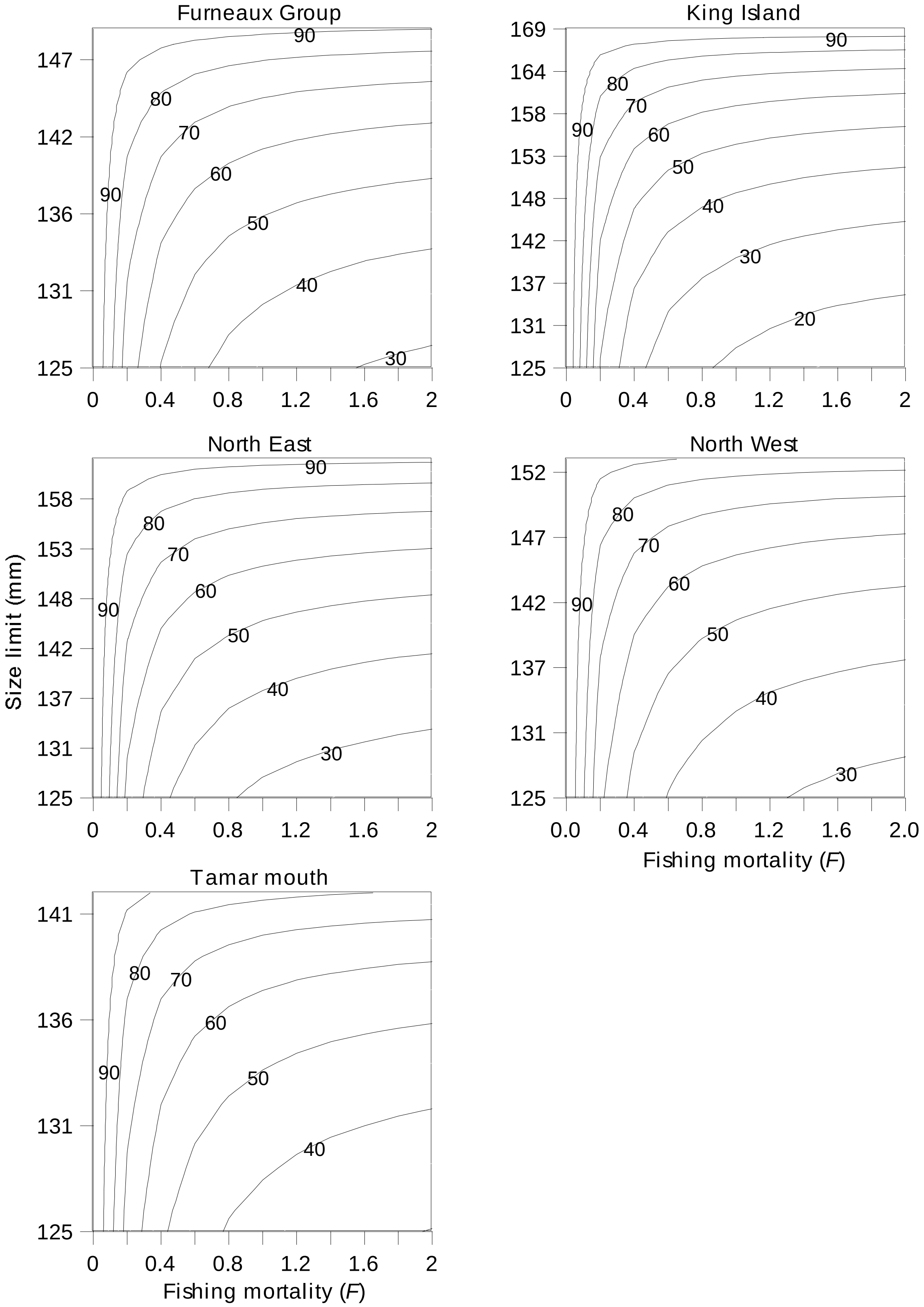

Fig. 18. Egg-per-recruit contour diagrams for *Haliotis laevigata* from the five regions. The value used of the instantaneous rate of natural mortality (*M*) was 0.2. Isopleths indicate the percentage of the virgin egg production conserved at different combinations of size limit and fishing mortality (*F*).

These analyses illustrate the sensitivity of EPR analyses to *M*: the greater the level of *M* the more egg production conserved at a given level of *F* and size limit. EPR analyses are also very sensitive to change in the maximum age (Fig. 19). An increase in the maximum age decreases the proportion of egg production conserved at a given level of *F* and size limit. The analyses reported in Table 14 were calculated at the level of $A_{99\%}$ rather than the actual maximum age found in the population.

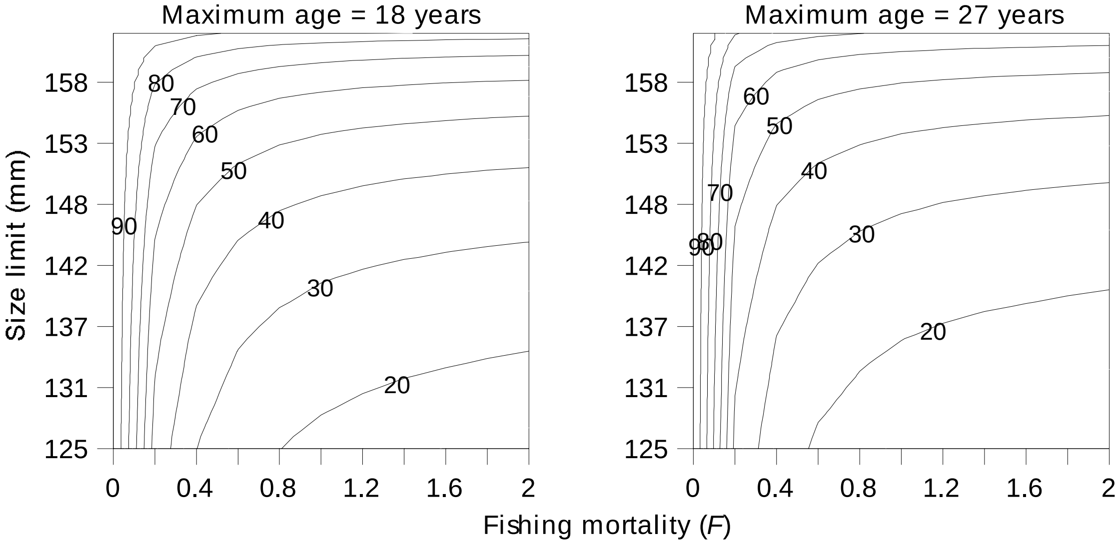

Fig. 19. Egg-per-recruit contour diagrams for *Haliotis laevigata* from the North east used to illustrate the sensitivity of egg-per-recruit analysis to the maximum age parameter. All the parameters used were the same in both analyses except for the maximum age. This was changed from $A_{99\%}$ (18 years) to the maximum age recorded in the region (27 years). Isopleths indicate the percentage of the virgin egg production conserved at different combinations of size limit and fishing mortality (*F*).

Table 14. Egg-per-recruit values expressed as a percentage of the total egg production in the absence of fishing. For each region values are given for two levels of natural mortality (*M*), several size limits and several levels of fishing mortality (*F*).

			Fishing mortality (*F*)									
Region	*M*	Size limit (mm)	0.2	0.4	0.6	0.8	1.0	1.2	1.4	1.6	1.8	2.0
Furneaux Group	0.1	135	66%	51%	44%	40%	37%	35%	34%	33%	32%	32%
		140	73%	60%	53%	49%	47%	45%	44%	43%	42%	41%
		145	83%	74%	68%	65%	63%	61%	60%	59%	58%	58%
		150	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%
	0.2	135	74%	61%	55%	51%	48%	46%	45%	44%	43%	42%
		140	80%	70%	64%	61%	58%	57%	56%	55%	54%	53%
		145	88%	82%	78%	75%	73%	72%	71%	70%	70%	69%
		150	100%	100%	100%	100%	100%	100%	100%	100%	100%	100%
King Island	0.1	145	51%	35%	29%	25%	23%	22%	21%	20%	20%	19%
		150	55%	41%	34%	31%	29%	27%	26%	25%	25%	24%
		155	61%	47%	41%	38%	36%	34%	33%	33%	32%	32%
		160	68%	57%	51%	48%	46%	45%	44%	43%	42%	42%
	0.2	145	62%	48%	42%	38%	36%	34%	33%	32%	31%	30%
		150	67%	54%	48%	45%	42%	41%	39%	39%	38%	37%
		155	72%	61%	56%	53%	51%	49%	48%	47%	47%	46%
		160	79%	71%	66%	63%	62%	60%	59%	59%	58%	58%
North East	0.1	140	56%	41%	35%	32%	29%	28%	27%	26%	26%	25%
		145	61%	47%	41%	37%	35%	34%	33%	32%	31%	31%
		150	66%	54%	48%	45%	43%	41%	40%	40%	39%	39%
		155	74%	64%	58%	55%	54%	52%	51%	51%	50%	50%
	0.2	140	67%	55%	49%	45%	43%	41%	40%	39%	39%	38%
		145	72%	61%	55%	52%	50%	48%	47%	46%	46%	45%
		150	77%	68%	63%	60%	58%	57%	56%	55%	54%	54%
		155	84%	76%	73%	70%	69%	68%	67%	66%	66%	65%
North West	0.1	135	58%	43%	36%	33%	30%	29%	28%	27%	26%	26%
		140	62%	48%	42%	38%	36%	35%	33%	33%	32%	31%
		145	68%	56%	50%	46%	44%	43%	42%	41%	40%	40%
		150	78%	68%	63%	60%	58%	57%	56%	55%	54%	54%
	0.2	135	68%	55%	49%	45%	43%	41%	40%	39%	38%	37%
		140	72%	61%	55%	52%	49%	48%	47%	46%	45%	44%
		145	78%	68%	63%	60%	58%	57%	56%	55%	54%	54%
		150	86%	79%	75%	73%	71%	70%	70%	69%	68%	68%
Tamar mouth	0.1	125	59%	42%	34%	30%	27%	25%	24%	23%	22%	21%
		130	63%	47%	40%	36%	33%	31%	30%	29%	28%	27%
		135	69%	55%	48%	44%	42%	40%	38%	37%	37%	36%
		140	79%	69%	63%	60%	57%	56%	54%	53%	53%	52%
	0.2	125	66%	51%	44%	39%	36%	34%	32%	31%	30%	30%
		130	71%	57%	50%	46%	43%	41%	40%	39%	38%	37%
		135	76%	65%	59%	55%	53%	51%	50%	49%	48%	47%
		140	86%	78%	73%	70%	68%	67%	66%	65%	64%	64%

Table 14 summarises the level of egg production likely to be conserved in each region at a range of size limits and values of *F*. For example, at a minimum size limit of 140 mm in the Furneaux Group, population egg production at a natural mortality of 0.1 and fishing mortality of 1.0 is 47 percent of the egg production of the unfished population. Derivation of these various EPR results using a range of possible parameter values allows an assessment of the impact of fishing on these abalone stocks to be made at several degrees of conservatism.

4. Discussion

4.1 Morphometry

Morphometric analyses were carried out in order to quantify the variability between regions, as well as to allow the detection of any changes in length-weight-shape characteristics that may occur through time. Changes in morphometry are particularly relevant to populations that presently are relatively unfished because there is evidence that shell quality improves and growth rates increase as a population of abalone is fished (Tarbath, 1999). The morphometric analyses conducted here therefore provide a useful baseline for reference in future studies.

4.2 Age and Growth Estimation

Many of the analyses and conclusions presented here depend on the relationship between numbers of shell layers and age. However, the assumption of two growth rings per year used here appears to be sound: The ring counts found in known-age abalone and the strong agreement between growth characteristics derived from age-length and the tag-recapture method provide strong verification of this relationship for greenlip abalone. The growth parameter L_∞ derived from tag-recapture data describes the maximum length of animals within a population. For age-length data this parameter describes the average maximum length of the oldest animals in the population. These parameters are therefore not strictly comparable (Francis, 1988). However, at the level of determination described in this study no differences between the parameters could be found between methods.

Whilst the interpretations of the data presented here appear to be sound, verification of the relationship between numbers of shell layers and age has not been confirmed across the entire geographic range of greenlip abalone in Tasmania. When a consistent maximum age is used in the analysis yield- and egg-per-recruit results are not greatly affected by the number of shell growth rings per year (Nash *et al.*, 1994). However, the results presented here demonstrate the strong sensitivity of egg-per-recruit analyses to the parameter of maximum age. Therefore it remains important to conduct ageing verification studies for greenlip abalone throughout the Tasmanian distribution of the species.

Von Bertalanffy growth parameters calculated in this study showed similar growth rates to those of greenlip abalone in South Australia (Shepherd and Baker, 1998). However, the theoretical maximum lengths (L_∞) in Tasmania appear to be smaller than those in South Australia.

In this study a corresponding increase was found in the number of major rings with an increase in brown rings. This suggests that the presence of brown rings may provoke the deposition of additional fine rings. Shepherd and Huchette (1997) found similar results for *H. scalaris* and suggested that similar results would occur in *H. laevigata*. They considered the number of brown rings to be an index of the extent of infestation. Fortunately such infestation appears to be less of a problem for greenlip abalone than blacklip. This is important because it increases the proportion of the population that have ageable shells. Therefore the extension of results calculated from the ageable population to the entire population under study can be done with more confidence.

4.3 Sexual Maturation, Fecundity and Sex ratio

4.3.1 Onset of Sexual Maturity

This study has shown that sexual maturation commences at about 3 years of age, and a steadily increasing proportion of successively older year classes is mature. Nearly all abalone are mature at 4 to 5 years of age. This is much younger than in blacklip abalone where full maturity is only achieved at about 10 to 12 years of age (Nash *et al.*, 1994).

In the Tasmanian blacklip abalone fishery, size limits have been established at the length at age of maturity plus two years. The rationale behind this practice has been to allow the abalone two years to reproduce once they become sexually mature. This rule of thumb was used in this study (Table 8), but the method has not been tested empirically for either species and may have limitations when applied to greenlip abalone. These limitations relate to the probability that recruitment is sporadic in greenlip abalone. The nature of recruitment in greenlip abalone is discussed further below. Sporadic recruitment would require that additional breeding seasons are required to ensure that all sexually mature abalone have had more than one chance to reproduce. It is therefore sensible to allow additional breeding seasons if applying this method of establishing size limits for greenlip abalone.

4.3.2 Fecundity

As an index of fecundity, gonad volume represents the potential fecundity only. Potential fecundity is probably greater than the true fecundity because all eggs in the gonad may not be released at spawning (Clavier, 1992). Therefore, the results of the egg-per-recruit analyses will not be affected if the proportion of ripe gametes that are released at spawning is not dependent on size. However, potential fecundity may not provide the same age-relative fecundity relationship as true fecundity: in abalone hatcheries young, small abalone spawn more frequently and vigorously than large, old abalone (Nash *et al*., 1994). If this is also true for wild greenlip abalone, the relationship between age and fecundity would be less steep than the volumetric indices of fecundity calculated here would suggest. A higher size limit would therefore not afford the increase in protection of egg production that the results presented here would indicate. This may be particularly important in regions such as King Island where the length-fecundity relationship was strongly allometric. Allometry suggests that the very large abalone are far more fecund. However, the fact that such abalone represent only a small proportion of the population and the possibility of infrequent and less vigorous spawning may substantially reduce the realised strength of this allometric relationship.

The use of gonad volume as a measure of fecundity also assumes that the length-gonad volume relationship or the age-gonad volume relationship does not, in relative terms, vary greatly throughout the reproductive cycle. This may be critical for *H. laevigata* because the spawning period of this species in Tasmania is relatively short. The differences in these relationships over the period of this study (Fig. 13) suggest that not all samples were taken when the populations were in peak reproductive condition. Sampling was scheduled in the period immediately prior to spawning. This was planned to ensure that the gonads of female abalone would be ripening. Unfortunately the large number of sites sampled meant that the sampling program extended over two months. At sites sampled close to the end of this period the length-fecundity power relationship could not be fitted to the data. This may have been due to an increased proportion of the abalone having already spawned prior to sampling.

The relationships calculated between length and fecundity were highly variable (Fig. 13). Whilst much of this variation in apparent fecundity may actually be caused by measurement error, reproductive studies of *H. rubra* in southern Tasmania have shown that there may be considerable variation in reproductive condition (and therefore fecundity) between individuals sampled at the same time (unpublished data). Measurement error is most likely caused by inaccurate tracing of the gonad cross-sectional area. Nash et al. (1994) found that measured gonad area was larger when pressure was applied to the conical appendage section during tracing. To avoid this difficulty we ensured that each conical appendage was hardened in alcohol prior to measuring its cross-sectional area.

4.3.3 Sex ratio

The significant departure from a one to one, male to female relationship at many sites could be caused by a combination of differing male and female growth rates and fishing. These effects are not examined here but a greater growth rate and maximum size in females would have the effect of increasing the selective pressure of the fishery on females.

Greenlip abalone tend to aggregate prior to, and during spawning (Shepherd, 1986). This behaviour is probably an adaptation to increase fertilisation success. An uneven sex ratio would mean that same sex aggregations would be more likely to be formed. This would be exacerbated where the density of the adult population has been reduced as a result of fishing such that the size of aggregations is small. Even in populations with an equal sex ratio 50 % of pairs and 25 % of triplet groups would contribute nothing to gamete production because of the respective probabilities that these groupings will be of the same sex. The consequence of an uneven sex ratio would therefore be reduced fertilisation success at spawning. Stock-recruitment relationships for greenlip abalone suggest that this would subsequently result in reduced recruitment to the fishery (Shepherd and Partington, 1995).

4.4 Mortality Estimation

Fortunately problems and complexities of mortality estimation caused by the existence of un-ageable greenlip abalone were negligible for most of the sites studied. This is because the un-ageable proportion of shells was generally very small and their size distribution approximately matched the ageable sample. Despite this the catch-curve analyses (Fig. 14), used here to estimate rates of instantaneous total mortality, rely on several other key assumptions:

- that all fully recruited age classes are equally vulnerable to sampling,
- that mortality rates are constant with age in the fully recruited year classes,
- that recruitment rates to the populations are constant over time, and,
- that the mortality rate is constant over time.

The youngest age class used in the estimation of total mortality (Z) for any region was five years of age. Analyses of the age at maturity suggest that these abalone were almost all mature, and because of their emergence into open habitat, equally vulnerable to capture. The first assumption of the catch-curve analysis therefore appears to be valid. The assumption of constant mortality across the fully recruited age classes has not been examined in Tasmanian greenlip abalone populations. If a marked decrease in mortality occurs with increasing age at the five regions described here, it would be evident as a trend in the frequency of the fully recruited age classes. These would describe a concave curve. This result was not found for the fitted points in the regressions for any of the regions (Fig. 14) and therefore suggests that the assumption of constant mortality rates for the fully recruited age classes was not violated.

Recruitment rates are probably not constant but it is reasonable to assume that, on average, they have been in the five regions surveyed. The regression lines fitted to the fully recruited age classes in Fig. 14 reflect this because they describe the average slope across several age classes. However, analysis on a regional scale will hide local fluctuations in recruitment. These fluctuations may be exacerbated by heavy fishing at some sites (such as the Waterhouse Island area). When fishing pressure has been so high that the density of adult abalone is greatly reduced fertilisation success is also likely to decline. Despite the tendency for greenlip abalone to aggregate before and during spawning (Shepherd, 1986), a reduced density and increased distance between spawning adults would mean that fewer aggregations would form, that aggregations would contain fewer abalone and that more aggregations would contain abalone of only one sex. Experimental studies have demonstrated that fertilisation success is highest when male and female adults are within two metres of one another and less than five percent at separations greater than 16 metres (S. Shepherd, pers. comm.). For these reasons it is likely that recruitment rate variation is likely to affect the estimation of Z by catch curve analysis on a local scale.

The epidemic nature of spawning in greenlip abalone also exposes the species to recruitment fluctuation. Such a reproductive strategy relies upon environmental conditions being favourable at the time of spawning to maximise fertilisation success. If conditions are not optimal reduced fertilisation success may result and be followed with consequent declines in settlement and recruitment.

The estimate of the instantaneous rate of natural mortality (M = 0.11, 10 % per annum) calculated here from the survival of known age abalone recovered from the Furneaux Aquaculture Pty Ltd lease area provides a useful lower estimate of the rate in other populations. It is likely that this rate underestimates natural mortality in other populations because of the isolated location of the abalone placed in the lease area. These abalone would probably have suffered less predation than abalone in the more complex and biologically-diverse main fishing areas. The relatively low overall density of the abalone in the lease area may also reduce the rate of natural mortality in this area (Shepherd and Godoy, 1989).

The estimate of M from the lease area was lower than any of the rates of $Z_{A99\%}$ calculated from longevity (Table 11). At sites of low fishing mortality $Z_{A99\%}$ was assumed to approximate M. Longevity-based estimates suggest that M in lightly-fished but not stunted populations (eg. Rebecca Bay, Disappointment Bay and Seal Bay) is about 0.2 to 0.25 (20 to 25 % per annum) (Table 11). Estimates of M from stunted populations do not appear to be useful for wider application to unfished areas. Values of M in stunted areas were much higher than at most fished sites. This suggests that density dependent mortality may be an important component of natural mortality in stunted greenlip populations as it is other abalone populations (Shepherd and Godoy, 1989). Density dependent mortality implies that the rate of natural mortality may change over time as the density of a population is altered. One of the key assumptions of mortality estimation by catch-curve analysis may therefore be violated.

4.5 Yield-per-recruit and Egg-per-recruit Analyses

This study aimed to provide estimates of the population parameters necessary for per-recruit analyses. If there were no relationship between stock size and subsequent recruitment, then a greater yield could be achieved from the greenlip stocks by fishing them at size limits lower than the current limits (Table 13, Fig. 15 and Fig. 16). However, evidence from other abalone fisheries indicates that abalone fisheries are prone to collapse because of recruitment failure (Breen, 1986; Tegner *et al.*, 1989). Whilst it is uncertain whether these declines were caused directly by recruitment overfishing (Breen, 1992), the possibility of recruitment overfishing occurring demands that a proportion of egg production be protected when size limits are established. The egg-per-recruit analyses given here provide a mechanism for determining the proportion of virgin egg production conserved at various combinations of size limit and fishing mortality under equilibrium conditions.

Unfortunately egg-per-recruit analyses are particularly sensitive to changes in parameters which are difficult to define. When M or the theoretical maximum age (A_{max}) is varied, the proportion of egg production conserved also changes greatly (Fig. 17, Fig. 18 and Fig. 19). Whilst egg-per-recruit analyses assume that rates of recruitment and mortality are in equilibrium, fluctuation in these rates is likely in greenlip abalone. Therefore it is sensible to construct these analyses conservatively and to interpret the results cautiously. In this study this was achieved by selecting a low rate of natural mortality (M). Shepherd and Baker (1998) argue that egg production should he conserved at 40 to 50 % of virgin levels for large greenlip abalone populations, and at even higher levels for more vulnerable small populations. In this study these thresholds were achieved at different size limits in each of the regions (Table 15). Even at high levels of fishing mortality the 150 mm interim size limit exceeds the 50 % threshold in the Furneaux Group and at the Tamar mouth. The interim size limit of 150 mm at King Island is insufficient to maintain more than 40 % of virgin egg production at moderate levels of fishing mortality (Table 15). These results suggest that the present interim size limits are within an appropriate range in the North east and North west but that they could be:

- raised at King Island,
- lowered in the Furneaux Group, and,
- set at a new lower level should fishing commence at the Tamar mouth.

Whilst this analysis presents a convenient range of size limits for each region, establishing size limits entirely on this basis may not be sensible. This is because of the limitations of egg-per-recruit analysis that have already been discussed. Furthermore blanket size limits may not provide enough protection for populations that are already overfished and in disequilibrium.

Table 15. Estimated size limits at which 40 % and 50 % of virgin egg production is conserved in each of the five greenlip-producing regions. Moderate and high levels of fishing mortality are compared (F = 0.6 and 1.0, 45 % and 63 % per annum die due to fishing, respectively). A rate of natural mortality (M) of 0.1 and a maximum age of $A_{99\%}$ (Equation 6) was used in all analyses. The old and interim size limits for each region are given for comparison.

	F = 0.6		F = 1.0		Existing size limits	
Region	40 % EPR threshold	50 % EPR threshold	40 % EPR threshold	50 % EPR threshold	Old limit	Interim limit
Furneaux Group	132	138	137	142	140	150
King Island	154	159	157	162	140	150
North East	144	151	148	153	140	150
North West	138	145	143	147	132	140
Tamar mouth	130	136	134	138	140	150

4.6 Implications for Management

Perhaps the most important limitation of the analyses presented here is the inability to accommodate variable recruitment to the populations. At heavily exploited sites gamete production would be very low if adult densities were so reduced that physical separation of adults denied the opportunity for successful fertilisation. Inability to find a mate of the opposite sex may also be exacerbated by the departure from an even sex ratio. These mechanisms could combine to cause greatly reduced recruitment and have been described as the likely cause of poor recruitment in depleted populations of greenlip abalone in South Australia (Shepherd and Partington, 1995).

Egg production and recruitment for greenlip abalone is probably best ensured by the conservative setting of size limits and by the maintenance of moderately low levels of fishing mortality. The size limits suggested in this study are based on conservative estimates of key parameters and allow for moderate increases in the level of fishing mortality. Whilst the establishment of conservative size limits is simple to apply uniformly this form of management cannot overcome the uneven distribution of diver effort which appears to be occurring in the greenlip fishery. The liberty of divers to fish anywhere, means that a reduction in total effort will not necessarily provide a reduction in fishing mortality in the most vulnerable populations. Uneven distribution of effort can occur because divers prefer fishing areas closer to their home port (eg. Great Dog Island and the Waterhouse Island areas). Hence more accessible populations tend to be those most exploited (evident as higher rates of F in Table 11) and those most in need of protection or restoration.

It is also important to understand that a chosen size limit will provide differing levels of protection to abalone populations at different localities. The analyses presented here assume that the sites sampled are generally representative of their regions. Locations exist within each region where peculiar growth and mortality rates mean that the local population is not well described by the biological parameters assumed for the region (Table 4). In the King Island region, where it is suggested that size limits be increased, slower growing stocks that do not reach the new size limit may be lost to the fishery. This may transfer the fishing effort elsewhere within the region and hence increase the fishing mortality on the remaining accessible populations. Several processes should counteract this:

- the greater protection afforded to smaller, slower growing populations may benefit the region by acting as a source of egg production,
- the increase in size limit will tend to better protect those stocks which might receive increased effort,
- the new size limit would be chosen such that it accommodates higher levels of fishing mortality than those currently estimated (F at 0.6 is greater than the estimated fishing mortality at any of the King Island sites (Table 11)).

Egg production and recruitment may also be enhanced by the protection of populations of high reproductive capacity. Shepherd and Baker (1998) proposed that populations of greenlip abalone may act as ‘source’ and ‘sink’ areas for gamete production and settlement. This notion suggests that closed areas may play an important role in the maintenance of egg production and rebuilding of populations. Abalone within a closed area may grow to a larger size where fecundity is maximal and they can aggregate into very large clusters where fertilisation success is high. A well-placed area will ensure that larvae are carried out of the closed area to enhance recruitment in downstream populations. Closed areas also provide important contrast between populations that is often required for research projects. A pressing need exists to define the relationships between aggregation structure, adult density and potential recruitment. Quantifying these relationships will be difficult but is nevertheless crucial if predictions of egg production are to be validated.

The perception of divers about the status of populations is also an important part of the establishment of appropriate size limits. The analyses presented here do not accommodate these perceptions. Where concern exists over the reproductive potential of a population it may be prudent to set interim size limits at conservative levels that allow extra capacity for the rebuilding of population. The limits suggested by egg-per-recruit analysis may then provide a baseline for the establishment of size limits in the longer term. Already depleted populations are likely to be in disequilibrium and therefore have high recruitment variability. Without adopting additional restoration measures these populations may never recover despite the establishment of more conservative size limits.

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