Abstract. - Populations of the New Zealand (NZ) black-footed abalone Haliotis iris were examined in two important fishing areas. Sizefrequencies were compared among three regions around Stewart Island in the extreme south of NZ, three regions of the Marlborough Sounds in the northern part of the South Island, and a site closed to commercial fishing in the North Island. Von Bertalanffy growth parameters were estimated from shell growth rings of subsamples from all regions. Markrecapture data were available for two regions, and independent estimates of von Bertalanffy parameters were calculated. Total mortality was estimated from catch curves and also from length-frequencies using the method of Fournier and Breen (1983). Yield-per-recruit (YPR) and egg-per-recruit (EPR) were calculated and two reference levels of fishing mortality, $\mathrm{F}_{0.1}$ and $\mathrm{F}_{25 \%}$, were estimated. Analyses showed that, despite previous evidence to the contrary, rings are not laid down annually in the regions we examined. For two fishing regions, the estimated current fishing mortality rates are greater than both $F_{0.1}$ and $F_{255}$, suggesting that the current fishery is more intense than can be sustained in the long term. YPR and EPR do not appear to be greatly affected by changing the minimum legal size. By decreasing $F$ to $F_{0.1}$, however, equilibrium egg production would increase from $18 \%$ to a more satisfactory level with little change in YPR. We discuss management strategies and argue that it would be prudent to decrease fishing mortality, thereby maintaining higher egg production at little sacrifice of YPR.

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# Population Structure, Ageing, and Fishing Mortality of the New Zealand Abalone Haliotis iris 

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The fishery for the abalone Haliotis iris (called "paua" in New Zealand) is now one of the largest abalone fisheries in the world, yet the biological basis for its management has only recently been examined in detail. Both the minimum legal size (MLS) for fishing and the permissible catch level were arbitrarily set for historical reasons that did not take into account the best yield and egg production of the fishery. Recent research has aimed at assessing whether the present levels of fishing are sustainable.
Individual Transferable Quotas (ITQs) for paua were implemented in 1986 and a Total Allowable Commercial Catch (TACC) was set in each of seven Quota Management Areas (QMAs), based on the previous catch histories of commercial fishers (Schiel 1991). The total catch of paua for the entire country is currently 1193 tons (whole weight).

Haliotis iris is a shallow-water species, endemic to New Zealand (NZ). It occurs around the entire coastline, but is most abundant in the cooler waters from Cook Strait southwards. It is found predominantly at depths of $<5 \mathrm{~m}$ (Schiel, unpubl. data). Fishing is restricted to free-diving, and no underwater breathing apparatus is allowed. Paua reach 195 mm (shell length) and the MLS is 125 mm .

The commercial value of the fishery has increased dramatically during the last five years (Schiel 1991). There are also a large recreational fishery and a continuing importance of both paua meat and shell to the indigenous Maori people.

The history of abalone fisheries worldwide shows that management is difficult and that populations are often overfished, causing a precipitous drop in commercial landings (Sloan and Breen 1988). The difficulties in management arise from the spatial patchiness and sedentary nature of abalone (Poore 1972b, Shepherd 1986, Sluczanowski 1986), an uncertain relationship between standing stock and recruitment (Prince et al. 1988, Breen 1991), and often a paucity of useful information on growth and mortality (Shepherd and Breen 1991). These uncertainties also apply to the NZ paua fishery, which occurs over most of the coastline including many remote places with rough sea conditions and difficult access.

Although the fishing of paua goes back to pre-colonial times (Best 1929), there is a relatively small history of research on the fishery (Schiel 1991). Growth and mortality rates have been studied for only a few sites in the South I. (Poore 1972a, Sainsbury 1982). Estimates of basic

population parameters are required to manage the fishery effectively. In this paper we assess the size structure, age structure, and mortality of paua populations.
We estimate 'age' from growth rings in shells and assess the usefulness of this ageing technique for paua. This is potentially one of the most powerful tools available for estimating growth and mortality rates (Shepherd and Breen 1991). Cross sections of H. iris
shells have obvious rings. These have previously been used to estimate age and growth (Murray and Akroyd 1984, Murray 1986, Hahn 1989), but no verification has been reported. Similar rings have been used elsewhere to age abalones. For instance, rings in $H$. tuberculata (in the English Channel) have been verified by growth studies (Forster 1967, Hayashi 1980). Verification is also reported in Japanese H. discus discus (Kojima et al. 1977) and the Korean H. diversicolor diversicolor
and $H$. d. aquatilis (Kim and Cheung 1985). Inoue and Oba (1980) suggest that shell circuli are annual for Japanese $H$. gigantea. Prince et al. (1988) describe a method for ageing Tasmanian $H$. rubra, based on the method of Munoz-Lopez (1976).

In two quota management areas that support substantial landings, we compare estimated levels of fishing mortality with estimates of appropriate levels of fishing mortality obtained from per-recruit modeling. We also compare growth and mortality estimates from shell growth rings with those obtained from other methods. Finally, we explore the consequences of altering the present MLS.

## Materlals and methods

## Fleld sampling

The size structure of emergent $H$. iris populations was examined around Stewart I., which comprises a major part of the southern fishery, and the Marlborough Sounds, which are a major part of the fishery in the northern part of the South I. (Fig. 1). Stewart I. is exposed to a range of weather conditions. The east coast is in the lee of prevailing westerly winds, but is occasionally subjected to severe easterly storms. The west coast of the island is often inaccessible due to the prevailing winds and a large onshore swell. During the time of our sampling, the swell was reduced to about 1 m . The northern side of the island is protected from the westerly winds but has a refracted westerly swell. Paua occur along the entire coastline of Stewart I.

The Marlborough Sounds are generally less exposed than Stewart I. Paua occur only at the outer margins of the Sounds, as the inner shores are protected and provide generally unsuitable habitat for paua. Northerly winds funnelling through Cook Strait are occasionally severe and can bring exposed conditions to most places where paua are fished. The eastern side of D'Urville $I$. is protected from westerly winds. Sites in the central portion of the Sounds are generally subjected to similar conditions of exposure to the north, while southeastern sites are protected from the west and north. One other site was used in this study.
Karori Rock is on the south coast of the North I. It is within an area closed to commercial fishing since 1974 after severe depletion of paua populations caused by both commercial and recreational fishing. This site is generally protected from severe swells but occasionally experiences severe northerly and southerly storms in Cook Strait.
Except at Karori Rock, sampling sites were chosen to be representative of commercially harvested sites. This was done in consultation with commercial divers
and, at Stewart I., a commercial diver assisted us in the field. During $15-25$ September 1989, 17 sites were assessed at Stewart I., and 19 sites during 17-23 October 1989, at the Marlborough Sounds. Karori Rock was sampled on 30 November 1989. Each sampling site was roughly 1 ha in area. Paua were collected, taken to a boat, measured to the nearest mm (shell length), and a subsample from each site was frozen and taken back to Wellington for weighing and ring counting. Remaining paua were returned to their habitat. The numbers collected at each site varied (range 125-548), depending on sea conditions and the abundance of paua. The goal was to collect several hundred paua at each site. To remove paua, we used a blunt trowel of a type commonly used by commercial divers, and took care not to cause damage. Paua less than 70 mm were not representatively sampled because they occupy cryptic inshore habitats and require different sampling techniques. We attempted to sample paua $>70 \mathrm{~mm}$ representatively by having each diver remove all paua as they were encountered. A total of 5790 (Stewart I.) and 8731 (Marlborough Sounds) paua were measured.
For analyses, we grouped sites by regions of Stewart I. and the Marlborough Sounds (Fig. 1) because we did not wish to assess fine-scale variability in parameters.

## Ageing and growth

Shells in the ring-count subsample were measured in length and then sectioned sagittally through the spire with a lapidary saw. Because the rings are obvious (Fig. 2) no further enhancement was necessary. Ring counts for all shells were done by the same experienced technician.
From the ring-count sample data we estimated the von Bertalanffy growth parameters with the non-linear least-squares procedure FISHPARM (Saila et al. 1988). We also estimated growth parameters from markrecapture data obtained at several sites (Fig. 1) in the northern Marlborough Sounds and around D'Urville I. (Talbot Murray, Min. Agric. Fish., P.O. Box 297, Wellington, pers. commun.). Abalone had been collected, tagged with a numbered plastic disc attached to the shell with epoxy putty, replaced, and recovered later. Most of the times-at-liberty were one year; increments for shorter and longer times (range 92-519 days) were adjusted pro rata. We estimated asymptotic length $\mathrm{L}_{\infty}$ and the Brody growth coefficient K from a FordWalford regression (Ricker 1975). For comparison with these results, we also calculated growth parameters from age estimates (ring counts) obtained from abalone in the same experiments (Talbot Murray, pers. commun.). The ring counts were done by the same technician, as explained above.


Figure 2
Growth rings in a cross section of a Haliotis iris shell.

## Mortality estimation

Age-length keys (Ricker 1975) were constructed from the ring-count data. The keys were used to estimate the catch curve from the length-frequency sample for each region; total mortality rate was then estimated from the regression of the natural $\log$ of estimated number-at-age on 'age' (Robson and Chapman 1961). The first 'age' included in the procedure was chosen to represent the first 'age' class with a mean length greater than minimum legal size.
Total mortality rates were also estimated from the length-frequency samples using the method of Fournier and Breen (1983), using a strategy similar to that of Tegner et al. (1989). To obtain the fishing mortality rate $F$, we subtracted an assumed value of $M=0.10$, based on the work of Sainsbury (1982), from the total mortality rate Z. Natural mortality rate is difficult to estimate, especially in fished populations (Shepherd and Breen 1991); Sainsbury used several methods to estimate $M$ in a population protected from fishing. The method of Fournier and Breen (1983) can estimate growth and mortality rates simultaneously but is better applied by constraining the growth estimates, to be consistent with independent estimates. We applied this method to length-frequencies from the northern Marlborough Sounds and D'Urville I., using the growth estimates obtained from mark-recapture data in those regions. This method could not be applied to the other
regions because we had no independent estimates of growth.
In using the Fournier and Breen (1983) method, the assumed number of age classes N was determined by examining results using different values of N . We chose the highest value for which the procedure estimated a substantial proportion of the population to be contained within each age-class. At unrealistically high values of N , the procedure estimates that some ageclasses are "empty." The parameter NFULL (the index of the first cohort whose abundance is used in estimating mortality) was chosen with reference to the mean cohort length and the minimum legal size. Estimated standard deviations of lengths-at-age around mean length-at-age were constrained to values near 4.1, based on examination of length-frequencies in which cohort modes were clear (Schiel, unpubl. data). $\mathrm{L}_{\infty}$ was unconstrained except for D'Urville I., where a minimum constraint was required to obtain estimates consistent with the mark-recapture data. Population proportions were left unconstrained unless the procedure made unrealistically high estimates for single age-classes. Variance of mean lengths from the von Bertalanffy growth curve and variance of the estimated population proportions from an exponential decay curve were both constrained to a maximum of 1.0. Sensitivity of the procedure to changes in N, NFULL, K, and the standard deviations of length-at-age was examined by varying these parameters (see Tegner et al. 1989).

## Modeling

Yield-per-recruit (YPR) modeling was done on a spreadsheet incorporating the YPR model of Ricker (1975). We report results from two regions: the northern Marlborough Sounds and D'Urville I. Lengthweight relations were calculated from field sampling results (Table 1). Egg production modeling was done for these regions using a simple spreadsheet model of the form described by Sluczanowski $(1984,1986)$. The additional information required for this modeling is the length-fecundity relation. Relevant data are available from Poore (1973), Sainsbury (1982), and Wilson (1987). Based on the size range of paua in each of these sources, we used Wilson's data to derive

$$
\text { Eggs }=\left(9.32 \times 10^{-12}\right) \times \text { shell length }(\mathrm{mm})^{8.408} .
$$

The natural mortality rate $M$ was assumed to be 0.10 . We assessed the sensitivity of the results to this assumption by varying M. For the northern Marlborough Sounds, we also varied $M$ and the size-at-firstcapture and developed the response surface of YPR

Table 1
Length-weight power curves for each of the regions of New Zealand examined. The relation is whole weight (g) $=\mathrm{a} \times$ (length (mm) ${ }^{\text {b }}$ ).

| Region | $n$ | a | b |
| :--- | :---: | :---: | :---: |
| Karori Rock | 278 | $3.593 \mathrm{E}-5$ | 3.305 |
| Stewart I. West | 495 | $5.308 \mathrm{E}-5$ | 3.169 |
| Stewart I. North | 416 | $3.918 \mathrm{E}-6$ | 3.718 |
| Stewart I. East | 499 | $2.994 \mathrm{E}-5$ | 3.303 |
| Marlborough D'Urville | 335 | $2.592 \mathrm{E}-5$ | 3.322 |
| Marlborough North | 497 | $2.470 \mathrm{E}-5$ | 3.339 |
| Marlborough South | 181 | $4.927 \mathrm{E}-5$ | 3.190 |

and egg production. For each region, the von Bertalanffy growth curves from mark-recapture data were used.

We held the age-at-first-capture constant at the first age-class with a mean length equal to or greater than 125 mm . Then we varied the instantaneous rate of fishing mortality, F , to estimate $\mathrm{F}_{0.1}$ and $\mathrm{F}_{25 \%} . \mathrm{F}_{0.1}$ is the fishing mortality rate at the point where yield-perrecruit increases with $F$ one-tenth as fast as it does at the origin. Although arbitrary, $\mathrm{F}_{0.1}$ is used by several major international stock assessment agencies as a guide to appropriate target fishing mortalities (Mace 1988). $\mathrm{F}_{25 \%}$ is the fishing mortality rate at which equilibrium egg production is $25 \%$ that of an equilibrium virgin population.

## Results

## Field sampling

Haliotis iris were abundant at all sites, despite more than 30 years of commercial fishing activity in all regions. It was not our intention to estimate densities, but an indication of abundance is given by the length of time it took to obtain our samples. The mean was 155 paua per diver-hour (SD 33.6) or about 32 kg whole wt per diver-hour.
The structure of paua populations varied considerably among the seven regions (Fig. 3). The three regions of Stewart I. show clear differences in the modes (Fig. 3A-C). The west coast region had the major mode at $140-145 \mathrm{~mm}$ shell length, well beyond the minimum legal size of 125 mm , and paua were found up to 187 mm . The major mode for the northern region was at $125-130 \mathrm{~mm}$. The east coast region had a higher proportion of smaller paua and the major mode was at 120 mm .
In contrast to Stewart I., length-frequencies for the three regions of the Marlborough Sounds were similar
to one another (Fig. 3D-F). The major modes were around 125 mm (MLS), and smaller paua were found in each region. There has probably been roughly similar fishing pressure in these three regions in recent times.

Although the Karori Rock site is closed to commercial activity, it is subjected to considerable illegal fishing (Schiel 1989). The major mode in length-frequency is at 130 mm (Fig. 3G). Because illegal fishing removes paua of all sizes, it reduces paua densities but does not necessarily change the population size structure.

## Ageing and growth

A typical ring-count frequency is shown for the Marlborough Sounds D'Urville I. region (Fig. 4). Paua appear to be fully recruited to the sampling procedure by 'age' 10 . The greatest ring count we observed was 34 at the west coast of Stewart Island. Growth rates were obtained from the ring count data for all sites (Table 2). Growth parameters from ring-count data and mark-recapture experimental data for two regions (Table 3) and the mean increments predicted from the two methods (Fig. 5) were compared. A large difference between the two methods was evident: the markrecapture data resulted in higher K estimates and larger $\mathrm{L}_{\infty}$ estimates; estimated growth from markrecapture data was much greater than from ring-count data. This pattern is the converse of what would be expected if the tagging procedure had retarded growth; therefore, we consider the mark-recapture data to be more reliable. The mark-recapture data are inconsistent with the assumption that one, or even two, rings are laid down annually.

## Mortallty estimation

Total mortality rates from the catch-curve analyses ranged from $\mathrm{Z}=0.216-0.425$ (Table 4). Mortality estimates based on the length-frequency analysis, and the parameters used to obtain them, are shown in Table 5 . The estimates varied when N, NFULL, K, and the standard deviation constraints were varied; the pattern of change was not consistent between data sets. Only variation in N caused large variation in estimated Z . The Methods describe an objective procedure for choosing N . The 'best' estimates (using the criteria described above) were $\mathrm{Z}=0.495$ and $\mathrm{Z}=0.507$ for the northern Marlborough Sounds and D'Urville regions, respectively. The extreme range observed over all parameter variations in the two data sets was $\mathrm{Z}=0.238-0.995$.

## Modeling

Growth rates used in modeling were those estimated from mark-recapture data (Table 3) for the northern


Flgure 3
Size-frequency histograms of Haliotis iris measured in September and October 1989.


Figure 4
'Age' estimates from growth ring counts ( $n$. 335 ) in one region (Marlborough Sounds D'Urville I.), assuming that one growth ring represents one year of age.

Marlborough Sounds and D'Urville I. regions. Growth estimates from ring count data were not used because of the discrepancy seen in Table 3. Estimates of $\mathrm{F}_{0.1}$ and $\mathbf{F}_{25 \%}$ resulting from YPR analyses are given in Table 6 for three assumed $M$ values. In all cases, $\mathrm{F}_{25 \%}$ was greater than the estimated $\mathrm{F}_{0.1}$ obtained from the same parameters.
The best estimates of actual fishing mortality rates, obtained from the procedure shown in Table 5 , were substantially higher than $F_{0.1}$ in both regions examined (Table 6). This result is not sensitive to the assumed $M$, although higher $M$ values increase $\mathrm{F}_{0.1}$ and decrease the estimated current level of F . Response surfaces in YPR and egg production resulting from variation in M and the size-atfirst capture are shown in Figures 6 and 7, respectively. These show the typical form of such surfaces (cf. Tegner et al. 1989). When M is higher, maximum YPR is obtained at a lower size for a given $F$, or at a higher $F$ for a given size. Egg production follows a simpler pattern, but is greater at a given combination of F and size-at-first-capture when M is greater. Yield and egg production resulting from different values of M and MLS are shown in Table 7.


Figure 5
A comparison of the length-specific growth increments predicted from the mark-recapture data (thin line) and from growth ring counts (thick line) in two regions of the Marlborough Sounds. Data points are the observed growth increments; predictions were based on data in Table 3.

Table 2
Estimates of von Bertalanffy growth parameters (with standard errors) from the growth ring-count data of Haliotis iris where $\mathrm{L}_{\infty}$ is the asymptotic length, K is the Brody coefficient (Ricker 1975), and $t_{0}$ is the theoretical age at length zero.

| Region | $n$ | $\mathrm{~L}_{\infty}$ | K | $\mathrm{t}_{0}$ |
| :--- | :---: | :---: | :---: | ---: |
| Karori Rock | 278 | $143.2(2.41)$ | $0.160(0.022)$ | $-8.4(0.96)$ |
| Stewart I. West | 495 | $153.3(1.63)$ | $0.143(0.017)$ | $-7.0(1.17)$ |
| Stewart I. North | 416 | $134.1(0.81)$ | $0.318(0.034)$ | $-5.9(0.54)$ |
| Stewart I. East | 499 | $130.9(1.21)$ | $0.283(0.027)$ | $-6.0(0.43)$ |
| Marlborough D'Urville | 335 | $131.1(1.79)$ | $0.210(0.022)$ | $-6.6(0.53)$ |
| Marlborough North | 497 | $135.0(3.06)$ | $0.114(0.018)$ | $-11.5(1.47)$ |
| Marlborough South | 181 | $134.8(2.68)$ | $0.291(0.042)$ | $-4.7(0.51)$ |

## Table 3

A comparison of von Bertalanffy growth parameters estimated from growth ring-count data from several sites in the D'Urville I. and northern Marlborough Sounds regions (Fig. 1) and mark-recapture data from experiments at the same sites (Talbot Murray, unpubl. data). Sample sizes are unequal because more animals were subjected to ring counting than marks were recovered.

| Place | Mark-recapture data |  |  | Ring-count data |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $n$ | $\mathrm{L}_{\infty}$ | K | $n$ | $\mathrm{L}_{\infty}$ |  | K | (SE) |
| D'Urville I. | 79 | 141.6 | 0.379 | 131 | 131.5 | (2.21) | 0.197 | (0.029) |
| Northern Marlborough | 53 | 144.5 | 0.285 | 180 | 126.4 | (2.65) | 0.214 | (0.052) |

## Discussion

## Size structure

Evidence from length-frequencies indicates that in some regions the fishery may still be sustained by the accumulated stock. Although reliable catch-per-uniteffort figures are not available for the commercial fishery, it is probable that the west coast of Stewart I. represents such a region. The weather and sea conditions render this region inaccessible for much of the year, but it is a favored place to fish when conditions permit because of the large sizes and abundance of paua. In contrast, sites on the east coast of Stewart I. are considerably more sheltered, generally accessible to fishing, and closer to a port. The observed population structure in the eastern region, with most paua below MLS, is consistent with a population in equilibrium with the fishery.
There are alternative explanations for the differences in size-frequencies. One possibility is a difference in growth rates among regions: $L_{\infty}$ could be smaller in the eastern region of Stewart I. than the western region. Another possibility is that the population structure seen at the west coast of Stewart I. may have resulted from a short period of good recruitment followed by poor recruit-

Table 4
Total mortality estimates, and their standard errors, from the catch curve method, based on growth ring-count data. Sample sizes are given for the ring-count and length-frequency samples.

| Region | Ring-count sample | Length sample | Z $\quad$ (SE) |
| :--- | :---: | :---: | :---: | :---: |
| Karori Rock | 285 | 285 | $0.16(0.022)$ |
| Stewart I. West | 319 | 1796 | $0.13(0.017)$ |
| Stewart I. North | 412 | 1332 | $0.19(0.022)$ |
| Stewart I. East | 313 | 2662 | $0.28(0.031)$ |
| Marlborough D'Urville | 173 | 2780 | $0.38(0.049)$ |
| Marlborough North | 263 | 4634 | $0.36(0.060)$ |
| Marlborough South | 90 | 1317 | $0.25(0.050)$ |
| Total | 1855 | 14806 |  |

Table 5
Estimates of total mortality rate Z based on length-frequencies, using the method of Fournier and Breen (1983). N is the assumed number of age classes; NFULL is the number of the first age-class included in the mortality estimate; "SDevs" are the standard deviations of lengths in the first and last age-classes; $T$ is the value of the objective function minimized by the procedure. Asterisks indicate constrained values.

| Region | N | NFULL | SDevs | $L_{\infty}$ | K | T | Z |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Northern Marlborough Sounds | 14 | 7 | $4.1^{*}$ | $4.2^{*}$ | 144.4 | $0.28^{*}$ | 92.8 |
| D'Urville I. | 12 | 6 | $4.2^{*}$ | $4.2^{*}$ | 138.0 | $0.37^{*}$ | 162.0 |


| Table 6 <br> Comparison of estimated fishing mortality rates ( F ) with the reference levels $F_{0.1}$ and $F_{25 \%}$ for two regions, and sensitivity of the estimates to assumed natural mortality rate $\mathbf{M}$. |  |  |  |
| :---: | :---: | :---: | :---: |
| Region | $\mathrm{F}_{0.1}$ | $\mathrm{F}_{25 \%}$ | Est. F |
| Northern Marlborough Sounds |  |  |  |
| $\mathrm{M}=0.05$ | 0.11 | 0.16 | 0.45 |
| $\mathrm{M}=0.10$ | 0.18 | 0.27 | 0.40 |
| $\mathrm{M}=0.15$ | 0.25 | 0.47 | 0.35 |
| D'Urville I. |  |  |  |
| $\mathrm{M}=0.05$ | 0.11 | 0.18 | 0.46 |
| $\mathrm{M}=0.10$ | 0.18 | 0.32 | 0.41 |
| $\mathrm{M}=0.15$ | 0.27 | 1.11 | 0.36 |

ment. A third possibility is that natural mortality is much higher in the eastern region of Stewart than in the other regions. Similarly, population size structures seen in the Marlborough Sounds could be explained by high natural mortality, recruitment variation, or stunted growth in some regions. Only repeated

Table 7
Northern Marlborough Sounds region: YPR (top) and egg production (bottom) for three different levels of assumed M, for three different minimum legal sizes. YPR is in grams whole weight; egg production is expressed as a percentage of the eggs produced by a virgin population.

| MLS | 115 |  | 125 |  | 130 |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| M | $\mathrm{F}_{\text {est }}$ | $\mathrm{F}_{0.1}$ | $\mathrm{F}_{\text {est }}$ | $\mathrm{F}_{0.1}$ | $\mathrm{F}_{\text {est }}$ | $\mathrm{F}_{0.1}$ |
| 0.05 | 219.0 | 196.1 | 230.6 | 199.0 | 236.5 | 205.4 |
| 0.10 | 175.9 | 151.1 | 176.2 | 151.1 | 171.9 | 147.0 |
| 0.15 | 139.0 | 126.3 | 132.5 | 122.2 | 182.9 | 114.4 |
| 0.05 | 7.4 | 33.4 | 9.9 | 35.0 | 12.8 | 34.1 |
| 0.10 | 14.0 | 31.1 | 18.1 | 33.3 | 12.5 | 36.6 |
| 0.15 | 22.6 | 31.1 | 28.2 | 34.6 | 33.9 | 39.1 |



Figure 6
Yield-per-recruit as a function of the natural mortality rate (M), fishing mortality rate ( F ), and the minimum legal size. In $\mathrm{A}, \mathrm{M}=0.05 ; \mathrm{B}, \mathrm{M}=0.1 ; \mathrm{C}, \mathrm{M}=0.15$.


Flgure 7
Egg production as a function of the natural mortality rate (M), fishing mortality rate ( F ), and the minimum legal size. In $\mathrm{A}, \mathrm{M}=0.05 ; \mathrm{B}, \mathrm{M}=0.1 ; \mathrm{C}, \mathrm{M}=0.15$.
sampling through time, and appropriate experimentation, can distinguish among these alternatives.

## Ageing and growth

Despite the fact that growth rings in $H$. iris are quite distinct, as has been reported for other species (Prince et al. 1988), they are evidently not annual in at least some populations. Predicted growth increments from ring count data were much less than observed incre-
ments from mark-recapture. This suggests that more than one ring is laid down annually, but it is not clear whether the deposition of growth rings follows a regular annual pattern. We examined the hypothesis that the growth rings are semi-annual, but predicted and observed growth increments still did not agree. Consequently, the ring counts overestimate age in two study regions. This appears to be borne out by lengthfrequency analysis of mortality in which the estimates are higher than those from catch curves.

Our experience underscores the need to validate age estimates from independent data (Beamish and McFarlane 1983). For H. iris, the use of growth rings leads to the erroneous conclusion in at least two populations that they are more lightly fished than indicated by length-frequency analysis based on mark-recapture data.

## Mortallty

For the reasons discussed above, we consider that the mortality rates based on ring counts are spurious for H. iris, at least for the regions examined. Mortality rates derived from length-frequency distributions are heavily dependent on the assumptions of the method. One critical assumption is that recruitment to the population is roughly constant. If recent recruitment has varied with any trend, analysis of a single lengthfrequency sample cannot provide a realistic estimate of mortality (Shepherd and Breen 1991). We have no data on annual variation of recruitment at our sampling sites. Interannual variation can be high in some species of abalone (Tegner et al. 1989), but it is systematic change in recent recruitment that causes estimates to be dubious. However, it is encouraging that our estimates of mortality are reasonably robust to variation in the input parameters (Table 5).

Other important assumptions are that natural mortality is age-independent (over the age range examined) and also constant for all areas. For abalones generally, the first assumption is not unreasonable for mature animals (Shepherd and Breen 1991) and, for H . iris, it is consistent with the conclusions of Sainsbury (1982). Our estimates of current fishing mortality rates are sensitive to the assumption that $\mathrm{M}=0.10$ (Table 6). This is the best estimate of natural mortality derived by Sainsbury (1982).

## Modeling and implications for management

Of the two reference points we use for evaluating fishing mortality rate in the $H$. iris fishery, $\mathrm{F}_{0.1}$ is smaller than $\mathrm{F}_{25 \%}$ for both regions. This result is insensitive to the assumed M and indicates that $\mathrm{F}_{0.1}$ management is more conservative than $\mathrm{F}_{25 \%}$ management.
The estimated current fishing mortality rates for both regions are greater than both reference levels of F ; this result is also insensitive to the assumed value of $M$. If the underlying assumptions hold, therefore, the current fishery is more intense than can be sustained in the long term in these regions. Egg production at the estimated present level of fishing mortality is about $18 \%$ (Table 7). This is lower than prudent management would probably require.

Both reference points are sensitive to several assumptions, similar to those discussed above: random recruitment variation, constant age-independent M , constant growth rates, and the assumed value of M (reviewed by Hancock 1979, Vetter 1988, Breen 1991).
The impact of varying the minimum legal size appears small in comparison with the sensitivity of YPR and egg production analysis to M (Table 7). Neither YPR nor egg production at equilibrium would be affected much by changing the MLS, at least over the range examined. Maximizing YPR by adjusting the MLS would require a much more precise knowledge of M. YPR is robust to changes in F, but decreasing $F$ to the reference level $F_{0.1}$ would increase equilibrium egg production; this would be true whatever combination of M and MLS is examined. This result is similar to that reported by Sluczanowski $(1984,1986)$ for Southern Australian abalones. He found that egg production could be increased markedly with little sacrifice in YPR in the fishery.
Because of the ease with which paua can be found in most sites, there is a temptation to assume that stocks are healthy and in no imminent danger of overfishing. However, based on our estimates of fishing mortality rates, the recent fishery may be simply removing an abundant accumulated stock at a rate greater than annual production in two study regions.

Our best estimates of fishing mortality rates are higher than the standard reference levels, indicating that fishing pressure should be reduced in these regions. Under an ITQ management regime, this can be addressed by reducing quotas in a QMA. Translating reductions in fishing mortality to reductions in TACCs for Quota Management Areas can be done by evaluating the Baranov catch equations (Ricker 1975). Another approach is to estimate maximum constant yields from historical catch data (Schiel 1989).

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