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ON THE SURVIVORSHIP AND HISTORICAL GROWTH OF THE SOUTH AFRICAN CAPE ROCK LOBSTER

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Natural survivorship parameters for male and female Cape rock lobsters *Jasus lalandii* are estimated using size-structure information from pristine sections of the population, such as animals in sanctuaries. It is assumed that these pristine subpopulations are at steady states, i.e. that annual juvenile settlement is constant, and that migration into and from these populations is negligible. The natural survivorship parameters are calculated in terms of parameters for somatic growth rate, which are obtained by fitting the Ford-Walford growth model to male and female tag data. The results indicate that female natural survivorship is consistently higher than that of males, and that the somatic growth rate of *J. lalandii* was considerably higher at the beginning of the century than during the past 25 years.

The commercial fishery for Cape rock lobster *Jasus lalandii* off the west coast of South Africa is the third most valuable in South Africa. However, catches declined from in excess of 10 000 tons in the 1950s and 1960s to less than 2 000 tons in the 1996/97 season. Recently, a size-based model has been used to assess the biomass of the resource and to calculate annual Total Allowable Catches (Bergh and Johnston 1992, Johnston and Butterworth 1995). Furthermore, a two-sex delay-difference model has been used to calculate current egg production as a precentage of pristine egg production (Cruywagen 1996). Key parameters in both these models are the natural survivorship of males and females.

Examination of the length frequency distribution of animals caught for tagging since 1969 does not reveal the existence of modes that could correspond to specific age-classes (Goosen and Cockcroft 1995, Cruywagen 1997). As the data are unsuitable for use of age-structured models, only methods relying on size structure can be used to determine natural survivorship.

A study that relied heavily on somatic growth rate was used to estimate natural survivorship of *Jasus lalandii* (Johnston and Bergh 1993). Since that study, considerably more information on somatic growth rate of the species has become available and has been analysed by Cruywagen (1997). In the present study, the adult natural male and female survivorship parameters are re-estimated using the new results on male and female somatic growth. Rather than deriving these from an involved size-structure model, as used by Johnston and Bergh (1993), a simpler method requiring fewer assumptions is used.

Other previous estimates of natural survivorship have been made. For data collected between 1969 and 1971 from Dassen Island and Cape Peninsula, Newman (1973) employed tag-recapture methods described by Ricker (1958) to estimate natural survivorship of adult males to be between 0.65 and 0.92. Using Beverton and Holt's (1956) equation, Pollock (1978) estimated natural survivorship for male rock lobster at Robben Island to be 0.64.

BIOLOGICAL BACKGROUND

A Cape rock lobster year is defined here as the period from 1 November until 31 October of the following year. Fishing traditionally takes place between November and March, the bulk of the catch being taken during the first two months of this period. Moulting is annual, males moulting between September and November and females between April and June. Mating takes place soon after females moult. Most mature females are in berry from July until October. Hatching peaks during October and November. The puerulus larvae settle about 14–18 months later, between December and April. *J. lalandii* is considered to be a non-migratory species (Pollock 1986).

On average, after settlement, it takes another five years for 50% of the females to reach sexual maturity (Pollock 1973, 1986), whereas it takes four years after settlement for males to reach 50% sexual maturity (Pollock 1973, 1986). Both males and females reach 50% maturity at 60–65 mm carapace length (Pollock 1986). The resource has been fished since the beginning

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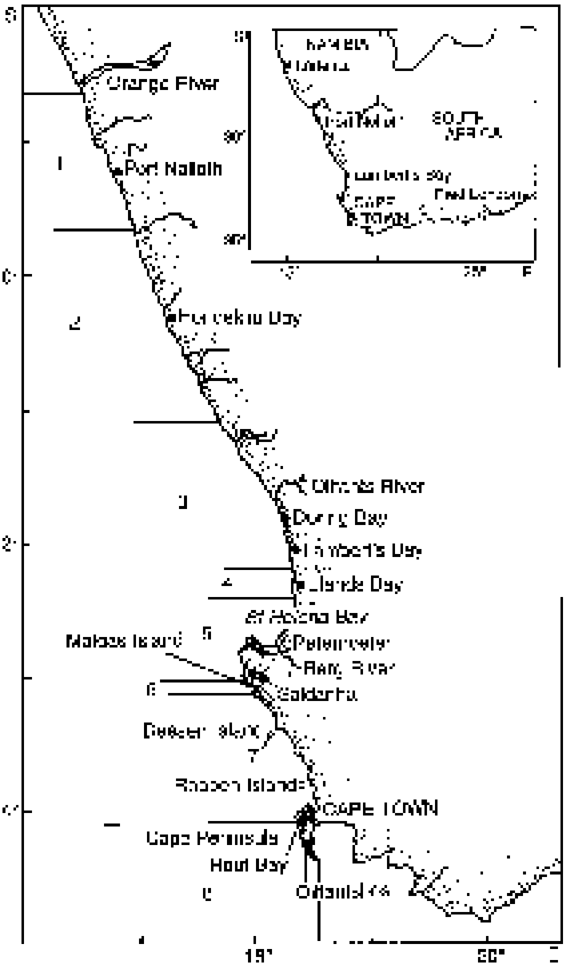

Fig. 1: The eight fishing grounds for Cape rock lobster off the west coast of South Africa referred to in the text

of this century, minimum allowable lengths over that period ranging between 98 and 75 mm.

Model equations

Beverton and Holt (1956) presented formulae for calculating instantaneous mortality when recruitment is throughout the year in a pristine or unfished population. Here, the calculation of instantaneous natural mortality when recruitment is at discrete intervals (in this example, once a year) is considered. The formula presented below is valid for a pristine or unfished population and is based on somatic growth rates and the specific population structure. The equations are derived in terms of natural survivorship (s), which is related to instantaneous natural mortality (M): $s = \exp(-M)$.

It is assumed that the growth model of Von Bertalanffy (1938) gives an adequate description of adult somatic growth, namely

$$L_t = L_\infty \left[1 - e^{-K(t-t_0)}\right] \quad , \qquad (1)$$

where L_t is the mean length of an individual of age t, L_∞ is the maximum or asymptotic body length, K is the Brody growth coefficient and defines the growth rate towards the asymptotic length, and t_0 shifts the growth curve along the age axis to allow for apparent non-zero body length at age zero. Note that, from this equation, the Ford-Walford model can easily be derived by eliminating t_0, namely

$$L_{t+1} = \alpha + \rho\, L_t \quad , \qquad (2)$$

where

$$\alpha = L_\infty\,(1 - e^{-K}), \quad \rho = e^{-K} \quad , \qquad (3)$$

Using the above relationships, the natural survivorship parameter for all animals of age a_{min} and older is expressed by

$$s = \frac{\bar{L} - L_{a_{min}}}{e^{-K}(\bar{L} - L_\infty) + L_\infty - L_{a_{min}}} \quad . \qquad (4)$$

Two alternative derivations for this natural survivorship formula are presented in the Appendix. Refer also to Hoenig (1987) and Hilborn and Walters (1992).

Ford-Walford growth parameters

As explained in the previous section, to calculate the natural survivorship for *J. lalandii*, the two parameters α and ρ appearing in the Ford-Walford growth model, or equivalently L_∞ and K in the Von Bertalanffy growth model, along with the average size of an individual ($\bar{L}$), in that part of the population that is under consideration ($L \geq L_{a_{min}}$), are required. How the Ford-Walford growth parameters were determined for the rock lobster population is discussed below.

As is evident from the long maturation period, *J. lalandii* is a slow-growing species. Also, modelling is complicated by the substantial effect of annual and spatial factors on somatic growth rates (Melville-Smith *et al.* 1995, Cruywagen 1997). The somatic growth rate of mature females is markedly lower than that of males, because mature females direct some energy into egg production.

MALES

Extensive tag-recapture studies for determining male somatic growth rates were undertaken during the 1968/69–1971/72 and the 1975/76–1994/95 seasons in various fishing areas, namely Port Nolloth (Area 1), Lambert's Bay and Doring Bay (Area 3), Elands Bay (Area 4), St Helena Bay (Area 5), Saldanha Bay (Area 6), Dassen Island (Area 7), Olifantsbos (Area 8) and Hout Bay (a sanctuary in Area 8) – Fig. 1. Information on these studies is summarized in Goosen and Cockcroft (1995). A total of 12 867 growth increments in carapace length of male lobsters (size range 60–150 mm) was measured. A generalized linear model, based on a Ford-Walford model and corrected for temporal and spatial changes in growth rate, was used to describe the data (Cruywagen 1997).

The generalized linear model which described best the tagging data is

$$\overbrace{L_{i,kj} + \Delta L_{i,kj} = \alpha + \rho L_{i,kj}}^{\text{Basic–Ford Walford model}}$$

$$+ \quad \overbrace{\sum_{v}\left[Y_v Q_{i,j,v}\right]}^{\text{Adjustment terms for years}}$$

$$+ \quad \overbrace{\sum_{w}\left[\mathrm{A_w X_{i,k,w}}\right]}^{\text{Adjustment terms for areas}} \quad + \overbrace{\varepsilon_{i,j,k}}^{\text{Error}} \qquad (5)$$

where the subscript i indicates a specific tagging return in year j and area k; j and v range over all the years, apart from 1994/95 for v; k and w range over all areas listed in Table I, apart from Hout Bay for w; $Q_{i,j,v} = 1$, if $j = v$, else $Q_{i,j,v} = 0$ and similarly $X_{i,k,w} = 1$, if $k = w$, else $X_{i,k,w} = 0$ (Cruywagen 1997). Therefore, $L_{i,j,k}$, refers to the length of animal i in year j and area k. Note that the error term captures all effects not explained by the regression model.

This describes somatic growth for the 1994/95 year in Hout Bay, with terms added to adjust the intercept parameter (α) to account for variations across years and areas. The magnitude of the adjustments to be made for annual and spatial effects to the intercept parameter are reflected by the respective year- and area-specific parameters Y and A. The parameters and the associated significance levels obtained from this fit are shown in Table I.

FEMALES

Compared to males, few female tag-recapture studies have been carried out. Data are only available for the 1969/70–1971/72 seasons (Newman and Pollock 1974). However, in 1992/93 and 1993/94 (Cockcroft and Goosen 1995) and in 1994/95 (Marine & Coastal Management [MCM], unpublished data) incremental growth studies were carried out by collecting females from the field, just before moulting and after they stopped feeding, and then keeping them in the laboratory until moulting.

Table I: Parameter values estimated by fitting the generalized linear model to tag-recapture growth data for *J. lalandii*. For the full model, refer to Equation 5. For both sets of parameters, the base case, i.e. the intercept value, refers to Hout Bay in 1994/95

Parameter	Estimate	*t*-value	Significance level	*SD*
Males				
Intercept (∝)	8.9609	34.59	0.0001	0.2590
Year (*y*)				
1968/69	1.8933	11.80	0.0001	0.1605
1969/70	2.4262	26.51	0.0001	0.0915
1970/71	2.5228	22.12	0.0001	0.1141
1971/72	2.9583	23.77	0.0001	0.1245
1975/76	2.2021	14.90	0.0001	0.1478
1976/77	1.5173	8.99	0.0001	0.1687
1977/78	1.2558	2.89	0.0038	0.4341
1978/79	2.3485	11.71	0.0001	0.2006
1979/80	3.0588	18.34	0.0001	0.1668
1980/81	1.5802	15.76	0.0001	0.1003
1981/82	2.1020	19.47	0.0001	0.1080
1982/83	1.8886	20.36	0.0001	0.0927
1983/84	2.4438	21.33	0.0001	0.1146
1984/85	3.1254	14.77	0.0001	0.2116
1985/86	1.3505	7.97	0.0001	0.1695
1986/87	0.2865	2.13	0.0331	0.1344
1987/88	1.5856	18.04	0.0001	0.0879
1988/89	1.1282	12.12	0.0001	0.0931
1989/90	0.5679	5.22	0.0001	0.1089
1990/91	−0.2815	−2.65	0.0081	0.1064
1991/92	−0.1788	−1.92	0.0556	0.0934
1992/93	−0.3740	−4.96	0.0001	0.0754
1993/94	−0.1251	−1.37	0.1717	0.0916
Area (*A*)				
1	−1.5342	−19.36	0.0001	0.0792
3	0.2518	2.37	0.0177	0.1061
4	0.3079	4.06	0.0001	0.0758
5	−1.3419	−14.28	0.0001	0.0940
6	0.2848	1.81	0.0707	0.1576
7	−0.3080	−4.07	0.0001	0.0758
8	−1.1037	−16.97	0.0001	0.0651
Size (*p*)	0.9224	319.30	0.0000	0.0029
Females				
Intercept (∝)	1.4522	4.48	0.0001	0.3240
Year (*y*)				
1969/72	1.1896	8.45	0.0001	0.1407
1992/93	−0.1148	−1.83	0.0679	0.0627
1993/94	−0.2228	−2.85	0.0046	0.0781
Area (*A*)				
Robben Island	−0.1631	−1.08	0.2825	0.1515
7	−0.5266	−3.39	0.0008	0.1554
8	−0.2555	−3.77	0.0002	0.0677
Size (*p*)	0.9821	209.60	0.0000	0.0047

All these data on female growth were combined into a set of 382 records, ranging over size-classes from 55 to105 mm carapace length (*CL*) for four areas; Dassen Island (Area 7), Cape Point (Area 8),

Table II: Mean carepace lengths of male and female *J. lalandii* when populations may have approached a pristine state

Year	Mean male length (mm)	Mean female length (mm)
Cape Peninsula (>62.5 mm)		
1912/16	122.0	–
Robben Island: east side (>62.5 mm)		
1962/63	87.9	–
1963/64	86.8	–
1964/65	94.2	–
1965/66	97.6	–
1966/67	97.6	–
Robben Island: west side (>62.5 mm)		
1972/73	85.7	73.0
1976/77	94.2	77.0
1977/78	100.0	79.0
Malgas Island (>72.5 mm)		
1985/86	102.4	83.5
Hout Bay (>87.5 mm)		
1984/85	104.1	–

the sanctuaries at Hout Bay (Area 8) and Robben Island (Area 7). Newman and Pollock (1974) did not distinguish between the tagging returns for the years 1969/70–1971/72. For the purpose of determining the Ford-Walford growth parameters, the data from those years were combined into a 1969/72 period.

To obtain the female growth parameters, generalized linear modelling similar to that described above for males, was carried out on the tag-recapture data. Again, the Ford-Walford growth model for Hout Bay in the 1994/95 season was taken as base case. The parameters correcting for period and spatial effects are shown in Table I.

From the above, the male and female asymptotic lengths (L_∞), as well as the Brody growth coefficients (K) for each area and year, can be calculated using Equations 3 and 5. However, for calculating survivorship parameters, the average somatic growth rates over an extended period of time should be used rather than just a single year's growth figures.

To obtain Ford-Walford model parameters representative of male and female growth over a period of time, the averages of the annual adjustment factors over the years for which they were available were used in Equation 5, instead of the actual annual adjustment factors. However, for illustrating sensitivity to these average values, growth parameters were obtained for males and females using the highest and lowest annual adjustment factors. These were used as upper and lower bounds respectively. For males, the average annual adjustment factor is 1.4701, the highest being 3.1254 (1984/85) and the lowest –0.3740 (1992/93). For females, taking into account that the 1969/72 adjustment factor represents three years, the average annual adjustment factor is 0.5385, the highest being 1.1896 (1969/72) and the lowest –0.2228 (1993/94). The average adjustment factor is calculated as $(3 \times 1.1896 - 0.1148 - 0.2228)/6$, because altogether six seasons are considered, including 1994/95, which was used as the basis season for regression purposes.

Survivorship calculations

In order to avoid confounding natural and fishing mortality in calculating instantaneous natural mortality rates, and hence natural survivorship parameters, only data from unfished subpopulations can be used. Furthermore, the assumption that there is no migration into and from the subpopulations must hold. Apart from the Ford-Walford growth parameters, the average size of individuals in that section of the population for which natural survivorship is to be calculated, is required. Because of the form of the above equations, the natural survivorship parameter must be calculated only for that portion of the population that is larger than a specified minimum size, and not for a specific size-class or groups of size-classes only.

GILCHRIST 1912–1916

One way of obtaining information on pristine size structure of the Cape rock lobster population is to examine the size composition of catches taken during the early development of the fishery. Johnston and Bergh (1993) reported on size frequencies of males in experimental hoopnet catches (c. 1912–1916), as documented by Gilchrist (1913, 1914 and 1918). Because the rock lobster fishery only started in earnest at the turn of the century, the size composition of these catches should be a reasonable approximation of the pristine size structure, if gear selectivity is ignored.

The hauls were made in depths of 5–30 m at Robben Island and neighbouring locations, namely Woodstock Beach, Milnerton, Green Point and Clifton. Sizes are reported for 25-mm size-classes, with the smallest class having a midpoint of 25 mm and the largest a midpoint of 200 mm *CL*.

As 50% of males reach sexual maturity between 60 and 65 mm *CL*, and because the Ford-Walford growth parameters for males are only valid for animals >60 mm, the average length of the animals >60 mm had to be calculated. Gilchrist's (1913, 1914 and 1918) were reported for size-classes spanning 25 mm. Therefore, to ensure that only mature rock lobsters were included, size-classes with a midpoint of 75 mm or more were selected for the calculations. This implies that the resulting survivorship value is valid for animals >62.5 mm.

The average male carapace length for animals >62.5 mm was 122 mm (see Table II). Ford-Walford parameters are not available for Robben Island. Instead, averages of the growth parameters for Areas 7 and 8, between which Robben Island is located, were used. By substituting these parameters into Equation 4, a value for natural survivorship was calculated. Using the Ford-Walford parameters describing minimum recorded growth gave a biologically unrealistic survival parameter that was larger than unity. This was because the asymptotic length of rock lobster at Robben Island, as predicted by the Ford-Walford model, was smaller than the average male length obtained from Gilchrist's (1913, 1914 and 1918) data. Even for the average growth scenario, an unrealistically high value of $s = 0.996$ was obtained (Table III).

Assuming no change in asymptotic length over time, these unrealistic values imply that the somatic growth rate of male rock lobster at the beginning of the century was much higher than the average growth rate since 1968/69, on which the Ford-Walford parameters are based. Even though hoopnets tend to select the larger animals in the population (D. E. Pollock, MCM, pers. comm.), so biasing survivorship values, this does not provide a satisfactory explanation for the high values of natural survivorship obtained.

HOUT BAY 1984/85

In the 1984/85 season, the fishing industry was allowed to catch a small (20 ton) quota of rock lobster in the Hout Bay Sanctuary, which had been unfished for more than 50 years. It was declared a sanctuary in 1933.

Males were sampled by baited traps. Length frequencies for 5-mm size-classes are available from a midpoint of between 90 and 135 mm. From this, an average male length of 104 mm was calculated for animals >87.5 mm. The results of the natural survivorship calculations are shown in Table III. As is the case with hoopnets, the results are likely to be biased because of gear selectivity. The magnitude of the bias would depend on the soaking time of the traps (A. C. Cockcroft, MCM, pers. comm.).

MALGAS ISLAND 1985/86

Estimates of the average carapace length of mature rock lobsters in a pristine population can also be obtained from size structure information from other experiments carried out in sanctuary areas. For example, Barkai

Table III: Calculated survivorship parameters for three growth scenarios: the highest growth recorded, the lowest growth recorded and the average growth over the period 1968/1969 to 1994/95 for both male and female *J. lalandii*. Note that different low, average and high growth parameters are calculated for each area as described in the text, using Equation 5 and the parameter values in Tables I and II

Male survivorship				Female survivorship			
Year	Low growth	Average growth	High growth	Year	Low growth	Average growth	High growth
Robben Island (>62.5 mm)							
1912/16	n/a	0.996	0.969				
Robben Island: east side (>62.5 mm)							
1962/63	0.960	0.897	0.848				
1963/64	0.955	0.890	0.840				
1964/65	0.982	0.929	0.886				
1965/66	0.991	0.942	0.902				
1966/67	0.991	0.942	0.902				
Robben Island: west side (>62.5 mm)							
1972/73	0.951	0.883	0.830	1972/73	n/a	0.953	0.900
1976/77	0.982	0.929	0.886	1976/77	n/a	0.970	0.930
1977/78	0.997	0.950	0.912	1977/78	n/a	0.976	0.940
Malgas Island (>72.5 mm)							
1985/86	0.970	0.915	0.871	1985/86	n/a	0.957	0.906
Hout Bay (87.5 mm)							
1984/85	0.970	0.876	0.805				

Table IV: Male survivorship parameters recalculated so as to be comparable with the female survivorship parameters in Table III, by using average, minimum and maximum Ford-Walford parameter values calculated from data collected over the same period as those for females. Note that different low, average and high growth parameters are calculated for each area as described in the text, using Equation 5 and the parameter values in Tables I and II

Year	Male growth parameters comparable to females		
	Low growth	Average growth	High growth
Robben Island: west side (>62.5 mm)			
1972/73	0.950	0.892	0.836
1976/77	0.884	0.806	0.735
1977/78	1.000	0.957	0.916
Malgas Island (>72.5 mm)			
1985/86	0.821	0.735	0.658

and Branch (1988) reported on size frequencies obtained off Malgas Island (Area 6). As Malgas Island has been a sanctuary since 1933, it is reasonable to assume that the population there is close to its pristine state.

Samples were collected by hoopnets in 1986 and recorded in 5-mm size-classes. The average length of males >72.5 mm was 102.4 mm, whereas for females >72.5 mm it was 83.5 mm. Because hoopnets tend to select larger animals, these averages are likely to be overestimate. The results of natural survivorship calculations are shown in Table III. For males, the growth parameters for Saldanha Bay (Area 6) were used. There are no growth parameters for females for Area 6, so those for Hout Bay were used. For areas in which female tagging data are available, the Hout Bay and Saldanha Bay growth rates for males were the most similar (Table I).

ROBBEN ISLAND 1963–1967, 1973 and 1977–1978

To remove any bias ascribed to gear selectivity, it is preferable to use information on size structure obtained from diving surveys. Such data are available for the Robben Island Sanctuary (Fig. 1). However, they were collected shortly after Robben Island's proclamation as a sanctuary in 1963.

Newman (1973) reported frequencies in 5-mm size-classes of divers' samples collected between 1963 and 1967 on the east side of the island. The average lengths obtained for males >62.5 mm are shown in Table II. Pollock (1978) documented size frequencies of divers' samples collected off the west side of Robben Island (c. 1973) for males and females. Pollock and Beyers (1979) reported on diving experiments off the west side of Robben Island in 1976/77 and 1977/78. Average lengths of mature males and females obtained from those surveys are also listed in Table II. The calculated survivorship parameters are presented in Table III. Although these size structure data are not biased by gear selectivity, the fact that Robben Island had been a sanctuary for such a short period before these surveys were carried out might bias the data and the results.

Comparing male and female survivorship

To compare natural survivorship parameters for males and females, the Ford-Walford growth parameters should be computed for comparable years. For females, tag-recapture growth data are available for six years, 1969/70–1971/72 and 1992/93–1994/95 (Table I). The average, minimum and maximum growth parameters obtained over this period were used in the above calculations. For the purpose of direct comparability, the average, minimum and maximum Ford-Walford intercept parameter values for males for the six years were calculated as 1.2049, –0.3740 and 2.9583 respectively.

Using these values, natural survivorship was recalculated for males at Robben Island for 1972/73 and 1976/77–1977/78 and at Malgas Island for 1985/86 (Table IV). Size-structure data are available for both sexes at Robben Island in 1972/73 and 1976/77–1977/78, and at Malgas Island in 1985/86. Comparing results presented in Table III and IV, it is evident that female natural survivorship is on average consistently higher than that of males, for those specific areas and years.

RESULTS AND DISCUSSION

The natural survivorship parameter for males, using average growth over all years for which data are available, but excluding data for 1912–1916 (Gilchrist 1913, 1914, 1918), ranges between 0.88 and 0.95 (Table III). These values agree with those obtained by Johnston and Bergh (1993). Assuming a somatic growth rate equal to the slowest growth attained since 1968/69, values of natural survivorship range from 0.95 to 1.00, which is, as expected, unrealistically high. On the other hand, assuming a somatic growth rate equal to the highest growth rate attained since 1968/69, natural survivorship ranges between 0.81 and 0.91.

Only when growth parameters, describing average or maximum growth are assumed, are biologically realistic survivorship parameters (<1) obtained for

Gilchrist's 1912–1916 data. However, the value of 0.996 for natural survivorship seems unrealistically high. This suggests that, historically, growth rates were considerably higher than those attained since 1968/69, when tagging studies commenced.

Using the lowest recorded female growth, a realistic survivorship parameter cannot be obtained. Assuming parameters that describe the average of all the recorded years, female natural survivorship ranges between 0.95 and 0.98, which still seems unrealistically high. This provides evidence for the hypothesis that female growth rates, as is the case for males (Cockcroft and Goosen 1995, Cruywagen 1997), are much lower currently than in the recent past.

Natural survivorship of males and females has been compared in areas where comparable size structure information is available, i.e. at Robben Island for 1972/73 and 1976/77–1977/78 and at Malgas Island for 1985/86. Female natural survivorship is consistently higher than that of males (Tables III and IV). There is no known biological reason why this should be the case, although females migrate inshore for a portion of the year when they are exposed to a different environment than males (Pollock 1986).

At Robben Island, commercial fishing took place some 10–15 years before the tagging studies were carried out. As males constitute about 80% of commercial catches (MCM, unpublished data), the impact of catches on the average of size of mature males would have been much greater than for females. In terms of Equation 3, this would have resulted in a lower calculated rate of survival of males. It is likely that fishing still influenced the population structure at that stage, even taking into account the very slow somatic growth rates and the longevity of rock lobsters. However, Malgas Island had been a sanctuary for 50 years when the diving surveys were carried out, and in this case the higher female natural survivorship cannot be explained by past fishing patterns.

The effect of restricted fishing on the structure of a rock lobster population is well demonstrated by the declaration of Robben Island as a sanctuary in 1963. The longer the period since this declaration, the higher are the mean length and survivorship parameters for adults. In other words, the survivorship parameters are less confounded by fishing mortality as the population recovers to its pristine level.

CONCLUSION

The method used here for determining natural survivorship depends critically on the stock being in equilibrium. This assumption very seldom holds, even for a pristine population, because, for example, environmental factors affect recruitment. However, as the calculations were carried out for four different fishing areas at various times during this century, it is probable that the results provide good indicative ranges for the value of the natural survivorship parameter.

Note also that the estimate of natural survivorship is intricately dependent on the estimates of mean length $\bar{L}$, on how representative the sampling above $L_{a_{min}}$ is, and on the parameter L_∞. Nevertheless, the results obtained here complement, and serve to improve confidence in, values of natural survivorship obtained from a full length-based model (Johnston and Butterworth 1995).

Results of this study suggest that natural survivorship of females is consistently higher than that of males. Furthermore, it seems that the somatic growth rate of the Cape rock lobster was considerably faster at the beginning of the century than during the past 25 years, assuming that asymptotic length has remained constant during that period.

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APPENDIX

Derivation 1

If $N_{0,t}$ represent the number of recruits belonging to a specific cohort (e.g. Cohort 0) in year t, then, assuming no fishing, it follows that

$$N_{i,t+i} = N_{0,t}\,\mathrm{e}^{-M_i} \quad , \qquad \text{(App. 1)}$$

Hoenig (1987) derived an explicit expression for natural mortality (M), in terms of the Von Bertalanffy growth parameters, from this equation. For completeness, the derivation is repeated here.

Considering a portion of the population between the ages a_{min} and a_{max}, the average length $\overline{L}$ of an individual, at time t, omitting t subscripts, is given by

$$\overline{L} = \frac{\sum_{i=a_{min}}^{a_{max}} N_i \overline{L}_i}{\sum_{i=a_{min}}^{a_{max}} N_i} \quad ,$$

where $\overline{L}_i$ is the average length of an individual in the ith age-class. By assuming steady state conditions, namely that $N_{0,t}$ is independent of time t, Equation App. 1 can be substituted into this relationship to give

$$\overline{L} = \frac{\sum_{i=a_{min}}^{a_{max}} \mathrm{e}^{-M_i}\,\overline{L}_i}{\sum_{i=a_{min}}^{a_{max}} \mathrm{e}^{-M_i}} = \frac{\sum_{i=a_{min}}^{a_{max}} \mathrm{e}^{-M}\,\overline{L}_i\,(1-\mathrm{e}^{-M})}{\mathrm{e}^{-Ma_{min}} - \mathrm{e}^{-M(a_{max}+1)}} \quad .$$

Different growth models may be substituted for $\overline{L}_t$, notably the seasonal oscillating growth model of Pauly and Gaschütz (1979). If, however, the simple non-oscillating Von Bertalanffy growth equation is selected, one obtains

$$\overline{L} = L_\infty - \frac{L_\infty(1-\mathrm{e}^{-M})\,[\mathrm{e}^{-a_{min}(M+\mathrm{K})} - \mathrm{e}^{-(a_{max}+1)(M+\mathrm{K})}]\,\mathrm{e}^{\mathrm{K}t_0}}{[1-\mathrm{e}^{-(M+\mathrm{K})}]\,[\mathrm{e}^{-Ma_{min}} - \mathrm{e}^{-M(a_{max}+1)}]} \; .$$

Assuming there is no reason to believe that the older age groups are under-represented, the a_{max} can be taken to be infinite and

$$\overline{L} = L_\infty - \frac{L_\infty\,(1-\mathrm{e}^{-M})\,\mathrm{e}^{-\mathrm{K}(a_{min}-t_0)}}{1-\mathrm{e}^{-(M+\mathrm{K})}} \quad .$$

Substituting $L_{a_{min}}$ into the Von Bertalanffy equation and then that result into the above equation, t_0 can be eliminated and the natural mortality rate becomes

$$M = \ell\mathrm{n}\left[\frac{\mathrm{e}^{-K}\,(\overline{L}-L_\infty) + L_\infty - L_{a_{min}}}{\overline{L}-L_{a_{min}}}\right] . \quad \text{(App. 2)}$$

Making the usual assumption that all cohorts comprise the same number of individuals when these individuals are of comparable age, this formula can be used to calculate instantaneous natural mortality for that portion of the population for which the Von Bertalanffy growth model holds. The natural survivorship parameter is thus expressed by

$$s = \frac{\overline{L}-L_{a_{min}}}{\mathrm{e}^{-\mathrm{K}}(\overline{L}-L_\infty) + L_\infty - L_{a_{min}}} \quad . \quad \text{(App. 3)}$$

Derivation 2

Here, an alternative derivation of M is presented using a delay-difference setup. Hilborn and Walters (1992) presented a similar derivation, but in terms of body mass rather than length-class, as is done here.

Assuming N represents the number of mature adults or, more precisely, the portion of the population for which the Von Bertalanffy growth model holds, t is the year and T is the time to maturity, then

$$N_t = sN_{t-1} + R\,(N_{t-T-1}) \quad , \qquad \text{(App. 4)}$$

where R (the number of recruits joining the population at the beginning of the year) is assumed to be a function of the population at time t-T-1, whereas, as before, $s = \mathrm{e}^{-M}$ is the natural survivorship. The total sum of the lengths of all animals in the population, at time t equal to and older than age a_{min}, can be expressed as follows:

$$L_t = \sum_{i=a_{min}}^{\infty} \overline{L}_i\,\mathrm{N}_{t,i} \quad ,$$

where $N_{t,i}$ refers to the numbers of animals aged i, in the mature population N_t, in year t.

Substituting the Ford-Walford model (Equation 2) and the delay-difference relationship (Equation App. 4) into this equation gives

$$L_t = s\alpha N_{t-1} + s\rho\,L_{t-1} + L_{a_{min}}R\,(N_{t-T-1}) \quad .$$

From Equation App. 4, it follows that, at equilibrium,

$$R^* = (1 - s)\, N^* \quad ,$$

where N^* represents the equilibrium population and R^*, is the equilibrium recruitment. Substituting this relationship into the above equation and assuming equilibrium conditions, with the average length given by $\bar{L} = L^*/N^*$, where L^* is the sum of all the lengths at equilibrium, it follows that

$$\bar{L} = s\alpha + s\rho\bar{L} + (1 - s)\, L_{a_{min}} \quad .$$

As before, by using relationships $s = \mathrm{e}^{-M}$ and Equation 3, the same expression for natural mortality (M) is obtained, as in the first derivation:

$$M = \ell\mathrm{n} \left[\frac{\mathrm{e}^{-\mathrm{K}}(\bar{L} - L_\infty) + L_\infty - L_{a_{min}}}{\bar{L} - L_{a_{min}}} \right] \quad ,$$

and so Equation App. 3 also follows.