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ESTIMATES OF GROWTH AND NATURAL MORTALITY OF THE BLACKLIP ABALONE (*HALIOTIS RUBRA*) IN TASMANIA

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Summary

Studies into growth and natural mortality of the blacklip abalone (*Haliotis rubra* Leach) were undertaken at three sites on the Tasmanian coastline. These sites were closed to abalone fishing for the course of the study. A total of 10,000 abalone were tagged during four separate tagging events at six-monthly intervals. One year following the final tagging event, an intensive recapture exercise took place at each site.

Growth was measured by analysis of length increments in tagged individuals. Mortality was measured by the rate of disappearance of the abalone *i.e.* the decline in probability that abalone from preceding tagging events were recaptured. The abalone were double tagged, and mortality estimates were adjusted for tag loss. To counter the effects of migration upon the rate of disappearance, a grid was set up in one study site, and the position of release and recapture of each abalone was recorded. At another site, a preliminary search was undertaken to find abalone within the site. Subsequent searching was undertaken with the intention that all parts of the site should receive the same level of effort to ensure equal representation of abalone from each tagging event. Research divers searched the third site initially, after which it was opened up to licensed abalone divers who were paid a reward for the return of tagged shells.

At two sites, the quantity of abalone recovered from the earliest tagging events was very small, which, after adjustment for tag loss produced instantaneous rates of disappearance of tagged abalone greater than 1.0. At the third site, large numbers of abalone marked in the earliest tagging event were recovered, producing a non-linear rate of disappearance. The high and disproportionate rate of disappearance was attributed predominately to overgrowing of tags by fouling organisms and it was subsequently not possible to determine rates of natural mortality from rates of disappearance. It was found that the useful life of the laminated disc tags could be as short as two years before they were completely hidden by fouling.

The requirement for structurally sound shells for successful attachment of tags caused inadvertent selection of smaller abalone and rejection of many larger abalone with brittle shells. Recovery rates of tagged shells were highest among smaller abalone, indicating that it was difficult to achieve successful tag attachment to large abalone. Estimates of growth rate were biased by the inability to adequately measure growth of these larger (older) abalone.

Samples from abalone populations were collected at all three sites both before and after the study. The shells were aged and used for growth and mortality analyses, and the results compared with the growth and mortality analyses of the tagged abalone. The relative differences in growth rate between sites observed in the mark-recapture study were mirrored in growth rates from the age-length study. This confirmed the belief that blacklip abalone lay down annual growth rings at these sites. Estimates of natural mortality from catch-curves were lower than the rates of disappearance from the mark-recapture study, but generally higher than those from earlier studies in other parts of the Tasmanian coast. Instantaneous rates ranged between 0.29 and 0.41.

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1. Introduction

This study was developed during the early 1990's as part of a strategy to manage the Tasmanian blacklip abalone (*Haliotis rubra* Leach) fishery by setting size limits that allowed a maximum sustainable level of production.

The quantity of abalone produced from the Tasmanian abalone fishery has fluctuated. Catch levels peaked in 1984 at about 4500 tonnes and sparked concern that abalone were being harvested at unsustainable levels. The following year saw the introduction of individual quotas for divers, and the total allowable catch (TAC) was fixed at 3806 tonnes. This was progressively reduced to 2958 tonnes in 1988. Then followed a sharp decline in TAC to 2100 tonnes in 1989, due to industry concern that abalone stocks were being reduced to low levels. There were fears that the fishery might decline in the way that many abalone fisheries in other countries had done, which had often been attributed to over-fishing.

Determining appropriate catch levels since the introduction of a TAC to the fishery has been a difficult task. To effectively manage a fishery, TACs should be set at the optimal level of sustainable fishing. Exactly what constituted a sustainable level of catch is the subject of much debate. Achieving this ideal will require understanding of the factors that drive population growth and some understanding of their interaction. If TACs are determined without regard to the productivity of stocks in terms of growth, recruitment and mortality, catch levels may be inappropriate and either fail to conserve stocks in a sustainable manner, or squander the resource by allowing too little to be taken.

Furthermore, while imposing a general constraint on the catching of all abalone stocks, a TAC may fail to prevent localised stock depletion. It is possible to fish stocks to unsustainable levels on a small scale, particularly if the economic benefits from such a fishery outweigh the cost of taking of abalone at low catch rates. Consequently, a TAC set on the fishery as a whole may fail to prevent localised stock collapse. Alternatively, TACs may be set too conservatively, causing more isolated stretches of coastline to receive minimal fishing pressure, to the economic detriment of the State.

Managers of the Tasmanian abalone fishery have made several attempts to account for variation in growth and its effect upon stock dynamics. Initially, the size limit was set at 6 inches (152 mm), but this was reduced to 5 inches (127 mm) in 1965 after more information about growth rates became available. In 1987, the minimum legal size of abalone was raised from 127 to 132 mm, and two years later, to 140 mm on most of the West and South Coast. These later changes to size limits were determined by adding the estimated length of two years growth to the size at which abalone in those areas became sexually mature, thus ensuring that stocks would have some years of breeding before being fished.

While undertaking these measures, it was recognised that they were crude and relatively imprecise. Size at sexual maturity can at best be only a generalised measure, because of the high variability in growth rates between adjacent stocks. The degree to which an increase in the size limit would increase levels of egg production was unknown, as was the effect of increased egg levels upon subsequent recruitment to the fishery.

In the late 1980’s, estimates of yield- and egg-per-recruit were made following a study of blacklip abalone stocks in Bass Strait (Nash *et al*., 1994), and were used to determine optimal size limits for a limited fishing season in that area in 1989. This work demonstrated the benefits that might flow to the fishery if similar studies were undertaken in other Tasmanian waters. However, the success of such work on a statewide basis depended upon better estimates of rates of growth and natural mortality than currently existed.

Abalone in the south of the State generally grow larger and faster than those from more northern waters (Nash, 1992). Because blacklip abalone become sexually mature at age rather than size (Nash *et al*., 1994), southern abalone mature at a greater size than their northern counterparts. The difference in growth is so large that some stocks in northern waters have average maximum sizes below the size limit, while more southern stocks may be taken while sexually immature.

Shell ageing techniques described by Prince (1988a) enabled rapid assessment of growth in blacklip abalone, and while such growth information was relatively easy to obtain, it depended upon the assumption that *H. rubra* laid down one growth ring in its shell each year. Prince (1988a) and Nash (1995) found strong evidence for this assumption in stocks at George III Rock and Shag Rock Bay respectively (both locations in south-eastern Tasmania), but McShane and Smith (1992) found it unwarranted after studying three populations in Victoria. There was no evidence for the assumption in other parts of Tasmania.

In conjunction with their shell ageing work, Prince (1991; 1988b) and later Nash (1995) developed a method for marking abalone by fastening disc tags into respiratory pores. This method had advantages over earlier marking techniques (which included tags fastened with wire and glue). Their work demonstrated that abalone growth rates could be reliably measured by analysis of length increments, and avoided the need to determine rate of deposition of growth rings inherent with their shell ageing methods.

Nash expanded his egg production study to include blacklip stocks from the south and east of the State (Nash, 1992). He noted that there was great variation in rates of mortality between different areas, which made it difficult to determine reliable estimates of egg production and yield. A further difficulty stemmed from the use of catch-curves to measure mortality, which again relied upon assumptions about the rate of deposition of growth rings.

Earlier work by Beinssen and Powell (1979) demonstrated a method that was not reliant upon successful age determination, and that could be used to measure the rate of instantaneous natural mortality (*M*) in populations of *H. rubra.* They measured the decline in rate of recapture of tagged abalone over time and from this, estimated *M* at 0.2.

The current study of natural mortality and growth among populations of blacklip abalone was developed from these earlier studies. It sought to meet the needs expressed by managers for better information with which to manage the industry. The project was predicated upon the assumption that some geographically intermediate stocks were optimally protected by the 132-mm size limit, given latitudinal trends in growth rates between northern and southern Tasmania (Nash, 1994).

By using mortality and growth parameters from this study, the level of egg production from such stocks may at some future stage be measured, and used as a standard by which to determine size limits for stocks at the geographic extremes of the State.

2. Methods

2.1 Site selection

Three sites were selected, one on the West Coast and two on the East Coast (Fig. 1).

On the West Coast, size-at-maturity analyses suggested that the 132-mm size limit extended good protection only as far south as Gannet Point, a series of rocky outcrops in the far north of the West Coast. A site at Couta Rocks, about 15 km further north was subsequently chosen. On the East Coast, the sites chosen were at Ironhouse Point, south of Falmouth and the other at Magistrates Point, south of Darlington on Maria Island.

Because we sought to measure only *natural* mortality, the study sites and surrounding areas at Couta Rocks and Ironhouse Point were closed to abalone fishing during the course of the study (September 1992 to March 1998). Magistrates Point is within the boundaries of the Maria Island marine reserve, and has been closed to fishing since the inception of an earlier tagging study in 1966. Because of the low level of effort in the industry at that time, it is likely that there has never been any significant disturbance to abalone populations at Magistrates Point.

All sites were protected from illegal fishing and amateur diving by their close proximity to nearby communities. The Ironhouse Point and Couta Rocks sites are both overlooked by local residents. Parks and Wildlife rangers drive past Magistrates Point several times a day. We are confident that the sites were not fished during the study period.

The sites chosen were generally sheltered, relatively easy of access, and featured extensive areas of reef shallow enough for prolonged diving. All sites had substantial quantities of blacklip abalone. They all featured large areas of sand bottom interspersed amongst the reef, which was felt might help prevent migration of abalone out of the study area.

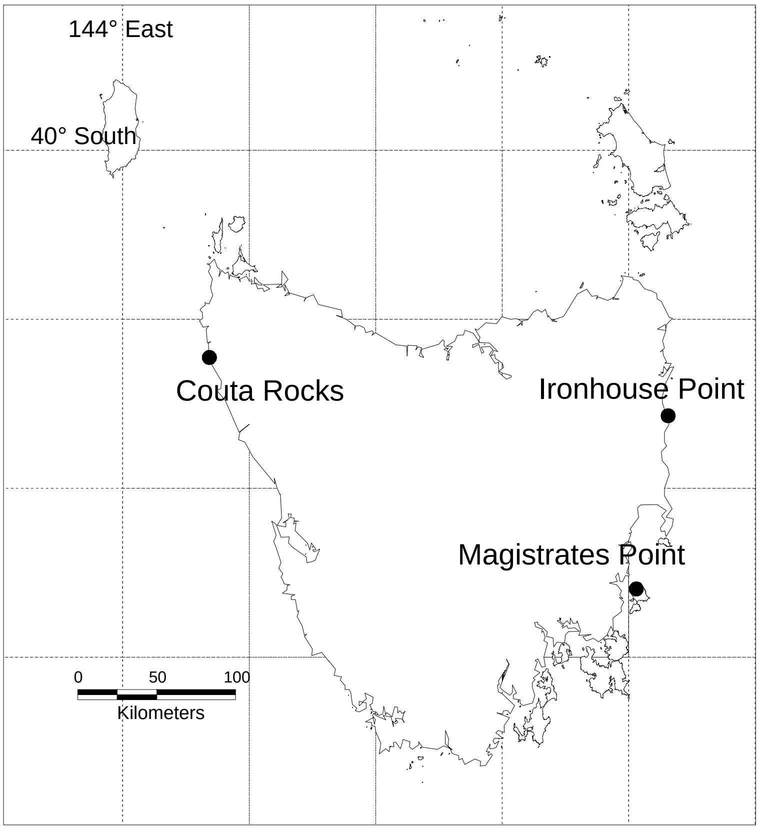


Fig. 1. The growth and mortality study was undertaken at three sites in Tasmania. On the north part of the West Coast, a site was chosen at Couta Rocks. Two sites were chosen on the East Coast - one at Ironhouse Point in the north, and the other (Magistrates Point) on the western shore of Maria Island.

2.2 Tagging of abalone

At all three sites, abalone were tagged in four discrete events between 1993 and 1995, at approximately six month intervals. At Ironhouse Point and Couta Rocks, 1000 abalone were usually tagged at each event, although the last tagging event at Couta Rocks was cut short by bad weather and only 350 abalone were tagged. The study area at Magistrates Point was much smaller and consequently only 500 abalone were released at each tagging event. A total of 2021 abalone were tagged at Magistrates Point, 4066 at Ironhouse Point and 3371 at Couta Rocks.

Abalone were selected randomly for tagging. However, those of shell-length less than 80 mm were not tagged because it was considered that the size of the tag may affect smaller abalone.

The tags used were made by Floy Tag and Manufacturing Incorporated, of Seattle, USA. They consisted of laminated plastic discs of between 12.5 and 15 mm diameter each uniquely numbered, and were obtained in several different colours. They were fastened to the abalone by plastic rivets of 3.2 mm diameter attached through open respiratory pores. During the first tagging event, white nylon rivets were used that were fixed by a special applicator. These rivets were particularly difficult to use and subsequent events used black nylon “Snap” rivets that could be closed by thumb pressure. The black rivets (part number 27SR0012) are distributed in Australia by NPA Pty Ltd of Kilkenny, South Australia.

Each abalone was marked with two tags. The first (open) respiratory pore (furthest from the growing edge) and third respiratory pores were the preferred sites for attachment. Respiratory pores were carefully reamed out to 3.2 mm hole-size with a drill bit, so that the rivets did not cause undue pressure and consequent crumbling of the shell. Every tagged abalone was checked to make sure that the tags were securely fastened. This tagging procedure has been used extensively in Tasmanian abalone research and generally follows that described by Prince (1991).

At Magistrates and Ironhouse Points, attachment of tags was done underwater to minimise stress to the abalone. The process of tagging abalone (which involves measuring and recording as well as attaching tags) takes much longer when done underwater than in a boat or on land. At Couta Rocks, where weather conditions limit diving opportunities, tagging usually took place in a boat because it was necessary to tag abalone as quickly as possible. However, during the first two tagging events at this site, some underwater tagging was done.

Great care was taken to ensure that the newly tagged abalone were firmly re-attached to the reef before the diver left them. Any abalone that showed signs of damage (cuts, bleeding or shell damage) were not tagged. It was recognised, though, that injured abalone may have been tagged without the animal’s immediate distress being detected. After each tagging event, a search of the release area was made to check for loose tags and injured or dying abalone. Usually, injured or dying abalone were indicated by the presence of numbers of fish, particularly wrasse. Dead and injured abalone or abalone with loose tags were removed from the water.

During the second and third tagging events, a search was undertaken for previously tagged abalone. Subsequently, several hundred abalone were measured underwater at each site. These data were used in the final growth analyses.

2.3 Migration

Observations were made of movement by tagged abalone at Magistrates Point. The study area at this site consisted of 100 metres of fringing reef along the rocky shore of the point (Fig. 2). At its eastern end was a sandy beach. Offshore from the reef, the bottom was sand. At the other (western) end of the site, off the end of the point, the reef ran out into deep water. The study site was divided along its length into five equal sections, each 20 metres wide. Galvanised chain was used to mark the boundaries. At each tagging event, an equal number of abalone were tagged in each of the five sections, and the position (section number) of each released abalone was recorded.

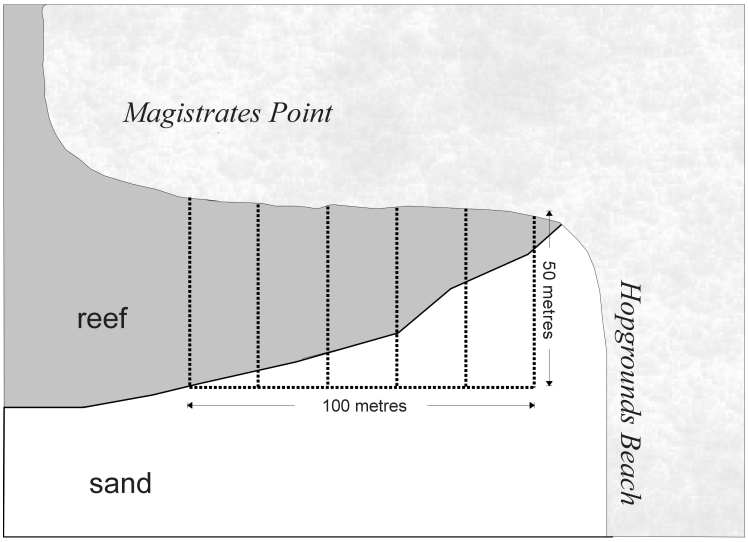


Fig. 2. The site at Magistrates Point, Maria Island, showing the structure of the grid and its position relative to the reef. Five distinct lanes were set out over the reef. The position of tagged abalone at both release and recapture with respect to the lanes was used to determine net movement over the tagging period.

When abalone were recovered from Magistrates Point, the section from which each abalone was taken was recorded. The net movement during the period of release was calculated by comparing the two positions.

At Ironhouse Point and Couta Rocks, no positional information was recorded when tagged abalone were released.

2.4 Search procedure

About one year following the final tagging event, research divers commenced recovery of tagged abalone. At all three sites, an initial search was made to determine if and how far abalone might have spread outside the study areas. Apart from this step, the search procedure differed at all three sites.

At Magistrates Point, a series of strip transects of one metre width was laid over the study area across each of the five sections (see 2.3), and each transect exhaustively searched for tagged abalone. The transects were divided into five metre segments, so that the net movement by each abalone relative to its release could be determined. The entire study area was searched in 15 days diving by four divers. This method of searching was thorough but very time consuming. During the course of the search it became apparent that abalone were concentrated at the sand-edge or close to the shore-line. In the middle ground between these two areas the reef was largely devoid of abalone. However, the design of the search dictated that these areas should be searched as rigorously as the areas that held abalone.

At Ironhouse Point and Couta Rocks the reef area was many times larger. It was realised that there were insufficient resources to carry out a thorough search of the entire reef, so a different search procedure was adopted. At Ironhouse Point, two licensed abalone divers were allowed to harvest abalone randomly from within and outside the site. Areas that were barren of abalone were quickly identified. Their catch bags were checked for tagged abalone and if any were found, the quantity and their location (determined with a hand bearing compass and a rangefinder) were recorded. The position of abalone on the reef was then used as a guide to locate the search area. Strip transects were placed over these areas and searched for tagged abalone.

At Couta Rocks, the area of reef was large, comparable with that at Ironhouse Point. However, the reef structure was much more complex than at either of the previous sites, with great variation in depth over short distances. Much of the reef was deeper than could be dived by research divers, such that the search techniques used at the other two sites were inappropriate. Subsequently, a series of radial swims were undertaken by research divers about a central point within the site over a three day period, and a considerable proportion of tagged abalone were recovered. The area was then made available to abalone fishing by the fishing industry and recreational divers, and a reward system for the shells of tagged abalone was instituted. Over the next two months, quantities of tagged abalone were recovered, mostly by two particular divers or from the factory which bought their catch.

The condition (*i.e.* whether alive or dead) and size at recovery of each abalone was recorded. At all three sites, the empty shells of dead tagged abalone were collected and their death was recorded.

2.5 Estimation of growth rates

Growth rates were estimated by two separate techniques at each site.

2.5.1 Growth rates from marked abalone

At Magistrates Point and Ironhouse Point, abalone were tagged in four separate events spaced approximately six months apart that took place in spring and late autumn. At Couta Rocks, one of the tagging events took place in late spring, but the otherwise tagging was done in summer and winter.

Marked abalone were recaptured and measured both during the six-monthly tagging events, where they were re-released, and at the completion of the study, where they were removed from the site and killed. Growth increments were analysed using a non-linear regression of Fabens (1965) re-parameterisation of the von Bertalanffy growth function

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

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.

2.5.2 Growth rates from aged shells

In addition to direct measurement of growth and mortality from marked abalone, a number of shells were collected and prepared for the purpose of counting growth rings. Samples of 200 or more abalone were collected randomly from among the stocks at each site both prior to, and at the end of the tagging study. The tagged shells recovered at the end of the tagging exercise were also aged, to enable a comparison between growth and mortality estimates from each method.

2.5.3 Ageing of shells

Shell lengths were measured, and a section cut from each shell that passed through its spire, exposing the growth rings. Using a binocular microscope, the number of rings were counted on each side of the section and a grade from 0 (bad) to 5 (good) assigned according to the clarity of each reading. The method is described extensively by Nash (1995) and enables counts to be made of rings in sections that are heavily bored, in contrast to the method used by Prince and others that counted rings from spire ground shells (McShane and Smith, 1992; Prince *et al*., 1988a). This undoubtedly adds to the rigour of the method and reduces potential bias caused by inability to count rings in older shells that may have a high incidence of borer damage. In this study, ring deposition was assumed to occur annually.

Analyses of aged shells used ring counts from the right hand side of the shell section, of clarity rating 3 or higher. Shells of lesser clarity usually exhibited large disparities between right and left hand side ring counts or had incomplete ring developments that made assignment of ages questionable. The right hand side of the section was used, because it has been established by Nash (1995) that this side produces more consistent readings.

2.5.4 Calculating growth rates from aged shells

The von Bertalanffy growth function

$$L_t = L_\infty \cdot [1 - e^{-K(t-t_0)}] \qquad (2)$$

was used to describe growth, where L_t is the length of the abalone at age t, L_∞ is asymptotic or average maximum length, K is the coefficient of growth and t_0 is the age at which L is zero. Growth curves were fitted by non-linear regression of age-length couplets.

2.6 Estimation of tag-loss

At the final recapture event, the number of tags remaining in each abalone was recorded. Using this data, it was possible to calculate the number of abalone that had lost both tags and that should have been recaptured, for each of the four marking events.

The method used to calculate tag loss is described extensively by Seber (1982) and Krebs (1989) where

R_A = number of tagged abalone recaptured with a tag in the first respiratory pore (*i.e.* the second tag is lost),

R_B = number of tagged abalone recaptured with a tag in the second respiratory pore (*i.e.* the first tag is lost), and

R_{AB} = number of tagged abalone with both tags present.

The number of abalone that should be recaptured from each tagging event is

$R = R_A + R_B + R_{AB}$ + { the number of abalone that have lost both tags }which is calculated

$$R = \frac{1}{1 - \frac{R_A R_B}{(R_A + R_{AB})(R_B + R_{AB})}}(R_A + R_B + R_{AB}) \tag{3}$$

2.7 Estimation of rates of mortality

Rates of mortality were estimated both from the decline in rate of recovery of tagged shells and from catch curve analysis of aged shells.

2.7.1 Rates of mortality derived from the decline in rate of recovery of tagged abalone

The rate of disappearance in populations of abalone at the three sites was estimated from the declining quantities of abalone recovered from preceding tagging events over the period of time they were at liberty.

It was assumed that the probability (p) of recovering a tagged abalone varies exponentially with time, such that

$$p = \alpha \cdot e^{-Xt} \tag{4}$$

where X is the coefficient of disappearance of the abalone, (and comprises the sum of the natural mortality, permanent migration and ongoing tag loss), and t is the time between release and recapture.

The constant α is defined

$$\alpha = \alpha_1 \cdot \alpha_2 \tag{5}$$

where α_1 is the probability that abalone are not lost to the study by tagging mortality or initial tag loss and α_2 is the efficiency of finding tagged individuals during the search.

It was initially assumed that α does not vary between any of the four tagging events, because the same tagging method was used throughout the study, so that initial tag loss should apply equally to each event. It was also assumed that the searching efficiency for individuals from each event is constant.

Equation (4) can be transformed to a linear form by taking the natural logarithm of both sides

$$\ln p = \ln \alpha - X \cdot t \qquad (6)$$

and X determined from the slope of the regression of the logarithm of the probability of recovering an abalone ($\ln p$) against time (t). To simplify analyses, time at liberty for each abalone was determined from the middle of the period of time encompassing the event during which it was tagged up to the middle of the period during which it was recaptured.

Because time was measured in units of days, the rate of disappearance (X) and its standard error were converted to annual rates by multiplying by 365.

2.7.2 Rates of mortality from catch curve analysis

Population samples of abalone were collected before and after the tagging study at all sites except Magistrates Point. The population samples were collected in a random manner from stocks in or adjacent to the study sites. The shells of the abalone were aged. At Magistrates Point, prior to the study, a sample comprising 284 abalone was collected and measured, but not aged.

Mortality rates were determined using catch curves developed both from samples taken at each of the three sites, and from the aged shells of tagged abalone recovered at the end of the study. The catch curves were developed using ring counts from the right hand side of the shell, of clarity rating 3 or higher. Ages were assigned to abalone shells of lesser clarity using age-length keys.

The catch curves were produced by plotting the natural logarithm of the frequencies of each age-class against age. Regression lines were fitted to data points that fell within the guidelines established by Pauly (1990). Assuming a constant rate of recruitment and rate of mortality with respect to age at each site, the slope of the regression line equals the negative instantaneous rate of mortality (Z).

3. Results

3.1 Estimates of growth rates

3.1.1 Growth rates estimated by analysis of mark-recapture data

Of the three sites, abalone grow largest at Magistrates Point (Fig. 3). Abalone from Ironhouse Point grow relatively quickly, but to a smaller maximum size than at Magistrates Point. Mean annual growth increments at Couta Rocks are approximately half those of the two East Coast sites.

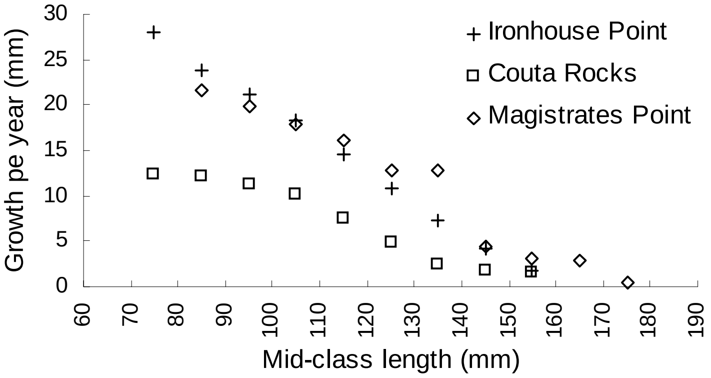


Fig. 3. Annual mean growth increments by 10 mm size-class at each of the three study sites.

Fig. 3 was developed from annual mean increments of grouped data (by 10 mm size-class), where size-classes at the extremes of the size-range are made up of relatively few individuals, and consequently have a disproportionate influence on the shape of the curve. Its inclusion is to illustrate differences in growth rates between sites, and was not used to estimate growth parameters.

Instead, growth parameters were determined by fitting recapture data to Faben’s (1965) re-parameterisation of the Von Bertalanffy growth model (Table 1).

Table 1. Growth rates estimated by analysis of mark-recapture data

The von Bertalanffy parameters K, L_∞ and t_0, derived from growth increments of abalone measured at the three study sites between 1994 and 1997. The parameters were derived from non-linear regressions of length against growth increment using Fabens’ (1965) model. The number of increments measured at each site is shown in the right hand column (n), standard errors are given in brackets and t_0 was later calculated assuming that an abalone of age 0 was 1 mm long.

Site	L_∞	K	t_0	n
Magistrates Point	160.6 (1.2)	0.40 (0.02)	-0.02	821
Ironhouse Point	152.6 (0.9)	0.52 (0.07)	-0.01	1153
Couta Rocks	147.4 (1.0)	0.27 (0.01)	-0.03	752

3.1.2 Growth rates determined from aged shells

Samples of shells collected at each of the study sites both before and after the study were measured. These measurements were plotted by frequency of each 5-mm size-class relative to the position of the 132-mm size limit (Fig. 4). Displacement of the mode to the right occurs in the post-study samples at both of the sites that were fished by commercial divers prior to the study (Couta Rocks and Ironhouse Point), which is assumed to be due to growth of the fished section of the population. At Magistrates Point where no fishing is undertaken, there is no clear shift in population size-structure.

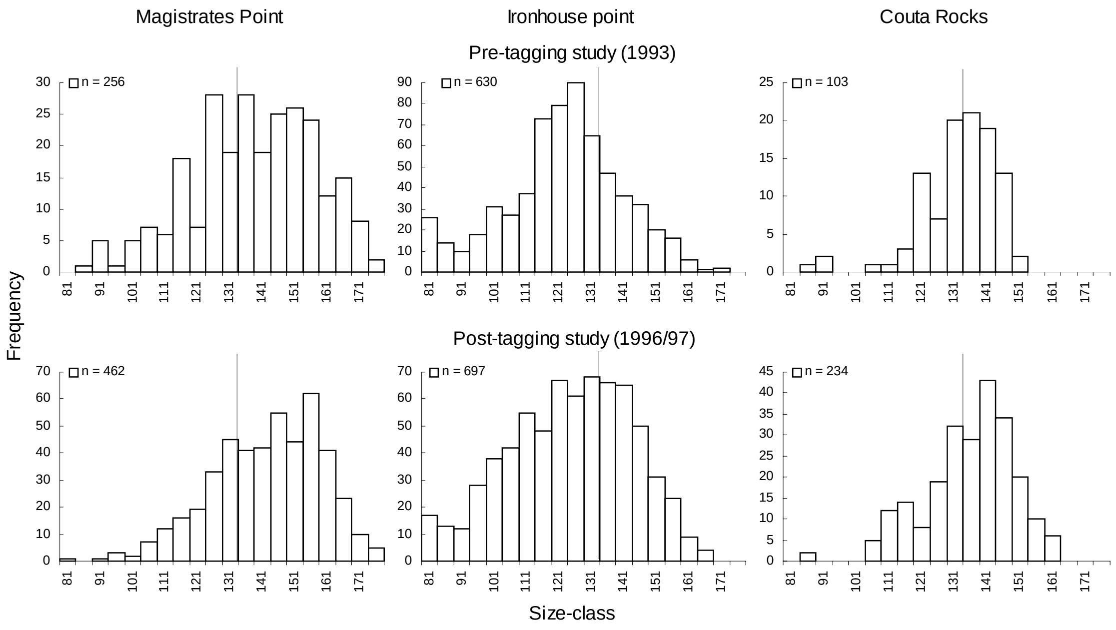


Fig. 4. The size-composition of randomly collected population samples of abalone taken before and after the tagging study. Size-classes are grouped by 5-mm intervals. The position of the size limit (132 mm), is indicated by a line drawn vertically after the 131-mm size-class. Sample size (n), is shown in each chart.

Growth curves and growth parameters derived from aged shells are summarised in Figs 5 to 9. The results from samples obtained before and after the tagging study are paired for the sake of comparison. It is assumed that these results illustrate the effect upon growth rates of the cessation of fishing in the area.

Growth curves from aged tagged shells are provided for comparison with the post-study growth curves. The tagged shell growth curves lack early data compared with the post-study curves. Attempts were made to statistically separate the growth curves using analysis of residual sum of squares without success.

There are two figures that do not compare growth before and after the tagging study. At Magistrates Point (Fig. 5) in 1993, abalone collected were measured then released and consequently shells are not available for ageing. The comparison is between a sample collected immediately after the tagging study and a sample collected two years following that. They illustrate the uniformity of growth rates over time that might be expected of an area which has never been fished.

The other exception is Fig. 9, which shows data from tagged shells from the mark-recapture study which were sectioned and aged. It was intended that the results from the analysis of aged tagged shells should be compared with growth rates from the mark-recapture study (Table 1), and that any differences in growth rates between the three sites would become obvious.

At Ironhouse Point (Fig. 6) the study site was fished by licensed divers up until the time that the first sample was collected. Essentially, Fig. 6 shows that young abalone from the post-study sample are larger than those caught earlier. Samples collected from an area 500 metres south (Fig. 7) that was not closed to fishing also show an increase in size for age among younger abalone. Like Fig. 6, it shows that growth rates may have changed in the area. Young abalone appear to be larger than in the earlier sample. Larger 10 and 11 year old abalone are not represented in the 1996 sample to the extent that they were in December 1993.

At Couta Rocks (Fig. 8), the earlier sample suffers from both inadequate sample size, and limited size-range. The second sample was collected some 400 metres south of the study site (but still within the boundaries of the reserve and therefore closed to fishing) and shows high ring counts found in abalone in this locality. Abalone here are reputed to be smaller than generally found on this section of the West Coast. However, this area is normally heavily fished, partly because of its close proximity to the launching ramp, and also because it consistently sustains good catch rates and large catches in spite of the fishing pressure.

Comparison of growth curves from aged tagged shells shows that older abalone from Magistrates Point are larger than at the other two sites, that abalone at Ironhouse Point grow comparatively quickly to a smaller average maximum size, and that abalone from Couta Rocks are the slowest growing of all three sites. These analyses were made with a limited number of small abalone (although abalone as small as 70 mm were tagged, they were aged after they had grown to a larger size) and the growth parameters may not reflect growth in the population at large.

It is important to note that the differences in growth rates between the three sites correspond with differences in growth obtained from the analyses of tag-recapture data (Table 1 and Fig. 3).

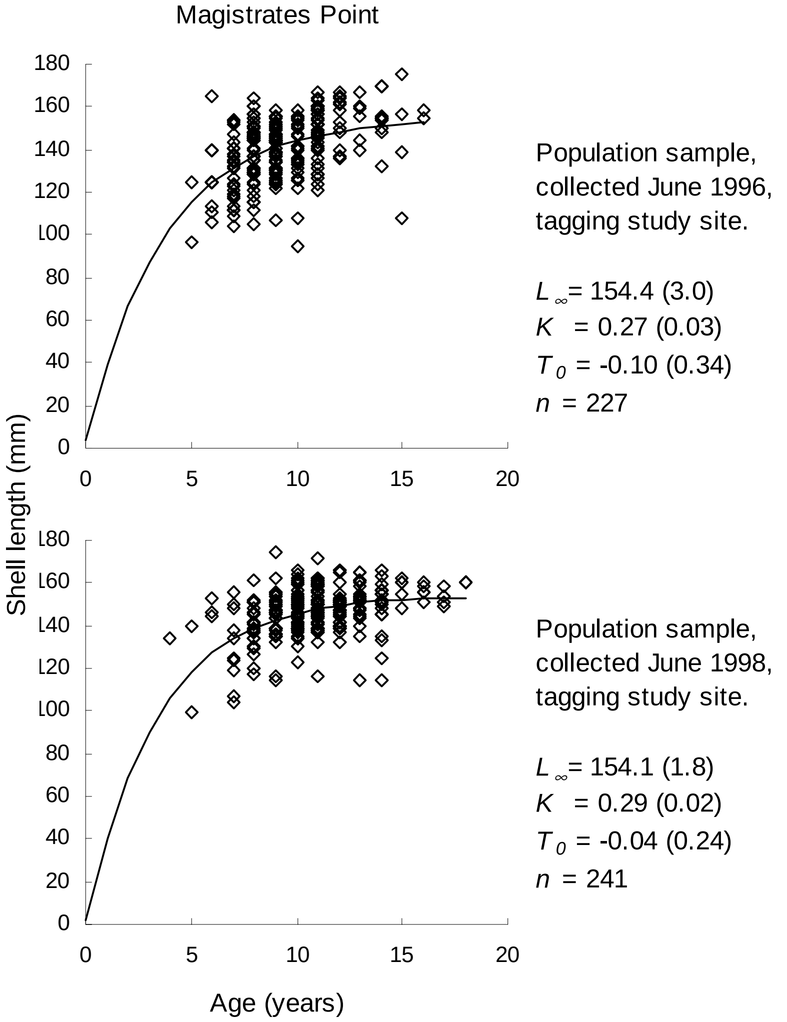
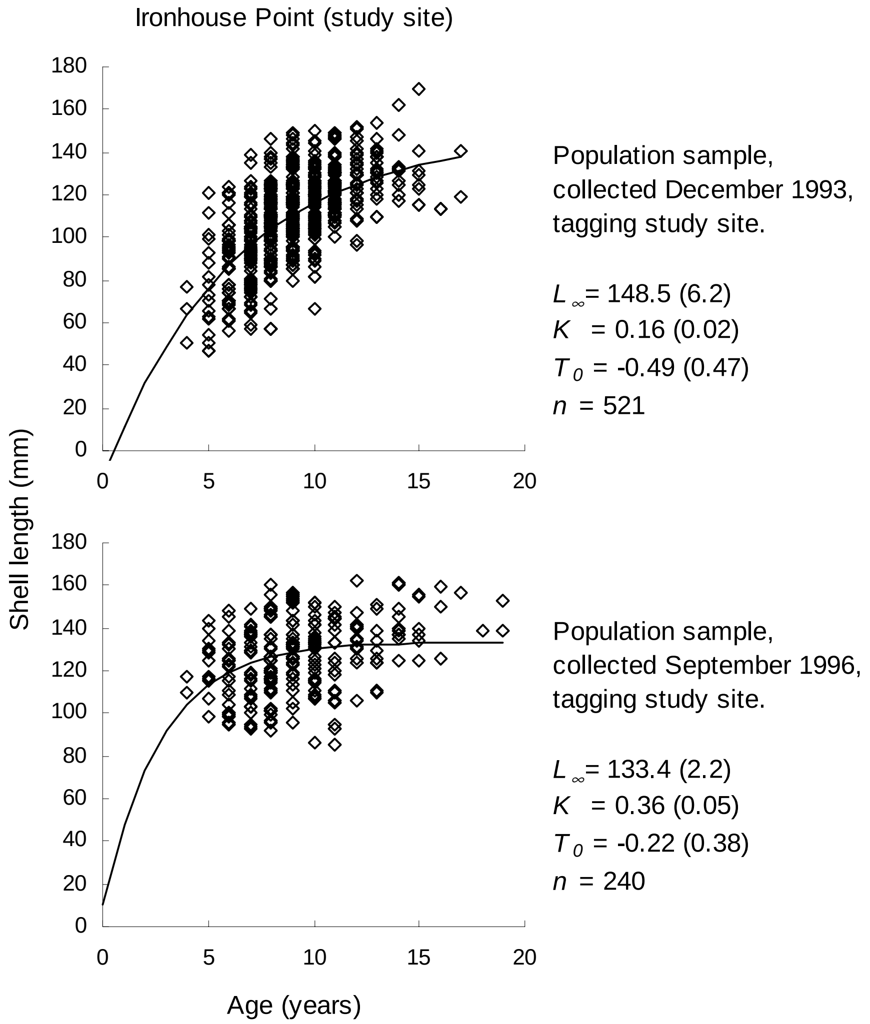


Fig. 5. The Von Bertalanffy growth function fitted to age-length data from blacklip abalone shells collected at Magistrates Point. Note that both these samples were collected after the tagging study had been finalised at this site. Standard errors for each growth parameter are given in brackets.



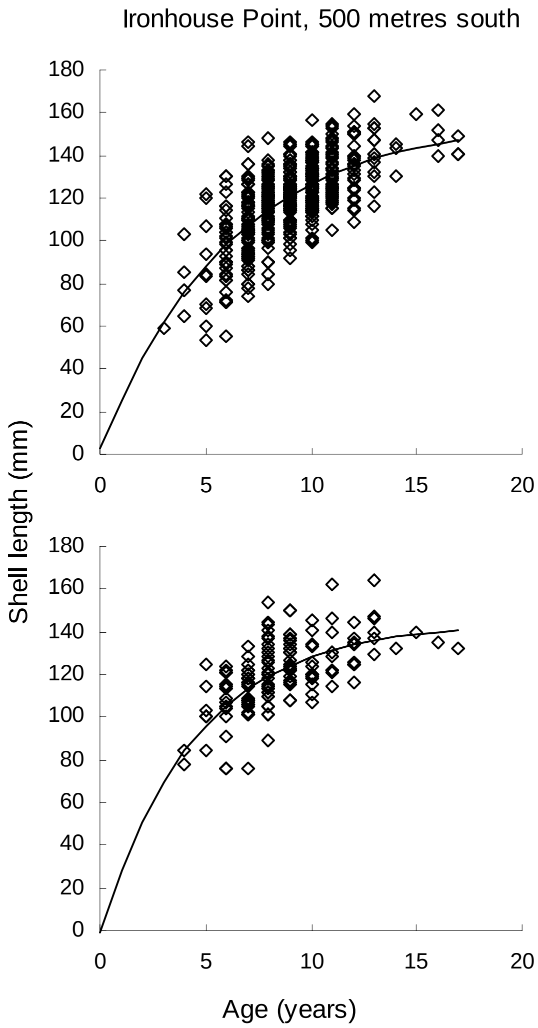
Population sample, collected December 1993, tagging study site.

L_∞ = 148.5 (6.2)
K = 0.16 (0.02)
T_0 = -0.49 (0.47)
n = 521

Population sample, collected September 1996, tagging study site.

L_∞ = 133.4 (2.2)
K = 0.36 (0.05)
T_0 = -0.22 (0.38)
n = 240

Fig. 6. The Von Bertalanffy growth function fitted to age-length data from blacklip abalone shells collected at the Ironhouse Point study site both before and after the tagging study. Standard errors for each growth parameter are given in brackets.



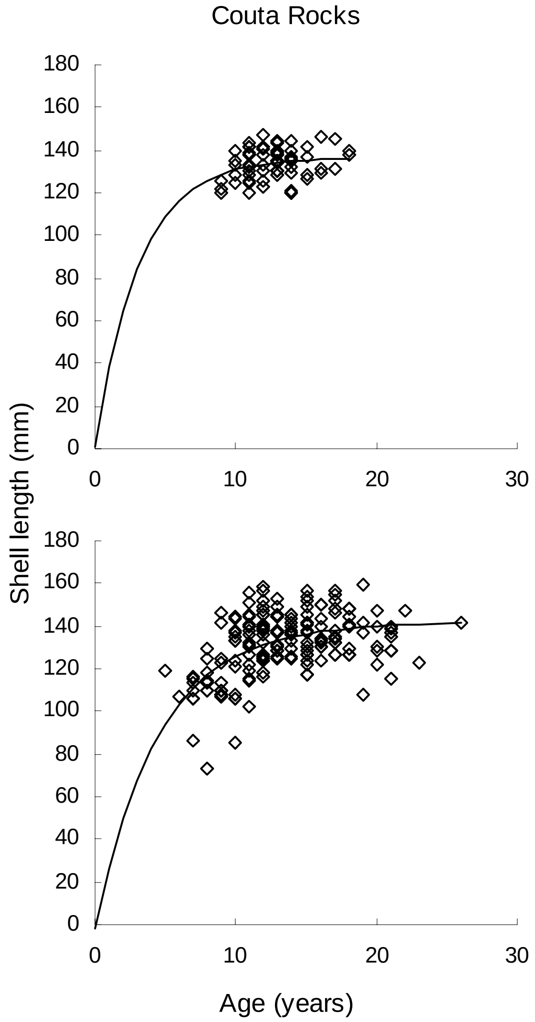
Population sample,
collected December 1993,
500 metres south of study site.

L_∞ = 157.7 (5.3)
K = 0.16 (0.01)
T_0 = -0.11 (0.43)
n = 528

Population sample,
collected November 1996,
500 metres south of study site.

L_∞ = 144.2 (4.4)
K = 0.22 (0.03)
T_0 = 0.03 (0.38)
n = 160

Fig. 7. The Von Bertalanffy growth function fitted to age-length data from blacklip abalone shells collected about 500 metres south of Ironhouse Point. This area was fished during the course of the study and abalone were collected to compare growth rates between fished and unfished stocks. Standard errors for each growth parameter are given in brackets.



Population sample,
collected September 1993,
study site.

L_∞= 136.4 (1.9)
K = 0.32 (0.05)
T_0 = -0.02 (0.16)
n = 70

Population sample,
collected January 1997,
400 metres south of study site.

L_∞= 141.6 (1.8)
K = 0.22 (0.02)
T_0 = 0.05 (0.37)
n = 190

Fig. 8. The Von Bertalanffy growth function fitted to age-length data from blacklip abalone shells collected at Couta Rocks. Standard errors for each growth parameter are given in brackets.

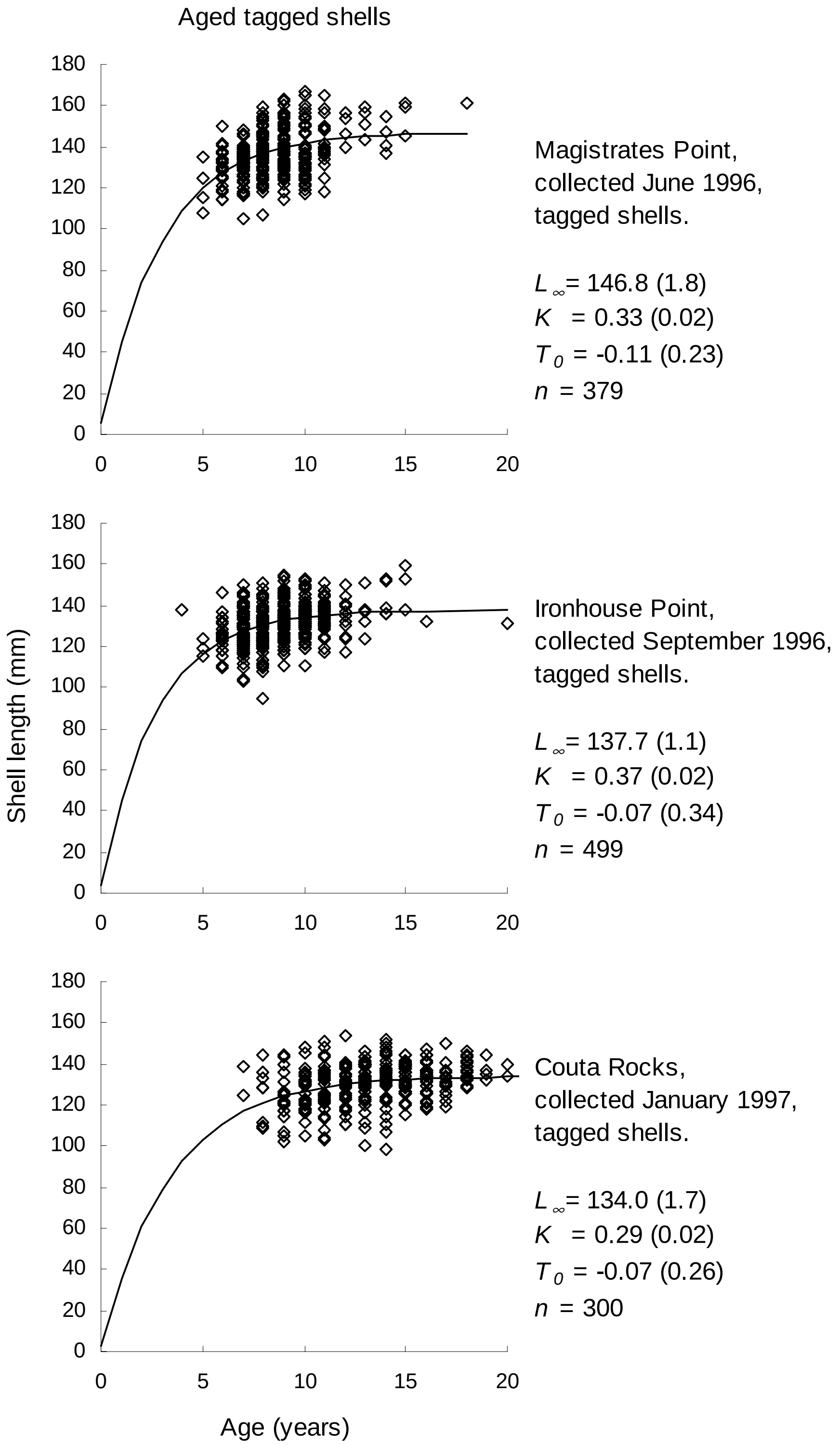


Fig. 9. The Von Bertalanffy growth function fitted to age-length data from tagged abalone shells from the mark-recapture study. Standard errors for each growth parameter are given in brackets.

3.2 Tag loss

Tagged shells were examined to determine causes of tag loss. At Ironhouse Point, 154 of the 4066 tagged abalone were recaptured more than once. Of these, 43 abalone had lost tags. Over half of these (25) had lost tags within 13 months of release. Of the remainder, tags were lost at some indeterminate time between 6 months following marking and their recapture several years later.

Subsequent analysis of tag loss following the methods of Seber (1982) and Krebs (1989) confirms that tag loss is not correlated with time, implying that tags are not lost at a steady predictable rate over the duration of the study.

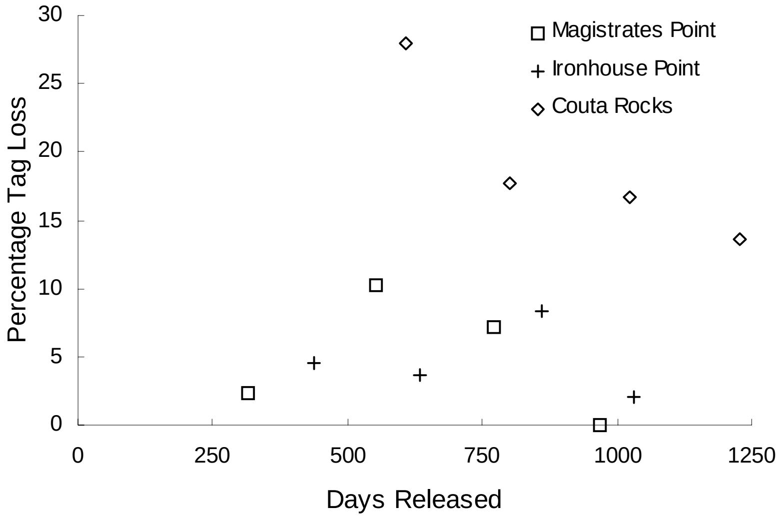


Fig. 10. Tag loss shown as percentage of the number of abalone nominally recaptured with no tags over the total number of abalone recovered from each of four tagging events, plotted against the average length of time (measured from day 0) that the tagged abalone were released.

Generally, tag loss was least from the earliest tagging event at all three sites (Fig. 10). By site, tag loss was least at Magistrates Point and Ironhouse Point. No tag loss was observed from abalone released at the earliest tagging event at Magistrates Point in 969 days. All abalone recovered from the first tagging event at this location were landed with no loss of tags from the first respiratory pore, which means that the number of abalone nominally recovered with no tags present is zero or in other words, total tag loss was zero. In contrast, of all the abalone released from the most recent tagging event at Couta Rocks, over 28 percent lost both tags within 610 days.

3.3 Migration

At Magistrates Point, which was the only site where the position of tagged and released abalone was recorded, there was no directional trend in movement of abalone.

At both of the larger sites, tagged abalone were recovered up to 500 metres from the study area. This demonstrates the potential movement of tagged abalone and caused great difficulty while searching for marked individuals scattered over such a large area.

3.4 Estimates of rates of mortality

3.4.1 Rates of disappearance in marked abalone

Regressions of the probability of recapture of tagged abalone against time (in days) are shown for each site in Fig. 11. The slopes of these regressions multiplied by 365 produce an annual rate of disappearance.

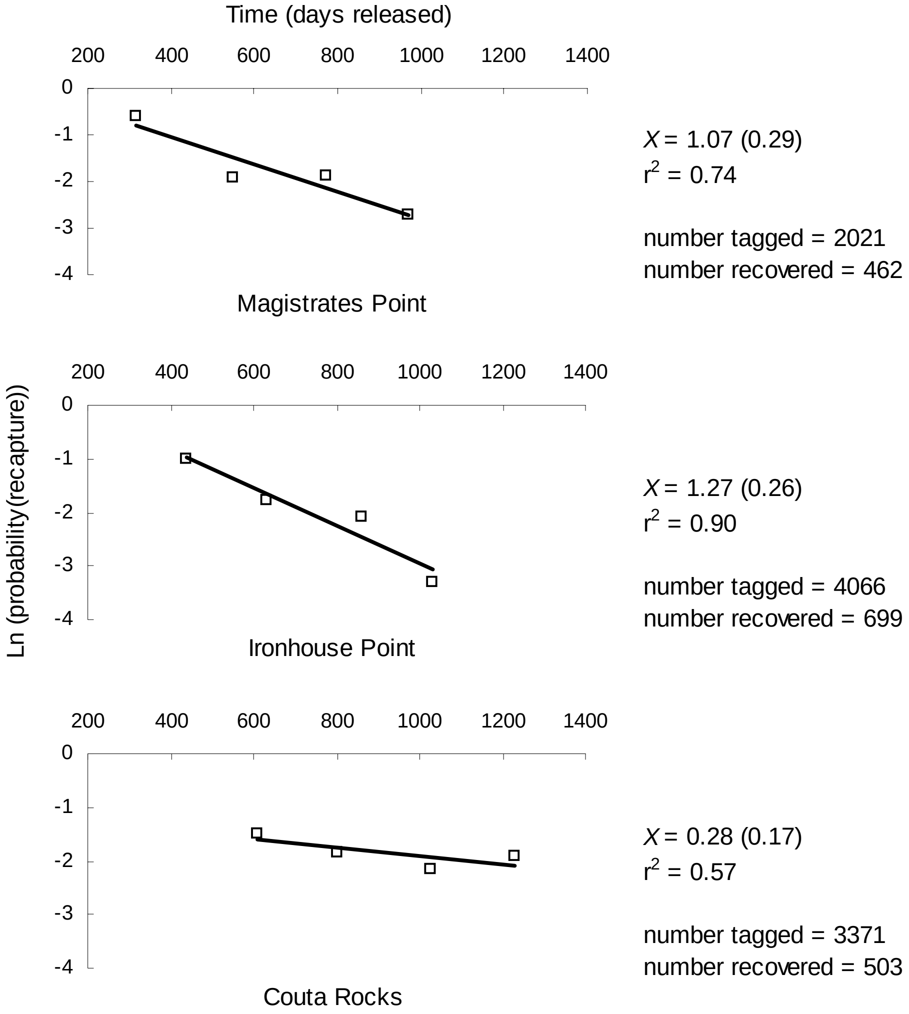


Fig. 11. Annual rates of disappearance (*X*) determined from the declining rate of recapture of tagged shells. The slope of declining rate of the natural logarithm of the probability of recapturing tagged abalone released in four separate events over a two year period, regressed against time in days then multiplied by 365, gives the instantaneous annual rate of total disappearance at each of the three study sites. Standard error for the rate of disappearance is shown in brackets.

The data have been modified to account for the effects of tag loss, so the number recovered at the right hand side of each chart includes the number of abalone nominally recovered from each event with no tags attached. Rates of disappearance were least at Couta Rocks, and greatest at Ironhouse Point.

While the probability of recapturing abalone from the most recent tagging event was greatest all three sites, it did not necessarily follow that recapture of tagged abalone was progressively less from the earlier tagging events. At Magistrates Point, more abalone were recovered from the second tagging event than from the tagging event which took place six months later. At Couta Rocks, recovery from the earliest tagging event was greater than from the following event, and almost as great as from the third event.

3.4.2 Mortality rates by catch curve analyses

The instantaneous annual rate of total mortality (Z) and the sample size (n) determined by catch curve analysis of population samples collected at or near the three sites and aged tagged shells are shown in Figs 12 to 14, and summarised below in Table 2.

Ironhouse Point (Fig. 13) and Couta Rocks (Fig. 14) were fished at least until mid 1993, and therefore Z represents both fishing and natural mortality.

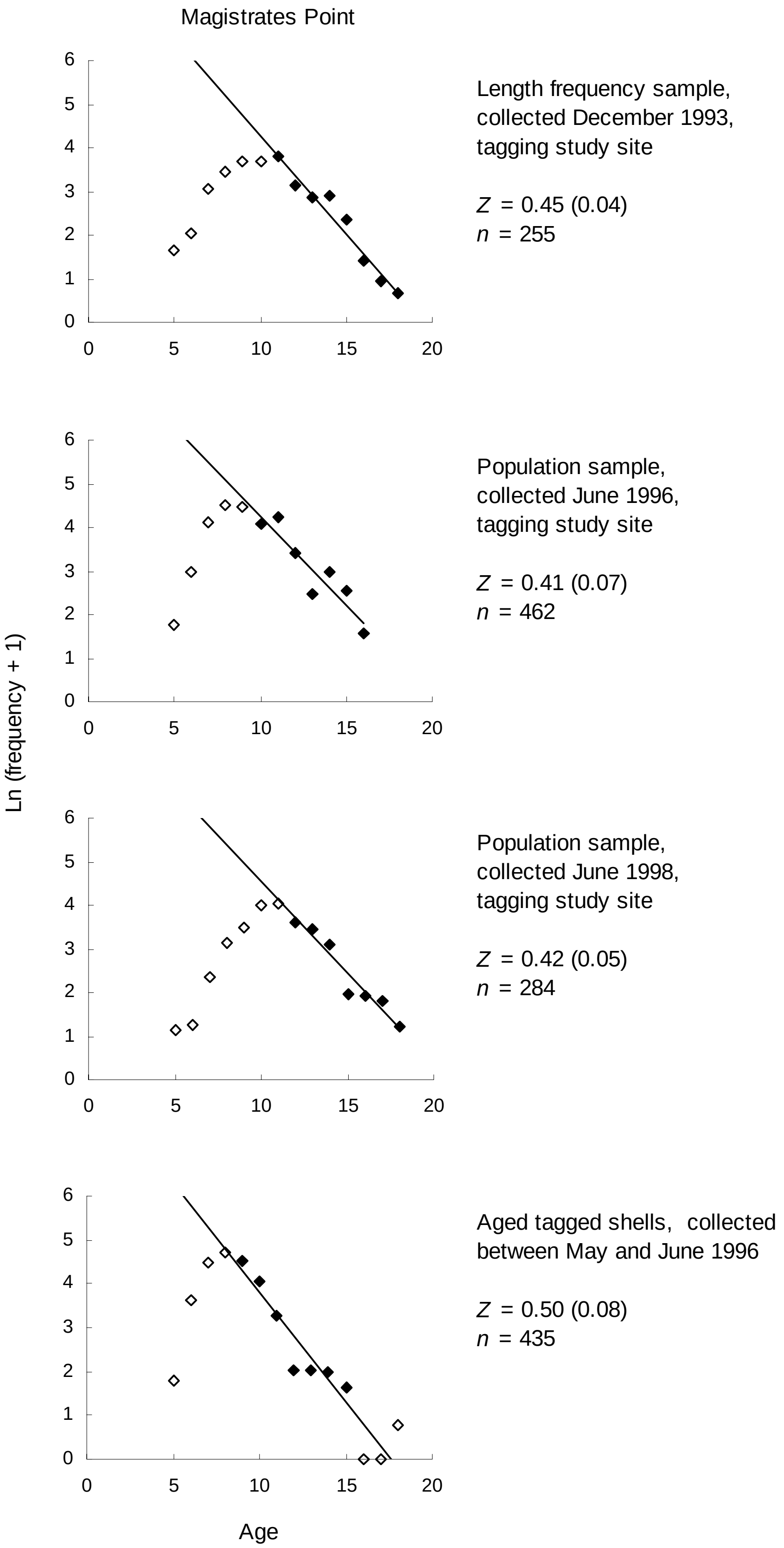
The December 1993 sample from Magistrates Point (Fig. 12) was returned to the water alive, and consequently no ageing data was available. Instead, an age-length key was derived from combined 1996 and 1998 samples, and applied to the 1993 length data. This was considered justifiable because there was no appreciable difference in growth rates between 1996 and 1998 (Fig. 5). The area has been an abalone reserve for many years prior to collecting the 1993 sample, and has probably never been fished, so it is considered unlikely that changes in abundance will cause density-dependent variation in growth rate.

Catch curves were also developed from the tagged shells which had been aged. Age-length keys were again used to assign ages to shells that could not be aged. The mortality rates from each of the three sites can then be compared with rates of disappearance from the mark-recapture study in Fig. 11.

Table 2. Summary of instantaneous rates of mortality from catch curve analyses

The shaded samples were collected either while the areas were still fished or just after they were closed to fishing, so incorporate fishing mortality. The standard error of the instantaneous rate of mortality is shown in brackets.

Site	Date	Z	n
Magistrates Point	December 1993	0.45 (0.04)	255
	June 1996	0.41 (0.07)	462
	June 1998	0.42 (0.05)	284
Ironhouse Point	October 1993	0.49 (0.04)	95
	December 1993	0.51 (0.05)	620
	September 1996	0.35 (0.04)	910
Couta Rocks	September 1993	0.45 (0.15)	102
	January 1997	0.29 (0.05)	235



Length frequency sample,
collected December 1993,
tagging study site

Z = 0.45 (0.04)
n = 255

Population sample,
collected June 1996,
tagging study site

Z = 0.41 (0.07)
n = 462

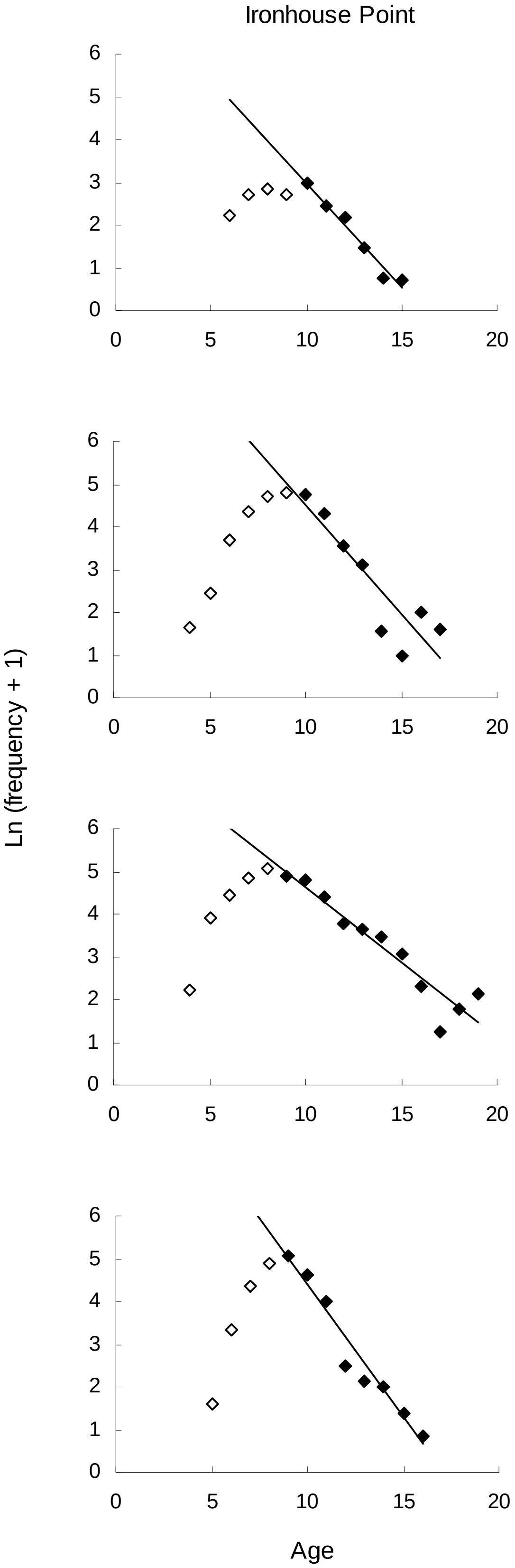
Population sample,
collected June 1998,
tagging study site

Z = 0.42 (0.05)
n = 284

Aged tagged shells, collected
between May and June 1996

Z = 0.50 (0.08)
n = 435

Fig. 12. Comparison of catch curves and rates of instantaneous mortality, from samples collected at the Magistrates Point study site both before and after completion of the tagging study, and from the recaptured tagged shells which were subsequently aged. The standard error of instantaneous mortality is shown in brackets.



Population sample,
collected October 1993,
tagging study site

Z = 0.49 (0.04)
n = 95

Population sample,
collected December 1993,
tagging study site

Z = 0.51 (0.05)
n = 620

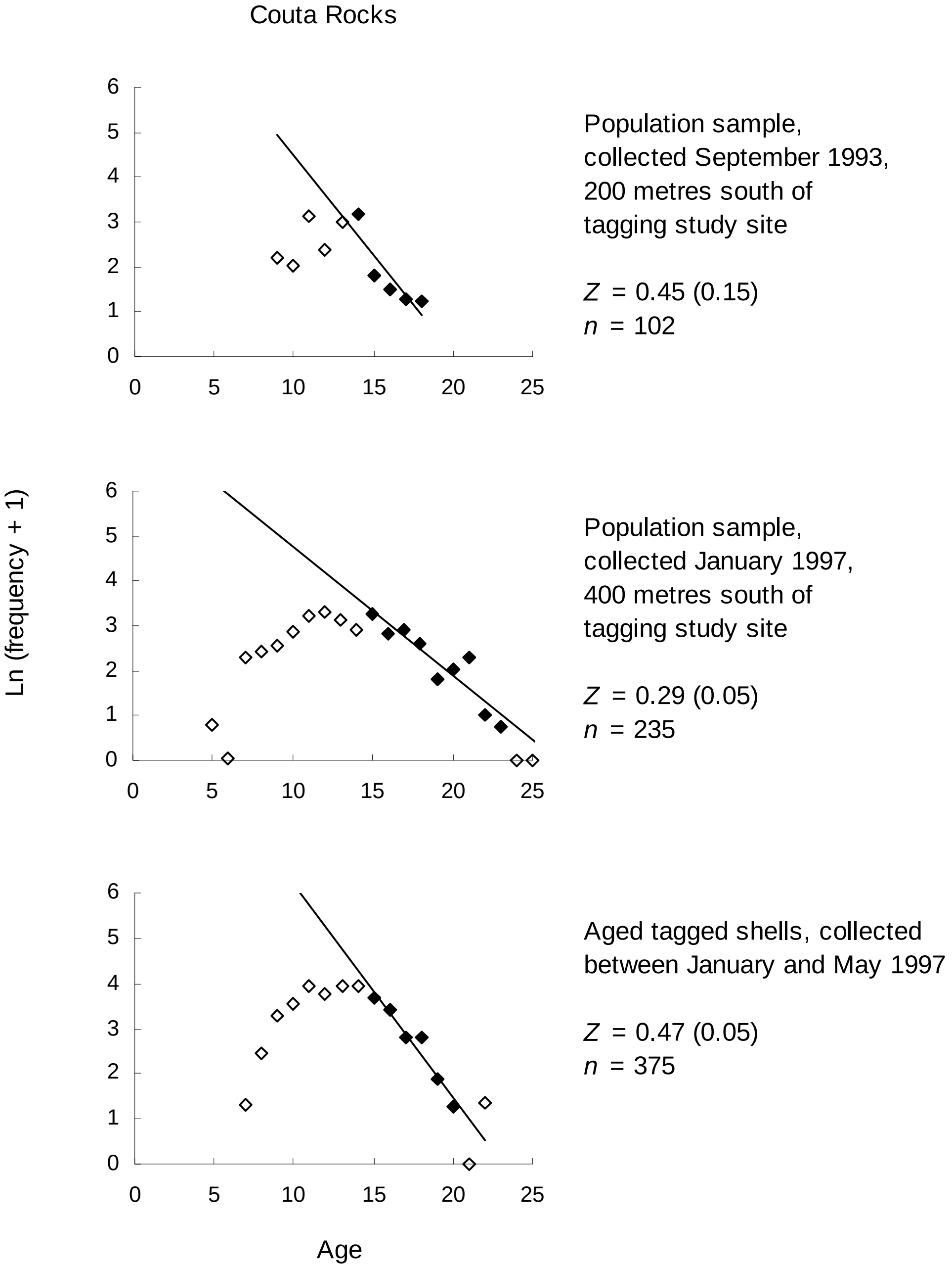
Population sample,
collected September 1996,
tagging study site

Z = 0.35 (0.04)
n = 910

Aged tagged shells, collected
between July and November
1996

Z = 0.62 (0.06)
n = 581

Fig. 13. Comparison of catch curves and rates of instantaneous mortality, between population samples and tagged shells. The population samples were collected at the Ironhouse Point study site both before and after the study and the tagged shells were recovered from the site at the end of the study, then subsequently aged. The standard error of instantaneous mortality is shown in brackets.



Population sample, collected September 1993, 200 metres south of tagging study site

Z = 0.45 (0.15)
n = 102

Population sample, collected January 1997, 400 metres south of tagging study site

Z = 0.29 (0.05)
n = 235

Aged tagged shells, collected between January and May 1997

Z = 0.47 (0.05)
n = 375

Fig. 14. Comparison of catch curves and rates of instantaneous mortality, between population samples and tagged shells. The population samples were collected from sites within 400 metres of the Couta Rocks study site both before and after the study and the tagged shells were recovered from the site at the end of the study, then subsequently aged. The standard error of instantaneous mortality is shown in brackets.

4. Discussion

4.1 Growth

4.1.1 Estimates of growth rate from growth increments

The growth rates from the mark-recapture study show that abalone from the most southern site on the East Coast (Magistrates Point) grow to the largest size, that Couta Rocks abalone grow at the slowest rate and at Ironhouse Point, abalone grow at a faster rate than at the other two sites, but to a smaller average maximum size than Magistrates Point (Fig. 3).

A comparison of growth parameters from various sites around the Tasmanian coastline shows that with the exception of George III Rock (where stocks are considered to be slower growing than those from adjacent reefs), abalone populations from the north of the state grow slower than more southern stocks (Table 3).

Table 3. Growth rates estimated by analysis of mark-recapture data

The von Bertalanffy parameters K, L_∞ and t_0, derived from growth increments of abalone measured at various sites around Tasmania between 1990 and 1996. The three study sites from this study are included for comparison. The number of increments measured at each site is shown in the right hand column (n), standard errors for L_∞ and K are given in brackets and t_0 was calculated assuming that an abalone of age 0 was 1 mm long.

Site	L_∞	K	t_0	n
South –East (Nash, 1995)				
George III Rock deep	153.2 (1.5)	0.46 (0.04)	-0.01	126
George III Rock shallow	153.9 (0.6)	0.41 (0.01)	-0.02	874
Stinking Bay	159.7 (1.8)	0.36 (0.01)	-0.02	491
Shag Rock Bay	182.2 (2.2)	0.44 (0.02)	-0.01	336
East				
Magistrates Point	160.6 (1.2)	0.40 (0.02)	-0.02	821
Ironhouse Point	152.6 (0.9)	0.52 (0.07)	-0.01	1153
North-West				
Couta Rocks	147.4 (1.0)	0.27 (0.01)	-0.03	752
Bass Strait Islands (Tarbath, 1999)				
Deal Island, Kent Group	131.8 (3.1)	0.40 (0.06)	-0.02	57
Long Islet, Hogan Group	146.4 (6.2)	0.23 (0.04)	-0.03	79

Effects of seasonal variation in growth upon estimates of growth rate

No allowances have been made for seasonal variation in growth, and for the timing of tagging and recapture with respect to periods of fast growth. It is necessary to consider whether some of the between-site differences in growth apparent in the mark-recapture study may be due to seasonal changes in the rate of growth.

In Tasmania, there is strong seasonal variation in growth of sexually mature blacklip abalone. Growth appears to be minimal in late autumn when gametogenesis takes place (Harrison and Grant, 1971) and winter, but increases in spring and continues through summer. Much of the tagging and recapture of abalone in this study took place in spring when growth of abalone is at its peak. However, while analysing growth data, growth has been treated as though abalone grew at a linear rate throughout the year, which meant that there was scope for biasing estimates of growth parameters by including or omitting a period of fast growth.

The seasonal nature of growth meant that there were growth increments collected over periods of low growth as well as growth increments collected over periods that incorporated an extra growing season. If most of the growth increments were measured between the end of one growing season and the start of another, then growth analyses would be affected by slow growth. Similarly, if abalone were tagged at the start of one growing season and recaptured at the end of one or more growing seasons, then the measured growth rates will be higher than really occur. Pinpointing exactly when growth periods start or stop may be critical.

Tagging (and some recapturing) was done during the period November to January (peak growth) and again in May to July (minimal growth). The final recapture event took place at Magistrates Point in May and June (minimal growth), Ironhouse Point from July to September (growth initially minimal but increasing) and at Couta Rocks from January to May (initially high growth reducing to low growth). At all three sites there was an interval of at least one year between the final tagging event and the recapture event.

It therefore follows that the growth rates from abalone at Couta Rocks may be positively biased (*i.e.*. estimates of growth are faster than really occurred), since a large proportion of the tagged abalone were recaptured at the end of a period of fast growth. However, if this bias could be eliminated, then the differences in growth rates between Couta Rocks and the other two sites would be increased, indicating the difference in growth rates cannot be attributed to seasonal factors.

The data set from this study is very complex with respect to the seasonal timing of growth and the protracted nature of recapturing tagged abalone defies categorising growth increments as seasonally affected or not, particularly when the time of the growth periods is only approximately known. Notwithstanding this, a small subset of growth data that could be seasonally categorised were subdivided into groups based on those that had an extra period of high growth and those that did not. Analyses of growth increments from the two groups produced similar growth parameters. A closer look at the data revealed that growth increments from each group had similar frequency distributions and that seasonality had no apparent effect upon the growth analyses. The six-monthly sampling strategy may have split the peak growing period in half at all three sites and consequently there may be no bias in estimates of growth rates caused by seasonal variation in growth.

Effects of shell condition upon estimates of growth rate

Difficulties were encountered while tagging abalone with brittle shells. Past experience at MRL with counting growth rings in brittle shells indicates that these abalone are from the older part of the population, with medium to large shells. However the largest shells in a sample are not necessarily brittle and are often from comparatively young abalone that exhibit fast growth rates. In this study, analysis of growth increments from tagged shells is therefore likely to reflect growth from younger abalone for a given shell length because the older ones had a lesser chance of being successfully tagged.

Analyses of growth increments may therefore over-estimate growth rates, particularly from Couta Rocks where a larger proportion of shells are brittle, heavily bored and where tag loss was highest.

4.1.2 Estimates of growth rate from aged shells

Rate of deposition of growth rings

Although it has been established that growth rings in the shells of *H. rubra* collected from two sites in southern Tasmania are laid down annually (Nash, 1995; Prince *et al*., 1988a), the process of ageing shells of abalone is complicated by a variety of factors. For example, it has been shown that adventitious rings may be deposited as a consequence of attack by shell boring organisms (Shepherd and Huchette, 1997), and that annual rings may be lost due to shell erosion (Shepherd and Turrubiates-Morales, 1997). In a Victorian study, a high proportion of shells collected for a growth study could not be aged because of shell damage by marine borers (McShane and Smith, 1992).

In this study, the between-site differences in growth from the mark-recapture study are reflected in the age-length growth analyses based upon annual growth rings. Importantly, early length at age from the growth curves corresponds with the growth increments observed in the mark-recapture study. For example, a 10 year old abalone from Couta Rocks in 1997 is approximately 120 mm shell length (Fig. 7) which means it has grown at an average rate of 12 mm per year. This growth rate corresponds well with the observed annual increment at this site (Fig. 3). At Ironhouse Point, the fitted model suggests that in 1996, a 5 year old abalone would be 100 mm shell length (Fig. 6), which again corresponds with the magnitude of the mean annual growth increment of smaller abalone (Fig. 3). There is similar correspondence between mean annual growth increment and length at age at Magistrates Point.

The importance of the correspondence between age-length and mark-recapture growth rates is that it provides strong evidence to support the assumption of annual growth rings and extends the range for which this assumption is valid beyond the south-east of the State.

Sources of error or bias

Brittle shells caused problems when counting rings from shell-sections of abalone, particularly those collected at Couta Rocks, and to a lesser extent from Magistrates Point. Some shells could not be reliably aged because of borer damage. These shells have high ring-counts indicating that they are either old or have laid down extra growth rings inside their shells as a result of borer attack. The shells are often thicker and heavier than shells that can be aged, and they are not necessarily the largest shells of the sample.

Fig. 15 Comparison showing the differences between the size-composition of shells that could be aged and the size-composition of the complete sample, collected from Couta Rocks, January 1997.

In Fig. 15, the size-distribution of shells from the 1997 sample collected at Couta Rocks that could be successfully aged is compared with those where ring-counts could not be reliably made. Between size-classes 130 and 150 mm, up to 30 percent of shells could not be aged, and consequently these shells were not included in growth analyses. In size-classes greater than 150 mm, the percentage of unageable shells diminishes. This means that abalone with unageable shells do not generally grow larger than 150 mm (*i.e.* they die before they reach this size). The effect of being unable to age these shells is to overestimate the rate of growth and has been discussed more extensively in an earlier study of blacklip abalone in Bass Strait (Tarbath, 1999).

Comparison of growth rates by site

One of the uses of sampling at the same site over time is to detect changes in growth rate that may reflect underlying changes in structure and abundance of the population. For example, after sampling at the Bass Strait islands both before and after fishing, it was found that high fishing pressure and consequent removal of large numbers of abalone caused the remaining abalone to grow at faster rates *i.e.* growth rates in these islands were density-dependent. In that study, higher growth rates became apparent after comparing size at sexual maturity and increased mean length for age of younger abalone (Tarbath, 1999).

At Magistrates Point, where there has been no fishing since the mid 1960’s, growth rates appear to be unchanged between 1996 and 1998 (Fig. 5). This is consistent with the hypothesis that abalone populations at this site are in equilibrium.

At the Ironhouse Point study site, where fishing ceased during the course of this study, growth rates among younger abalone appear to have increased between 1993 and 1996 (Fig. 6). If the relationship between reduction in abalone density and increased growth rate was valid, growth rates in the study site should fall, not increase, because abalone abundance should increase as a consequence of the cessation of fishing. While abalone abundance was not directly measured in this study, divers who fished the site when it was re-opened to fishing initially had high catch rates, presumably due to an increase in abundance of legal-size abalone.

What then, is the significance of the change in growth rates at this site, and how does it relate to abalone abundance?

The first consideration to be made is that the study in the Bass Strait islands was undertaken from samples collected over a much longer period than the study at Ironhouse Point. The cause of density-dependent effects on growth (presumably competition for food and home-sites, or physical contact with other abalone causing transmission of parasites and disease) may need to be present for some time before they are manifested as measurable changes in growth. The interval between sampling at Ironhouse Point may be too short to detect changes in growth, and the difference in size among the younger age-classes in Fig. 6 may be unrelated to abalone abundance.

Secondly, changes in growth rate will be more apparent in younger abalone because they grow at a faster rate than older abalone. Any difference in size between young abalone collected over time is therefore easier to detect. However, it is more difficult to collect adequate samples of young abalone (because they are cryptic) and growth analyses are usually based on the shells of older (emergent) abalone. Nash, Sellers, Talbot, Cawthorn and Ford (1994) found that generally, mature (emergent) abalone were larger than immature (cryptic) abalone for a given age. In Fig. 6, there are relatively fewer young abalone in the 1996 sample than in the 1993 sample, and although those from the 1996 sample are larger for their age, this may be due to inadequate sampling from cryptic habitat rather than changes in growth rate.

Thirdly, the level of fishing pressure at Ironhouse Point has usually been low compared with that experienced at the Bass Strait islands. Abalone stocks around Ironhouse Point and nearby Paddy’s Head were seldom fished prior to the study. The aggregations of abalone here are thinly concentrated, being sporadically distributed about the reef, which itself is of limited area. Furthermore, the region is difficult to access because of the distance (30 kilometres) from the boat ramps at Bicheno and St Helens. A boat ramp with restricted access was constructed at Ironhouse Point during the 1980’s, but divers quickly found that the abalone stocks in the area took a long time to recover between fishing and that good catches were infrequent (G. Myers, pers. comm.). Therefore, at Ironhouse Point, changes in fishing pressure and consequent abalone abundance may be too little to cause an appreciable change in growth rate.

Finally, samples collected 500 metres south of the Ironhouse Point site (outside the study area and therefore exposed to fishing) show that in 1996, most of the abalone in the 5 to 7 year-classes were larger than their 1993 counterparts (Fig. 7). Again, because of the small number of abalone involved, it is not clear whether this is due to increased growth rates or just reflects inadequate sampling of cryptic habitat. The increase in size of young abalone is common to both sites, and consequently is unrelated to changes in abundance at the study site.

At Couta Rocks, insufficient young abalone were collected and aged in 1993 to compare with the more recent sample.

4.2 Mortality and the disappearance of tagged abalone

The rates of disappearance of tagged abalone at Ironhouse Point and Magistrates Point are too high to be the result of natural mortality alone (Fig. 11). At Magistrates Point and Couta Rocks there is non-linear variation in the proportion of abalone recovered. There was a high proportion of abalone recovered from the second tagging event, while less abalone were recovered from the following event. At Couta Rocks, the rate of disappearance is much closer to that which might be expected from natural mortality alone, but the recovery rate from abalone tagged at the earliest tagging event was inexplicably high. The standard error of the rate of disappearance is high in all three cases.

Several factors affect the recovery of marked individuals:

(a) mortality of tagged fish due to the process of tagging,

(b) migration of fish from the release area,

(c) loss of tags from living fish,

(d) mortality of tagged fish due to natural causes (Beverton and Holt, 1957).

It then follows that estimates of rates of natural mortality derived from rates of disappearance of tagged fish may be confounded unless allowances are made for the effects of the first three factors.

4.2.1 Mortality of tagged fish due to the process of tagging

Great care was taken to ensure that only undamaged tagged abalone were released. At the end of each of the four tagging exercises, divers searched the release area for dead or dying abalone. Because very few dead tagged abalone were found, it was considered that the process of tagging had no detrimental effect upon the abalone and consequently there was no significant effect on estimates of natural mortality due to the tagging process.

4.2.2 Migration of fish from the release area

The effect of migration is less predictable. Nash (1995) had earlier found that *H. rubra* made unidirectional movements of at least 300 metres along a rocky shoreline at Stinking Bay in southern Tasmania. It was believed that the presence of extensive areas of sandy bottom around each site would limit movement of abalone out of the study area.

Comparison between positions of release and recapture found no net migration at Magistrates Point. Abalone could only migrate from this site by travelling westward, along the reef, out to the end of the point. Preliminary searches in this area recovered only one abalone outside the site. A (separate) study outside the site has never recorded the presence of tagged abalone. We are certain that migration was not a factor in the high rate of disappearance of tagged abalone at Magistrates Point.

A tagging program took place at the southern end of Hopfields Beach in 1966, several hundred metres to the south of Magistrates Point. None of the abalone recovered in that exercise were found to have moved more than a few metres from their release site (Harrison, 1967).

Conversely, at the other two sites, tagged abalone were recovered at distances of up to 500 metres from the study area. At Ironhouse Point, a local resident found tagged abalone in shallow water on a point about 500 metres south of the site. Research divers found tagged abalone at a rocky outcrop 300 metres south-east of the site. Abalone from all four tagging events were recovered from this rock, perhaps indicating that if distance travelled was a function of time, then abalone, particularly from the earlier tagging events could potentially travel much greater distances. When the Ironhouse Point site was established, sand coverage over the reef was more extensive, and it was thought that the abalone might be contained within the study area. During the course of the study, much of the sand was removed and rocky patches formed into unbroken reef extending for great distances offshore and along the shore southward, allowing the abalone to migrate.

At Couta Rocks it was realised that abalone had migrated from the study area when a population sample was collected from reef 400 metres south of the site. From a sample of 375 abalone, 6 were found with tags from the two earliest tagging events. Commercial divers later recovered tagged abalone from the entire reserve area, which is bounded by rocky coast extending about 500 metres both north and south of the tagging site. Following the conclusion of field work at Couta Rocks, divers fished this short section of coast intensively, to the extent that it was estimated about 10 tonnes of abalone were taken here in the year that followed (M. Stephenson, pers. comm.). It is most likely that because of this coverage that all abalone habitat within the region was sampled which negates the effect of migration outside the immediate study area.

Migration out of the study area is therefore considered to be a confounding factor only at Ironhouse Point.

4.2.3 Loss of tags from living fish

Incomplete recovery of marked animals due to tag loss is complex. There are two types of tag loss. The first type takes place during a relatively short period after release of marked fish. It does not affect the rate of disappearance of marked individuals and is measured by the constant *a* in equation 7. The second type is an ongoing (*i.e.* throughout the life of the study) process of shedding of tags and contributes to the rate of disappearance (Beverton and Holt, 1957).

Examination of tag loss over time indicates that in this study, ongoing tag loss was negligible (Fig. 10). Furthermore, from examination of tagged shells, it was generally noticeable that nacre was deposited over the tips of the rivets by 12 months, and that once this process had started, it became much more difficult to remove the tag. Prince (1991) found that within three months of tagging, over 50 percent of abalone had begun coating the end of the rivet with nacre, and that 13 months after tagging, over 30 percent had firmly cemented the rivet in place, thus increasing the rate of retention.

It is apparent that tag loss was least from abalone released at the start of the study (Fig. 10). A different style of rivet was used to attach the tags to abalone during the first tagging event at all three sites. This type of rivet was difficult and time-consuming to apply, and during the following three tagging events, its use was discontinued in favour of a design that was much simpler to use. Alternatively, tag loss from the first tagging event may have been lower because divers were less experienced and were more cautious in their approach to tagging and took more time to ensure that tags were adequately fastened and would not fall out.

Tag loss in this study was recorded as the physical disappearance of tags. However effective tag loss may occur in more subtle ways that were not measured. Other forms of tag loss include erosion of numbers on the tags and bent or broken tags, caused by abalone abrading the tags against rocks. It has also been noted that where tags are attached to the abalone, they may become obscured by overgrowing of epibiota (McShane, 1988; Shepherd, 1998; Shepherd and Godoy, 1989). At the Marine Research Laboratories, it has frequently been observed that abalone collected from areas of past tagging studies are found to bear tags when the epibiota has been removed from their shells.

Population samples from Couta Rocks and Ironhouse Point collected at the end of the study were both found to contain tagged abalone when the shells were cleaned some months later. Some of the tags were recent and indicate that overgrowing may take place within two years. At both sites, fouling was caused by growth of encrusting coralline algae on the shells. At Magistrates Point divers became aware of the need to carefully examine heavily fouled abalone in case tags were missed. Here, fouling was caused by a variety of organisms including sponges, bryozoans and various algae. The fouling was quite obvious and divers were able to check heavily fouled shells for tags. However the degree of build up (of encrusting corallines particularly) on abalone was deceptive, and a great many abalone must have been missed.

Fig. 16. The white arrows point to two moderately encrusted Floy disc tags riveted to the shell of an abalone. The abalone had been released for only twelve months, and probably would have escaped detection had the diver not examined bumps on the shell near the respiratory pores of the abalone. (*Photo R. Officer*)

Shepherd (1998), in a recent study of tagged juvenile abalone, found higher rates of disappearance using the Beinssen-Powell method than in a parallel study that compared temporal change in abalone density. He concluded that the Beinssen-Powell method tended to overestimate *M* and the density method underestimated *M*.

The high rates of disappearance of abalone at Ironhouse Point and Magistrates Point can be mostly attributed to overgrowing of tags. At Couta Rocks, and to a lesser extent Magistrates Point, the rate of disappearance was non-linear. Early tagging events produced a greater rate of recovery than could be attributed to a linear rate of migration or overgrowing of tags. This may be due to seasonal effects upon settlement and growth of fouling organisms. Tags on abalone released at different times of the year may be fouled by organisms that have differing capacities to foul tags, or limit settlement of encrusting corallines on tags by some inherent anti-fouling property. Different rates of recovery may be attributable to the use of tags of varying colours during different tagging events. While it is not suggested that divers could recover abalone with tags of a particular colour more efficiently, some colours may transmit light at rates more favourable to the settlement and growth of fouling organisms.

4.2.4 Size-composition of tagged abalone

Due to the high rates of disappearance of tagged abalone, it was decided to age their shells and determine rates of mortality from catch curves (Figs 12 to 14). All three sites showed higher rates of mortality than catch curves from the population surveys, and initially it appeared that there must be a link between mortality and the tagging process. However, after a comparison of size-compositions of tagged abalone with size-compositions from population samples (Fig. 4, Fig. 17) it appeared that the tagged abalone were not a representative sample of the stocks in those areas.

At two of the sites, the size-composition of the sample tagged by divers (Fig. 17) differs markedly from that obtained in population samples (Fig. 4). In all four tagging events at Ironhouse Point, the modal size-class of tagged abalone was 121 mm or less, while that of population samples was 5 mm higher at the start of the study rising to 15 mm towards the end. At Magistrates Point, divers also tagged a higher proportion of small abalone than would be found in samples randomly selected from the population.

Because of the bias towards smaller abalone when tagging, the recaptured abalone tend to be smaller (and younger) than those from population samples, which were randomly collected and not selected by size.

Consequently, catch curves prepared from the aged tagged shells at these two sites feature steeper regression lines than those from the population samples because there is a greater frequency of younger age-classes (Figs 12 to 14). This immediately discounts the value of these particular mortality estimates, and raises the possibility that the mark-recapture estimates of mortality are affected by size-selected bias.

Further investigation of size-selected bias among tagged abalone shows that the smaller size-classes are recaptured at proportionally greater levels than larger size-classes (Fig. 17). At Magistrates Point and Ironhouse Point this infers that larger abalone have a greater rate of disappearance (by mortality, migration or overgrowing of tags) than smaller abalone. At Couta Rocks, it probably just means that the tags fell out of the larger abalone at a greater rate.

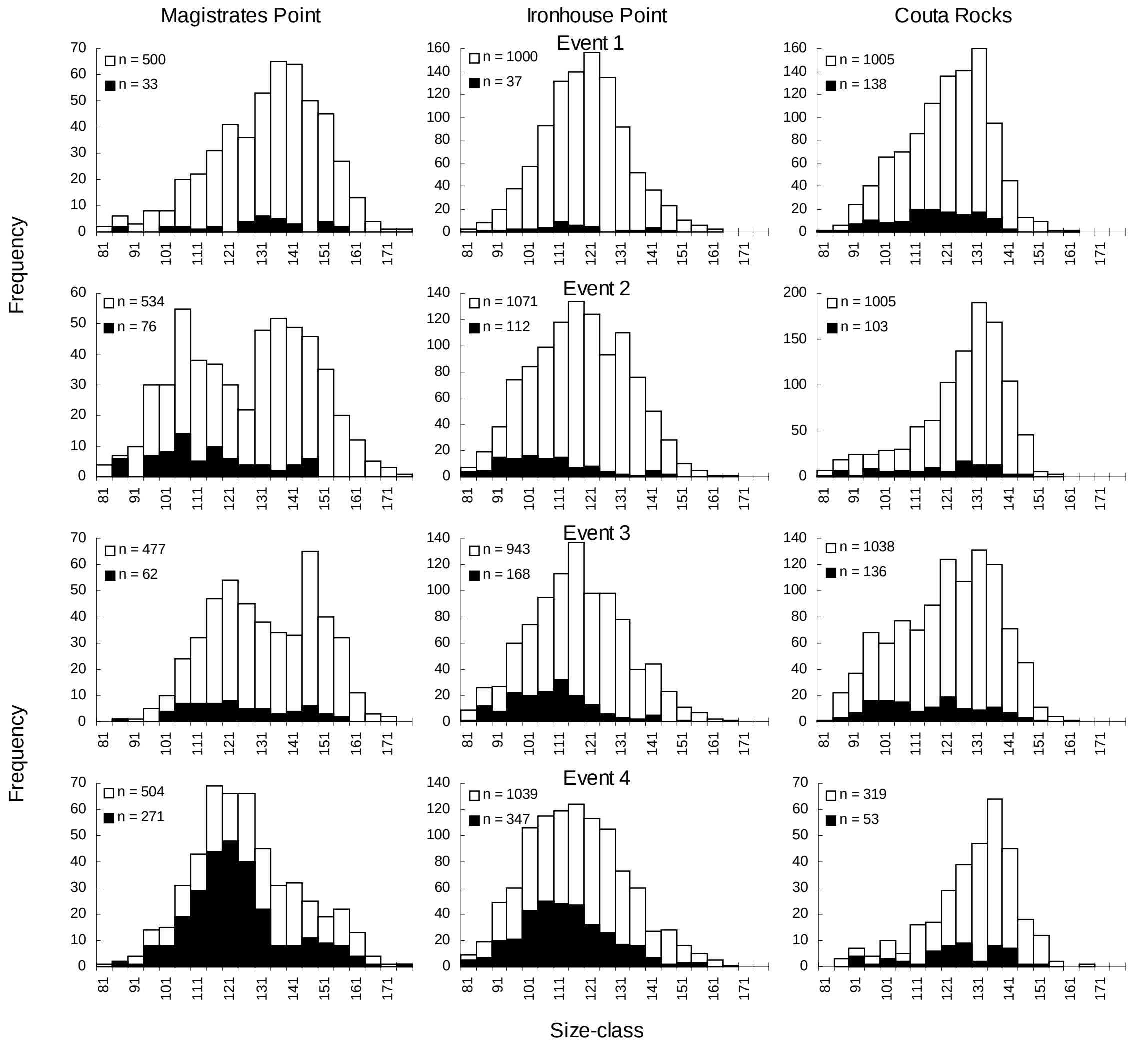


Fig. 17. The size-composition of tagged abalone, showing the proportion of tagged abalone recovered by size-class. Length-frequency distributions of the initial length of released (un-shaded) tagged abalone and initial length of recaptured (shaded) tagged abalone are shown thus:

- Each column of four charts is from the site the name of which appears at the top of the figure,
- Each row of three charts is specific to one of the four tagging events that took place at approximately six-monthly intervals, Event 1 being the earliest.

The size-class is grouped at 5-mm intervals and is spaced so that the size limit (132 mm) falls on a class boundary. The legend in each chart shows the total number of abalone tagged at each site for each tagging event, and the total number of tagged abalone recaptured from that event.

It was subsequently found that size-selected bias when tagging underwater at Ironhouse and Magistrates Point was inadvertently caused by divers attempting to ensure that tag loss was minimised. The shells from many larger (older) abalone become brittle due to marine borers tunnelling through the shell. The process of tagging involves selecting an abalone at random and reaming out two respiratory pores to attach the tags. At this point, shells from many of the larger abalone would start crumbling around the pores, and the holes would become too large for successful attachment of the rivet. The divers would then abandon that abalone, and select another one.

In contrast, researchers tagging abalone aboard the boat at Couta Rocks did not have the luxury of being able to pick and choose from a seemingly endless array of abalone. They were limited to what the diver had brought up, and did not have a great range to choose from. About 10 abalone were collected by divers and brought to the surface. If a shell was found to be brittle, the people in the boat often made two or three attempts to find a respiratory pore that was strong enough to withstand the compressive forces of the rivet and would persevere with abalone that divers tagging underwater would have abandoned. The abalone were then tagged and measured, and placed over the side in bags. Divers would collect the bag of abalone and return them to the reef, where they were individually placed foot down to the substrate, and guarded from attack by wrasse or being washed off the rock by the surge until they had established a secure hold on the reef. Divers recall that when they replaced the freshly tagged abalone on the bottom, tags would occasionally fall out of the shell, or become loosened by rubbing against or becoming attached to the feet of other abalone in the bag. This may partially explain the high rate of initial tag loss at Couta Rocks (Fig. 10).

4.3 Mortality rates from aged shells

Rates of mortality derived from catch curves depend upon several critical assumptions. The first is that the abalone can be successfully aged. We found support for our ageing technique and assumption of annual growth rings when comparing length-at-age models with growth increments at all three sites (4.1.2).

We have assumed that natural mortality occurs at the same level for each age-class within a sample. Earlier work with this species in Tasmania found that mortality declines with age to year 3, but from then to year 7 was approximately constant (Prince *et al.*, 1988b).

We have also assumed that a constant rate of recruitment occurred across the range of age-classes within a sample. There is no evidence to support this assumption, and given variability in predator abundance and environmental factors, constant rates of recruitment during the period represented by the sample is unlikely.

In contrast to the rates of disappearance from the mark-recapture study at Ironhouse and Magistrates Points, estimates of mortality derived from catch curves fall within a range of values that are more commonly associated with death by natural causes. For example, Shepherd and Breen (1992) list several values of M in the range 0.19 to 0.70 for adult blacklip abalone. Prince estimated M between 0.28 and 0.45 for emergent abalone at George III Rock in south-east Tasmania (Prince, 1989).

Alternatively, if natural mortality is calculated using the method described by Hoenig (1983) where

$$M = -(\ln(\frac{N_t}{N_0}) / t ,$$

and N_0 is the initial number of fish in the population, N_t is the number of fish that will reach maximum age t in the population (which is frequently assumed to be 1 percent), then for the range of maximum ages between 15 and 20 years such as were found at Magistrates Point and Ironhouse Point, values of M could be expected to range between 0.30 to 0.23. These are generally lower than values found by catch curve analysis in this study.

Mortality rates at Magistrates Point (the un-fished reserve) were virtually unchanged between 1996 and 1998. Z was measured at about 0.41 which is higher than the generally accepted rate of 0.2 for adult *H. rubra*, found by Beinssen and Powell in eastern Victoria (1979) or Nash in un-fished populations in Bass Strait (Nash *et al*., 1994). That mortality is higher at Magistrates Point than Ironhouse Point and Couta Rocks (which were both fished before the study) may reflect greater abundance of abalone, as Shepherd found in a similarly un-fished population of *H. laevigata* (Shepherd, 1990). Shepherd also noted long-term oscillations in population size and rates of mortality (between 0.02 to 0.86, mean 0.38) and concluded that the rate of mortality was density-dependent.

Presumably the decrease in mortality rates at the two formerly fished sites over the duration of the study reflects the absence of fishing mortality. If this is the case, then instantaneous fishing mortality (F) is about 0.15 per annum at Ironhouse Point (Fig. 13). This is much lower than that found by Beinssen (1979) who estimated F at 0.8 and 1.05, or Sanders and Beinssen (1996) (F averaged about 0.4 over a 5 year period), but similar to that of McShane (1989) who estimated fishing mortality at 0.16. All three studies used methods other than catch-curve analysis. The low rate of F at Ironhouse Point is consistent with information we have received about catch and effort in the region (see 4.1.2, *Comparison of growth rates by site*).

At Couta Rocks in 1993, the high standard error of Z masks changes in mortality (Fig. 14). The sample was small (102) and may not be representative of the population.

Abalone at Couta Rocks become fully emergent several years later than at the other sites (Fig. 14). Because earlier studies have shown that emergence takes place when abalone are sexually mature (Prince *et al*., 1988b), (Nash, 1992), it implies that the age of sexual maturity is later here. At Ironhouse and Magistrates Points, age-classes are completely emergent by about age 10. Blacklip abalone from the North Coast and the Bass Strait islands (Nash *et al*., 1994) also appear to be fully emergent at this age, while abalone from the Gardens (East Coast), Ketchem Bay (South Coast) and Top Rocks (South-West) become fully emergent slightly later at age 13 (Nash, 1992).

5. Conclusions

The mortality study by the mark-recapture methods of Beinssen and Powell was confounded by a variety of factors including overgrowing of tags, migration and size-selectivity that were not anticipated when the study was initiated. This type of study is very demanding of resources if it is to be undertaken successfully, particularly at the stage involving recapture of tagged abalone. The promotion of a tag-reward scheme and subsequent recapture of tagged shells by licensed abalone divers and processors proved very successful.

Clearer results might be obtained if the study was run with multiple tagging events over a shorter duration (perhaps just one year, instead of three years). While the mortality estimates from such a study would relate only to that period of time, there would be less confounding effects with which to contend, and greater familiarity with the study site may bring advanced warning of problems. In short-term studies however, there may be problems detecting significant changes in disappearance between tagging events.

Future studies of this nature should provide greater emphasis on recapturing (by temporary marking) and recording abalone at each tagging event. This would benefit the study because the rate of disappearance of the abalone would be more closely monitored (and confounding effects detected earlier). It would also permit the parallel use of survival estimation techniques (*e.g.* those described by Lebreton (1992)) on at least part of the tagged stock. The number of tagging events should be expanded, because regressions of just four data points tend to have a high degree of variability.

Because of fouling, the type of tags used has proved unsuitable for long-term use. Where abalone are tagged for long periods, tags need to have some sort of anti-fouling properties or be raised well above the surface of the shell so that they are not overgrown by epibiota. This study has also demonstrated that the rivet-into-respiratory-pore technique of Prince (1991) is unsuitable for abalone with brittle shells, and its use may induce size-selective bias.

Estimates of growth rate and average maximum size from the three sites derived from both growth increments and aged shells show a common trend. They support the commonly held belief of latitudinal trends in growth rates between northern and southern Tasmania and the work of earlier researchers (Nash *et al.*, 1994).

Perhaps the most important outcome of the study is the evidence confirming the assumption of annual growth rings at the three sites. This enables us to extend the area over which we can develop age-based growth information from the south-east to the north-east and west of the State, and enhances our knowledge of the biology of stocks in those areas.

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