

## **Legal Minimum Lengths and the Management of Abalone Fisheries**

Authors: Malcolm Haddon, and Fay Helidoniotis

Source: Journal of Shellfish Research, 32(1) : 197-208

Published By: National Shellfisheries Association

URL: <https://doi.org/10.2983/035.032.0126>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## LEGAL MINIMUM LENGTHS AND THE MANAGEMENT OF ABALONE FISHERIES

MALCOLM HADDON<sup>1\*</sup> AND FAY HELIDONIOTIS<sup>2</sup>

<sup>1</sup>CSIRO Wealth from Oceans, GPO Box 1538, Hobart, TAS 7001, Australia; <sup>2</sup>Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart, Tasmania 7001, Australia

**ABSTRACT** A management strategy evaluation framework was used to simulate multiple populations making up a management or quota zone for Australian blacklip abalone (*Haliotis rubra*). The simulation was conditioned on the properties of blacklip abalone and its fishery on the east coast of Tasmania. Abalone are well known for exhibiting spatial heterogeneity in their biological properties. Each population in the simulation was represented by a size-based population dynamics model and had biological properties of growth, maturation, emergence from crypsis, and mortality specific to each population; the range of these properties varies to different degrees in the different quota zones around Tasmania. The simulation was used to compare the effects of applying different legal minimum length (LML) regulations on the fishery. Because of spatial heterogeneity in growth, a single LML within a zone has always been a compromise between underprotecting some populations and overprotecting others. The simulation was used to determine the protection afforded the overall mature biomass and the variation likely among different populations, and how these populations then responded to exploitation. In addition, when setting an LML within a zone, an analysis was made, using the simulation, of the potential trade-offs between the total allowable catch (TAC), the number of abalone needed to take that TAC, the proportion of the mature biomass protected by the LML, and the stock depletion level after fishing with different LMLs but the same TAC.

**KEY WORDS:** abalone, legal-minimum-length, fisheries, management, spawning biomass, protection, trade-offs

### INTRODUCTION

In Tasmania, the management of the abalone fishery (95% blacklip abalone, *Haliotis rubra* and 5% greenlip abalone *Haliotis laevigata*) uses a number of regulatory instruments (Tarbath & Gardner 2011). These include (1) divers require an abalone license (123 available); (2) a total allowable catch (TAC) is allocated as individual transferable quota in 5 different quota zones around the state, plus a separate greenlip quota; (3) to distribute effort further, catch caps are placed on some statistical reporting blocks within zones, and these caps are effectively loose competitive TACs; and (4) each zone has at least 1 legal minimum length (LML). In addition, ad hoc block closures are sometimes put in place in areas thought to need resting. The spatial management measures (zones, TACs, catch caps, and ad hoc closures) aim to distribute the catch in a manner that avoids local depletion whereas the different LMLs around the state aim to preserve some (unspecified and unknown) level of spawning biomass. All of these management tools are commonly used elsewhere.

In Tasmania, the guideline for setting the LML for a zone is to estimate the average size at maturity and then add 2 y of growth. Although there are no prescribed methods for how to do this, in practice, the average growth increase expected for 2 y is added to the average size at 50% maturity; the expected growth increments are those predicted by the inverse logistic (Haddon et al. 2008). Unfortunately, there is a great deal of spatial heterogeneity among separate populations of abalone in terms of their biological properties relating to growth and maturity. Thus, any LML selected for relatively large geographical areas (like a quota zone) is always a compromise between providing more than 2 y protection to the relatively slow-growing populations and less than 2 y of protection to the faster growing populations. Because of this problem, despite the so-called 2-y

rule being included in the Tasmanian abalone management plan (currently under revision), in practice, it can only be used as a guideline rather than a regulation.

Initially, in Tasmania, the LML was set statewide at 127 mm in 1962, but now each zone has its own minimum length regulations; Tarbath and Gardner (2011) provide a detailed history of developments. Even within a zone different areas can have a different LMLs if the variation of localized abalone populations makes that desirable, although no zone currently has more than 2 LMLs (Fig. 1). Because of the compromise nature of the protection afforded different populations by a given LML, suggestions for changing an LML are often controversial among the abalone industry. Increasing an LML will increase the protection of mature biomass, with currently unknown but assumed precautionary consequences, but it will also lead to a reduction in the amount of catch that can be taken from some of the less productive populations. Assuming the TAC is not reduced, increasing an LML will thus lead to greater pressure being placed on more productive populations. This increased pressure may be offset by the larger abalone weighing more, which implies that fewer abalone would be required to make up the same weight of catch. However, if the LML is increased too much, then fewer animals will be able to grow to legal size, catches will be reduced, and the quality of the product may decline because older individuals are sometimes reported to develop thicker shells, have a lower relative meat yield, and even develop a discoloration of the foot tissues. Discussions about what constitutes the most appropriate LML for different stocks are hampered because it remains unknown what level of mature biomass protection is required to secure a stock's sustainability. It is also unknown what level of protection is provided to the spawning biomass by a given LML, or how changing an LML might affect the potential catch from an area, either as weight or in terms of the number of individuals needed to take a given catch.

A number of abalone fisheries around the world have exhibited significant declines in their production (Hobday et al.

\*Corresponding author. E-mail: Malcolm.Haddon@csiro.au  
DOI: 10.2983/035.032.0126

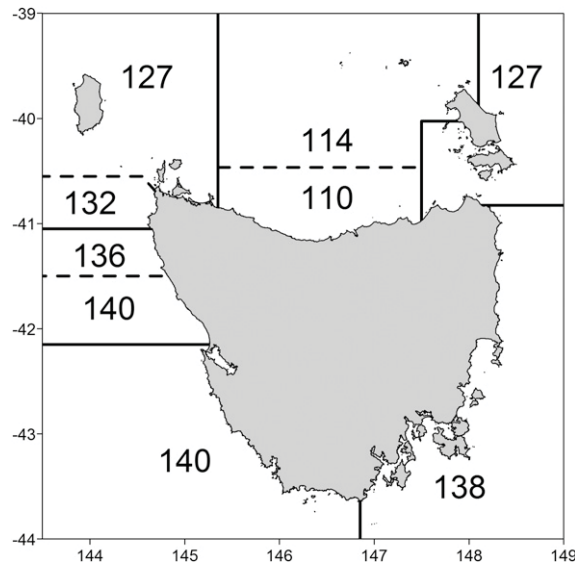


Figure 1. Schematic map of Tasmania with the recent articulation of different legal minimum lengths (LMLs) in millimeters for blacklip abalone (*Haliotis rubra*) around Tasmania, Australia. Solid lines separate different quota zones; dashed lines indicate LML subdivisions within zones. Revisions are continually being suggested, with recent attention being paid to the Northeast and Northwest, both of which are in the same quota zone.

2001, Hamasaki & Kitada 2008, Neuman et al. 2010, Searcy-Bernal et al. 2010), and although the exact reasons for such declines are varied, an important aspect is a failure to recruit in adequate numbers to maintain the stocks. Being relatively sedentary, the successful reproduction of abalone is sensitive to the effects of severe depletion brought on by fishing, disease, or environmental change (e.g., sea temperature and weed cover). Although disease and environmental changes are not easily managed, depletion of mature biomass brought about by fishing should be manageable through the combined influence of an LML and a TAC. Trade-offs are expected between the TAC set and the LML selected to avoid depletion of mature biomass. The risk of depletion of the mature biomass is likely to be greater if catches are close to and potentially higher than the maximum productivity of a stock. In such cases, setting an LML that secures a proportion of the mature biomass becomes important for ensuring sustainability. If, however, the TAC is low relative to the productivity, then the LML can be set at a lower size, with a lower risk of depleting mature biomass. This trade-off could be useful if smaller sizes commanded premium prices in commercial markets, which has sometimes happened in the Tasmanian live export market; however, the exact character of this trade-off is currently unknown. In terms of contributing to sustainable fishing, because the weight-at-length relationship is exponential, the numbers of abalone required to take a given TAC will be less with a larger LML; this is also part of the trade-offs that should be considered when setting an LML.

Here we present how we use a management strategy evaluation simulation framework (Appendix 1) to examine how different LMLs interact with a typical range of biological variation exhibited within a simulated abalone quota zone and lead to an array of different protection levels across the various populations. In this way, we can determine the proportional protection

of mature biomass expected from different LMLs and the range of protection levels afforded populations having different productivity. At the same time, the trade-off between the TAC, the numbers required to take the TAC, and the proportion of mature biomass protected by different LMLs were assessed by determining the TACs that led to the same target level of stock depletion under different prescribed LMLs.

The objectives of the work were, therefore, (1) to develop a simulation framework capable of mimicking an abalone fishery made up of numerous populations, each with somewhat different biological properties; (2) to determine the proportion of mature biomass secured by different LMLs in simulated populations with known properties; and (3) to determine the trade-off between LML and number of abalone required to take a TAC while inducing the same level of depletion of mature biomass in a simulated fished population.

## MATERIALS AND METHODS

### The Simulation Framework

Spatial structuring is a fundamental aspect of an abalone stock, and this is included by simulating multiple, separate populations (in this case, 70), each with its own set of particular biological properties. The choice of 70 separate populations enabled the full range of biological properties to be expressed given the random allocation of values, but the actual number of populations is arbitrary and the management strategy evaluation framework can simulate as many or as few as wanted. Each population is based on a model with size-structured population dynamics. Each size-structured model has 105 length classes of 2 mm between 2 mm and 210 mm, with the 210-mm size class acting as a plus group that sums any animals predicted to grow larger than this by the predicted growth dynamics. The sex ratio is assumed to be 1:1 and the sexes are not distinguished, but there are separate vectors of numbers-at-size for the cryptic and emergent components of the stock; this was necessary because the size at emergence differs among populations, which in turn affects the availability of different size classes. The time step is annual, with natural mortality being implemented in 2 halves, with the remaining dynamics in between so as to spread the effects of natural mortality across the implied annual dynamics. All recruitment is into the cryptic component and all fishing mortality is imposed on the emergent component. Growth is described using a size-transition matrix (see Appendix 1, Eqs (5) and (6)), with somewhat different growth for each population. Because the emergent and cryptic components are modeled separately, the model equations differ from earlier size-structured models (e.g., Breen et al. 2003), particularly in the annual dynamics and in the model initiation (Appendix 1). The dynamics involve interactions between growth, survivorship, and recruitment (as in previous models), but the interactions between the emergent and cryptic components of each population can also be important.

### Biological Data

There is insufficient information available to fit the simulation framework to a real quota zone in any of the jurisdictions within Australia. Although there are detailed and adequate amounts of catch and catch rate data, data on growth and on size at maturity are only available in sufficient quantities to

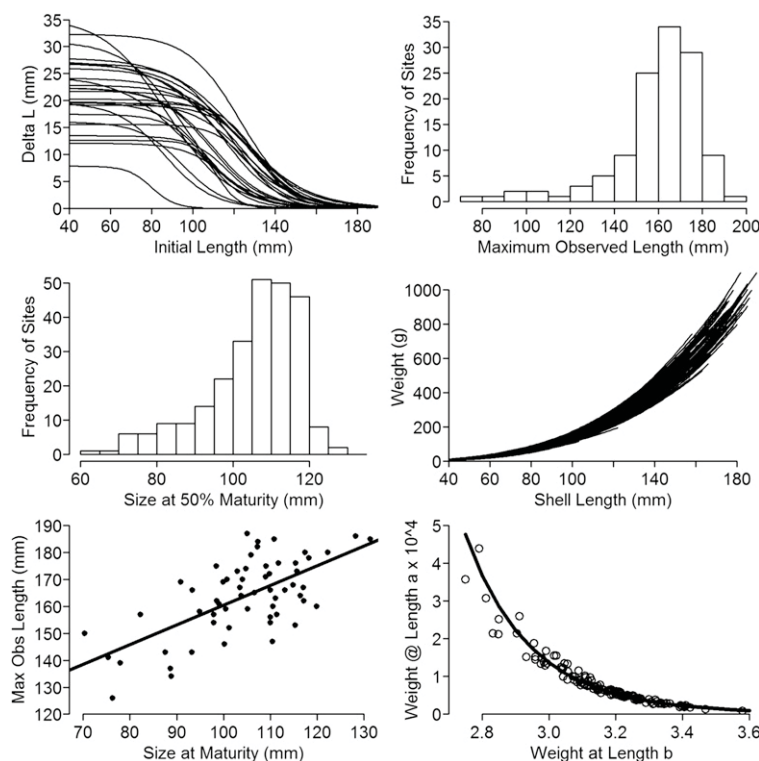


Figure 2. Examples of variation observed in the biological properties of populations of blacklip abalone (*Haliotis rubra*) at different sites around Tasmania. (Top left) Spread of the predicted average growth increments for 27 different populations. (Top right) Observed maximum lengths seen in 122 different sites. (Middle left) The distribution of the size at 50% maturity at 258 sites east of longitude 146.5. (Middle right) The distribution of the expected weight at length at 122 sites (truncated at the maximum length observed at each site). (Bottom left) The relationship between size at maturity and maximum observed length (both the relationship and its variability are required in the simulations). (Bottom right) The relationship between the 2 parameters,  $a$  and  $b$ , of the weight-at-length relationship (Eq (9)).

reinforce the intuition from previous studies that abalone stocks are spatially heterogeneous in their biological properties at small spatial scales (Fig. 2), potentially as small as tens to hundreds of meters (Prince et al. 1987, Helidoniotis et al. 2011). However, by selecting some of the biological properties at random from the range available (generally characterized with either normal or log-normal distributions), then simple linear and nonlinear relationships between variables can be used to determine related parameters in equations describing processes such as growth, size at maturity, and size at emergence. Thus, for example, it was only necessary to select 2 out of the 3 parameters describing growth in each population because there was a tightly fitting linear surface relationship found among the 3 growth parameters across the 27 populations studied for growth characteristics. In an analogous fashion, there was a tightly fitting logarithmic relationship between the 2 parameters describing the weight-at-length relationship for 122 separate populations, which could be used to simplify the allocation of this biological property to each simulated population. Not only were there relationships among the parameters of curves describing particular biological properties, but also there were relationships among the various biological properties within populations. For example, populations that have a smaller size at maturity also have a smaller maximum length and often a lower weight-to-shell length relationship (Fig. 2). These variables all have an influence on the relative productivity of different populations. Using these relationships simplified the conditioning of the simulation framework onto a particular quota zone using the data available in Tasmania. The equations describing the

dynamics, and the supporting equations describing growth, size at maturity, weight at length, selectivity, size at emergence, and other processes affecting the biology and fishery for each population are detailed in Appendix 1.

#### Calculation of Mature Biomass Protected

There are numerous ways in which an estimate of the proportion of mature or spawning biomass protected in a given population by a given LML can be calculated. Here we compare the total unfished mature biomass or  $B_{00}$ , estimated by applying Eq (11) to the equilibrium unfished size structure, obtained from Eqs (23) and (24), with the unfished mature biomass vulnerable to fishing,  $B_0^M$ , estimated using Eq (12). Observations from the fishery imply that the use of logistic selectivity around the LML is more appropriate than assuming knife-edged selectivity at the LML, as in Eq (17). However the vulnerable mature biomass is calculated, the proportion,  $P^{Sp}$ , of mature biomass protected by a given LML in any year  $t$  is

$$P^{Sp} = \frac{(B_0^{Sp} - B_0^M)}{B_0^{Sp}}. \quad (1)$$

This represents the maximum amount of protected spawning biomass, because when the stock begins to be depleted (i.e., the subscript time is no longer 0), this can also lower the amount of spawning biomass below the LML.



### *Simulating a Quota Zone*

A quota zone is defined as a subdivision of the overall fishery that includes multiple populations (in this case, 70 populations), but are managed with the same LML. To explore the effect of different LML values on the level of protection afforded a particular quota zone, replicate simulations consisting of 70 populations were generated. The production curve for each population was characterized numerically by repeatedly applying an array of constant harvest rates (0.01–0.4 in steps of 0.01), each for 50 y, to estimate the equilibrium yield and concomitant depletion level at each harvest rate; 50 y was always sufficient to achieve equilibrium. The number of simulations for each population was thus 40 different harvest rates at 10 different LMLs (121–127 mm, and 130–140 mm in steps of 2 mm), giving a total of 400. Each of the 40 different harvest rates gave rise to an equilibrium yield. The maximum sustainable yield (MSY) across the zone for each LML scenario was thus estimated by finding the maximum equilibrium yield possible by summing the individual equilibrium yields from each of the 70 populations for each harvest rate. For each population, the proportion of the mature biomass protected by each of the given LML scenarios was calculated using Eq (1), and the average for the zone was obtained by using the sums of the  $70 B_0^{Sp}$  and  $B_0^M$ .

The biological minimum length (BML) is the outcome of applying the 2-y rule to each population separately. The curves describing the proportion mature at a given size and the growth characteristics were different for each population, so the BML also varied among the 70 populations.

### *Simulating Catching the TAC*

Before exploring further the dynamics relating to alternative LMLs, each zone was depleted to approximately  $0.4B_0$  by applying a constant harvest rate until the desired depletion level was approximated. This initial depletion was used to simulate the behavior of an active fishery, rather than always starting with pristine, unfished populations.

The relative productivity of each population was characterized by determining what proportion of the total MSY was generated in each population. Catches were allocated to each population by multiplying the TAC by this vector of proportions and adding a small amount of normal random noise. The individual catches were applied to randomly selected populations and to prevent the TAC being excessively over- or under-caught, once 25, and again once 50, populations had been exposed to fishing the remaining TAC was reallocated to the remaining unfished populations, which would either increase or decrease their respective catches appropriately. Each simulation consisted of 50 replicates of 70 populations fished for 50 y, and each year the numbers required to take the predicted catch were estimated using Eq (18). This simulation implies that some populations may become overfished whereas others are possibly underfished, which reflects the variation in localized catch levels and assumed depletion levels seen in the Tasmanian fishery (Tarbath & Gardner 2011).

### *The Impact of Different LMLs on Yield and Spawning Biomass Protected*

Size-at-maturity values were selected such that zones containing 70 populations could be simulated with BMLs, averaged over 20 replicate zones, that approximated 4 chosen sizes:

122 mm, 127 mm, 132 mm, or 138 mm. By setting LMLs also of 122 mm, 127 mm, 132 mm, and 138 mm for each of the 4 BMLs, it was possible to consider how the MSY and the proportion of the mature biomass protected by the LML varied across the 16 possible combinations. Naturally, the combinations with the smaller BMLs (from a smaller size at maturity) generated smaller MSYs, because the average maximum size was also smaller; comparisons were thus limited to the 4 LMLs within each BML.

### *The Number of Abalone Required for a Given Catch*

The LML for blacklip abalone on the Tasmanian east coast has previously been 127 mm but is now 138 mm, which is a compromise reflecting the BML observed across more than 200 east coast populations (unpubl. data). To examine the effect of these 2 LMLs, relative to the average BML, on the number of abalone required to achieve the same catch and the same level of depletion, comparisons were made of outcomes when LMLs of 127 mm and 138 mm were applied to 50 replicate zones that had an average BML of 138 mm. With 70 populations, the total MSY across each of these replicate zones was approximately 750 t (more precisely, the values were 756 t at an LML of 127 mm and 751 t at an LML of 138 mm). The simulations applied 4 different TACs (650 t, 675 t, 700 t, and 750 t) at the 2 different LMLs. Before imposing any fishing, each replicate zone was depleted to approximately  $0.4 B_0$  by iteratively searching for and applying the fishing mortality, which, when applied repeatedly, generates the required  $0.4 B_0$ . With each predepleted replicate zone, the selected TAC was applied in each year for 50 y, and in each year the actual catch, the mature biomass, the depletion level across the zone, and the number of abalone taken in the catch are recorded. The median values in each year for these 4 variables, across the 50 replicates, were then compared across the 4 TAC levels and the 2 LML settings.

## RESULTS

### *Individual Populations*

Within individual populations, the size at 50% maturity and the BML interact with the growth characteristics to influence the proportional numbers at size and, in conjunction with the LML, the proportion of mature biomass secured from fishing pressure (Fig. 3). A larger size at maturity correlates to a larger  $L_{50}$  growth parameter, and, even when the other growth parameters remain the same, this leads to abalone growing to a larger and heavier final size. When the LML aligns with the BML, then the proportion of the mature biomass protected from fishing tends to be just above ~20% (Fig. 3). However, if the LML is set above the BML, the protection can become much greater, which would prevent access to a significant proportion of the animals in such populations. Alternatively, if the LML is set too small, then the proportion protected can be relatively small, which could lead to sustainability problems (Fig. 3).

### *The Range of Protection Within Zones*

When the size at 50% maturity is set such that the expected BML averaged across 20 simulated zones should be 138 mm the spread of the  $Max\Delta L$ , from Eq (7), the size at maturity, the maximum length, and the BML are all described by approximately

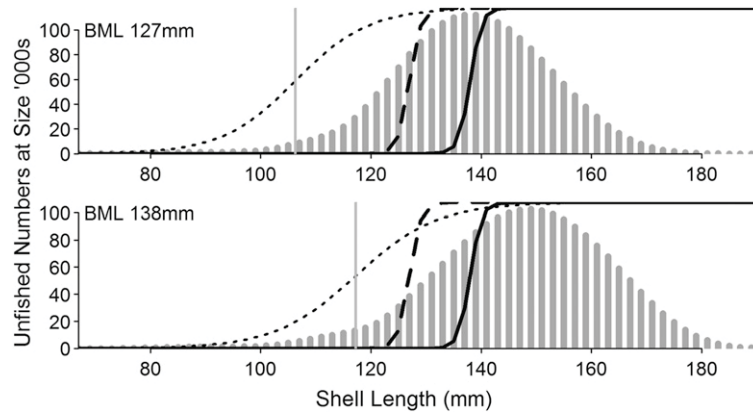


Figure 3. The unfished size distributions of emergent abalone when the size at 50% maturity (vertical gray line) is 105.3 mm and 116.3, leading to biological minimum length (BML) values of 127 mm and 138 mm, respectively. In each graph, the dotted line is the curve describing the proportion mature at a given size. The left-hand selectivity curve, the dashed line, is centered around 127 mm; and the right-hand selectivity curve, the solid line, is around 138 mm. With a BML of 127 mm, the mature biomass protected by a legal minimum length (LML) of 127 mm was 20.0%, but was 47.0% with an LML of 138 mm. With a BML of 138 mm, the mature biomass protected in this population by an LML of 127 mm was only 7.1% and was 22.2% with an LML of 138 mm.

normal distributions. However, the unfished mature biomass,  $B_0$ , and MSY are both distributed in a log-normal fashion (Fig. 4). This general pattern was common across each predetermined BML. For the BML of 138 mm, the range of maximum yields extended to just above 70 t and the percent protection of mature biomass ranged from 5.5%–66.6%, although the higher levels of protection were mostly limited to those populations with maximum yields less than 10 t. If the percent of mature biomass protected is plotted against the related size at maturity and the MSY for each population, the relative protection is distributed unevenly across its range, with fewer populations having the smallest size-at-maturity values (Fig. 5). Most of the populations

with the highest levels of mature biomass protection only have relatively low expected yields. Combinations of high yield and high protection do not appear common (Fig. 5), reflecting that the highest yields are likely to derive from populations that grow fastest and largest.

#### Percent Protection of Mature Biomass with Increasing LML

When replicate zones are simulated, the variation in the average BML generated in each zone becomes evident, and the effect of different LMLs on the percent protection afforded the mature biomass can be illustrated (Fig. 6). In each of the

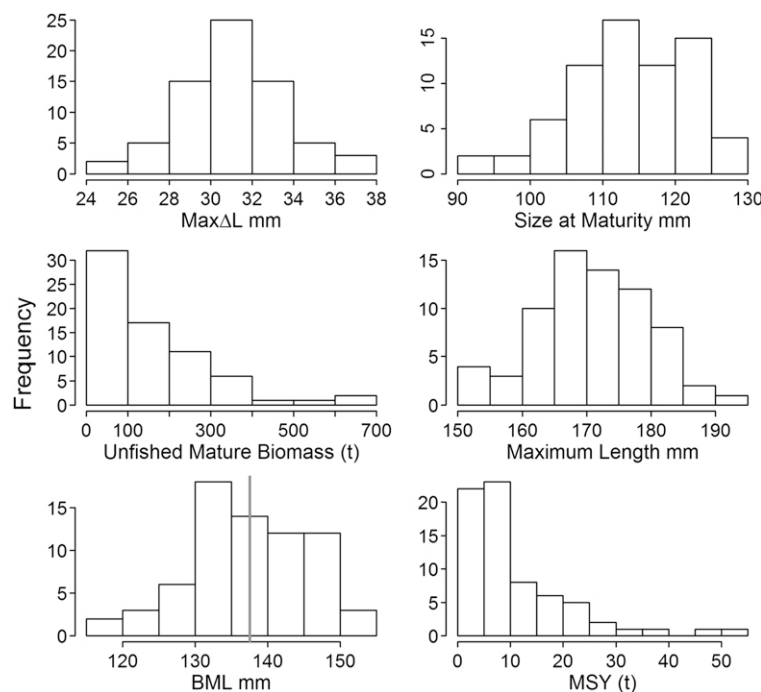


Figure 4. The properties of 70 abalone populations in a simulated zone in which the mean biological minimum length (BML) across 20 simulated zones is expected to be 138 mm. Max $\Delta$ L is one of the parameters describing growth, the maximum length is the length after 23 y of growth, and the BML is the biological minimum length, where the vertical line is the average for this example zone at 137.5 mm. MSY, maximum sustainable yield.

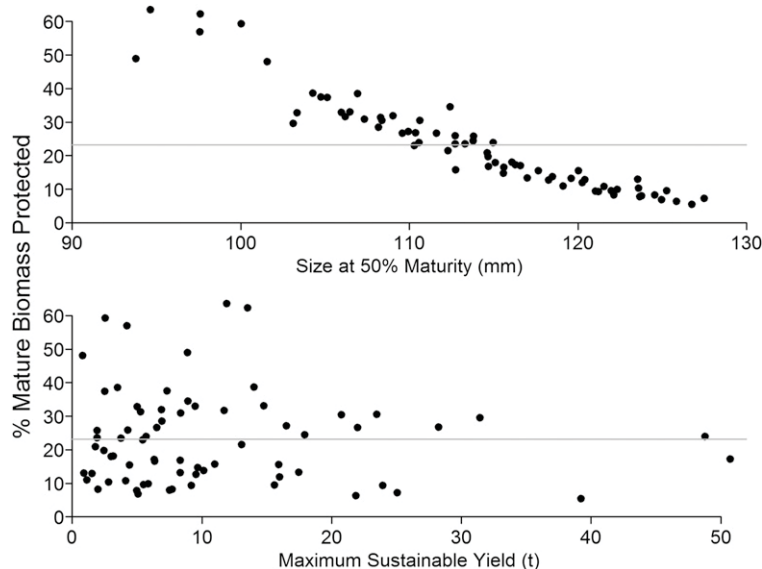


Figure 5. With a biological minimum length of 137.5 mm and a legal minimum length of 138 mm, the average percent protection of mature biomass was 23.2% (the horizontal line in both graphs), with a range from 5.4–63.5%. The total maximum sustainable yield across the zone was 756.9 t, with a range across populations from 0.9–47.4 t.

4 cases, when the LML matches the average BML, approximately 20% of the mature biomass is afforded protection, although a BML of 122 mm leads to protection slightly less than 20%, and that from a 138-mm BML being slightly more. If the LML is set at or more than 10 mm below the BML, the percent protection of mature biomass declines below 10%. The trends representing the average percent protection for each BML are all approximately parallel to each other (Fig. 6). The variation within each zone is much greater than the averages between zones (compare Fig. 5 with Fig. 6).

#### Variation of MSY with LML

The LML imposed on replicate zones influences the selectivity of fishing, and this in turn influences the average MSY across each set of replicate zones. For each of 4 average BML scenarios (122 mm, 127 mm, 132 mm, and 138 mm), the MSY varied in a smooth manner, depending on the imposed LML

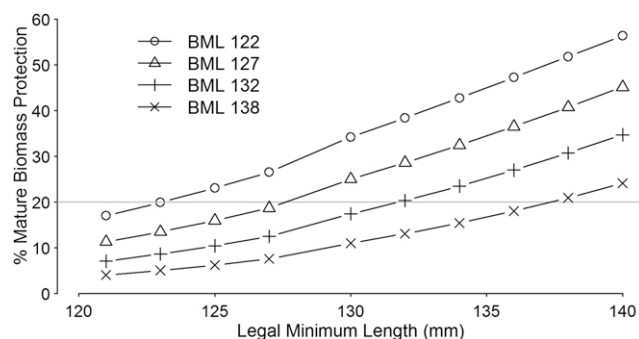


Figure 6. The percent protection afforded mature biomass at 10 different LML for four different average BML values. For each combination of BML and LML, the lines in each case are the average protection level. The fine horizontal line is at 20% protection. The top line and data points relate to the BML of 122 mm while the bottom line and points relate to the BML of 138 mm.

(Fig. 7). In each of the 4 cases, the maximum MSY is always predicted to occur at an LML that is 2–4 mm smaller than the associated BML (so, the percent protected mature biomass is less than 20%). There is a transition of the curves from a shallow dome shape for the BML of 138 mm, with a maximum at an LML of 134 mm, to a continually declining curve for the BML of 122 mm, with its maximum at the lowest LML of 121 mm (Fig. 7). The curves for the BML of 132 mm and 138 mm are relatively flat but slightly domed. In the simulations, with a BML of 138 mm, the average MSY at an LML of 138 mm was approximately 5 t less than at an LML of 127 mm (<1% difference). However, for the BML-138-mm case, given that the overall mean across all replicate zones and different LMLs was 726 t, and the range across individual zones was 558–915 t,

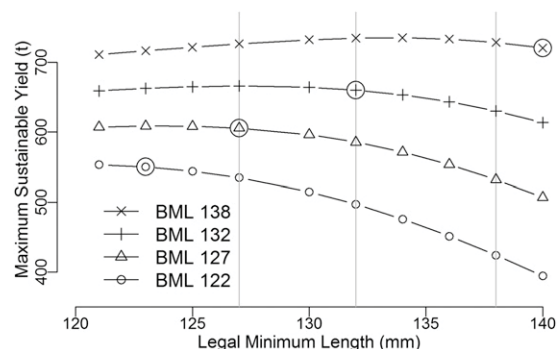
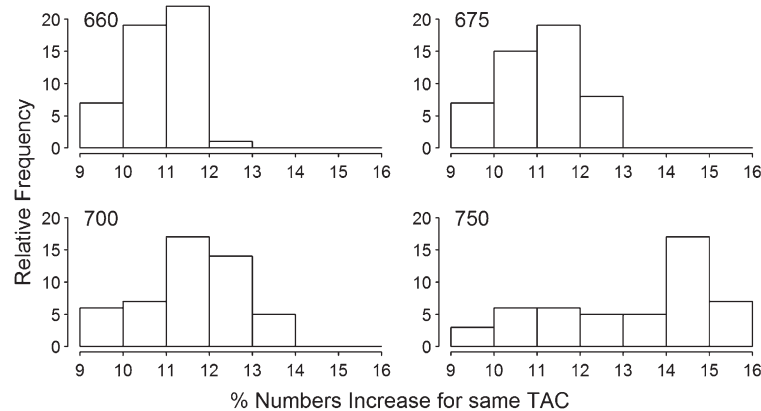


Figure 7. The manner in which the average maximum sustainable yield (MSY) across 20 replicate zones changes relative to 40 combinations of 4 biological minimum lengths (BMLs; 122 mm, 127 mm, 132 mm, and 138 mm) and 10 legal minimum lengths (LMLs; 121 mm, 123 mm, 125 mm, 127 mm, 130 mm, 132 mm, 134 mm, 136 mm, 138 mm, and 140 mm). The maximum size and weight of abalone are influenced by the BML, so the absolute MSY for the BML of 122 mm was naturally smaller than that generated by a BML of 138 mm. The circled points are where the average BML matches the LML; these are never at the maxima of each curve.



**Figure 8.** The average increase in the percent of numbers needed to catch the same total allowable catch (TAC) when the biological minimum length is 138 mm and the legal minimum length (LML) is 138 mm relative to an LML of 127 mm. The numbers at the top left of each graph are the TAC applied. There were 50 replicate zones in each case.

a difference of 5 t is not significant. A similar argument could be made for the BML-132-mm case; however, for the BML-127-mm case, although an LML of 121 mm suggests an MSY only 2 t greater, an LML of 132 mm would lower the expected TAC by 20 t (3.4%), and an LML of 138 mm would lower the TAC by 73 t (12.1%). For populations with smaller BMLs, imposing a smaller LML than the BML affects the MSY far less than imposing a larger LML (Fig. 7).

#### *Changes in Numbers of Abalone in the Catch with LML*

When the LML is smaller, the fishery can take smaller and lighter abalone, so the expectation is that, for a given zone, the number of animals needed to land a given TAC will be greater for an LML of 127 mm than for an LML of 138 mm. In terms of the percentage increase in numbers of abalone required when fulfilling the TAC at 127 mm rather than 138 mm, both the average increase in the percentage and the spread of the increases required become larger as the TAC increases; in all cases, an average increase of more than 10% is required (Fig. 8). Given that the numbers required for a TAC between 650 t and 750 t are between 1,360,000 and 1,830,000, the differences between using an LML of 127 mm and 138 mm can vary between 148,000 and 236,000 animals depending on the TAC imposed (Table 1).

In this simulation, the percent protection afforded the mature biomass by the 2 different LMLs of 127 mm and 138 mm was 8.1% and 22.2%, respectively. Applying a different given TAC for 50 y led to different final depletion levels for the 2 treatments. To obtain the same depletion level required taking a smaller TAC with the LML of 127 mm. The simulated zones had an average total MSY of about 750 t, and applying a TAC of 750 t with an LML of 138 mm led to the median depletion after 50 y approaching a new equilibrium of approximately 30%  $B_0$ , whereas a TAC of 675 t led to the zones remaining at approximately 40%  $B_0$ . With an LML of 127 mm, a TAC of 650 t was required to achieve approximate stability, but a TAC of 750 t led to the median depletion across the replicated zones declining steadily downward to approximately 22%  $B_0$ , with no indication of the stock reaching equilibrium (Fig. 9, Table 1). To obtain a depletion level of 40%  $B_0$  after 50 y of fishing at an LML of 127 mm, one needs a TAC of 650 t, but at an LML of 138 mm, a TAC of 675 t can be taken. As the TAC allocated gets closer to the total MSY, then the difference between the 2 LMLs

to get the same depletion level increases. Thus, to finish at approximately 30% depletion, a TAC of about 700 t and 750 t is required by the 127-mm and 138-mm LMLs, respectively (Fig. 9, Table 1).

Fishing at an LML of 127 mm when the BML is 138 mm greatly affects the size distribution of emergent abalone. By summing the size distributions of emergent abalone across the 70 populations, in either case the resulting size distributions after 50 y of fishing at 750 t are very different (Fig. 10). The size distribution when fishing at an LML of 138 mm is relatively steep, from about 138 mm up to about 165 mm, and the mode of legal animals is highest at the LML. Fishing at an LML of 127 mm, the size distribution is flatter between 127 mm and about 165 mm, but the mode of the fished animals is at 130 mm rather than 127 mm (Fig. 10). The range of the size distribution when the stock is at 40%  $B_0$  is wider when fishing at an LML of 127 mm relative to fishing at an LML of 138 mm, ranging from 127–181 mm relative to 138–170 mm.

## DISCUSSION

This appears to be the first time that a size-structured simulation model has been used to examine interactions between the

**TABLE 1.**

**The numbers of abalone required to take a given total allowable catch (TAC) when the biological minimum length is 138 mm under 2 different legal minimum lengths (LMLs).**

TAC	Increase (%) <sup>*</sup>	LML 127 mm		LML 138 mm	
		Depletion <sup>†</sup>	<i>n</i> (1,000s) <sup>‡</sup>	Depletion <sup>†</sup>	<i>n</i> (1,000s) <sup>‡</sup>
650	10.5	0.401	1,509	0.432	1,361
675	10.6	0.357	1,603	0.403	1,428
700	11.1	0.332	1,688	0.352	1,492
750	12.7	0.224	1,832	0.315	1,596

<sup>\*</sup> The average percent increase in numbers, across 50 replicate zones and 50 y, required to take the same TAC under an LML of 127 mm rather than an LML of 138 mm. All simulated zones started at a depletion level very close to 0.4 $B_0$ . <sup>†</sup> The median stock level after 50 y of applying the TAC. <sup>‡</sup> The median numbers required to take the TAC in the 50<sup>th</sup> year of fishing.



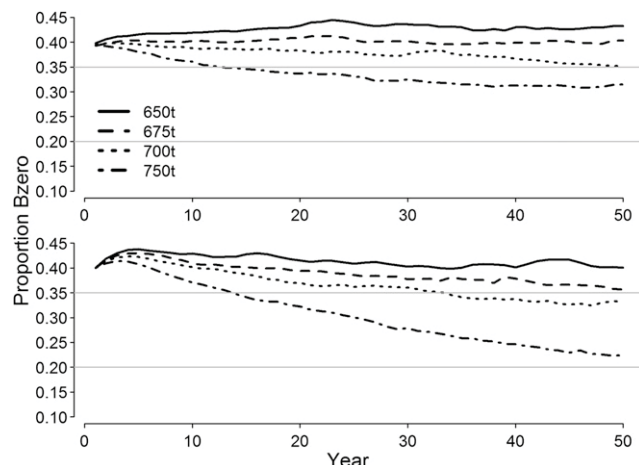


Figure 9. Different responses of a zone with a biological minimum length of 138 mm leading to an average total maximum sustainable yield of ~750 t depleted to approximately  $0.40 B_0$  and then exposed to 50 y of 4 different total allowable catch (TAC) levels. The top graph illustrates the imposition of an LML of 138 mm whereas the bottom graph indicates the response under an LML of 127 mm. The 2 horizontal gray lines are at  $0.20 B_0$  and  $0.35 B_0$ . Note the y-axis begins at  $0.1 B_0$ . The top line in both cases relates to a TAC of 650 t; the bottom line, a TAC of 750 t.

LML, the TAC, the percent mature biomass protection, and the number of animals needed to take a given catch. The use of such a simulation is the only plausible way to examine the trade-offs between the objectives of maximizing the TAC, maximizing the proportion of the mature biomass protected, and minimizing the numbers of abalone required to take a given catch.

The origin of the 2-y rule used for setting the LML in Tasmania appears to have been simple intuition, although in Tasmania essentially the same rule (allowing 2 y of significant spawning) is used to set the minimum size for scallops (*Pecten fumatus*). In Australia, Tasmania appears to be the only state that attempts to make an explicit relationship between the size at maturity and the LML imposed on particular abalone fisheries.

#### Individual Populations

The maximum yield per recruit (an equilibrium concept) for blacklip abalone appears to occur at sizes a few millimeters smaller than the BML, as evidenced by the maximum MSY for a particular BML always occurring with an LML between 2 mm and 4 mm smaller than the BML. For the most highly productive populations, if the LML is approximately close to the BML, there is little difference in the potential yield and the proportion of the mature biomass protected brought about by small adjustments in the precise LML implemented. However, for less productive populations (with smaller BMLs), changes in potential yield and proportion of mature biomass protected were more sensitive to increases in LML. This reflects the continued debate in Tasmania about setting LML values in the north of the state where both growth and size at maturity tend to be expressed at smaller sizes, and is also far more variable than farther south, leading to greater difficulty in finding a compromise LML that is effective across large geographical areas.

#### Individual Zones

The relationship between the proportion of mature (spawning) biomass protected, the BML (size at maturity plus 2 y of growth), and the LML imposed is a simple rising curve (Fig. 6). It suggests that the use of the 2-y rule is a reasonable compromise when adopting a wide-ranging LML. When the LML approximates the average BML, then it prevents excessive under- and overprotection within a zone. However, if a zone is fished using an LML that is 5–10 mm smaller than the BML, then there is a much greater risk of depletion for any given TAC than if fishing closer to the BML. Conversely, if the LML is set 5–10 mm above the BML, then—especially for populations with smaller BMLs—there can be very great overprotection such that significant losses in potential yield will occur (Fig. 7).

It should be noted that the time taken for depletion to occur can be quite extended. In the simulations, dropping whole zones from about  $0.4B_0$  to about  $0.2B_0$  could take 50 y. However, in that time, some of the component populations within the zone became so depleted that commercial fishing was no

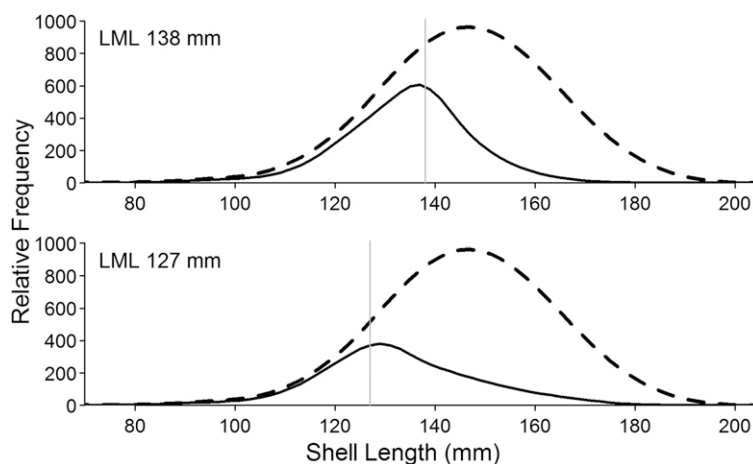


Figure 10. The expected size distribution of emergent abalone with an average biological minimum length of 138 mm and a total maximum sustainable yield of 751 t, fished at 750 t. In each case, the outer curve is the unfished size distribution and the lower curve is after 50 y of fishing at 750 t, leading to depletion levels of 31.5% and 22.4%  $B_0$  for the 138 mm and 127 mm legal minimum lengths (LMLs), respectively. The depletion level relates to the mature biomass both below the LML and any residual biomass above the LML.

longer viable. If the fishing were occurring at levels well above the sustainable yields, then depletion times could be much shorter.

Given the variation typically observed within a quota zone, it is the case that a single LML constitutes a compromise between underprotecting some populations and overprotecting others. However, populations that are highly productive as well as overprotected appear to be uncommon. This is understandable because most highly productive populations are only highly productive in absolute terms because their members grow large and heavy relatively quickly. Very highly protected populations would undoubtedly be underused; however, to be so overprotected implies that their size at maturity must be small relative to many other populations within the zone, and it is highly unlikely they would be very productive. Nevertheless, individual divers may have localities with which they are familiar made effectively unavailable given an increase in LML, so controversy will undoubtedly remain. The dome shape of the MSY-to-LML curves for the higher BML values (132 mm and 138 mm) indicate that smaller LMLs in such circumstances may lead to growth overfishing. Increasing the LML in this circumstance may lead to increased yields from such populations that would mitigate any increased impacts expected on the more highly productive populations.

#### *Variation of MSY and Numbers of Abalone Caught with LMLs*

The intuition that increasing an LML would lead to a serious decline in the available yield from a zone appears valid when a zone is already being fished close to its average BML. However, if a zone was being fished with an LML well below its average BML (for example, Tasmania's east coast has an average BML of approximately 138 mm but was originally fished at 127 mm), then potential yields would not decline to any large extent by moving the LML closer to the BML. An additional advantage would be that the number of animals required to take an equivalent TAC would be expected to decline by at least 10% because they become larger and heavier. Despite this decrease in the number of abalone harvested, the larger LML (127–138 mm) decreases the exploitable biomass by more than 10%, so that the fishing mortality rate will automatically be larger (the same TAC from a smaller exploitable biomass equals a higher harvest or fishing mortality rate). This does not automatically imply a lower catch rate, because the catchability of the larger abalone may be rather different from the relatively smaller animals. But, because of this effect, large changes should not be made to LML values to avoid rapid changes in the fishery.

In the north of Tasmania, where BMLs can be much smaller, it seems likely that there remain regions in which the LML is inappropriately high, and this is preventing the reasonable harvest of available resources. Experimental trials using smaller LMLs have been used in the northwest in defined regions, and discussions and revisions of LML boundaries and levels are ongoing.

The expected difference in the size distribution of legal-size abalone under 2 different LMLs is large. When the zone is depleted to approximately  $0.4 B_0$ , the size distribution under an LML of 127 mm is wider than under an LML of 138 mm (Fig. 10). This implies that the fishery under an LML of 138 mm would be more dependent on new recruits than when under an LML of 127 mm. The size distribution available for capture is another

one of the trade-offs that should be considered when selecting a particular LML for a zone. If the size distribution found with the 127-mm LML is preferred, then a more conservative TAC would be required to counterbalance the reduction in protection of the mature biomass so that the impact of the TAC on depletion levels remains stable. Currently, it is still unknown what level of spawning biomass to protect using an LML to ensure against a stock collapse.

#### *Protection of Mature Biomass*

The east coast of Tasmania was fished at 127 mm from 1962 to 1987, after which the statewide LML was increased to 132 mm; this was increased in the eastern zone to 136 mm in 2002 and 138 mm at the end of 2006. This means that, for decades, many populations on the east coast only had relatively minor mature biomass protection. These circumstances make such populations vulnerable to failure in recruitment success. If severe depletion of underprotected populations coincides with 1 or 2 y of negligible recruitment, then the spawning biomass could be reduced to very low levels, leading to effective collapse for these populations. This is one potential explanation for why some highly productive populations on the east coast went from 8 y of landings more than 100 t with a maximum of almost 300 t during the late 1970s and early 1980s, down to just more than 10 t a year following such catches. There are many instances of abalone fisheries around the world where very high catches are followed by collapse and greatly reduced yields that fail to recover. Even a small LML may give the impression that it would provide a minimum secure breeding stock; however, the self-sustaining nature of reproduction in abalone populations and the vagaries of successful recruitment suggest that LML values that are relatively close to the size at maturity are risky. Although many years may go by without apparent problems, if a depleted state coincides with years of weak or no successful recruitment, then particular populations could decline to very low levels from which they may never recover. This would be a particular danger if fishing was proceeding at higher than sustainable levels. The simulations also suggest that slow population declines could occur over decades, even without recruitment failure, which adds a further risk to maintaining an LML that is smaller than the BML. Setting the LML close to the average BML for an area does not risk the loss of significant amounts of yield, but offers the potential for reducing the risks of stock collapse, particularly in the face of adverse recruitment events. It can be recommended that any LML chosen should take into account the average size at maturity, leaving a significant buffer before permitting fishing mortality. If growth data are not available for some areas, some proxy, perhaps related to some fraction of the maximum observable size, could potentially be used instead.

#### ACKNOWLEDGMENTS

This work was funded jointly by the Commonwealth Scientific and Industrial Research Organisation, the University of Tasmania, and the Australian government's Fisheries Research Development Corporation as part of FRDC project 2007/020. We also thank Dr. Craig Mundy and David Tarbath of the University of Tasmania's abalone team for access to data and discussion.

## LITERATURE CITED

- Breen, P. A., S. W. Kim & N. L. Andrew. 2003. A length-based Bayesian stock assessment model for the New Zealand abalone *Haliotis iris*. *Mar. Freshw. Res.* 54:619–634.
- Haddon, M., C. Mundy & D. Tarbath. 2008. Using an inverse-logistic model to describe growth increments of blacklip abalone (*Haliotis rubra*) in Tasmania. *Fish. Bull.* 106:58–71.
- Haddon, M. 2011. Modelling and quantitative methods in fisheries. 2<sup>nd</sup> edition. Boca Raton: Chapman & Hall/CRC. 449 pp.
- Hamasaki, K. & S. Kitada. 2008. The enhancement of abalone stocks: lessons from Japanese case studies. *Fish. Fish.* 9:243–260.
- Hastings, N. A. J. & J. B. Peacock. 1975. Statistical distributions. London: Butterworths. 130 pp.
- Helidoniotis, F., M. Haddon, G. Tuck & D. Tarbath. 2011. The relative suitability of the von Bertalanffy, Gompertz and inverse logistic models for describing growth in blacklip abalone populations (*Haliotis rubra*) in Tasmania, Australia. *Fish. Res.* 112:13–21.
- Hobday, A., M. J. Tegner & P. L. Haaker. 2001. Over-exploitation of a broadcast spawning marine invertebrate: decline of the white abalone. *Rev. Fish Biol. Fish.* 10:493–514.
- Neuman, M., B. Tissot & G. Vanblaricom. 2010. Overall status and threats assessment of black abalone (*Haliotis cracherodii* Leach, 1814) populations in California. *J. Shellfish Res.* 29:577–586.
- Prince, J. D., T. L. Sellers, W. B. Ford & S. R. Talbot. 1987. Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*: Mollusca: Gastropoda). *J. Exp. Mar. Biol. Ecol.* 106:243–263.
- Searcy-Bernal, R., M. R. Ramade-Villanueva & B. Altamira. 2010. Current status of abalone fisheries and culture in Mexico. *J. Shellfish Res.* 29:573–576.
- Tarbath, D. & C. Gardner. 2011. Tasmanian abalone fishery—2010. Institute of Marine and Antarctic Studies, Hobart. University of Tasmania. 110 pp.

## APPENDIX 1: THE SIZE-BASED MODEL

## Model Variables

Terms in bold type are matrices or vectors. Subscript  $t$  relates to year, subscript  $L$  relates to length class, and superscript  $Sp$  or  $Ex$  relates to spawning or mature and exploitable biomasses, respectively. Superscripts  $E$  and  $C$  relate to emergent and cryptic components, respectively. Superscript  $M$  relates to being mature and exploitable.

## Model Structure

The mortality schedules can differ between the cryptic and emergent population components, especially if a constant initial fishing mortality is applied to the emergent population, and exactly how the fishing mortality is implemented in the model needs to be reflected in the equilibrium and dynamics equations. The model structure adopted has half of natural mortality occurring followed by growth and fishing mortality, followed by the remaining natural mortality, which spreads the effects of natural mortality across the implied dynamics within a year.

## Population Dynamics

If survivorship is implemented as half of  $M$ , the natural mortality—that is,  $\mathbf{C}_S = e^{-\frac{M}{2}}$  for cryptic and  $\mathbf{O}_S = e^{-\left(\frac{M}{2}\right)}$  for emergent—twice in the year (different terms are used to enable different natural mortality values in cryptic relative to emergent habitats), with other dynamics between the survivorship (natural mortality) events, then the dynamics can be represented as

$$\mathbf{N}_{t+1}^E = \mathbf{O}_S[\mathbf{G}\mathbf{O}_S(\mathbf{N}_t^E + \mathbf{E}\mathbf{N}_t^C)] \quad (2)$$

and

$$\mathbf{N}_{t+1}^C = \mathbf{C}_S[\mathbf{G}\mathbf{C}_S(\mathbf{N}_t^C - \mathbf{E}\mathbf{N}_t^C)] + \mathbf{R} \quad (3)$$

where  $\mathbf{N}_t^E$  and  $\mathbf{N}_t^C$  are vectors of numbers-at-size in year  $t$  for emergent and cryptic abalone, respectively, with  $n$  size classes;  $N_{t,L}^E$  would be emergent numbers at size  $L$  in year  $t$ ,  $\mathbf{G}$  is a square growth transition matrix ( $n \times n$ ) specific to each population but the same for both sexes, and for cryptic and emergent portions of each populations,  $\mathbf{E}$  is a square 0 matrix ( $n \times n$ ) with the proportion emergent by size class, Eq (4), arranged along the

diagonal elements, and  $\mathbf{R}$  is a vector ( $n$ ) of recruitment numbers (generally 0 except for the smallest size classes).

## Emergence

Transfer from crypsis into emergence is described using a standard logistic equation (Haddon 2011, p. 360):

$$E_L = \frac{1}{1 + e^{-Ln(19)(L-L^E50)/(L^E95-L^E50)}} \quad (4)$$

where  $E_L$  is the proportion of size class  $L$  that is emergent, and  $L^E50$  and  $L^E95$  are logistic parameters for the emergence curve being the lengths at which 50% and 95% of cryptic animals become emergent, respectively.

## Growth

The elements of the growth transition matrix,  $G_{i,j}$ , are defined by

$$G_{i,j} = \begin{cases} \int_{-\infty}^{L_i + \frac{LW}{2}} \frac{1}{\sqrt{2\pi}\sigma^j} e^{-\left[\frac{(L_i - \bar{L}_j)}{2(\sigma^j)^2}\right]^2} dL & L_i = L_{Min} \\ \int_{L_i - \frac{LW}{2}}^{L_i + \frac{LW}{2}} \frac{1}{\sqrt{2\pi}\sigma^j} e^{-\left[\frac{(L_i - \bar{L}_j)}{2(\sigma^j)^2}\right]^2} dL & L_{Min} < L_i \leq L_{Max} \end{cases} \quad (5)$$

where  $LW$  is the class width in millimeters;  $\bar{L}_j$  is the expected mean length of animals starting in size class  $j$ ;  $L_{Min}$  and  $L_{Max}$  are the minimum and maximum size class considered, respectively; and  $\sigma^j$  is the expected standard deviation for length class  $j$ . To ensure that all columns sum to 1.0 and to make  $L_{Max}$  a plus group, the final row of the matrix is modified for each column  $j$  as

$$G_{LMax,j} = G_{LMax,j} + \left(1 - \sum_{i=L_1}^{L_{Max}} G_{i,j}\right) \quad (6)$$

The expected mean size following growth for each initial size class  $j$  is defined using an inverse logistic growth curve that has been found to describe blacklip abalone growth well (Haddon et al. 2008):

$$\bar{L}_j = L_j + \frac{Max\Delta L}{1 + e^{Ln(19)(L_j - L_m50)/(L_m95 - L_m50)}} + \epsilon_{L_j} \quad (7)$$

where  $L_{m50}$  and  $L_{m95}$  are the logistic parameters for the growth curve being the length at which the growth increment is 50% and 95% of the maximum, respectively, and  $Max\Delta L$  is the maximum growth increment for the inverse logistic curve describing abalone growth. Variation around the mean expected growth increment is assumed to be normal with a standard deviation,  $\sigma^j$ , that varies with the growth increment (Haddon et al. 2008):

$$\sigma^j = \frac{Max\sigma^j}{1 + e^{Ln(19)(L_j - L_{m95})/(210 - L_{m95})}} \quad (8)$$

where  $Max\sigma^j$  is the maximum standard deviation describing the variation around the mean expected growth increment, the point at which variation is 5% of the maximum is set at 210 mm and the 50% point is set at  $L_{m95}$ .

#### Weight at Length

The weight ( $W_L$ )-at-length ( $L$ ) relationship has the usual power form with parameters  $a$  and  $b$ :

$$W_L = aL^b \quad (9)$$

#### Mature Biomass

Maturity at size,  $m_L$ , is described by another logistic curve using parameters  $\alpha$  and  $\beta$ , such that the size at 50% maturity is  $-(\alpha/\beta)$ , and the interquartile distance is  $2Ln(3)/\beta$ :

$$m_L = \frac{e^{(\alpha+\beta L)}}{1 + e^{(\alpha+\beta L)}} \quad (10)$$

and mature or spawning biomass in year  $t$ ,  $B_t^{Sp}$ , is estimated using

$$B_t^{Sp} = \sum_{L=L_{Min}}^{L_{Max}} m_L W_L N_{t,L}^E + m_L W_L N_{t,L}^C \quad (11)$$

where  $N_{t,L}^E$  and  $N_{t,L}^C$  are, respectively, the emergent and cryptic numbers at size  $L$  in year  $t$ , which recognizes that some mature animals may remain in crypsis. The mature biomass vulnerable to fishing is estimated using

$$B_t^M = \sum_{L=L_{Min}}^{L_{Max}} m_L s_{t,L} W_L N_{t,L}^E \quad (12)$$

which is the same as the exploitable biomass except it also includes the proportion mature at a given size.

#### Selectivity, Harvest Rate, and Exploitable Biomass

Selectivity for length  $L$  in year  $t$ ,  $s_{t,L}$ , is described by another logistic curve:

$$s_{t,L} = \frac{1}{1 + e^{-Ln(19)(L - L_{s50})/(L_{s95} - L_{s50})}} \quad (13)$$

where  $L_{s50}$  and  $L_{s95}$  are logistic parameters for the selectivity curve being the lengths at which 50% and 95% selection occurs, respectively. The model can be conditioned on known or simulated catches in year  $t$ ,  $C_t$ , expressed as annual harvest rates  $H_t$ —that is, the removals are determined from the catches divided by the exploitable biomass in year  $t$ :

$$H_t = \frac{C_t}{B_t^{Ex}} \quad (14)$$

The exploitable biomass is estimated as the sum of the numbers of emergent abalone at size times the selectivity at size and the weight at size:

$$B_t^{Ex} = \sum_{L=L_{Min}}^{L_{Max}} s_{t,L} W_L N_{t,L}^E \quad (15)$$

where the numbers of emergent abalone are estimated as

$$N_{t,L}^E = G_{i,L} O_L^E N_{t-1,L}^E + E_L N_{t-1,L}^C \quad (16)$$

Alternatively, if knife-edged selectivity is assumed to occur at the LML, then the theoretical  $B^{Ex}$  could be calculated as

$$B_t^{Ex} = \sum_{L=L_{ML}}^{\max} W_L N_{t,L}^E \quad (17)$$

However, in Tasmania, the selectivity around the LML is not knife-edged because divers try to err on the side of caution when harvesting from the seabed by targeting animals slightly larger than the LML, so a logistic selectivity curve centered on the LML appears more appropriate (although this still means that a small proportion of sublegal abalone could be observed, which corresponds to occasional observations in commercial catches).

#### Numbers in Catch

To estimate the number and weight of abalone taken in the catch required the harvest rate,  $H_t$ , the selectivity,  $s_L$ , and the numbers of emergent abalone  $N_{t,L}^E$ :

$$N_t^H = \sum_{L=2}^{210} H_t s_L N_{t,L}^E \quad (18)$$

Including the weight at length generates the catch weight:

$$C_t = \sum_{L=2}^{210} H_t s_L W_L N_{t,L}^E \quad (19)$$

#### Recruitment Processes

Recruitment is described using a vector with all new recruits allocated to the first size class and all other size classes being set to 0. A Beverton-Holt stock recruitment relationship was assumed, with  $a$  and  $b$  parameters that were restructured in terms of steepness,  $h$ ; unfished mature biomass,  $B_0^{Sp}$ ; and the average unfished recruitment level,  $R_0$ :

$$a = \frac{4hR_0}{5h-1} \quad \text{and} \quad b = \frac{B_0(1-h)}{5h-1} \quad (20)$$

Using this reparameterization the Beverton-Holt relationship becomes

$$R_{t+1} = \frac{4hR_0 B_t^{Sp}}{(1-h)B_0^{Sp} + (5h-1)B_t^{Sp}} e^{\varepsilon - \sigma_R^2/2}, \quad \varepsilon = N(0, \sigma_R^2) \quad (21)$$

The expected residual error distribution around the recruitment is log-normal;  $\sigma_R$  is the standard deviation of the natural logarithm of the recruitment residuals, and  $-\sigma_R^2/2$  is a bias correction term that ensures that the time series of estimated recruitments relates to the mean rather than the



median recruitment level (Hastings & Peacock 1975). If the  $\sigma_R$  term is set as a very small number, the recruitment will be effectively deterministic.

$A_0$  can be defined as the mature stock biomass that would develop given a constant recruitment level of 1. Thus, at a biomass of  $A_0$ , distributed across a stable size distribution, the resulting recruitment level would be  $R_0 = 1$ .  $A_0$  acts as a scaling factor in the recruitment equations by providing the link between  $R_0$  and  $B_0^{Sp}$ .  $A_0$  can thus be estimated by setting the annual recruitment level to 1, obtaining the equilibrium size distribution using Eqs (23) and (24), and then applying Eq (11). At the virgin biomass per recruit,  $A_0$ , the average unfished recruitment level,  $R_0$ , is related directly to the unfished mature, or spawning, biomass,  $B_0^{Sp}$ :

$$B_0^{Sp} = R_0 A_0 \quad (22)$$

In the simulations, the relative size of each population is defined by randomly selecting (from a log-normal distribution) an initial unfished average recruitment,  $R_0$ , which, given the equilibrium size distribution, provides an estimate of the population's unfished mature biomass  $B_0^{Sp}$ .

#### Model Initiation

Given constant growth,  $\mathbf{G}$ , constant recruitment,  $\mathbf{R}$ , defined as  $R_0$ , and constant natural mortality,  $\mathbf{C}_S$  and  $\mathbf{O}_S$ , which are each the survivorship from half the natural mortality, then at equilibrium the cryptic component of an unfished population,  $\mathbf{N}^{C*}$ , is defined as

$$\mathbf{N}^{C*} = (\mathbf{I} - [\mathbf{C}_S \mathbf{G} \mathbf{C}_S (\mathbf{I} - \mathbf{E})])^{-1} \mathbf{R} \quad (23)$$

where  $\mathbf{I}$  is a unit matrix. Consequently, the equilibrium number of emergent abalone,  $\mathbf{N}^{E*}$ , in an unfished population is

$$\mathbf{N}^{E*} = (\mathbf{I} - \mathbf{O}_S \mathbf{G} \mathbf{O}_S)^{-1} \mathbf{O}_S \mathbf{G} \mathbf{O}_S \mathbf{N}^{C*} \quad (24)$$

To avoid having to begin each simulation in an unfished state, it was necessary to be able to produce a simulated zone that was depleted to a required level relative to the unfished state. To do this, first an unfished zone was produced using Eqs (23) and (24), and then an iterative search was begun that applied a slowly increasing annual harvest rate to the standard dynamics, as in Eqs (2) and (3), until the required depletion level had been achieved. In this way, the recruitment dynamics were included in the dynamics of the simulated zone.