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Yield- and egg-per-recruit analyses for the New Zealand rock lobster, *Jasus edwardsii*

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Abstract The effects of different values of the instantaneous natural (M) and fishing (F) mortality rates and the minimum legal size on the yield- and egg-per-recruit of *Jasus edwardsii* were estimated for 10 areas around New Zealand. At the current assumed value for M of 0.10, the yield-per-recruit of females was insensitive to changes in F or the minimum legal size, whereas the yield-per-recruit of males was maximised at relatively low levels of F and large values for the minimum legal size. Egg-per-recruit (EPR) values varied considerably among areas. The weighted average exploited EPR as a percentage of the unfished EPR for the North and South Islands combined was 27%, and it is not clear if current levels of egg production are sufficient to sustain the population. At the current minimum legal size, a large reduction in F below the current estimated value is required to increase EPR values substantially. Increasing minimum legal size at the current level of F would result in modest increases in EPR. The goals of maximising yield- and egg-per-recruit do not conflict, provided fishing mortality is not reduced below about 0.4.

Keywords New Zealand; rock lobster; *Jasus edwardsii*; egg-per-recruit; yield-per-recruit; fishery management

INTRODUCTION

Estimates of yield and egg production are important for the management of an exploited fish population. In theory, total yield from the population can be maximised through the proper combination of controls on size at first capture and exploitation rate. However, there are 2 quite separate and distinct aspects to maximising the yield from a population: maximising yield-per-recruit (YPR) and maximising recruitment. Because the relationship between spawning stock size and subsequent recruitment (the stock–recruitment (S–R) relationship) is unknown for many fish stocks, the most common approach is to assume constant recruitment and estimate the effects of size at first capture and exploitation rate on yield using analytical YPR models. Use of these YPR models ignores the fact that a relationship between stock and recruitment may exist, and that recruitment is likely to decline and ultimately fail if stock size is reduced to low levels.

A partial solution to this problem is to estimate the effects of size at first capture and exploitation rate on egg production using analytical egg-per-recruit (EPR) models. However, EPR models suffer the same limitation as YPR models, i.e., the relationship between egg production and recruitment is usually not known (e.g., Sluczanowski 1984). Therefore, the usual approach has been to estimate EPR as a percentage of the EPR of an unfished stock, and then qualitatively judge if current egg production is sufficient to sustain the population.

Estimates of maximum equilibrium yield for the New Zealand red rock lobster, *Jasus edwardsii*, population from the North and South Islands combined have been made using stock production models (Saila et al. 1979; Annala & Esterman 1986; Fogarty & Murawski 1986). YPR models for females and males from the Gisborne area have also been developed (Saila et al. 1979). However, estimates of EPR and population egg production for *J. edwardsii* have not been made, nor has the relationship between egg production (spawning stock size) and subsequent recruitment been determined.

Until recently, the minimum legal size (MLS) regulations for *J. edwardsii* provided for a minimum tail length (TL) of 152 mm, except for Otago where the MLS is 127 mm*. A TL of 152 mm corresponds to an average carapace length (CL) of about 93 mm for females and 100 mm for males. A TL of 127 mm corresponds to an average CL of about 79 mm for females and 82 mm for males (Breen et al. 1988). All measurements in this paper are given as CL in mm, which is a more precise measure of size than TL.

Past and recent estimates of the instantaneous fishing mortality rate (F) around New Zealand are high, greater than 1.0 in many cases (Annala 1977, 1979, 1980, unpubl. data; Saila et al. 1979). Size at onset of maturity (SOM) of females, defined as the size at which 50% of the females are mature, varies considerably from less than 60–64 mm CL near Gisborne to 121 mm CL near Stewart Island (Annala et al. 1980). Thus, the SOM ranges from well below to well above the MLS. Based on this maturity schedule, and assuming that the abundance of females is proportional to the 1985 landings (Sanders 1986), at least 70% of all females on the North and South Islands breed at least once before being harvested at the current MLS and exploitation rates.

The effects of the current MLS (given the wide range in SOM) and high exploitation rate on yield and egg production are unknown. The purpose of this study is to estimate the YPR and EPR of *J. edwardsii* at the current levels of MLS and F from 10 areas around New Zealand (Fig. 1). The effects of different combinations of MLS and F on YPR and EPR, and the values of these 2 parameters that maximise YPR and optimise EPR are also investigated. Implications of the model results for management of the fishery are then discussed.

METHODS AND MATERIALS

The model

Our model is derived from the generalised crustacean YPR and EPR model of Caddy (1977, 1979), which has assumptions similar to the YPR models of Beverton & Holt (1957) and Ricker (1975). Caddy's

approach is to analyse the catch and egg production from a series of moult groups, rather than from a series of age classes as in the traditional methods. The model incorporates size-specific inputs for moult increments and moult frequency, size at first and full capture, proportions mature, and individual fecundity. Caddy's model has been modified for use with American lobsters (Campbell & Robinson 1983; Campbell 1985, 1986). We also modified Caddy's model to take into account aspects of the biology of *J. edwardsii* not adequately described by the original model or the modified versions. These modifications are described below.

An empirical growth function describes length of a given moult group as a function of length in the previous moult group. In spiny lobsters moult increment decreases and intermoult period increases with increasing size (Aiken 1980). Growth is represented by:

$$CL_{m+1} = a + b CL_m \quad (1)$$

where CL is carapace length, m indexes moult group and a and b are regression constants. The relation between length and weight is described by:

$$W_m = a (CL_m)^b \quad (2)$$

where W is weight. The relation between fecundity and length is described by:

$$f_m = a (CL_m)^b \quad (3)$$

where f is the number of eggs produced by a mature female in moult group m.

For males larger than the MLS, survival is described simply by:

$$\exp[-(F + M) t_{i_m}] = \exp(-Z t_{i_m}) \quad (4)$$

where F, M, and Z are the instantaneous coefficients of fishing mortality, natural mortality, and total mortality, respectively, and t_{i_m} is the length of the intermoult period. For females, survival is complicated by the legal protection of egg-bearing individuals ("berried" females). For the egg-bearing period, t_e , females are subject only to natural mortality; for the rest of the year fishing mortality occurs.

*On 1 June 1988 the minimum legal size (MLS) for *Jasus edwardsii* was changed from a tail length measure for areas other than the Otago Controlled Fishery Area. The new MLS is based on the width of the second abdominal segment measured across the pleural spines. The new MLS is 54 mm for males and 58 mm for females, which are the New Zealand equivalents to 152 mm tail length (Breen et al. 1988). In the Otago Controlled Fishery Area, the tail length measure remains in effect.

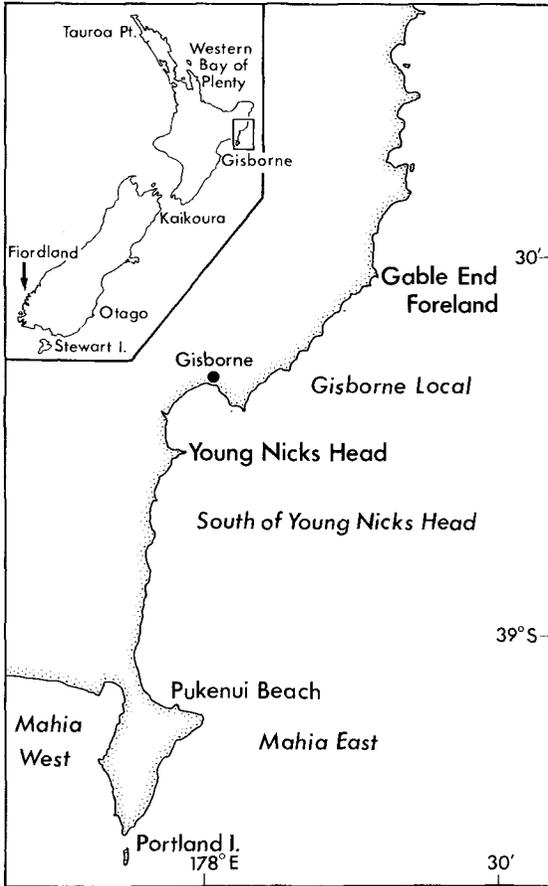


Fig. 1 Locations of sample areas around New Zealand.

Survival of mature females is thus:

$$\exp[-(F+M)(t_{i_m} - t_e) - M t_e] = \frac{\exp(-F t_{i_m} + F t_e - M t_{i_m})}{\exp(-F t_{i_m} + F t_e - M t_{i_m})} \quad (5)$$

If the real proportion of mature females in moult group m is Pr_m , then overall survival of females is:

$$(1 - Pr_m) \exp(-Z t_{i_m}) + Pr_m \exp(-F t_{i_m} + F t_e - M t_{i_m}) \quad (6)$$

Catch in numbers for males in moult group m is:

$$CN_m = [F / (F + M)] N_m [1 - \exp(-Z t_{i_m})] \quad (7)$$

If it is assumed that mean weight remains constant for a moult group, then catch in weight is:

$$C_m = [F / (F + M)] N_m W_m [1 - \exp(-Z t_{i_m})] \quad (8)$$

Similarly for immature females, catch in weight is:

$$C_m = [F / (F + M)] N_m W_m [1 - Pr_m] [1 - \exp(-Z t_{i_m})] \quad (9)$$

For mature females, egg bearing is considered to occur immediately after moulting, and fishing is considered to take place after the egg-bearing period (biologically realistic assumptions). The weight of catch of mature females is:

$$C_m = \frac{[F / (F + M)] N_m W_m Pr_m \exp(-M t_e) (1 - \exp[-Z(t_{i_m} - t_e)])}{(10)}$$

Finally, total catch and total egg production are obtained by assuming a population in stable equilibrium with the mortality rates specified, and summing over all moult groups:

$$C_{tot} = \sum_{m=1}^{\max} C_m \quad (11)$$

$$Egg_{tot} = \sum_{m=1}^{\max} N_m Pr_m f_m \quad (12)$$

The approach of Caddy (1977, 1979) was to develop a model with input parameters easily measurable in the field. In his model, the proportion of mature females, Pr_m , was estimated from field observations of maturity-at-length. However, this approach is not correct except in calculations where F in the model is the same as F in the field population. Because of differential mortality on immature females caused by protection of berried females, the observed proportion of mature females at various carapace lengths will vary with F , generally increasing as F increases.

Our approach is to use the apparent proportion of mature females, APr_m , from field observations of maturity-at-length made in a population for which an estimate of F is available. We estimate the probability PM_m that an immature female in moult group m will be mature in group $m + 1$; i.e.,

$$NI_{m+1} = (1 - PM_m) NI_m \exp(-Z t_{i_m}) \quad (13)$$

where NI_m is the number of immature females in moult group m .

The apparent proportion of mature females in moult group m , APr_m , is determined by plotting observed proportions of maturity at various carapace lengths on probability paper, fitting a curve, and then reading APr_m for each length m . The probability of maturation PM_m is then estimated with a simple simulation. If no maturation had occurred between moult classes m and $m + 1$, then the number of immature females would be simply:

$$NI_{m+1} = NI_m \exp[-(\hat{F} + M) t_{i_m}] \quad (14)$$

where \hat{F} is the estimated fishing mortality rate in the population where maturity was observed. The actual

number of immature females, based on observation, would be:

$$NI_{m+1} = (1 - APr_{m+1}) N_{m+1} \quad (15)$$

where N_{m+1} is the total female abundance calculated from the survival rate (Equation 6) of females in the previous year class. PM_m is estimated by comparing these 2 quantities:

$$PM_m = 1 - \frac{(1 - APr_{m+1}) N_{m+1}}{NI_m \exp[-(\hat{F} + M) t_{im}]} \quad (16)$$

In the EPR model, PM_m is used to calculate the abundance of immature females in each moult group (Equation 13). The proportion mature Pr_m for use in Equations 6, 9, and 10 is calculated directly from the number of immature females and the total number of females:

$$Pr_m = 1 - (NI_m / N_m) \quad (17)$$

The egg-bearing period varies around New Zealand from 3 to 6 months each year (Annala 1983). The catchability of females is very low (effectively zero) during the moulting period, with mating and egg extrusion occurring from a few hours to 5 weeks after the moult (McKoy 1979). As a result, few mature females without external eggs are caught between about March and October, so the external egg-bearing period was assumed to be 6 months (0.5 year) for all areas.

Individual variability in growth rates was not modelled, and an average growth rate for each moult group was used. Natural mortality was assumed constant for all moult groups. The total number of eggs produced was estimated before fishing mortality was applied.

Yield was estimated by summing the catch for each moult group (Equations 8, 9, and 10) starting with 1000 "recruits" reaching an arbitrary size (55 mm CL for females; 80 mm CL for males). Egg production was estimated by summing the number of eggs produced by females in each moult group starting with 1000 female "recruits" in the smallest moult group (55 mm CL). The model was run with various combinations of MLS, F, and M to assess the effects of changes in MLS and mortality rates on yield and egg production. MLS varied from 79 to 119 for females and from 82 to 122 for males. The lower values correspond to the present MLS in Otago. The largest number of moult groups used was 32 for females and 25 for males. The average size of the largest moult group generally corresponded well with the largest sizes observed in the fishery. F was varied from 0.0 to 2.0. For most runs $M = 0.1$; to examine sensitivity M was varied to 0.05 and 0.20 in some runs.

Input data

The data used as input for the model are shown only for 1 area (Fiordland) in Table 1. The data used for all areas are available from the authors (Annala & Breen 1988).

Estimates of growth rate were separated into the 2 components, moult increment and moult frequency. These components were usually estimated from recapture data from tagged rock lobsters and came from a number of published and unpublished sources (Street 1969, 1980; McKoy & Esterman 1981; McKoy 1985; Annala & Bycroft 1988; Annala unpubl. data; Booth unpubl. data).

Table 1 Growth rate, maturity, and fecundity data for *Jasus edwardsii* from Fiordland. CL, carapace length in mm.

	Females		Males	
Postmoult CL = a + b (Premoult CL)				
a	6.11		8.94	
b	0.966		0.981	
r ²	0.962		0.946	
n	406		249	
CL range	79.1–130.9		78.6–150.8	
Intermoult period (t _{im}) in years				
	CL	t _{im}	CL	t _{im}
	72.5	0.67	82.5	0.58
	77.5	0.73	92.5	0.61
	82.5	0.83	102.5	0.65
	87.5	0.93	112.5	0.69
	92.5	0.96	122.5	0.74
	97.5	1.0	132.5	0.81
	180.0	1.0	142.5	0.90
			152.5	1.0
			220.0	1.0
Proportion mature (Pr _m) at midpoint of 5 mm CL size class				
	CL	Pr _m		
	72.5	0.0		
	77.5	0.27		
	82.5	0.49		
	87.5	0.67		
	92.5	0.81		
	97.5	0.84		
	102.5	0.93		
	107.5	0.98		
	112.5	0.97		
	117.5	1.0		
Fecundity = a CL ^b				
a		0.0567		
b		3.18		
r ²		0.592		
n		19		
CL range		90–118		

An arithmetic relationship such as Equation 1 generally provided a better fit to growth increment data than either a power or exponential relationship, so the former was used for all areas. The intermoult period (t_{im}) of each CL class was estimated from data on annual moult frequency and equalled the reciprocal of the moult frequency. The functional form of the relationship between intermoult period and CL was not calculated, and the empirical data were used as direct inputs to the model. The model uses linear interpolation to estimate intermoult period for each moult group m .

The relationship between weight and CL calculated for males and females from Stewart Island (Annala & Bycroft 1985) were used for the model runs for Otago, Stewart Island, and Fiordland. The relationships calculated for the Gisborne area (Saila et al. 1979) were used for the remaining areas.

The proportions of sexually mature females in each CL class, based on the presence or absence of ovigerous setae or eggs, were estimated from the raw data analysed in Annala et al. (1980). In some cases the estimates were made by combining data from a number of areas or using data from adjacent areas. The relationships between fecundity and CL were taken from Annala & Bycroft (1987).

Natural mortality has not been measured directly. Instead, a value of 0.10 has been considered the best estimate of M . The model was run with $M = 0.05, 0.10, \text{ and } 0.20$ to bracket the expected true value of M .

Fishing mortality rates have been estimated for Otago (Annala 1977) and the Gisborne area (Annala 1979, 1980; Saila et al. 1979), and in many cases were 1.0 or greater. These estimates were based on studies done in Otago in the 1960s and in Gisborne in the mid 1970s. Nominal fishing effort (total number of pots and days fished) has increased considerably since (Ministry of Agriculture and Fisheries (MAF) unpubl. data), and F has undoubtedly increased also. Therefore, a value of $F = 1.0$ for both sexes is considered the best minimum estimate of the current level of F . This estimate is consistent with data from the late 1970s and early 1980s from Gisborne, Kaikoura, Stewart Island, and Fiordland (Annala unpubl. data).

Sensitivity of the model was examined briefly by varying parameters one at a time. The input data for Western Bay of Plenty females were used. Values of YPR and EPR at $F = 1.0$ and $MLS = 93$ mm CL were used for comparison with the test results. Because variation of some parameters caused greater change in the absolute value of YPR than in shape of

the isopleths, change in YPR relative to the maximum value observed in any set of runs was examined.

The parameters varied were a and b in Equations 1, 2, and 3, estimated lengths of the intermoult period when less than 1.0, apparent proportion mature when less than 1.0, and the estimated fishing mortality rate \hat{F} of the population in which maturity was observed (Equation 16).

RESULTS

Yield-per-recruit

The YPR isopleths at 3 values of M (0.05, 0.10, and 0.20) for females and males from Fiordland are shown in Fig. 2. Fiordland was chosen for illustration because the growth of both sexes is well described from this area (Annala & Bycroft 1988), and the model results appeared representative of those from other areas. For both sexes, the YPR at a given value of the MLS and F decreased as M increased. For females, there were small domes in the isopleths at low values of F (0.20–0.40) for $M = 0.05$, but the curves for $M = 0.10$ and 0.20 were relatively flat with no pronounced maxima. For males, there were pronounced domes in the isopleths at low values of F (0.10–0.20) for $M = 0.05$ and 0.10 , but the curves for $M = 0.20$ were relatively flat with no pronounced maxima.

The value of F that maximised YPR at the current MLS , and the MLS that maximised YPR at the current estimated minimum value of $F = 1.0$, for females and males from around New Zealand, are shown in Table 2 for the assumed value of $M = 0.10$. For females, maximum YPR occurred at high levels of F (about 1.0 or greater) for all areas except Otago, where the maximum occurred at $F = 0.40$ – 0.60 . The YPR isopleths for all areas were relatively flat, and the maximum YPR was only 0–4% greater than existing levels. At $F = 1.0$, the relationship between YPR and MLS was relatively flat, and the MLS that maximised YPR varied between 79 and 101 mm CL. For all areas except Otago, changing the MLS to the value that maximised YPR resulted in a YPR only 0–4% greater than existing levels. For Otago, the MLS that maximised YPR (93–95 mm CL) was approximately equal to the MLS for the rest of New Zealand, and resulted in a YPR 15% greater than the existing level.

For males, maximum YPR occurred at relatively low levels of F (0.15–0.80). For Western Bay of Plenty, Gisborne Local, South of Young Nicks Head, Kaikoura, and Stewart Island, the curves were

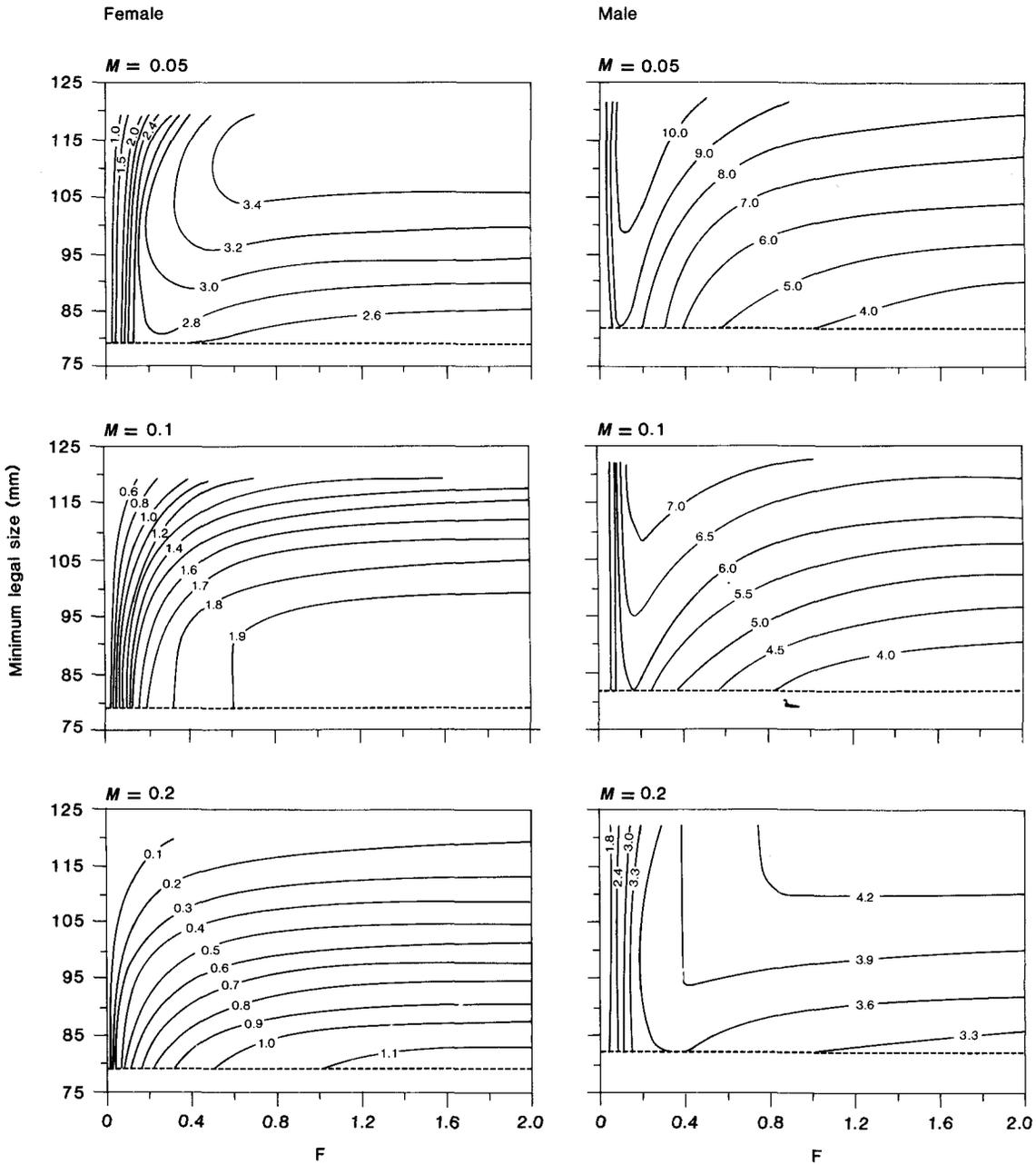


Fig. 2 Yield-per-recruit ($g \times 10^{-2}$) isopleths at 3 different values of the instantaneous natural mortality rate (M) for male and female *Jasus edwardsii* from Fiordland.

relatively flat, and maximum YPR values were only 1–9% greater than existing levels. For the other 5 areas, the domes were more pronounced, and maximum YPR values were 12–41% greater than

existing levels. At $F = 1.0$, the MLS that maximised YPR was larger than the existing MLS, and was larger than 122 mm CL (the maximum size used in the model) for most areas. YPR at the MLS that

maximised YPR was 4% to at least 35% greater than existing levels. For Otago, YPR at a MLS of 100 mm CL (equivalent to the rest of New Zealand) was 20% greater than the existing level.

The effects of varying M, F, and the MLS on the model results for all areas are presented and discussed in more detail in Annala & Breen (1988).

Egg-per-recruit

The isopleths of EPR as a percentage of the EPR of an unfished stock at 3 values of M (0.05, 0.10, and 0.20) for Fiordland are shown in Fig. 3. The results from Fiordland again appeared representative of those from other areas. At the current MLS of 93 mm CL, a large reduction in F below the current estimated minimum value of 1.0 to less than about 0.4 would be required to increase EPR substantially. At F = 1.0, EPR increased only gradually as the MLS increased, and a relatively large increase in the MLS would be required to increase EPR significantly.

The EPR of an unfished stock with M = 0.10 varied considerably (up to 24 ×) between areas (Table 3). The EPR as a percentage of the EPR of an unfished stock at F = 1.0 at the current MLS also

varied considerably between areas, ranging from a low of 1.2% in Otago to a high of 36.8% at Kaikoura. The exploited EPR values for Otago and Stewart Island were very small (0.001×10^9 and 0.006×10^9 eggs-per-recruit, respectively) and were only 0.4% and 2.1% of the largest exploited EPR value (0.285×10^9 eggs for Kaikoura). To allow comparisons to be made between areas, these calculations were based on a recruit size of 55.0 mm CL, which is the lower boundary of the smallest size class in which egg-bearing females have been observed for any area (Annala et al. 1980).

A weighted estimate of the EPR as a percentage of the unfished EPR for all areas on the North and South Islands combined at the current MLS with F = 1.0 and M = 0.10 was also calculated. The estimates of EPR at F = 1.0 and M = 0.10 for Northland, Bay of Plenty, Gisborne, Canterbury-Marlborough, Otago, Stewart Island, and Fiordland were taken directly from Table 3. The EPR for Wellington-Hawkes Bay was conservatively estimated as 30%, based on the SOM for this area (Annala et al. 1980). Taranaki and Westland were not included in the analysis because of the small size of the fisheries

Table 2 Yield-per-recruit (YPR) in g at the current minimum legal size (MLS) at F = 1.0, the value of F that maximises YPR (F_{max}), the YPR at F_{max} , the percentage increase in YPR at F_{max} over YPR at F = 1.0, the MLS that maximises YPR at F = 1.0 (MLS_{max}), the YPR at MLS_{max} at F = 1.0, and the percentage increase in YPR at MLS_{max} over the YPR at the current MLS at F = 1.0. F, instantaneous fishing mortality rate; instantaneous natural mortality rate = 0.1.

Area	YPR at current MLS with F = 1.0	F_{max} at current MLS	YPR at F_{max} (% increase)	MLS_{max} with F = 1.0	YPR at MLS_{max} with F = 1.0 (% increase)
Females					
Tauroa Point	295	1.0–2.0	295 (0%)	97–101	300 (2%)
Western Bay of Plenty	250	1.4–2.0	255 (2%)	95	255 (2%)
Mahia East	140	1.0–2.0	140 (0%)	79–93	140 (0%)
Mahia West	110	1.0–2.0	110 (0%)	79–93	110 (0%)
Kaikoura	135	1.0–2.0	135 (0%)	79–87	140 (4%)
Otago	240	0.4–0.6	250 (4%)	93–95	275 (15%)
Stewart Island	240	0.6–2.0	240 (0%)	97	245 (2%)
Fiordland	195	1.0–2.0	195 (0%)	85–93	195 (0%)
Males					
Tauroa Point	480	0.2	550 (15%)	>122	>610 (>27%)
Western Bay of Plenty	385	0.6–0.8	390 (1%)	108–114	400 (4%)
Gisborne Local	365	0.6–0.8	370 (1%)	106–114	380 (4%)
South of Young Nicks Head	415	0.4	440 (6%)	>122	>495 (>19%)
Mahia East	480	0.15	675 (41%)	>122	>650 (>35%)
Mahia West	450	0.15–0.2	570 (27%)	>122	>585 (>30%)
Kaikoura	390	0.2	425 (9%)	>122	>470 (>20%)
Otago	330	0.2	370 (12%)	112–122	420 (27%)
Stewart Island	405	0.4	430 (6%)	>122	>475 (>17%)
Fiordland	525	0.2	670 (28%)	>122	>700 (>33%)

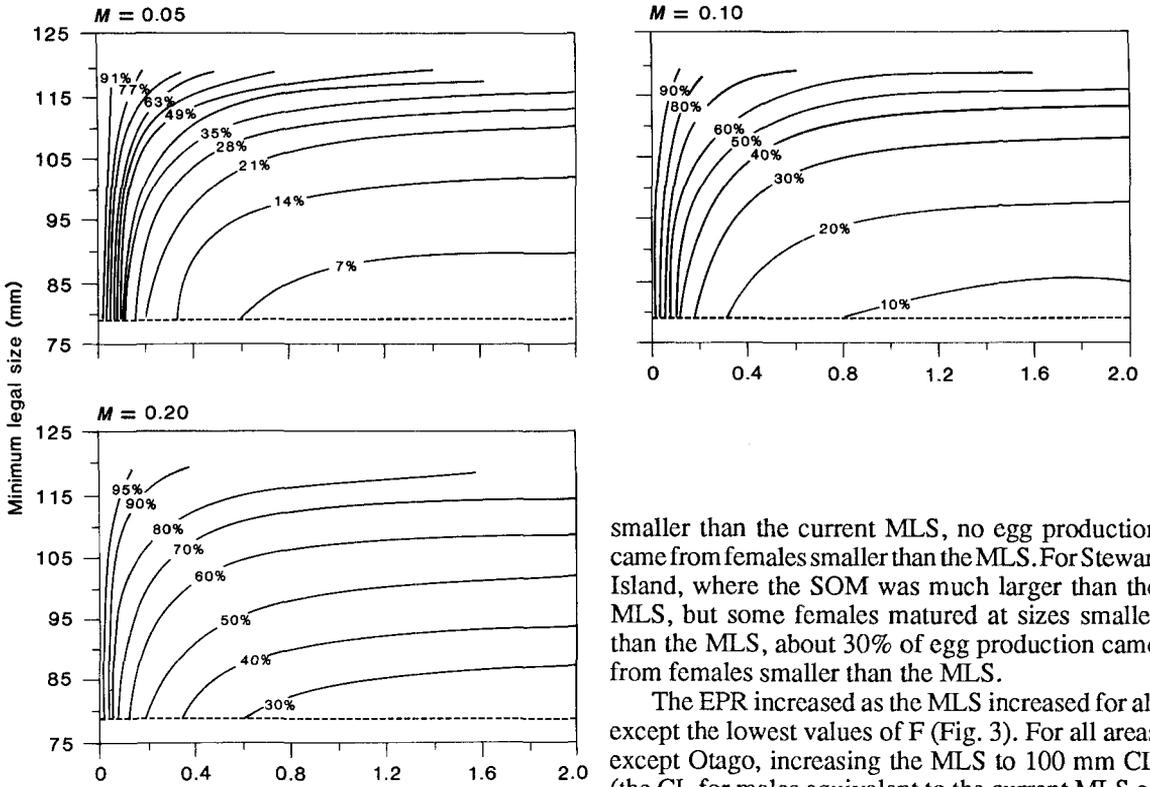


Fig. 3 Egg-per-recruit (as a percentage of the egg-per-recruit of an unfished stock) isopleths at 3 different values of the instantaneous natural mortality rate (M) for *Jasus edwardsii* from Fiordland.

(only 1.8% of the 1985 landings). The EPR estimates for the individual areas were multiplied by a weighting factor to estimate the weighted EPR. The weighting factor was the 1985 area landings divided by 1985 total landings (Sanders 1986) to give an estimate of abundance, times the EPR of an unfished stock from the area (Table 3). The weighted EPR equalled 27%.

At the current MLS with $F = 1.0$ and $M = 0.10$, at least 73% of the total population egg production for Western Bay of Plenty, Mahia East, Mahia West, Kaikoura, and Fiordland, where the SOM was much smaller than the MLS, was from females smaller than the MLS (Table 3). For Tauroa Point, where the SOM was approximately equal to the MLS, 52% of egg production came from females smaller than the MLS. For Otago, where the SOM was much larger than the MLS, and no females matured at sizes

smaller than the current MLS, no egg production came from females smaller than the MLS. For Stewart Island, where the SOM was much larger than the MLS, but some females matured at sizes smaller than the MLS, about 30% of egg production came from females smaller than the MLS.

The EPR increased as the MLS increased for all except the lowest values of F (Fig. 3). For all areas except Otago, increasing the MLS to 100 mm CL (the CL for males equivalent to the current MLS of 152 mm tail length) resulted in an increase in EPR of 24–45% (Table 3). For Otago, increasing the MLS to 100 mm CL resulted in an increase of nearly 9-fold. The weighted EPR for all areas on the North and South Islands combined at a MLS of 100 mm CL with $F = 1.0$ and $M = 0.10$ equalled 36%.

Sensitivity

Results of sensitivity tests for data for Western Bay of Plenty females are shown in Table 4. All parameters were changed by 10% for the test except b in Equation 1, where a 5% change was considered the maximum possible error, and b in Equation 2, where a change of -1% resulted in a 12% decrease in final size.

Yields were sensitive to none of the parameters tested. Egg-per-recruit was very sensitive to changes in parameters describing growth-per-moult (Equation 2) and to the observed proportion mature at various lengths. Much of the sensitivity to growth parameters stems from the nature of the equation. Small changes in either a or b in Equation 2 caused successively larger changes in each length-at-moult. This in turn resulted in a greatly altered length of time for breeding before exposure to the fishery in the model.

DISCUSSION

For females, the relationship between YPR and F at $M = 0.10$ was relatively flat, indicating that YPR cannot be increased by regulating F. The relationship between YPR and MLS at $M = 0.10$ was also relatively flat, suggesting that, with the exception of Otago, YPR cannot be increased by changing the MLS. With the exception of Otago, there was a positive relationship between YPR and SOM at a given value of MLS and F, i.e., a greater YPR was produced in areas with a larger SOM, as a result of the faster growth rate of females to the MLS from areas with a large SOM (data in Annala & Breen 1988: table 1).

For males, maxima occurred in the relationship between YPR and F at $M = 0.10$ at relatively low values of F for all areas, suggesting that YPR can be increased by reducing F from the current high levels. With the exception of Otago, there was a positive relationship between maximum YPR and growth rate, with maximum YPR greater for areas with faster growth rates (data in Annala & Breen 1988: table 1).

Annala (in press) investigated the effects of fecundity, SOM, and growth rate on the EPR of *J. edwardsii* from the same 8 areas used in this paper. Those results suggested that EPR was positively related to fecundity and negatively to SOM. There was no significant relationship between EPR and growth rate.

At the current MLS with $M = 0.10$, a large reduction in F to less than 0.4–0.6 was required to produce a substantial increase in EPR for most areas (Annala & Breen 1988). At the current MLS with $M = 0.10$, the YPR curves for females were relatively flat down to $F \approx 0.4$, and reducing F to this level did not result in a decrease in YPR. However, YPR

declined substantially for F values less than 0.4. At $F = 1.0$ with $M = 0.10$, an increase in the MLS resulted in an increase in EPR. At $F = 1.0$ with $M = 0.10$, the YPR curves for females were relatively flat, and increasing the MLS did not result in a significant change in YPR. Thus, the goals of maximising EPR and YPR do not conflict, provided F is not reduced below about 0.4.

A major constraint in this type of analysis is that an increase in egg production does not necessarily result in an increase in recruitment at a later date. The effects of changes in egg production on subsequent recruitment vary, depending on the functional form of the S–R relationship. One point that all S–R relationships have in common is that they pass through the origin, i.e., when spawning stock size is zero, subsequent recruitment is zero. Therefore, recruitment is likely to decline and ultimately fail if stock size is reduced too far. However, the minimum stock size necessary to prevent a precipitous decline in recruitment and stock collapse remains unknown for most species.

Egg production estimates from EPR analysis can be used to estimate whether egg production is sufficient to permit a fished population to persist, even when data are lacking on the levels of stock and recruitment. Sissenwine & Shepherd (1987) have suggested that if the fishery has been relatively stable and there is no evidence of a decline in recruitment and subsequent landings, then EPR should be maintained at least at current levels. This can be achieved by regulating F and/or the MLS. Breen (1986) suggested, from examination of stock-recruit curves, that 50% egg production is nearly always adequate; but that few fishery managers would be comfortable with egg production rates less than 25%.

Table 3 Number of eggs-per-recruit (EPR) of an unfished stock, EPR at an instantaneous fishing mortality rate (F) = 1.0 at the current minimum legal size (MLS) (% of EPR of an unfished stock), EPR at $F = 1.0$ with $MLS = 100$ mm carapace length (CL), and percentage of total egg production by females smaller than the current MLS at $F = 1.0$. Instantaneous natural mortality rate (M) = 0.10. Recruit size = 55.0 mm CL.

Area	EPR of unfished stock	EPR at $F=1.0$ at current MLS (% of EPR of unfished stock)	% of egg production from females < current MLS at $F = 1.0$	EPR at $F=1.0$ with $MLS = 100$ mm CL as % of EPR of unfished stock
Tauroa Point	1.357×10^9	0.232×10^9 (17.1)	52	21.4
Western Bay of Plenty	1.155×10^9	0.247×10^9 (21.4)	73	27.2
Mahia East	0.910×10^9	0.265×10^9 (29.1)	86	42.0
Mahia West	0.758×10^9	0.262×10^9 (34.6)	90	46.7
Kaikoura	0.775×10^9	0.285×10^9 (36.8)	87	50.2
Otago	0.056×10^9	0.001×10^9 (1.2)	0	11.4
Stewart Island	0.329×10^9	0.006×10^9 (1.7)	30	2.6
Fiordland	0.580×10^9	0.108×10^9 (18.7)	73	24.5

Bannister & Addison (1986) have extended the "classical" YPR and EPR modelling approach for the European lobster (*Homarus gammarus*) by coupling S-R curves to known YPR and spawning stock biomass per recruit curves to generate total yield and biomass estimates. They used the method of Shepherd (1982) to generate a variety of S-R relationships (the functional form of the S-R relationship for *H. gammarus* is unknown), and then used simulation techniques to investigate the effects of various combinations of F and MLS on total yield and biomass. Because the functional form of the S-R relationship for *J. edwardsii* is unknown, an approach similar to that of Bannister & Addison (1986) could be used to estimate the effects of various S-R assumptions on biomass and yield for the New Zealand rock lobster fishery.

Management implications

The fishery for *J. edwardsii* on the North and South Islands combined has been relatively stable since the initial peak landings in the mid 1950s. Since 1956 landings have ranged from a low of 2987 t in 1975 to a high of 5295 t in 1966 (Sanders 1986). (The degree of under-estimation of landings increased during the mid 1970s because the incidence of under- or non-reporting of landings during this period was greater than during earlier or later years owing to problems with the fisheries statistics system.) Landings have increased steadily since the low in 1975, and in 1984 totalled 4950 t, the highest since 1968.

Table 4 Results of sensitivity tests on the yield-per-recruit (YPR) and egg-per-recruit (EPR) models. The changes shown are the percentage difference between a run with the real data and a run with the alteration shown. Values compared were results for Western Bay of Plenty females at an instantaneous fishing mortality rate (F) = 1.0 and a minimum legal size of 93 mm carapace length. For YPR, the ratios of YPR at F = 1.0 to the maximum YPR were compared.

Parameter	Magnitude of change	Effect on YPR	Effect on EPR
a (Equation 1)	+10%	0.00%	0.00%
b (Equation 1)	+5%	+0.29%	0.00%
a (Equation 2)	+10%	-1.59%	+25.76%
b (Equation 2)	-1%	+0.56%	+43.47%
a (Equation 3)	+10%	0.00%	0.00%
b (Equation 3)	+10%	0.00%	-5.85%
Intermoult period when less than 1.0	+10%	-0.39%	-5.01%
Proportion mature when less than 1.0	+10%	-0.03%	+44.30%
\hat{F} (Equation 15)	+10%	+0.03%	-11.62%

However, there has been considerable geographic variation in landing trends since 1979, which may reflect regional differences in the state of the rock lobster stock. Landings from the Otago and Southern fisheries (where EPR values are very low) have declined, while landings from the remaining North and South Island fisheries (with the exception of the small Taranaki and Westland fisheries) have increased (MAF unpubl. data). Puerulus settlement rates in Otago and Southland have been much lower than rates for some areas along the east coast of the North Island (pers. comm. J. Booth), which suggests lower recruitment in these former 2 areas. Moreover, nominal effort (total number of pot-lifts) has substantially increased, and catch per pot-lift substantially decreased, during recent years (especially 1984 and 1985) in most areas (MAF unpubl. data), which suggests that stock size may be declining. Thus, it is not clear from the available data whether the current levels of EPR are sufficient to sustain the rock lobster population.

The EPR curves for all areas at the current MLS were relatively flat for high levels of F, and an increase in F beyond 1.0 will not result in a substantial decline in EPR. However, recruitment can decline and stocks collapse precipitously at low spawning stock sizes caused by excessive fishing effort. Therefore, EPR should not be allowed to decrease below current levels, and where possible should be increased as long as YPR is not substantially reduced.

If egg production needs to be increased, then the options available are either to increase the MLS or decrease F. Substantial increases in EPR can only be brought about by large reductions in F (Fig. 3), to levels less than half the estimated current minimum level of 1.0. On the other hand, EPR can be modestly increased by increasing the MLS without reducing F.

Because of the large differences in egg production between areas, and because the origins of larvae settling in various areas around New Zealand are not known, it is important to identify the areas that are the primary sources of larvae. If certain areas are found to produce most of the larvae that successfully survive to the puerulus settlement stage, then it may be necessary to regulate the harvest in these specific areas if spawning stock size and recruitment are being reduced to critically low levels. This could be accomplished by increasing the MLS or by reducing F by using catch quotas and/or effort controls, prohibiting the taking of females, or banning fishing entirely.

Some mature females appear to have refuges in time and/or space in certain areas. A number of

large, mature females tagged in Fiordland have been recaptured and released for up to 6 consecutive years only while they were egg-bearing and not available to the fishery. These animals have not been recaptured outside the egg-bearing period (Annala unpubl. data). Similar refuges may also exist at Stewart Island (McKoy unpubl. data). Thus, there may be a "pool" of mature females that are unavailable to the fishery because of behavioural or other reasons. The extent of this refuge population and its impact on egg production is unknown.

A management issue often discussed in the past is that of raising the MLS in the Otago area. The model results suggest that increasing the MLS in Otago to the MLS for the rest of New Zealand would result in a substantial increase in YPR for both sexes (15% for females and 20% for males with $M = 0.10$). Moreover, increasing the MLS for females to 93 mm CL would result in an increase in EPR to 7% of that of an unfished stock. A complicating factor in Otago is the existence of at least occasional migrations of rock lobsters from Otago to the Southern area (Street 1971). The frequency of these migrations and their impact on recruitment to and subsequent yield from the fishery are unknown.

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