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Stock assessment and risk analysis for the whiskery shark (*Furgaleus macki* (Whitley)) in south-western Australia

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Abstract

The current status of the whiskery shark (*Furgaleus macki*) stock in south-western Australia was assessed using an age and sex structured model. The best estimates of total and mature biomass in 1997/1998 were 38.8% of virgin, and 23.0% of virgin, respectively. The 95% confidence intervals for total biomass were 22.7-47.2%, and for mature biomass were 13.4-36.4%. Thirteen scenarios were used to test the sensitivity of the model to catch and effort, biological, and gear parameters. The estimates of current biomass were most sensitive to variations in catch and effort data. A scenario testing the use of raw catch and effort data produced unrealistically low estimates of current biomass, while a scenario testing the hypothesis that there had been no efficiency increases in the fishery over time indicated that biomass was currently higher than indicated by the best estimate. The remainder of the scenarios tested produced estimates of total biomass between 32 and 40% of virgin, and mature biomass would be at least 40% of virgin by 2010/2011 (a management committee target), that the total biomass in 2010/2011 will not be below that of 1996/1997, and that the stock would collapse. The results of risk analysis indicates that to achieve at least a 50% probability for the first two biological reference points, annual catches would need to be below 190 tonnes until 2010. The probability of a population crash before 2010 is approximately 5% when future catches are 175 tonnes, and greater than 50% when catches are above 280 tonnes. Risk analysis indicates that there is a need to substantially reduce commercial catches if the target set by the management committee is to be met. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Elasmobranch fisheries have a history of overexploitation and collapse (Anderson, 1990). However, in a small number of cases long-term fisheries have been achieved. For example, Australia's Southern Shark Fishery has fished for school (*Galeorhinus galeus*) and gummy (*Mustelus antarcticus*) sharks (Stevens et al., 1997; Walker, 1998) for over 60 years. To achieve sustainable elasmobranch fisheries, research on the status of populations is essential so that resource managers can regulate fisheries at appropriate levels.

Elasmobranchs are caught world-wide both as target species and as by-catch. Bonfil (1994) estimated

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that the global catch in the early 1990s was probably in excess of one million tonnes. Despite this there has been limited research on the status of populations. In the situations where research has been undertaken a variety of approaches have been used to assess the status of elasmobranch populations. These include: using tagging data to estimate mortality rates and their impact on the stocks (e.g. Holden, 1968; Grant et al., 1979; Simpfendorfer, 1999a); demographic analysis to estimate instantaneous rates of population increase (e.g. Smith and Abramson, 1990; Cailliet, 1992; Cortes, 1995, 1998; Sminkey and Musick, 1996; Au and Smith, 1997; Simpfendorfer, 1999b); production models based on catch and effort or fishery independent survey data (e.g. Otto et al., 1977 in Anderson, 1990; Marques de Silva, 1987); and dynamic pool models structured by age, sex and/or area (e.g. Walker, 1992; Punt and Walker, 1998).

The whiskery shark, Furgaleus macki, is a moderately sized species of the family Triakidae endemic to the waters of south-western and southern Australia (Last and Stevens, 1994). A demersal gillnet fishery operates in south-western Australia to catch F. macki, as well as Carcharhinus obscurus (dusky shark) and M. antarcticus (gummy shark). This fishery developed as a small scale longline fishery during the 1940s (Heald, 1987). The introduction of monofilament gillnets, hydraulic net haulers, and the displacement of fishers from other fisheries during the 1970s, resulted in a dramatic increase in fishing effort, placing considerable pressure on shark stocks (Heald, 1987; Simpfendorfer and Donohue, 1998). In 1975, Fisheries Western Australia (the government agency responsible for the management of fish resources) commenced the collection of detailed catch and effort data for all commercial fisheries, including the shark fishery.

Fishing effort continued to increase in the 1980s as markets developed for shark flesh and effort was diverted from other fisheries (Simpfendorfer and Donohue, 1998). In the early 1980s fishing patterns changed, with fishers switching from targeting *F. macki* to targeting *C. obscurus*. This was the consequence of decreasing catch rates for *F. macki* and an improved understanding of the *C. obscurus* stock. The falling catch rates of *F. macki* (and other species) in the mid-1980s raised concerns about the status of the stock and resulted in the introduction of a management plan that included limited entry, effort controls and gear restrictions aimed at ensuring sustainability for the fishery (Lenanton et al., 1989). In 1995 the committee providing advice on the management of the fishery recommended a limit reference point of 40% of virgin biomass to be achieved by the 2010/2011 season (Simpfendorfer and Donohue, 1998). Subsequently, a number of reductions in allowable fishing effort were implemented in attempts to reach the limit reference point for *F. macki* (and those set for other species).

With the introduction of more intensive management for the fishery a research project was implemented to provide improved biological and fishery data for the commercially important shark species. The ultimate purpose of this project was to provide information on the status of the shark stocks to fishery managers. The aim of this paper is to: (1) present raw catch and effort data, methods of correcting for incomplete data, and corrected catch and effort data for *F. macki*, (2) describe an age-structured method for assessing the status of the population, (3) provide information on the current status of *F. macki* in south-western Australia, and (4) report the results of a risk analysis used to assess the impact of future catch levels on the status of the population.

2. Methods

The definitions of the symbols and notation used within equations in this paper are given in Appendix A.

2.1. Catch and effort data

Catch and effort data for use in the assessment of the status of the *F. macki* population were obtained from compulsory monthly fishing returns supplied by commercial fishers to Fisheries Western Australia. The amount of fishing effort (e.g. type of gear, quantity of gear, and number of days fished) and catches (by weight) of individual species are reported monthly by one degree geographic blocks. These catch and effort data have been collected since 1975, although in some years compliance to the provision of catch returns was poor. To account for missing fishing returns the values of annual catch and effort were

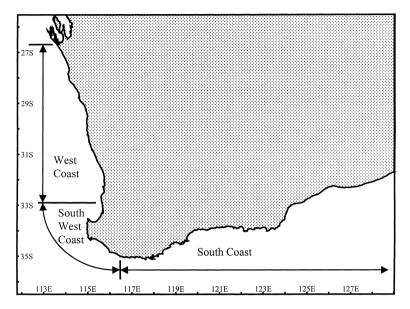


Fig. 1. Map showing the boundaries and management zones of the shark fishery in south-western Australia.

adjusted by the proportion of fishing returns not lodged. This resulted in catch and effort levels being increased by 25% in 1986, 35% in 1987, and 5% in all other years prior to the start of the 1989/1990 season. Since the start of the 1989/1990 season the provision of returns has been strictly enforced and no corrections were applied to this period.

To determine the level of catch and effort for F. macki the data for all vessels that captured sharks between 27°S and 128°E (Fig. 1) were extracted from the Western Australian catch and effort database. The catch data were corrected for fishers who did not accurately report the species composition of their catch. In most cases these fishers reported their catch simply as "shark" or "other shark". This practice was especially common in the years soon after the introduction of compulsory reporting of data by individual species. A number of quantitative criteria ("other shark" less than half of the total catch for a month, catch not recorded exclusively against one species, and either F. macki or C. obscurus recorded) were used to determine if a fisher had accurately reported the species composition of his catch. If a fisher's monthly return met these criteria then the record was considered a "good report" for that month. A record not meeting these criteria was considered a "bad report" for the month. The corrected total catch of each

species, in each region (regions corresponded to the three management zones of the fishery, see Fig. 1), was

$$\hat{C}_{s,r} = \frac{C_r C_{s,r}^{\rm G}}{C_r^{\rm G}},\tag{1}$$

and the total catch of each species over all regions was

$$\hat{C}_s = \sum_r \hat{C}_{s,r}.$$
(2)

Since more than one fishing method is used to catch sharks, the effort was standardised into gillnet equivalent units. Gillnet equivalent effort was calculated by taking the total shark catch of "good reports" using gillnets and calculating their gillnet CPUE by region

$$CPUE_r^{GN} = \frac{C_r^{GN}}{E_r^{GN}},$$
(3)

and applying this CPUE to the total catch for a region to calculate the gillnet equivalent effort:

$$\hat{E}_r = \frac{C_r}{\text{CPUE}_r^{\text{GN}}}.$$

The total gillnet equivalent fishing effort was calculated by summing all regional values:

$$\hat{E} = \sum_{r} \hat{E}_{r}.$$
(4)

The abundance of *F. macki* was assumed to be proportional to the catch rate of the commercial fishery.

In calculating the average annual catch rate of *F. macki*, catch rates were first calculated for each one degree geographic block within the range of the fishery:

$$U_{j,t} = \frac{\sum_{i} C_{i,j,t}^{G}}{\sum_{i} E_{i,j,t}^{G}}.$$
(5)

by multiplying the effective effort by 1.00+0.02t, where *t* is the number of years since 1975.

2.2. Model structure

The dynamics of the *F. macki* population were modelled using an age and sex structured simulation approach. Dynamics of the stock were assumed to be described by

$$N_{a+1,g,t+1} = \begin{cases} N_{0,g,t+1}, & a = 0, \\ (N_{a,g,t} - \hat{C}_{a,g,t}) e^{-M}, & 1 \ge a > x_g, \\ (N_{a,g,t} - \hat{C}_{a,g,t} + N_{a-1,g,t} - \hat{C}_{a-1,g,t}) e^{-M}, & a = x_g. \end{cases}$$
(8)

Blocks in which there were less than 100 gillnet equivalent effort units had highly variable catch rates and were regarded as too imprecise for inclusion in the analysis. Catch rates for each block were estimated as the mean of a whole financial year (referred to from here on as a year) as fishing in many blocks was infrequent. The average annual catch rates (y_t) were obtained by fitting the multiplicative loglinear model:

$$\log(U_{j,t}) = u + y_t + A_j + e \tag{6}$$

using the Generalised Linear Models procedure in SAS. The area effect (A_j) weighted the catch rates by the fishable area (depth less than 200 m) within each one degree geographic block.

The average annual catch rates of *F. macki* were used to calculate effective effort, a measure of effort which is assumed to remain proportional to the fishing mortality regardless of changes in the distribution of fish and fishing effort (Gulland, 1983),

$$E_t^{\rm E} = \frac{\hat{C}_t}{y_t}.\tag{7}$$

Effective effort was used as the measure of effort in the model described below. To take account of increasing efficiency in the fishery as a result of better equipment (e.g. larger vessels, GPS, and more effective net configurations), and increasing knowledge, a second calculation of effective effort was made based on the assumption that there was an annual 2% increase in efficiency. The efficiency increase was implemented

Recruitment to the fishery was assumed to follow a Beverton–Holt style stock–recruitment relationship,

$$N_{0,g,t} = \frac{S_t}{(b+cS_t)} P_{g=f}^{\prime\prime\prime},$$
(9)

where

$$S_{t} = \sum_{a=m}^{x} N_{a,g=f,t} P_{a}' P_{a}'.$$
 (10)

The stock-recruitment parameters (*b* and *c*) were calculated from the known reproductive characteristics of the species, the virgin recruitment (R^*) and the proportion of R^* that recruits when S_t is 20% of the virgin level (Hilborn et al., 1994),

$$b = \frac{S^*(1 - ((z - 0.2)/0.8z))}{R^*},$$
(11)

and

$$c = \frac{(z - 0.2)}{0.8zR^*}.$$
 (12)

The values of R^* and z were estimated in the model fitting process.

The catch in numbers of each sex, at each age, in each time period were calculated by

$$\hat{C}_{a,g,t} = N_{a,g,t} v_{a,g} F_t, \tag{13}$$

where the fishing mortality for each time period was

$$F_t = \frac{Y_t}{B_t^{\rm e}},\tag{14}$$

and the exploitable biomass was

$$B_t^{\mathbf{e}} = \sum_g \sum_a N_{a,g,t} w_{a,g} v_{a,g}.$$
(15)

The use of gillnets in the fishery necessitated the inclusion of a vulnerability (selectivity) term in the model. Vulnerability was expressed as a gamma function following the method of Kirkwood and Walker (1986), and using stretched mesh size (MS) of the gillnets measured in inches:

$$v_{a,g} = \left(\frac{L_{a,g}}{\alpha\beta}\right)^{\alpha} e^{\alpha - L_{a,g}/\beta},$$
(16)

where

$$\alpha\beta = \theta_1 \,\mathrm{MS},\tag{17}$$

$$\beta = -\frac{1}{2}((\theta_1 \,\mathrm{MS}) - (\theta_1^2 \,\mathrm{MS}^2 + 4\theta_2)^{1/2}). \tag{18}$$

The values of θ_1 and θ_2 were taken from values estimated by Simpfendorfer and Unsworth (1998a) on the basis of experimental work.

Growth was assumed to follow the von Bertalanffy growth equation, with the length of age class and sex

main target species (see Section 1). Both values of q were estimated in the model fitting process.

Total biomass for each year was calculated by

$$B_t = \sum_g \sum_a N_{a,g,t} w_{a,g},\tag{21}$$

where

$$w_{a,g} = lwaL_{a,g}^{hvb},\tag{22}$$

with weight measured in kilograms and length measured in centimetres.

Similarly, the mature female biomass was calculated as

$$B_{t}^{m} = \sum_{a=m}^{x} N_{a,g=f,t} w_{a,g}.$$
 (23)

2.3. Initial state

To account for the impact of fishing prior to the collection of detailed catch and effort information, the state of the population in 1975 was determined by

$$N_{a+1,g,1975} = \begin{cases} R_0 P_g''', & a = 0, \\ N_{a,g,1974} e^{-(M+F_0)}, & 1 \ge a > x_g, \\ N_{a,g,1974} e^{-(M+F_0)}/(1 - e^{-(M+F_0)}), & a = x_g, \end{cases}$$
(24)

determined for the middle of the year:

$$L_{a,g} = L_{\infty,g} (1 - e^{-K_g(a + 0.5 - t_{0,g})}).$$
⁽¹⁹⁾

The estimated catch rate in the model was calculated as a function of catchability and exploitable biomass:

$$\hat{U}_t = q_t B_t^{\rm e}.\tag{20}$$

Two values of q were used, one for the period from 1975 to 1981, and a second for the period from 1982 to 1997. During the first period fishermen mostly targeted *F. macki*, while from 1982 *C. obscurus* was the

where

$$R_0 = \frac{X_0 - b}{X_0 c}.$$
 (25)

The value of F_0 was estimated in the model fitting process and represents the estimated level of fishing mortality prior to 1975. The eggs per recruit in the pre-1975 population were calculated as

$$X_0 = \sum_{a=m}^{x} N_{a,g,0}^* P'_a P'_a P'''_{g=f},$$
(26)

where

$$N_{a+1,g,0}^{*} = \begin{cases} 1, & a = 0, \\ N_{a,g,0}^{*} e^{-(M+F_{0})}, & 1 \ge a > x_{g}, \\ N_{a,g,0}^{*} e^{-(M+F_{0})} / (1 - e^{-(M+F_{0})}), & a = x_{g}. \end{cases}$$
(27)

Virgin biomass is calculated as

$$B_0 = \sum_{g} \sum_{a} N_{a,g,0} w_{a,g},$$
 (28)

where

$$N_{a+1,g,0} = \begin{cases} R^*, & a = 0, \\ N_{a,g,0} e^{-M}, & 1 \ge a > x_g, \\ N_{a,g,0} e^{-M} / (1 - e^{-M}), & a = x_g. \end{cases}$$
(29)

Virgin mature female biomass was calculated by

$$B_0^{\rm m} = \sum_{a=m}^{x} N_{a,g=f,0} w_{a,g}.$$
 (30)

2.4. Model fitting

The model was fitted to catch rate data using the likelihood function:

$$LL = -\left(\frac{SSQ}{2\sigma^2}\right) - \left(n\ln\left(\sqrt{\sigma^2 2\pi}\right)\right),\tag{31}$$

where

$$SSQ = \sum_{t} [\log(U_t + 0.000001) - \log(\hat{U}_t + 0.000001)]^2$$
(32)

with $U_t = y_t$. A constant (0.000001) was added to U_t to enable the log-transform of zero values. Residual values from preliminary fitting of the model showed that values larger than 0.0000001 produced biased results. The model was fitted using the Solver function in Microsoft Excel to provide estimates of five unknown parameters (R^* , z, F_0 , $q_{1975-1981}$, and $q_{1982-1996}$). Random starting values for each of the unknown parameters were used. The value of z was constrained to fall within the range 0.205 (slightly greater than the 0.200 theoretical minimum) and an upper bound is given by

$$z_{\max} = \frac{S^*}{4R^* + S^*}.$$
 (33)

The derivation of this constraint is given in Appendix B.

The calculation of SSQ required that the variance of the residuals was equal for the two time periods for which different q values were used (1975–1981 and

1982–1996). To achieve this an iterative approach to function maximisation was used. First, the function was maximised using no correction for variance. Next, the variance of the residuals for each of the periods were calculated. Residual values were standardised by dividing by the residual variance for the appropriate period. The function was then re-maximised. This process was repeated until there was no change in the residual variance values for both periods.

Confidence intervals for the parameter estimates were calculated using bootstrapping. New sets of catch rate data were generated by randomly sampling residuals from the original fitted model (with replacement), correcting for the variance for the appropriate period (see above) and the number of observations $(\sqrt{n+1/n})$, and adding them to the catch rates estimated by the model. The model was then re-fitted using the new catch rate data. Five hundred sets of bootstrapped data were created. Ninety five per cent confidence intervals were calculated as the 2.5 and 97.5 percentiles of the resulting 500 sets of parameter estimates.

2.5. Projection of the fishery into the future

To determine the impact of future harvest strategies, the population was projected into the future using the model specified above. Recruitment variability was assumed to be described by a normal distribution with a mean of zero and standard deviation (σ^{r}) of 0.2. There are no published studies describing recruitment variation in elasmobranchs, but Punt and Walker (1998) assumed a σ^{r} between 0 and 0.4 for *G. galeus*. In the present study we chose the midpoint of Punt and Walker's range (σ^{r} : 0.2).

A constant annual yield harvest strategy approach was taken to projecting the model forward since fisheries managers had requested information on the appropriate future catch levels. Future catches in the fishery were assumed to be held constant after 1997, with levels between 0 and 350 tonnes tested. It was assumed that the fishery did not take exactly the designated catch each year, but rather came within 10%. To achieve this, a deviation to the catch calculated from a uniform random variate ranging from -10 to 10% was added to the designated catch each year (e.g. for 200 tonnes designated future catch, the actual catch ranged from 180 to 220 tonnes). This

represents implementation error in the constant annual yield harvest strategy. To project the population into the future it was necessary to estimate the value of F_t required to make the actual catches. This was done by searching for the value of F_t that gave the required catch.

2.6. Biological parameters

Biological parameters utilised by the model were mostly taken from published information on *F. macki*. Simpfendorfer and Unsworth (1998b) have described the reproductive biology, Simpfendorfer et al. (2000) the age and growth, and Simpfendorfer and Unsworth (1998a) the gillnet mesh selectivity parameters. The only parameter for which data were not available for *F. macki* is natural mortality (*M*). The value of *M* was estimated using the method of Hoenig (1983) that utilises a relationship between maximum age and total

Table 1

Biological parameters used in the age and sex structured model for F. macki

mortality. Simpfendorfer et al. (2000) examined age and growth in an exploited population, and based on this study it was assumed that in an unexploited population maximum age was 15 years for females and 13 years for males. The values of the biological parameters used in the model are given in Table 1.

2.7. Sensitivity tests

To investigate the sensitivity of the assessment to variations in catch and effort, fishery and biological data, 15 scenarios with various combinations of parameters were tested (Tables 2–4). The base case (scenario A) represents the best understanding of the population based on the currently available information. Scenarios B, C and D investigated the sensitivity of the model to variations in the catch and effort data (Table 2). Risk assessment was not undertaken for scenarios B and C. Scenarios (E–K) investigate the

Parameter	Value	Units	Source
Growth			Simpfendorfer et al. (2000)
Female			• · · ·
Κ	0.369	year ⁻¹	
L_{∞}	120.7	cm	
t_0	-0.544	year	
Male			
Κ	0.423	year ⁻¹	
L_{∞}	121.5	cm	
t_0	-0.472	years	
Length–weight			Simpfendorfer and Unsworth (1998a)
lwa	1.63E-5		L V V
lwb	2.733		
Selectivity			Simpfendorfer and Unsworth (1998a)
θ_1	173.70		1
θ_2	26415		
Natural mortality			Hoenig (1983) relationship
M	0.27	year ⁻¹	
Reproduction			Simpfendorfer and Unsworth (1998b)
P'	19		()
P''	0.5		
P'''	0.5		
$P'_{a}^{'}$ $P''_{a}^{''}$ $P'''_{g=m}$ $P'''_{g=f}$	0.5		
Age			Simpfendorfer et al. (2000)
m	6	years	1
x	15 (female)	years	
	13 (male)	years	

Table 2

Scenario	Name	Catch data	Effort data	Efficiency (% annual)
A	Base case	Corrected	Effective	2
В	Raw catch and nominal effort	Raw	Nominal	0
С	Nominal effort	Corrected	Nominal	0
D	No efficiency	Corrected	Effective	0
				0

^a The parameters not specified are the same as those of the base case (scenario A).

Table 3

Specification of scenarios for the assessment of the F. macki population: models testing sensitivity to variations in biological parameters^a

Scenario	Name	M (year ⁻¹)	m (years)	x (male/female) (years)	P''	$K^{\mathrm{b}}(\%)$
А	Base case	0.27	6	13/15	0.5	100
Е	Low M , high x	0.23	6	16/18	0.5	100
F	High M , low x	0.35	6	10/12	0.5	100
G	Double $0+M$	0.27 (0+0.54)	6	13/15	0.5	100
Н	Low m	0.27	4	13/15	0.5	100
Ι	High m	0.27	8	13/15	0.5	100
J	Annual breeding	0.27	6	13/15	1.0	100
Κ	Low growth rate	0.27	6	13/15	0.5	80

^a The parameters not specified are the same as those of the base case (scenario A).

^b Proportion of value given by Simpfendorfer et al. (2000).

sensitivity to variation in age, growth, natural mortality and reproduction (Table 3). For scenarios E and F (variation in M) the maximum age and natural mortality (using the Hoenig (1983) method) were changed. The effect of varying the CV of recruitment for the risk assessments was tested with scenarios L and M (Table 4). Scenarios N and O examined the sensitivity to changes in mesh selectivity, with the high and low values taken as the upper and lower 95% confidence intervals given by Simpfendorfer and Unsworth (1998a) (Table 4).

2.8. Risk assessment

Risk assessment was used to estimate the probability that a particular event would occur within a specified time given specified harvest strategies. The probability of three different events was assessed. Firstly, that the biomass target set by the Management Committee for the fishery would be met (i.e. total biomass at least 40% by 2010/2011). Secondly, that the total biomass in 2010/2011 would be equal to, or larger than, the total biomass in 1996/1997, and thirdly, that the *F. macki* stock would fail, as indicated by there being insufficient exploitable biomass to cover the annual catches at any time during the period from 1996/1997 to 2010/2011.

The *F. macki* population was projected forward using the results of each of the 500 bootstrapped data sets for each of the scenarios tested except B and C. Five hundred trials of each data set were used. The results from scenarios L and M were used to test the sensitivity of the results to the CV of recruitment. Assuming that the probability of each of the remaining scenarios (excluding B, C, L and M) was equal the overall probability of each of the specified events

Table 4

Specification of scenarios for the assessment of the *F. macki* population: models testing sensitivity to variations in gear and model specification parameters

Scenario	Name	σ^{r}	θ_1	θ_2
А	Base case	0.2	173.70	26415
L	High σ^{r}	0.3	173.70	26415
М	Low σ^{r}	0.1	173.70	26415
Ν	Low selectivity	0.2	171.84	22000
0	High selectivity	0.2	175.52	31779

occurring, given a designated catch, was taken as the mean of the results from the remaining scenarios.

3. Results

3.1. Catch and effort data

Catches of *F. macki* reported by commercial fishers in Western Australian waters since 1975 have varied between 94 and 508 tonnes (Table 5). Catches adjusted for fishers who did not provide species specific data on their returns have varied between 162 and 611 tonnes. The proportion of catch attributed to "good reporters" has increased steadily since the mid-1970s, from 50–60% to nearly 91% in 1996/1997. Catches of *F. macki* between 1979/1980 and 1992/ 1993 were between 380 and 500 tonnes, except for 1981/1982 when the catch was 611 tonnes and 1987/ 1988 when the catch was 583 tonnes. Since 1993/1994 the catches have fallen, ranging between 216 and 261 tonnes.

Nominal fishing effort (i.e. that reported by fishers) increased more than an order of magnitude from the mid-1970s to a peak in 1987/1988 (Table 5). After reaching this peak, nominal effort has fallen steadily as a consequence of management decisions, and in 1997/1998 was much less than half of the maximum reported level. Effective effort calculated without any efficiency increase showed a similar trend to that of nominal effort. However, the effective effort calculated with a 2% annual efficiency factor resulted in a higher peak effort level and higher current levels of effort. The catch rate calculated using the adjusted catch and effective effort with the 2% annual efficiency factor fell steadily during the late 1970s and early 1980s (Table 5). Since the mid-1980s the catch rate has remained relatively stable.

3.2. Model fit

The predicted catch rates from the model provided a good fit to the observed data (Fig. 2). In most cases the observed values fell within the 95% confidence inter-

Table 5

Catch, effort and catch rate values for F. macki by financial year from 1975/1976 to 1997/1998

Year	Raw catch (kg)	Adjusted catch (kg)	Catch from good reports (%)	Nominal effort (km gn h)	Effective effort (no efficiency) (km gn h)	Effective effort (2% efficiency) (km gn h)	Catch rate (no efficiency) (kg km gn h^{-1})	Catch rate (2% efficiency) (kg km gn h^{-1})
1975/1976	94262	161679	58.3	64691	65756	65756	2.46	2.45
1976/1977	138716	213652	64.9	67610	77105	78647	2.77	2.71
1977/1978	177868	345587	51.5	98053	119877	124720	2.88	2.75
1978/1979	186557	272754	68.4	100825	95395	101234	2.86	2.67
1979/1980	267180	388509	68.8	144173	160165	173368	2.43	2.23
1980/1981	290992	413099	70.4	165128	193103	213201	2.12	1.93
1981/1982	508382	610879	83.2	198634	299465	337246	2.04	1.79
1982/1983	390068	492804	79.2	270775	340466	391088	1.45	1.25
1983/1984	289807	388645	74.6	295477	346702	406217	1.12	0.95
1984/1985	278405	399089	69.8	439543	344571	411794	1.16	0.97
1985/1986	318428	481429	66.1	572425	569115	693748	0.85	0.69
1986/1987	336291	441362	76.2	600743	628075	780933	0.70	0.56
1987/1988	412168	583127	70.7	786687	749161	950117	0.78	0.61
1988/1989	324644	447028	72.6	665386	497416	643461	0.90	0.70
1989/1990	314268	409592	76.7	557851	570149	752299	0.72	0.55
1990/1991	402835	493594	81.6	516733	501489	674939	0.98	0.73
1991/1992	367946	433264	84.9	434428	443969	609474	0.98	0.71
1992/1993	297808	371513	80.2	445135	504432	706327	0.74	0.53
1993/1994	186179	226905	82.1	381944	421647	602215	0.54	0.38
1994/1995	211291	261291	80.9	350226	401521	584940	0.65	0.45
1995/1996	192011	233802	82.1	331149	355849	528773	0.66	0.44
1996/1997	196750	216748	90.8	327306	338324	512786	0.64	0.42
1997/1998	185449	231843	80.0	309795	293136	453182	0.79	0.51

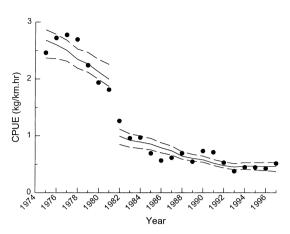


Fig. 2. Observed catch rate data for *F. macki* in south-western Australia (closed circles) and predicted catch rates from the model for the base case (scenario A) (solid lines) and 95% confidence intervals (dashed lines).

val for the predicted value. The size of the confidence intervals was greater in the period from 1975 to 1981 than for the period from 1982 to 1997. Comparison of the residuals between these two periods showed that the variation was higher for the later period (Fig. 3a), confirming the need for correction of the residuals in the fitting process. After correction the distribution of residuals was similar for both periods (Fig. 3b).

The population parameters (R^* , z and F_0) that provided the best fit for each of the scenarios tested, and their 95% confidence intervals (CIs), are given in Table 6. Values of $q_{1975-1981}$ and $q_{1982-1997}$ are not presented as they are scaling parameters. In all scenarios $q_{1975-1981}$ was greater than $q_{1982-1997}$.

Values of R^* varied considerably between scenarios. The base case (A), low age at maturity (H), and both mesh selectivity sensitivity tests (N and O) had very similar values, all towards the low end of the range from all scenarios. Two scenarios had lower values of R^* — low M and high x (E), and annual breeding (J). All other scenarios had R^* values greater than that of the base case. Highest values occurred for the two scenarios where uncorrected catch and/or effort was used (B and C). In all scenarios the best estimate of R^* was towards the lower end of the 95% CI. In only two scenarios (B and H) did the 95% CI of the R^* values reach limits set during the optimising procedure. On the basis of the 95% CI there were no significant differences between R^* in scenarios A, C, D, G, H, I, J,

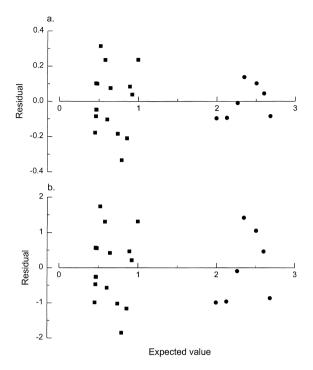


Fig. 3. Residual plots for the base case model (scenario A) for 1975–1981 (circles) and 1982–1997 (squares): (a) without correction for period variance, and (b) with correction for period variance. See text for details of correction for variance and fitting procedure.

K, N and O. The value for scenario B was significantly higher than that for A, D, E, J, K, N and O; while scenario F had a significantly higher value than J and E. Scenario E had a significantly lower R^* value than B, D, F, G, I and K.

Values of z varied less between each of the scenarios than did R^* (Table 6), mainly due to the constraints placed on the fitting procedure. Unlike the limits for R^* which were used to eliminate values that appeared to be unreasonable and speed the fitting process, the limits on z were imposed because of biological constraints. In all but four of the scenarios the 95% CI reached both the upper and lower limit set. In all scenarios the best estimate of z was at, or near, the upper limit of the allowable range. On the basis of the 95% CI there were no significant differences between z values for any scenarios.

Estimates of F_0 for all scenarios were less than 0.08 (Table 6). Highest values of F_0 were for the scenarios based on an uncorrected catch and/or effort (B and C).

Scenario	<i>R</i> *	z	F_0
A	284700 (273000–591200)	0.496 (0.205*-0.496*)	0.0032 (0.0002-0.0499)
В	1602700 (860000–10000000*) ^b	0.340 (0.205*-0.496*)	0.0739 (0.0000-0.1490)
С	643200 (223400-5689700)	0.276 (0.205*-0.496*)	0.0181 (0.0000-0.0856)
D	326900 (290200-843500)	0.468 (0.205*-0.496*)	0.0027 (0.0000-0.0472)
E	214800 (190300-290200)	0.562 (0.205-0.591*)	0.0042 (0.0003-0.0490)
F	555000 (519700-2972800)	0.326 (0.205*-0.326*)	0.0011 (0.0000-0.0583)
G	406700 (387400-1126700)	0.428 (0.205*-0.428*)	0.0022 (0.0000-0.0509)
Н	284900 (217400-1000000*)	0.342 (0.205*-0.558)	0.0015 (0.0000-0.0778)
Ι	401600 (376300-2710200)	0.362 (0.205*-0.362)	0.0011 (0.0000-0.0443)
J	263300 (231800-506100)	0.565 (0.205*-0.663*)	0.0045 (0.0000-0.0561)
К	363400 (316700-628800)	0.410 (0.205-0.496*)	0.0019 (0.0000-0.0700)
Ν	284800 (273000-540000)	0.496 (0.206-0.496*)	0.0032 (0.0002–0.0489)
0	284200 (272600-562000)	0.496 (0.205*-0.496*)	0.0032 (0.0000-0.0493)

Table 6 Population parameters from 13 different scenarios for *F. macki* population off south-western Australia^a

^a Values indicated are the best estimate and 95% confidence intervals calculated from the solutions of 500 bootstrapped data sets (in parentheses).

^b Asterix indicates that range was constrained by limits placed on the optimising procedure.

The 95% CI of F_0 for all scenarios ranged from close to 0 to more than 0.044, indicating no significant differences between scenarios.

3.3. Current status

The estimate of the 1997 total biomass from the base case (scenario A) was 38.8% of virgin (CI 22.7-47.2%), and for mature female biomass was 23.0% (CI 13.4-36.4%) (Table 7). The lowest estimates of 1997 biomass were for scenario B (uncorrected catch and effort) with 7.8% total (CI 4.3-98.2%) and 5.3% mature female (CI 3.2-97.1%). The highest estimate of biomass was in scenario D (no efficiency increase), where total biomass was 50.5% (CI 22.8-61.7%) and mature female biomass 35.1% (CI 16.5-50.9%). For the remaining scenarios the best estimates of total biomass were between 32.0 and 40.1%, and for mature female biomass between 21.2 and 30.3% (Table 7). The 95% CIs for biomass estimates indicated that there was no significant differences between the 1997 levels of total or mature female biomass for all scenarios.

To illustrate the trend in biomass levels through time the annual estimates of total and mature female biomass (and 95% CIs) for the base case (scenario A) are illustrated in Fig. 4. Total biomass declined consistently between 1975 and 1993, but since has been much more stable. Mature female biomass declined more rapidly than total biomass between 1975 and 1981, continued to decline between 1982 and 1992, and since 1993 has been slowly increasing. The best fit to the data indicates that total and mature female biomass were close to 100% of virgin level in 1975. However, some bootstrap results that had higher levels of F_0 indicated lower levels of biomass in 1975, resulting in the large 95% CI.

Table 7

Estimates of the 1997/1998 level of total and mature biomass for the *F. macki* population off south-western Australia from 13 different scenarios (see text for description of scenarios)^a

Scenario	$B_{\rm t}$ (% virgin)	$B_{\rm m}$ (% virgin)
A	38.8 (22.7-47.2)	23.0 (13.4–36.4)
В	7.8 (4.3–98.2)	5.3 (3.2-97.1)
С	32.0 (4.0-64.8)	26.8 (3.8-59.6)
D	50.5 (22.8-61.7)	35.1 (16.5-50.9)
Е	38.7 (28.9–49.8)	22.3 (14.1-36.4)
F	38.2 (6.2-47.0)	29.6 (5.0-38.7)
G	38.3 (14.4-46.8)	24.9 (10.0-38.0)
Н	38.7 (13.9-50.1)	23.3 (5.8-35.9)
Ι	36.8 (7.0-46.6)	30.3 (6.4-41.1)
J	39.4 (20.4–49.5)	21.2 (10.2-35.5)
Κ	40.1 (18.9–50.1)	28.0 (11.8-37.0)
Ν	39.5 (24.8-48.9)	23.5 (14.2-35.3)
0	39.1 (22.6-49.0)	23.4 (13.6–37.5)

^a Values indicated are the best estimate and 95% confidence interval calculated from the solutions of 500 bootstrapped data sets (in parentheses).

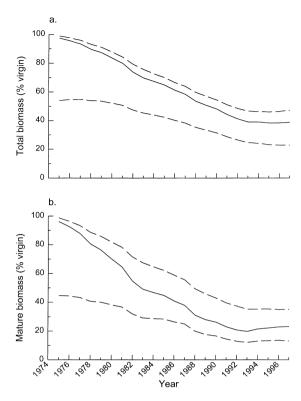


Fig. 4. Trends in (a) total biomass, and (b) mature female biomass (solid lines) between 1975 and 1997 with 95% confidence intervals (dashed lines). Confidence intervals are based on the results of refitting the model to 500 bootstrapped catch and effort data sets (see text for details).

3.4. Risk assessment

The probability curves of achieving each of the three reference points varied widely between scenarios, but most fell within a 20% probability band for any given catch level (Fig. 5). Mean probability curves were located centrally within the spread of the results for individual scenarios, indicating that they accurately represented a summary of the results. The mean probability curves for achieving 40% total biomass by the 2010/2011 season, and increasing biomass from 1996/1997 to 2010/2011, are similar (Fig. 5a and b). The mean probability of meeting these targets decreases slowly at annual catches less than 100 tonnes, and then falls more rapidly. A 50% chance of achieving the target of 40% total biomass by 2010/ 2011 occurs at an annual catch of approximately 195 tonnes; the 50% chance of achieving the increased

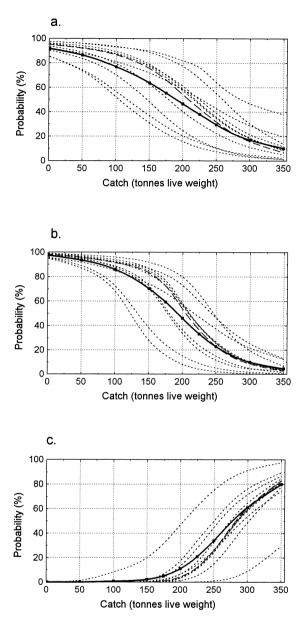


Fig. 5. Results of risk analysis for *F. macki* in south-western Australia. The probability of achieving three different biological reference points was tested: (a) total biomass is greater than 40% in the 2010/2011 season, (b) total biomass in the 2010/2011 season is greater than or equal to that in 1996, and (c) stock failure. Solid lines represent mean probability of each reference point being achieved assuming equal probability of scenarios (see text for scenarios included). Dotted lines represent probabilities for individual scenarios (except the base case), and the dashed line represents the probability for the base case. Actual annual catches were randomly selected from a range within 10% of indicated annual catches (see text for details).

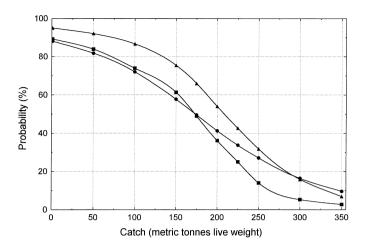


Fig. 6. Comparison of the results of risk analysis for the total biomass being at least 40% of virgin by the 2010/2011 season with three different levels of σ^{r} . Squares, $\sigma^{r}=0.1$; triangles, $\sigma^{r}=0.2$; and circles, $\sigma^{r}=0.3$.

biomass target by 2010/2011 occurs at an annual catch of approximately 190 tonnes. The mean probability of a crash in the stock (defined as the predicted catch exceeding the exploitable biomass) was insignificant at annual catches below 150 tonnes, but increased to a 50% chance at annual catches of approximately 280 tonnes (Fig. 5).

The three values of σ^{r} tested (0.1, 0.2 and 0.3) produced similar results, as illustrated by the similarity between the probability curves for the 40% biomass reference point (Fig. 6). The scenario with $\sigma^{r}=0.2$ produced the most optimistic curve, while scenario with $\sigma^{r}=0.1$ produced the least optimistic curve. At low catch levels the $\sigma^{r}=0.3$ scenario had probabilities similar to the $\sigma^{r}=0.1$ scenario, but at catches above 250 metric tonnes probabilities were similar to the $\sigma^{r}=0.2$ scenario.

4. Discussion

4.1. Current status of F. macki

The best estimate for the current status of the *F. macki* population off south-western Australia is that total biomass in 1997/1998 was 38.8% of the virgin level, and the mature female biomass was 23.0% of the virgin level. These levels represent significant declines in the population since 1975 when the model indicates

that biomass was probably above 95% of the virgin level. The prediction by the model that 1975 biomass was close to virgin levels is consistent with information available on shark catches during this period. Although no species-specific data are available, total annual shark catches prior to 1975 were mostly less than 300 tonnes (Simpfendorfer and Donohue, 1998). At these levels, *F. macki* catches were probably less than 100 tonnes. Simulations of the virgin population with annual catches of 100 tonnes indicate that the population would decline at less than 1% per year (Simpfendorfer, unpublished data).

Two sources of uncertainty were examined in this study. Firstly, 13 different scenarios were tested to investigate the uncertainty that resulted from possible errors in the initial parameters used in the model (catch and effort data, and biological and gear parameters). Secondly, uncertainty that resulted from possible errors in the catch and effort data were investigated using bootstrapping to give 95% confidence intervals for each of the scenarios. The use of these techniques showed that the range of possible results for the assessment of the F. macki population were broad across all of the scenarios tested. The smallest estimate of current total biomass was 4.0% of virgin, and the highest 98.2% of virgin. However, in all but one scenario (raw catch and effort data) the population showed a substantial decline in biomass over the period from 1975 to 1998. This leaves little doubt that the fishery has had a major impact on the stock, but that further research is required to reduce the uncertainty as to the size of this reduction.

The sensitivity tests run using different data in the model indicated that changes in the catch and effort data resulted in the largest changes in the estimates of 1997 biomass. In particular the results indicate the need for catch and effort data to be closely examined for errors such as not reporting species composition data, and non-submission of data. Failure to correct for these types of errors in the *F. macki* assessment resulted in estimates of 1997 biomass that were lower than the other scenarios, and that had extremely wide 95% confidence intervals.

The removal of the 2% annual efficiency increase from the catch rate data resulted in a substantial increase in the estimate of the 1997 level of biomass. This occurred because in this scenario (D) catch rates in the fishery since 1975 had not fallen as low as scenarios using the 2% efficiency correction. Since abundance is assumed to be proportional to catch rate the biomass would therefore have decreased less. The efficiency factor was included to simulate the impact of the introduction of new technology (e.g. depth sounders, radar, GPS and net haulers) and the increased knowledge and ability of skippers (e.g. identification of optimum fishing grounds and gear configurations). The level of annual increase was chosen arbitrarily due to the lack of data. Another approach to including efficiency increases would be to include a few large increases to more closely simulate the introduction of new equipment. However, this factor does not allow for the increasing knowledge and operating skill of fishers that occurs more gradually over time. Research to quantify the efficiency increases in the fishery over time would significantly enhance the accuracy of the assessment for F. macki.

The importance of the catch and effort data in determining the 1997 biomass results from the assumption of the model that abundance is proportional to the catch rate. Simple examination of the catch rate time-series suggests a greater level of population decline than suggested by the model. This is a result of the use of different values of q for the periods before and after 1981. Initial model runs using a single q from 1975 to 1998 failed to produce feasible results because the catches since 1983 could not be

sustained if the biomass had declined as sharply as suggested by the catch rate data (Simpfendorfer, unpublished data). The use of two different q values assumes that the behaviour of the fishery was different in these two periods, a fact supported by observations of changing target species (see Section 1). Therefore, assessment of the population without understanding the behaviour of the fishery would have led to a more pessimistic result, and possibly produced unnecessary management action.

Changes in biological parameters and gear selectivity had much lower impacts on the estimated current status of the population than did changes in catch and effort data. This indicates that further biological research is unlikely to substantially change the results of the assessment. Thus future research targeted at further refining the catch and effort data may have the greatest benefit.

The greater reduction in the mature female biomass, as compared to the reduction in total biomass, indicates that fishing has impacted more heavily on mature animals than on juveniles. This is largely a result of the selectivity of the demersal gillnets that are used in the fishery. Simpfendorfer and Unsworth (1998a) showed that the mesh sizes used in the fishery (16.5 and 17.8 cm) resulted in the capture of animals in the size range of sub-adult and adult individuals. In addition to the selectivity of the gear, it appears that small juvenile *F. macki* (<90 cm) rarely occur on the gillnet fishing grounds, or have a cryptic nature (Simpfendorfer and Unsworth, 1998a;Simpfendorfer, unpublished data), making their capture even less likely.

4.2. Risk analysis and management of the fishery

The risk analysis for *F. macki* indicates that future catches need to be reduced to achieve the biomass target set by the Management Committee (40% of virgin level by 2010). This is despite the best estimates of current biomass being close to 40% of virgin. This is an indication that the high levels of catch during the 1980s were achieved by depleting the biomass rather than by taking surplus production. To achieve a 50% probability of success of having the target biomass above 40% of virgin by the year 2010, the risk analysis indicates that annual catches will need to be less than 190 tonnes. Similar results were obtained for at least maintaining the current level of biomass because

current biomass is estimated to be close to 40% of virgin.

On the basis of the results from the model, and the risk analysis, continued catches at levels above 200 tonnes will result in there being a significant risk of the fishery exploiting the stock at a level where severe depletion would occur. In the short term, this level of exploitation is unlikely to cause extinction of the stock since the risk analysis was for the catch being greater than exploitable biomass (mostly sub-adult and adult). The risk to the population in the longer term, however, comes from the fishery having multiple target species. This could result in high levels of fishing effort being maintained to target other species, but with a continued catch of F. macki pushing the stock closer to extinction. Since the current study used a constant catch approach to projecting the F. macki catch forward it was not possible to investigate this impact. However, future work using a constant fishing mortality approach would be useful in understanding how the F. macki stock would be impacted by this type of phenomenon. Such an approach is possibly important given that Casey and Myers (1998) reported such a situation for the barndoor skate (Raja laevis) in the western North Atlantic where fishing for groundfish has depleted the population so that it is close to extinction.

The development of this modelling technique, and its application to the assessment of the F. macki population, has provided resource managers with information on which to base decisions about the future management of the fishery. In response to the results of this assessment the Management Committee responsible for the fishery has instituted a phased reduction of fishing effort over five years (Simpfendorfer, unpublished data). The aim of these new measures is to reduce the effort in the fishery, especially that targeted at F. macki. Ongoing assessment of the impact of these management measures will be required to ensure that they achieve the desired effects. Further refinement of assessments for F. macki will depend on the collection of more detailed biological data, and the inclusion of more detail in the model (e.g. inclusion of spatial structure, data from tagging studies, and size composition data). These refinements would further improve the information available to fisheries managers, and provide increased understanding of the F. macki population and the impact of the fishery.

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Appendix A. Notation

a	000
a	age
A_j	block effect for block <i>j</i>
b	a parameter of the Beverton-Holt
	stock-recruitment curve
B_t	the biomass at time t
B_t^{e}	exploitable biomass at time t
B_t^{m}	mature female biomass at time t
$B_{ m v}$	virgin biomass
$B_{ m v}^{ m m}$	virgin mature female biomass
с	a parameter of the Beverton-Holt
	stock-recruitment curve
$\hat{C}_{a,g,t}$	catch in numbers of F. macki of age a
	and sex g at time t
$C_{i,i,t}^{\mathrm{G}}$	catch of <i>F. macki</i> by "good reporting"
<i>'J</i> , <i>'</i>	fisher I in block j at time t
C_r	catch of all sharks in region r
$C_r \\ C_r^{ m G}$	catch of all sharks in region r by "good
7	reporting" fishers
$C_r^{\rm GN}$	catch of total shark in region <i>r</i> by "good
	reporting" fishers using gillnets
$\hat{C}_{s} \ C^{ m G}_{s,r}$	corrected total catch of species s
C^{G}	catch of species s in region r by "good
	reporting" fishers
$\hat{C}_{s,r}$	corrected total catch of species <i>s</i> in
	region r
$\begin{array}{c} C_t \\ \hat{C}_t \end{array}$	observed catch of time period t
$\hat{\hat{C}}_{t}$	estimated catch in time <i>t</i>
$CPUE_r^{GN}$	catch per unit effort of total shark in
ere_r	region r by "good reporting" fishers
	using gillnets
P	error
$e \\ \hat{E}$	total gillnet equivalent effort over all
L	regions
$E_{i,j,t}^{\mathrm{G}}$	fishing effort of "good reporting" fisher
$\boldsymbol{\nu}_{i,j,t}$	<i>i</i> in block <i>j</i> at time <i>t</i>
\hat{E}_r	total gillnet equivalent effort in region
L_r	
	r

E_r^{GN}	nominal effort in region r by "good
	reporting" fishers using gillnets
E_t^{E}	effective effort in time t
F_0	pre-1975 fishing mortality
$\vec{F_t}$	instantaneous rate of fishing mortality
g	sex
K_{g}	parameter of the von Bertalanffy func-
<i>g</i>	tion for sex g
$L_{a,g}$	the length of a fish of age a and sex g
L _{a,g} LL	log likelihood
lwa	parameter of the length-weight rela-
iwa	
11.	tionship
lwb	parameter of the length-weight rela-
7	tionship
$L_{\infty,g}$	parameter of the von Bertalanffy func-
	tion for sex g
m	age at maturity
Μ	instantaneous rate of natural mortality
MS	mesh size
$N_{a,g,t}$	number of fish of sex g and age a at the
	start of time t
$N^{*}_{a,g,0}$	pre-1975 number per recruit
$N_{a,g,v}$	number of animals of age a and sex g in
	the virgin population
P'_a	number of pups per pregnant female at
	age a
$P_a'' P_g'''$	proportion of females pregnant at age a
$P_{a}^{\prime\prime\prime\prime}$	proportion of embryos of sex g
q_t°	catchability at time t
R^*	the recruitment at virgin biomass
R_0	pre-1975 recruitment
$\tilde{S_t}$	egg production at time t
Ś*	unexploited egg production
SSQ	sum of squares
$t_{0,g}$	parameter of the von Bertalanffy func-
0,8	tion for sex g
и	overall mean catch rate of <i>F. macki</i>
$U_{j,t}$	catch rate of <i>F. macki</i> in block <i>j</i> at time <i>t</i>
\hat{U}_t	predicted catch rate at time t
$v_{a,g}$	vulnerability of a fish of age a and sex g
· a,g	to the fishing gear
W _{a,g}	weight of a fish of age a and sex g
	maximum age of sex g
$\begin{array}{c} x_g \\ X_0 \end{array}$	pre-1975 eggs per recruit
	average annual catch rate for time t
$\frac{y_t}{Y_t}$	catch in weight at time t
-	
Z	the proportion of R^* obtained at 20% of the focundity of virgin biomeda
	the fecundity of virgin biomass

α	gamma	function	gear	selectivity	para-
	meter				
β	gamma	function	gear	selectivity	para-

- meter
- σ variance of residuals
- θ_1 constant of proportionality between $\alpha\beta$ and MS
- θ_2 variance of length of sharks captured (constant across all mesh sizes)

Appendix B. Derivation of the upper bound of z

The Beverton-Holt stock-recruitment relationship is represented by

$$R_t = \frac{S_t}{a + bS_t},\tag{B.1}$$

where

$$b = \frac{S^*(1 - ((z - 0.2)/0.8z))}{R^*},$$
 (B.2)

and

$$c = \frac{z - 0.2}{0.8zR^*}.$$
 (B.3)

This equation can be rewritten for the number of recruits resulting from each egg:

$$\frac{R_t}{S_t} = \frac{1}{b + cS_t}.\tag{B.4}$$

This equation approaches a maximum of 1/b when egg production approaches zero, and asymptotes towards zero as egg production approaches infinity. For the fish stock, the minimum value is reached when it is in its virgin state (i.e. at S^*), when recruits per egg is R^*/S^* . That is recruits per egg ranges from R^*/S^* when the fish stock is unexploited to a maximum

$$\frac{R^*}{S^*} \left(\frac{4z}{1-z}\right) \tag{B.5}$$

when egg production approaches zero. For the Beverton-Holt stock-recruitment relationship, the factor

$$\left(\frac{4z}{1-z}\right) \tag{B.6}$$

~ ~ ~

represents the maximum level of compensation by the fish stock for the increased mortality of fishing.

If both recruitment and egg production are measured in the same units, then the ratio of R_t/S_t may not exceed 1. In this case, this imposes the condition on z that when the ratio R_t/S_t is a maximum,

$$\frac{R^*}{S^*} \left(\frac{4z}{1-z}\right) \le 1. \tag{B.7}$$

This can be rearranged to give

$$z \le \frac{S^*}{4R^* + S^*}.\tag{B.8}$$

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