

**Abstract.**—Growth of the blacklip abalone, *Haliotis rubra*, was estimated from 1,464 individuals that were tagged and left at large for up to five years at seven sites in New South Wales, Australia. Both the shape of the fitted growth curves and the average growth rates differed significantly among sites, separated by only 1–20 km. There was also significant variation in the growth of individual abalone within sites and this variation differed among sites. Abalone at sites where they grew quickly reached larger lengths and were morphologically different from those at sites where they grew slowly. For example, the shells of abalone from sites where they grew slowly were wider and heavier at a given length than those from sites where they grew quickly. The implication that rates of growth in width are less variable than growth in length suggests that a minimum legal width limit may be more appropriate than the present size limit that is based on length. A minimum legal width limit would redistribute fishing effort away from sites where abalone grow in length quickly towards sites where they grow slowly, including sites which are presently unfished because few individuals reach the minimum legal length. If this were possible, it would reduce the differences in exploitation among sites which, at present, have the potential to seriously deplete populations at sites where individuals grow quickly.

# Covariation between growth and morphology suggests alternative size limits for the blacklip abalone, *Haliotis rubra*, in New South Wales, Australia

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Legal restrictions on the minimum size of individuals allowed to be harvested are used to manage many fisheries. The theory behind their use asserts that by delaying the harvest of individuals until they have grown to a certain size, both yield and egg production can be increased (Beverton and Holt, 1957). Appropriate minimum size limits have traditionally been estimated by considering average rates of growth, mortality, and reproduction (Goodyear, 1993). Spatial variation in demography can complicate the use of a single size limit for a stock by making different size limits appropriate in different areas. Enforcement of different size limits over large spatial scales is possible (e.g. Guzmán del Prío, 1992), but if demography varies over small distances, appropriate size limits are difficult to enforce.

A common finding of studies on the growth of abalone has been that individuals at different sites can grow at markedly different rates (Sainsbury, 1982; Breen, 1986; Tegner et al., 1989). Despite this, there have been few systematic attempts to determine the spatial scale over which differences in growth occur (see Day and Fleming, 1992, for a review). Nonetheless, it

is apparent that growth can vary among regions separated by hundreds of kilometers (Nash, 1992) and among sites separated by tens of kilometers (Breen, 1986). As well as differing in their rate of growth, abalone that grow quickly will, in general, reach larger sizes than abalone that grow slowly (e.g. McShane, 1992; Nash, 1992). Consequently, many abalone fisheries contain populations with individuals that grow very slowly to only small sizes (Sloan and Breen, 1988; Tegner et al., 1989; Nash, 1992). Because minimum legal sizes are, in general, enforced over areas larger than those over which such variation in growth can occur, these sites often remain unfished.

Commercial fishing of abalone *Haliotis rubra* in New South Wales (NSW), Australia began in the early 1960's. Initially, divers harvested abalone of any size, but in 1973 a minimum legal length limit of 100 mm was introduced. This length limit was chosen to ensure that abalone recruiting to the fishery had reproduced at least once after reaching sexual maturity at approximately 80–90 mm. As fishing pressure increased through the 1970's and 1980's, it became apparent that the length limit of 100 mm

was not conserving enough egg production (Hamer, 1983). In response, the minimum legal length limit was increased in a series of increments from 100 mm in 1979 to 115 mm in 1987. An unfortunate consequence of these increases was the concentration of fishing effort at sites where abalone grew quickly and to large sizes (see also McShane, 1992). Because of this high level of effort and the limited dispersal of larval abalone (Prince et al., 1987), such sites were often overexploited, whereas in other areas where abalone grew more slowly to smaller sizes the populations were underexploited.

In this study, we describe a tagging study of variation in the growth of *Haliotis rubra* at seven sites along the NSW coast. These sites were grouped into four locations encompassing most of the geographical range of the fishery. This provides an indication of the variability in growth of the species at three spatial scales: among locations separated by hundreds of km, among sites separated by 1–20 km, and among individual abalone within the sites. In addition we describe morphological differences among the abalone that appear to be related to their rate of growth. This link between growth and morphology suggests that a minimum legal width limit may be more appropriate than the present size limit based on length.

## Materials and methods

### Sites and tags used

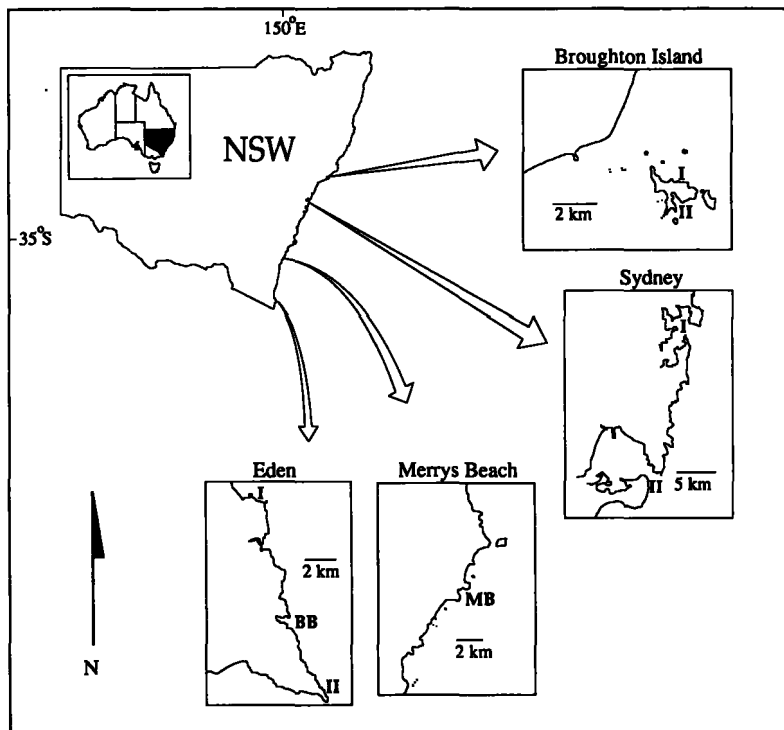
Abalone were tagged at seven sites, spanning almost 1,000 km of coastline, that were chosen because they were commonly used by commercial divers in the NSW abalone fishery (Fig. 1). Six of the sites were grouped into three locations (Broughton Island, Sydney, and Eden) each with two sites (referred to as I and II) separated by between 1 and 20 km. The single site at Merrys Beach was approximately midway between those at Sydney and Eden (Fig. 1). Supplementary tagging was also done at Bittangabee Bay near Eden (Fig. 1). This site was not commonly used by commercial fishermen because few individuals reached lengths above the 115-mm minimum legal limit. Estimates of growth parameters for Bittangabee Bay were not calculated separately because only 20 individuals were recaptured. These abalone were, however, used in the estimation of a growth

curve for all recaptured individuals and in the relationship among morphological variables (see below).

Small ( $\approx 2 \times 10$  mm), numbered plastic tags were attached to abalone with a cyano-acrylate glue between 20 May 1975 and 3 October 1981. This procedure required that abalone be removed from the water and their shells dried with compressed air before tagging. Individuals were chosen to make the size range at tagging representative of the population at each site. The maximum diameter (i.e. length) of each shell was measured to the nearest 0.5 mm, and the abalone were then replaced in the area near where they were collected. Samples of these tagged abalone were recaptured at opportunistic times between 11 December 1975 and 18 May 1982.

### Patterns in growth

Estimates of growth were obtained by using procedures based on a mark-recapture analogue of Schnute's (1981) general growth model (see Francis, in press). Schnute's model relates size to age by several parameters, including two ( $a$  and  $b$ ) which combine to describe a range of traditional growth curves including the von Bertalanffy ( $a > 0$ ,  $b = 1$ ), Richards



**Figure 1**

Map of Australia (inset) and New South Wales (NSW), showing the position of eight sites within four locations where blacklip abalone, *Haliotis rubra*, were tagged. Sites I and II within each location are as indicated on the maps; BB = Bittangabee Bay, MB = Merrys Beach.

( $a > 0, b < 0$ ), logistic ( $a > 0, b = -1$ ), and Gompertz ( $a > 0, b = 0$ ) models (Schnute, 1981). Francis (in press) reparameterized this model to express observed increments in length during tagging ( $\Delta Y$ ) as a function of the observed length at tagging ( $Y_t$ ) and time at liberty ( $\Delta t$ ). The model can be reparameterized further, so that growth can be described in terms of average annual growth for individuals of a given size (see Francis, 1988a). The general model where both  $a \neq 0$  and  $b \neq 0$ , was

$$\Delta Y = -Y_t + \left[ Y_t^b e^{-a\Delta t} + c(1 - e^{-a\Delta t}) \right]^{\frac{1}{b}},$$

where

$$a = \ln \left[ \frac{y_2^b - y_1^b}{\lambda_2^b - \lambda_1^b} \right],$$

$$c = \frac{y_2^b \lambda_1^b - y_1^b \lambda_2^b}{\lambda_1^b - y_1^b + y_2^b - \lambda_2^b}, \text{ and}$$

$$\lambda_1 = y_1 + g_1 \text{ and } \lambda_2 = y_2 + g_2.$$

The model was fitted to the observed increments by using maximum likelihood (Francis, 1988b). Parameters estimated during this process include the mean annual growth rates ( $g_1$  and  $g_2$ ) at two sizes ( $y_1$  and  $y_2$ ) and the parameter  $b$ . These parameters together combine to define the parameter  $a$ , and hence the shape of the fitted growth curve.

Several other parameters were also considered, and were included in the model if they significantly improved the fit (see Francis, 1988b). Two parameters describing seasonal variation in growth were examined by replacing  $\Delta t$  above with  $\Delta t + (\phi_r - \phi_t)$  where for any time ( $t_i$ )

$$\phi_t = \frac{u(\sin(2\pi[t_i - w]))}{2\pi}$$

and  $t_t$  and  $t_r$  are the times at tagging and recapture. The parameters  $u$  and  $w$  then describe the amplitude and phase of seasonality in growth, respectively. A parameter describing variation in growth among individuals was also examined, where the mean ( $\mu_g$ ) and standard deviation ( $\sigma_g$ ) of the expected increment in length were related by

$$\sigma_g = v\mu_g,$$

where  $v$  is the coefficient of variation in growth. A parameter describing contamination by outliers was

also examined, but it never added significantly to the model (see Francis 1988b).

The error model used considered errors due to variation in growth and measurement by

$$\Delta Y_{obs} = \Delta Y \varepsilon_g + \varepsilon_m,$$

where the observed increment in length ( $\Delta Y_{obs}$ ) was a function of that predicted by the growth model ( $\Delta Y$ ) and errors due to variation in growth ( $\varepsilon_g$ ) and measurement ( $\varepsilon_m$ ), assuming  $\varepsilon_g \sim N(1, \sigma_g)$  and  $\varepsilon_m \sim N(\mu_m, \sigma_m)$ . As such,  $\mu_m$  represents measurement bias (i.e. consistent difference in measurement between marking and recapture) and  $\sigma_m$  represents random error in measurement. Since better estimates of the growth parameters can be achieved when both  $\mu_m$  and  $\sigma_m$  are known (Francis, in press), they were estimated by repeatedly measuring the same set of shells ( $n=50$ ) after the tagging program had finished. Measurement bias was disregarded ( $\mu_m=0$ ) because the same people used identical techniques to measure abalone at tagging and recapture. Random errors in measurement among replicate readings and among readers were similar in size, and as a consequence  $\sigma_m$  was set to 0.65 for all analyses. Following fitting of the model, plots of residuals against length at tagging and time at liberty were investigated for any systematic lack of fit.

The parameters  $y_1$  and  $y_2$  should be chosen to span the lengths at tagging and to enable reliable estimates of  $g_1$  and  $g_2$  (Francis, 1988b). Because of differences in the length of abalone tagged among the sites, appropriate sizes for  $y_1$  and  $y_2$  also differed among sites. To facilitate comparison,  $y_1$  and  $y_2$  for each site were chosen from three standard lengths: 65, 90, and 115 mm. At sites where few small abalone were tagged, annual growth rates were estimated at 90 and 115 mm. Alternatively, at sites where few large abalone were tagged, annual growth rates were estimated at 65 and 90 mm. Once fitting of the model was completed, the annual growth rate at the third standard length was also calculated. This growth rate is defined by the parameters chosen during fitting of the model. Comparisons among estimated parameters were made by using  $t$ -tests.

To facilitate the comparison of our estimates of growth with those previously published, we also fitted the traditional von Bertalanffy growth model. This was done within the framework described above (see Francis, 1988b). To further aid the comparison of growth rates among studies, we converted the traditional von Bertalanffy parameters estimated from tagging data ( $k$  and  $L_\infty$ ) to parameters describing estimates of annual growth at the standard sizes used in this study. This was also done for previously pub-

lished estimates of growth derived from tagging studies in which similar tagging methods were used.

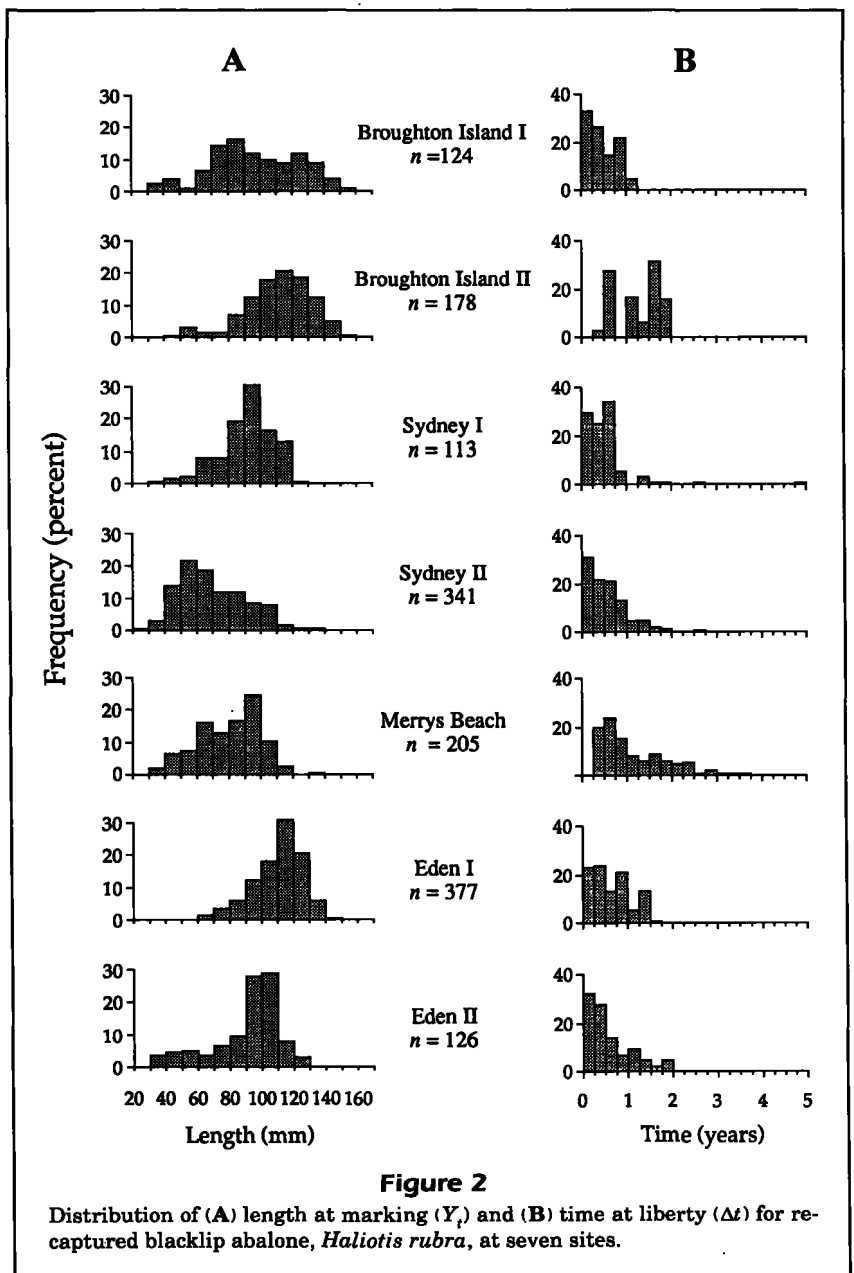
### Relation of growth to morphology

The shells of 390 recaptured abalone were retained for further measurement. This allowed us to relate present morphology of the shells to past growth rates. Few shells were retained from Broughton Island I or Eden I because the abalone were used in separate experiments to estimate fishing mortality. Measurements taken included the maximum and minimum diameters (length and width), the width of the ventral ridge of the shell at the aboral margin (ridge), and the dry weight of the shell. Relationships among these variables were investigated by correlation. To relate present morphology to past growth, the length of all shells was related to their width, weight (log transformed), and ridge by using multiple linear regression. The residuals from this relationship then indicate whether a shell is longer or shorter than expected given the other morphological variables. In a similar way, all the tagging data were combined into one growth model. The residuals from this growth model then indicate whether an abalone has grown faster or slower than expected. By averaging the residuals from the morphological relationship and the growth curve across all individuals at a site, any relationship between rates of growth and shell morphology among sites should be apparent.

### Results

A total of 1,464 abalone were recovered from the seven sites. At tagging, these individuals ranged in size from 15 to 152 mm, with a mean size of 91.1 mm (SE=0.7). The size of recaptured abalone at tagging differed among sites. Few of the individuals recaptured at Broughton Island II and Eden I were small when tagged (Fig. 2A). In contrast, few large abalone were recaptured from Merrys Beach, both sites in Sydney, and from Eden II.

Tagged abalone were at large for a period between 8 and 1,736 days, although most (98%) of the individuals were recaptured within two years of release. The range of times between tagging and recapture of abalone differed among sites (Fig. 2B). There were generally shorter times between tagging and recapture in Broughton Island I and Sydney I, and longer times at Merrys Beach (Fig. 2B). During the tagging period increments in size ranged from -8 mm to 84 mm, with an average of 11.8 mm (SE=0.4). Negative growth may have been caused by erosion of the shell.



## Patterns in growth

The shape of the fitted growth curve differed significantly among sites ( $t$ -tests,  $P < 0.05$ ; Table 1). At Broughton Island I and Sydney I, the fitted growth curve was similar to a traditional von Bertalanffy shape ( $a > 0$ ,  $b = 1$  in Table 1), whereas at Eden II it was more similar to a Gompertz shape ( $a > 0$ ,  $b = 0$  in Table 1), and at Merrys Beach more similar to a logistic shape ( $a > 0$ ,  $b = -1$  in Table 1). All curves were asymptotic and expected growth approached zero (Fig. 3B). The size at which expected growth equalled zero differed among sites and ranged from 118 mm at Merrys Beach to 151 mm at Broughton Island II (Fig. 3B; Table 1).

Estimates of average annual growth rates differed significantly among the seven sites (Table 1). Abalone at the two sites on Broughton Island had faster rates of growth than all other sites. At Broughton Island II a 65-mm abalone was expected to grow to the 115-mm length limit in approximately 18 months (Fig. 3A). Above 115 mm, growth declined rapidly so that in the next year expected growth was less than 10 mm. The rate of decline in growth rate then slowed, and growth was expected to continue until 151 mm (Fig. 3; Table 1). In contrast, growth at Sydney I was much slower; a 65-mm individual was expected to take almost 9 years to grow to 115 mm (Fig. 3A). Growth rate declined at an approximately constant rate throughout life (i.e. approximating a von Bertalanffy growth curve) until individuals were expected to have no growth at 126 mm (Fig. 3; Table 1). At Merrys Beach, abalone were expected to grow from 65 mm to 90 mm within a year, but then growth declined rapidly and individuals were expected to grow only just above the minimum length limit of 115 mm (Fig. 3A). Growth rates at Sydney II and Eden II were not significantly different at any of the standard sizes (Table 1).

There was significant variation in growth among individual abalone within all sites (Table 1). Variation in growth among abalone at Merrys Beach was significantly less than that at all other

sites and significantly greater at Broughton Island II, Sydney I, and Eden I ( $t$ -tests,  $P < 0.05$ ). The standard deviation of the observed growth increment ranged from 0.29 times the expected increment at Merrys Beach to 0.87 times the expected increment at Eden I (Table 1). This range implies that two-thirds of the abalone at Merrys Beach will grow between 0.71 and 1.29 times the expected increment, whereas at Eden I, two-thirds of the abalone will grow between 0.13 and 1.87 times the expected increment (Fig. 4).

Parameters representing seasonal variation in rates of growth significantly improved the fit of the model at three of the seven sites (Table 1). At Broughton Island II, peak growth rates occurred during late October at 1.9 times the minimum growth rate in late April. In contrast, peak growth rates at both Sydney II and Eden I occurred in December at a rate 2.0 and 2.9 times the minimum, respectively

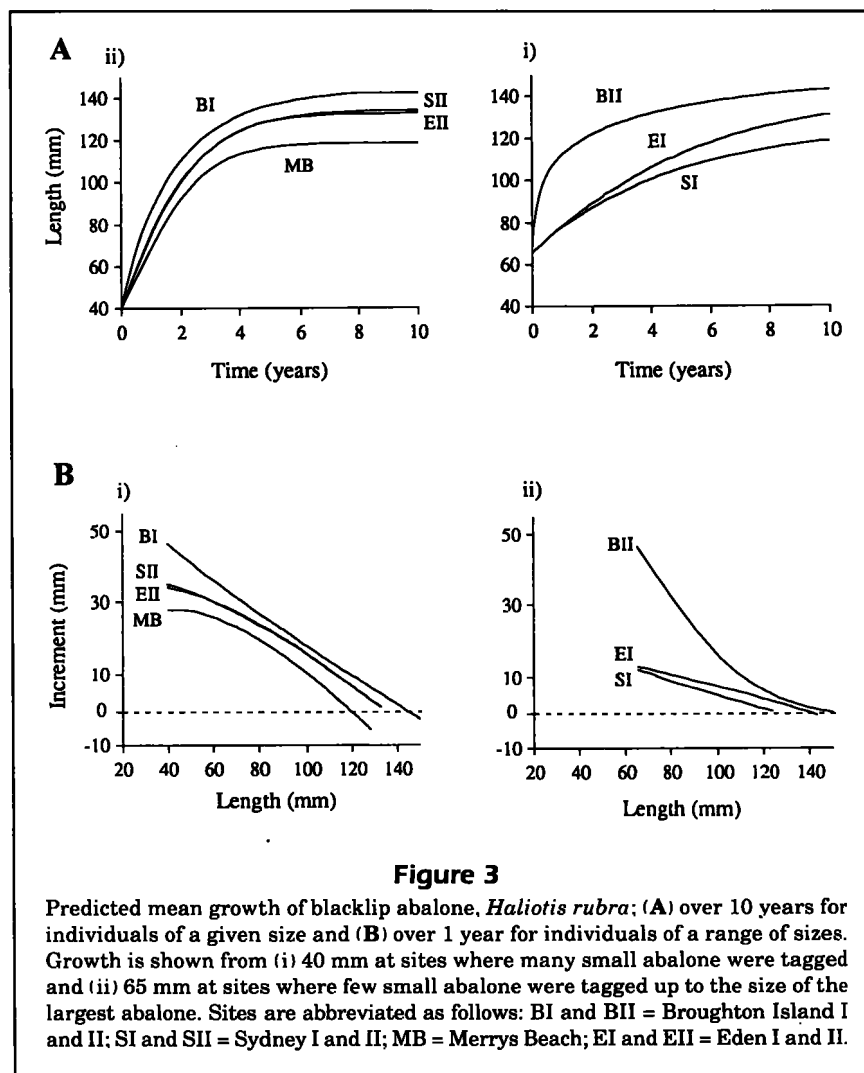
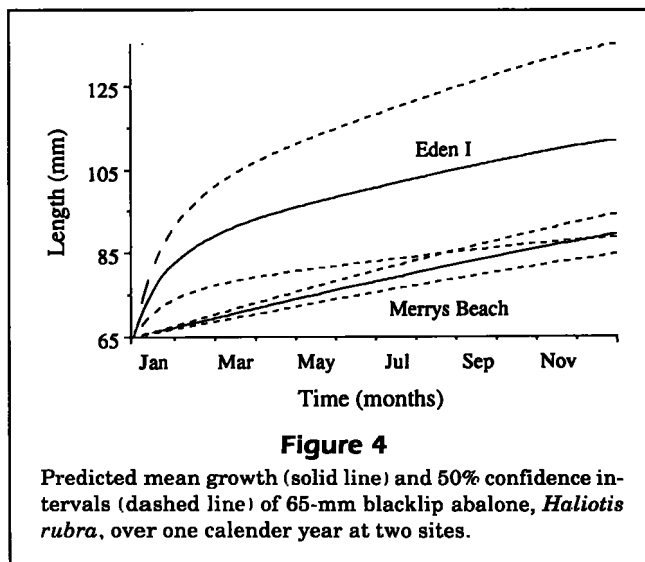


Table 1

Estimates of growth parameters and their standard errors (in brackets) for blacklip abalone, *Haliotis rubra*, from tag returns at seven sites. Parameters estimated during fitting are shown in light type; those defined by the fitted parameters are shown in bold. Expected annual growth rate at 65, 90, and 115 mm is shown as  $g_{65}$ ,  $g_{90}$  and  $g_{115}$ , respectively. See Materials and Methods section for a description of other parameters. Blanks occur where parameters did not add significantly to the fitted model.

Parameter	Site						
	Broughton Island		Sydney			Eden	
	I	II	I	II	Merrys Beach	I	II
<b>Curve shape parameters</b>							
$b$	1.33 (0.30)	7.58 (1.13)	1.33 (0.41)	0.25 (0.09)	-0.74 (0.12)	0.50 (0.37)	0.04 (0.10)
$a$	<b>0.59 (0.13)</b>	<b>0.11 (0.05)</b>	<b>0.20 (0.06)</b>	<b>0.66 (0.08)</b>	<b>0.89 (0.08)</b>	<b>0.22 (0.04)</b>	<b>0.71 (0.14)</b>
<b>Growth rate parameters</b>							
$g_{65}$ (mm·year <sup>-1</sup> )	<b>33.68 (1.52)</b>	46.93 (2.78)	12.25 (0.77)	28.66 (0.78)	24.63 (0.60)	<b>12.71 (0.92)</b>	28.80 (0.96)
$g_{90}$ (mm·year <sup>-1</sup> )	22.24 (0.95)	24.11 (1.39)	6.91 (0.52)	19.58 (0.67)	15.22 (0.34)	9.14 (0.49)	19.87 (0.69)
$g_{115}$ (mm·year <sup>-1</sup> )	11.52 (0.62)	8.36 (0.62)	<b>2.06 (0.91)</b>	<b>8.87 (0.77)</b>	<b>2.21 (0.42)</b>	4.86 (0.28)	<b>8.85 (1.40)</b>
<b>Seasonal parameters</b>							
$u$ (year)		0.31 (0.08)		0.48 (0.05)		0.33 (0.07)	
$w$ (year)		-0.19 (0.01)		0.00 (0.01)		-0.01 (0.03)	
<b>Growth variability parameter</b>							
$v$	0.54 (0.04)	0.73 (0.05)	0.76 (0.06)	0.48 (0.02)	0.29 (0.01)	0.87 (0.05)	0.39 (0.02)
Asymptote (mm)	143	151	126	133	118	140	133
Largest abalone (mm)	151	152	124	132	130	143	129
$n$	124	178	113	341	205	377	126



(Fig. 4). At Broughton Island I, Sydney I, Merrys Beach, and Eden II there was no evidence of any significant seasonal variation in growth rates (Table 1).

### Relation of growth to morphology

There were differences in the morphology of abalone among sites. For example, the shells of abalone recaptured from Merrys Beach were, on average, wider, heavier, and had a larger ridge than individuals of the same length from Sydney II (Fig. 5). There was a significant difference among sites in the slope of each of the relationships ( $t$ -tests,  $P < 0.05$ ), suggesting that the difference in morphology of individuals among sites changed with length. The shell of a 100-mm abalone from Merrys Beach was, on average, approximately 5 mm wider, 8.3 g heavier, and had a 1.7 mm larger ridge than the shell of a 100-mm abalone from Sydney II (Fig. 5). Differences in the width and ridge of shells among the sites increased with length, whereas differences in the weight of shells decreased with length (Fig. 5). The width, weight, and ridge of all shells were each significantly correlated with the other variables (width vs. weight  $r = 0.76$ ; width vs. ridge  $r = 0.58$ ; weight vs. ridge  $r = 0.68$ ;  $n = 390$  for all correlations).

Abalone from sites where their average growth was faster were morphologically different from those

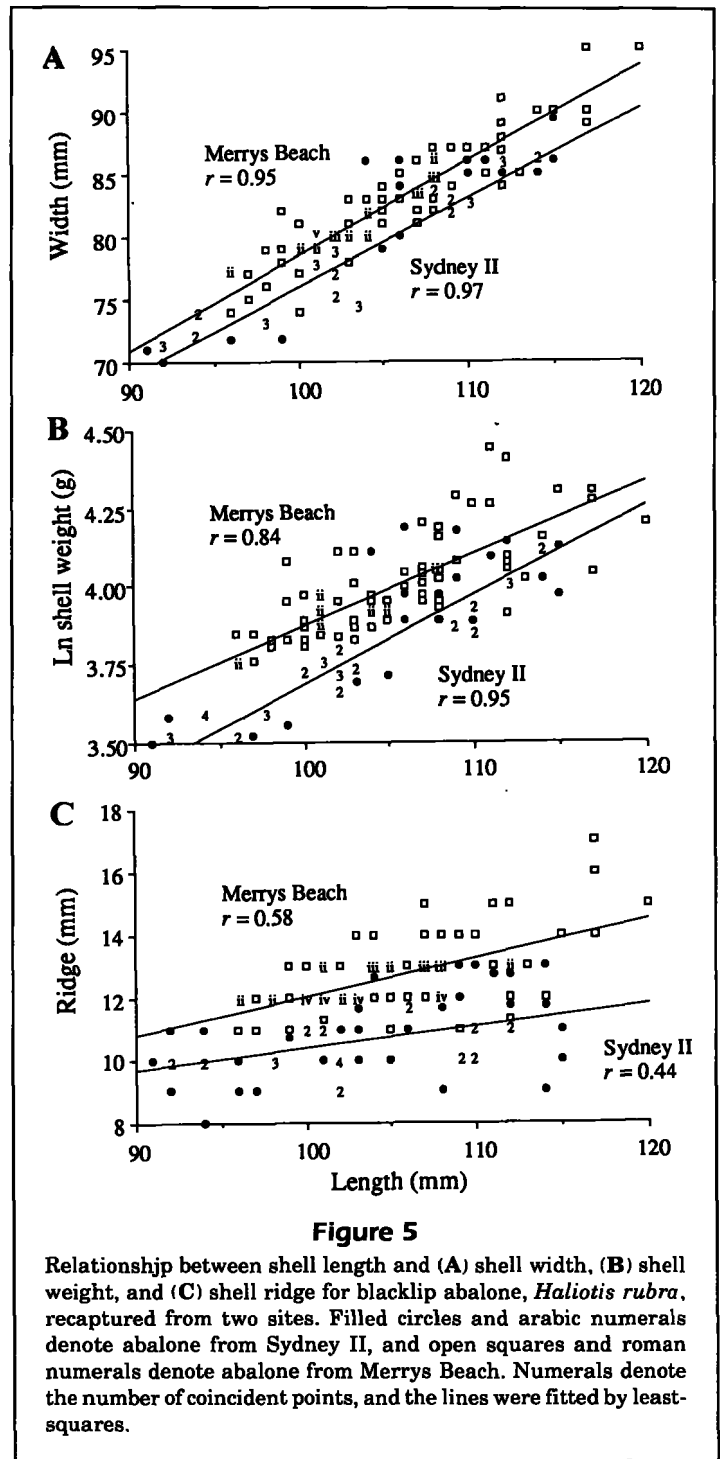
where their average growth was slower (Fig. 6). The residuals of the general growth model were significantly higher at sites such as those at Broughton Island, Sydney II, and Eden II than at Eden I, which was, in turn, significantly higher than Merrys Beach and Sydney I, or Bittangabee Bay (*t*-tests,  $P < 0.05$ ; Fig. 6). This ranking corresponds closely with the estimates of average growth rates in Table 1. The residuals of the relation between length and the independent variables width, weight, and ridge were generally higher at sites where growth was also high (Fig. 6). That is, given their width, weight, and ridge, abalone at sites where they grew quickly were longer than those where they grew slowly. Alternatively, shells of abalone of a given length at sites where they grew quickly were thinner, lighter, and had a smaller ridge than those at sites where they grew slowly.

**Discussion**

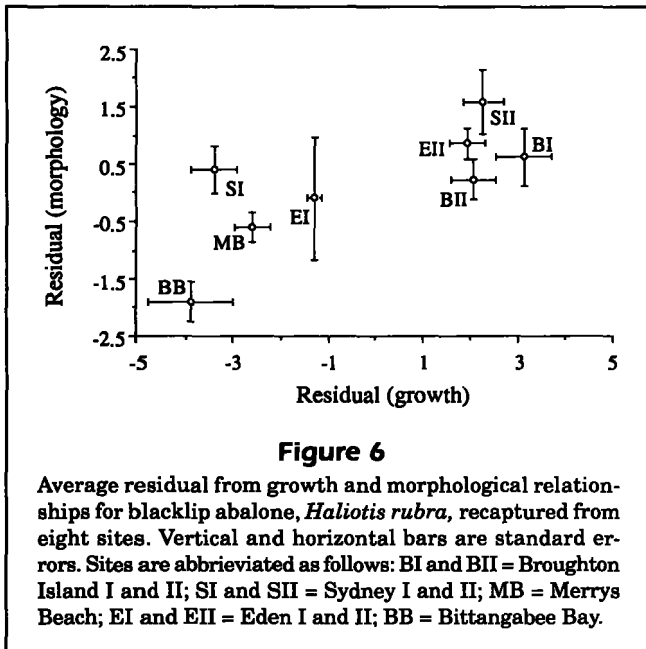
**Patterns in growth**

The intense spatial variation in growth that we observed for *Haliotis rubra* in NSW appears to be characteristic of abalone populations worldwide (Day and Fleming, 1992). At the smallest spatial scale, there was significant variation in the growth rate of abalone within sites. At a larger scale, both average rates of growth and the magnitude of within-site variation differed among sites separated by only 1–20 km. Perhaps the most likely explanation for variation in growth over these smaller spatial scales involves variation in the supply of food, related to local habitat and hydrographic conditions (Day and Fleming, 1992). At the largest spatial scale, average growth rates at the two sites on Broughton Island were significantly higher than all others. Broughton Island is approximately 300 km farther north than any of the other sites, and abalone around the island are likely to be exposed to higher water temperatures than abalone farther south. Water temperature is known to affect the growth rate of abalone (Day and Fleming, 1992), but the trend in NSW stands in contrast to that found for *H. rubra* in Tasmania, where abalone grow more slowly in the warmer, northern areas (Nash, 1992).

Several previous studies have found a relation between the rate of growth and maximum size of abalone at a site (Shepherd and Hearn, 1983; McShane et al., 1988; Sloan and Breen, 1988; Nash, 1992). In



general, abalone at sites where they grow quickly reach larger sizes than those at sites where they grow slowly. A similar situation appears to exist in NSW where abalone from the two sites on Broughton Island had the fastest average growth rates and reached the largest shell lengths (i.e. >150 mm, Table 1). In comparison, the slowest average growth rates



were recorded at Sydney I where the largest abalone was smaller than those at all other sites (i.e. 124 mm, Table 1). Despite this general relationship, slow rates of growth were recorded at Eden I, but growth was expected to continue until 140 mm, and many abalone were found over 130 mm in length.

Direct comparison of growth rates estimated by different studies are complicated by the variety of methods used for tagging and analysis. For example, tags attached by wire through an abalone's respiratory pore can affect growth (McShane et al., 1988), and growth parameters estimated from tagging and age-length data need to be interpreted differently (Francis, 1988a). Any comparison of growth rates among studies can also be confounded by the growth model used to fit the observed increments (e.g. compare estimates of growth from the different models used in Tables 1 and 2). When fitted with a similar growth model to past studies, our estimates of the growth of abalone in NSW span almost the entire range of those from similar studies in other states of Australia (Table 2). In addition, estimates of growth at the two sites on Broughton Island are consistently higher than any previously reported natural growth rates for the species.

### Relation of growth to morphology

Differences in the morphology of individuals among populations have been reported for a range of gastropod species including abalone (see review by Vermeij, 1980). Despite the significance of variation

in the morphology of *Haliotis rubra* in NSW, differences among sites were not large (e.g. compare with those of Breen and Adkins, 1982). There was also substantial variation in the morphology of individuals within sites. Despite little evidence, explanations for the variation in morphology of abalone usually concentrate on environmental rather than on genetic factors (McShane et al., 1988). As for other gastropods, it is likely that all aspects of shell growth that result in morphological differences are influenced by a variety of factors including exposure to wave action, diet, and water temperature (Tissot, 1992; Belda et al., 1993). Although we only present evidence to suggest that differences in morphology of the shell exist among populations of *Haliotis rubra*, there is also evidence for related morphological variation in the soft tissues (McShane et al., 1988).

Differences in the morphology of *Haliotis rubra* among sites were related to differences in growth. At sites where they grew slowly, the shells of abalone were wider, heavier, and had a broader ridge than those at sites where they grew quickly. These observations are similar to those made on other species of abalone (e.g. Breen and Adkins, 1982; Shepherd and Hearn, 1983; Tissot, 1988) and perhaps are not surprising considering that the processes proposed to influence both growth and morphology are similar. Inclusion of the slow-growing population at Bittangabee Bay strengthened the relation between growth and morphology that was evident among the seven sites where extensive tagging was done. Extensive tagging was not done at Bittangabee Bay because few animals grow above the present 115-mm legal length limit and hence the site is rarely fished by commercial divers. Because of the relationship between the maximum size reached by abalone at a site and their growth rate, very slow growing sites are rarely visited by commercial divers and, consequently, were not chosen for tagging in this study. As a result, our estimates of growth represent the higher end of the range of growth rates for abalone in NSW.

The increased width and weight of shells from abalone that grew slowly in length imply that rates of shell growth in width and weight are more consistent among sites than growth in length. This might be explained by increased synthesis of the organic matrix of the shell when energy is plentiful (Palmer, 1992) and can be devoted to expansion of the mantle at the growing edge and hence to rapid growth in length (Belda et al., 1993). Alternatively, when less energy is available, reduced synthesis of the organic matrix may result in a slower expansion of the growing edge of the mantle, causing slower growth in length and proportionally more growth in width and weight (Vermeij, 1980). Such an explanation would



not require any variation in the rate of incorporation of calcium-carbonate, which may continue regardless of the rate of synthesis of the organic matrix (see similar arguments for fish otoliths in Gaudie and Radtke, 1990). Because calcium-carbonate dominates a shell by weight (Palmer, 1992), if the rate of incorporation of calcium-carbonate was similar among different populations, the total weight of the shell might be a reliable indicator of the age of the abalone (see the literature on use of the weight of otoliths to age fish, e.g. Worthington et al., in press). The ability to age abalone is obviously desirable, but much doubt exists about present techniques of ageing, particularly for *Haliotis rubra* (McShane and Smith, 1992). This uncertainty emphasizes the need to investigate alternative methods to age abalone, one of which may be shell weight (Worthington et al., unpubl. data).

### Potential for alternative size limits

The present 115-mm minimum legal length limit is enforced along the entire coast of NSW for both the commercial and recreational fisheries. This size limit was chosen by considering average rates of growth, mortality, and reproduction in an attempt to maximize yield from the entire stock. The intense spatial variation in growth that we have described creates several problems which combine to restrict the effectiveness of the length limit. For example, because the 115-mm length limit was chosen by considering average rates of growth, it is less appropriate for sites where abalone grow faster or slower than average. At sites where they grow quickly, abalone rapidly reach the minimum legal length and may be harvested before contributing significantly to levels of egg production. Because of the limited dispersal of larval abalone (Prince et al., 1987), such sites have a limited capability to recover after fishing and hence may easily become overexploited. In contrast, at sites where they grow slowly, abalone take a longer time to reach the minimum legal length limit, and few are removed by divers. Consequently, rates of egg production may be high but they do not contribute

**Table 2**

Comparison of estimates of growth for blacklip abalone, *Haliotis rubra*. Note the estimated growth of abalone below 80 mm from Prince et al. (1988) was determined by analysis of size-frequency distributions; all other estimates were derived from tags glued to the external surface of the shell. Expected annual growth rate at 65, 90, and 115 mm is shown as  $g_{65}$ ,  $g_{90}$ , and  $g_{115}$ , respectively.

Study and location	$g_{65}$	$g_{90}$	$g_{115}$	$L_{\infty}$	$k$
	(mm·year <sup>-1</sup> )			(mm)	(year <sup>-1</sup> )
Shepherd and Hearn, 1983					
South Australia	21.3	14.1	6.9	139	0.34
	21.3	14.4	7.6	143	0.32
	26.4	18.0	9.7	144	0.41
McShane et al., 1988					
Victoria	13.1	6.8	0.5	117	0.29
	16.5	9.2	1.8	121	0.35
	16.1	10.2	4.3	133	0.27
Prince et al., 1988					
Tasmania	21.0	12.6	6.3	140	0.29
McShane and Smith, 1992					
Victoria	26.9	19.2	11.5	152	0.37
	16.5	9.2	1.8	121	0.35
	7.8	4.3	0.8	121	0.15
<b>This study, NSW</b>					
Broughton Island					
I	38.0	25.7	13.3	142	0.68
II	28.0	19.8	11.5	150	0.40
Sydney					
I	16.3	9.3	2.3	123	0.33
II	32.1	21.1	10.1	138	0.58
Merrys Beach	22.6	11.7	0.9	117	0.57
Eden					
I	18.0	12.1	6.2	141	0.27
II	30.4	17.9	5.5	126	0.69

significantly to other populations because of the restricted dispersal of larvae (see also Tegner, 1993). In addition, because of the link between growth rate and the maximum length of abalone at a site, as the maximum length of abalone at the site is below the minimum length limit, many populations can never be fished. Different length limits related to the growth of abalone at a site would be desirable, but considering the small spatial scales over which significant differences in growth can occur, their enforcement would be impractical.

An alternative approach to applying different length limits would be to enforce a size limit based on shell width. Because of the differences in morphology of abalone among sites with different growth rates, a width limit would allow individuals from sites where they grow slowly to be removed at shorter lengths than those where they grow quickly. This

would have two potentially desirable consequences. First, it would distribute effort more evenly across sites with the entire range of growth rates. This would occur because more abalone could be collected from sites where they grow slowly, and less would be available at sites where they grow quickly. Following the progressive increase in length limit during the 1980's, most fishing became concentrated at sites where abalone grew quickly (see also McShane, 1992). As described above, the length limit at these sites was also lower than appropriate, which in combination with the intense fishing effort, so that populations at sites where growth was fast were exploited at considerably higher rates than those for other populations.

The second desirable consequence of enforcing a width limit would be to allow the collection of abalone from sites that are presently unfished because abalone grow very slowly and few reach the minimum legal length (i.e. as stunted abalone). If an appropriate width could be chosen, more abalone would be available for collection at sites where they grow slowly, making it viable for divers to visit such sites. There is some evidence to suggest that growth rates of individuals at sites where they appear stunted are limited by a lack of available food (Shepherd and Hearn, 1983). By removing individuals, more food may be available to those that remain and their growth rates may, in turn, increase.

Considering the frequency of studies reporting covariation in growth and morphology of abalone, we suggest that alternative size limits appear to have the potential to improve the management of many abalone fisheries. The intense spatial variation in growth and related differences in morphology of *Haliotis rubra* in NSW, and the ease with which shell width can be measured, make a size limit based on width a potential alternative to the present length limit. The application of a width limit would allow abalone that have grown at different rates to be harvested at different lengths, essentially enforcing different length limits over very small spatial scales. As a consequence, the potentially damaging imbalance in exploitation rates among sites with different rates of growth in length would be avoided.

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