GROWTH AND MORTALITY RATES AND STATE OF EXPLOITATION OF SPINY LOBSTERS IN TONGA

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Abstract

An analysis was made of length frequency data for the spiny lobsters, Panulirus penicillatus *and* P. longipes, *caught on coral reefs in Tonga. The length data were used to estimate both growth and mortality parameters for populations caught around the main island, Tongatapu, and the Ha'apai islands in the centre of the Tonga archipelago. Growth parameters were computed by the interactive ELEFAN computer method and were consonant with those of other tropical spiny lobsters. The results suggested that mortality rate for males is somewhat higher than for females and is much greater in Tongatapu than in Ha'apai. Yield-per-recruit analysis showed that the Tongatapu fishery is being subjected to growth overfishing and that harvests could be substantially increased by raising the size at first capture. The implications for management and the recommended size increases for the legal minimum harvestable size of lobsters in Tonga are discussed.*

Résumé

On a procédé à une analyse des données de fréquences de tailles relative aux langoustes, Panulirus penicillatus *et* P. longipes, *capturées sur les récifs coralliens de Tonga. Les données de tailles ont servi à l'évaluation des paramètres de croissance et de mortalité des populations évoluant au large de l'île principale de Tongatapu et des Iles de Ha'apai situées au centre de l'archipel des Tonga. Par la suite, les paramètres de croissance ont été calculés à partir d'une méthode informatique interactive appelée ELEFAN et on a pu ainsi constater qu'ils correspondaient aux données relatives à d'autres espèces de langoustes tropicales. Les résultats obtenus semblent indiquer que les taux de mortalité des mâles sont légèrement supérieurs à ceux des femelles et beaucoup plus élevés à Tongatapu qu'à Ha'apai. L'analyse du rendement par recrue indique que les stocks de Tongatapu font l'objet d'une exploitation des spécimens en pleine croissance alors que les récoltes pourraient augmenter sensiblement si l'on ciblait davantage les individus de plus grande taille. On examine par ailleurs dans le document résumé ici l'incidence de cette situation sur la gestion de la ressource ainsi que la question du seuil de croissance en deçà duquel la pêche de la langouste de Tonga devrait être interdite.*

Introduction

Despite their relatively great economic importance there are few reliable estimates of growth and mortality rates for tropical Indo-Pacific spiny lobsters. The only really detailed work has been accomplished in Western Australia (*P. cygnus*), in Hawaii (*P. marginatus*) and in the Caribbean Sea (*P. argus*). Estimates of growth parameters and mortality rates are summarised in Table 1, which also gives the calculated values of the growth performance indices, Ø and Ø' (Munro and Pauly, 1983; Pauly and Munro, 1984). It is well established that the largest spiny lobsters are usually males, presumably a result of superior growth rates. This is reflected in the growth performance indices.

The material upon which this analysis is based consists of separate sets of length frequency samples of male and female *Panulirus penicillatus* and *P. longipes*, measured at Tongatapu and Ha'apai between February 1984 and January 1985. Data collections were organised by Dr L. Zann of the Institute of Marine Resources of the University of the South Pacific. Zann (1984) gives details of the research project in Tonga, of the fishery and of the reproductive characteristics and behaviour of the lobsters.

Data collection and analysis

Samples were collected from February 1984 to January 1985 from lobsters landed in Tongatapu and at two islands in the Ha'apai group. Information on sample sizes is summarised in Table 2. The largest samples were of male *P. penicillatus* at Tongatapu (N = 3364 in 12 monthly samples ranging in size between 93 and 637 individual measurements). Measurements are of carapace length (L), along the mid-dorsal line from between the horns to the rear margin of the carapace.

Table 1: Growth and mortality parameters and growth performance indices for species of spiny lobsters

Source	Species/ location	Sex	CL	W_∞	K	M	a	b	Ø'	Ø
Ebert & Ford	*P.penicillatus*	M	146.5	2133	0.211	0.284	0.002	2.773	3.66	1.54
1986	(Enewetak)	F	96.5	580	0.580	0.244	0.002	2.773	3.73	1.61
Zann (1984)	*P.penicillatus*	M					0.237	1.727		
	(Tonga)	F					0.006	2.571		
Phillips et al.	*P.cygnus*	M &	113.5		0.495	0.226	0.003	2.744	3.80	
(1980)	(W. Aust)	F								
Munro	*P.argus*	M	190.0	4700	0.215	0.400	0.003	2.738	3.89	1.78
(1974)	(Caribbean)	F	190.0	4700	0.215	0.600	0.003	2.738	3.89	1.78
Uchida &	*P.marginatus*	M	127.7		0.270				3.64	
Tagami	(Oahu,	F	106.0		0.386				3.64	
(1984)	Hawaii)									
	(Necker Is)	M	124.6		0.263				3.61	

Note: CL = asymptotic carapace length; W_∞ = asymptotic weight, K = coefficient of growth, M = coefficient of natural mortality; a = constant in length (mm)/weight (g) relationship; b = exponent in l/w relationship; ø' and ø = growth performance indices in terms of length and weight.

The size frequency data were analysed using the 'Kiel version' (December 1986 update) of the ELEFAN I and

II programs (Brey and Pauly, 1986). After experimentation, the size frequency data were compiled into 0.5 cm groups for analysis. One-centimetre size classes were too coarse and caused detail to be lost.

Table 2: Sample sizes and distributions for male and female *Panulirus penicillatus* and *P. longipes* sampled at Tongatapu and Ha'apai between February 1984 and January 1985

	P. penicillatus				*P. longipes*			
	Tongatapu		Ha'apai		Tongatapu		Ha'apai	
	Male	Female	Male	Female	Male	Female	Male	Female
Feb	93	87	1314	755	132	181	22	46
Mar	261	228	70	52	47	48	0	0
Apr	146	180	534	516	55	69	33	41
May	330	253	474	363	25	35	72	67
Jun	117	81	380	332	16	10	86	64
Jul	254	76	75	64	180	85	14	11
Aug	344	86	0	0	191	129	0	0
Sep	510	207	316	225	101	80	26	30
Oct	496	150	0	0	167	126	0	0
Nov	637	230	112	139	285	291	21	15
Dec	158	36	91	87	72	50	26	15
Jan	318	113	0	0	132	118	0	0
Total	3364	1727	3366	2533	1403	1222	300	289

The protocol adapted for the analysis is as follows:

(i) The monthly size frequency distributions for each sex, species and area are converted to percentage frequencies, weighted by the square root of the sample size and, where there are gaps in the sampling, also weighted with respect to the time interval which the sample 'represented'. The weighted samples are then summed to give the best representation of the annual average size frequency distribution of the catches. These are all routines which are available within the structure of the ELEFAN programs.

(ii) The annual average size frequency distributions by sex, species and area are then used to obtain a first estimate of the asymptotic size (L_∞) and of the ratio of the coefficients of mortality to growth (Z/K) from a Wetherall plot (embodied in the ELEFAN 2B program) (Wetherall, 1986; Wetherall et al, 1987).

(iii) The monthly size frequency distributions for each sex and species are then restructured using the ELEFAN 1A program, to highlight the peaks and troughs (Brey and Pauly, 1986) and the results are inspected to identify the most likely 'starting point', normally a highly conspicuous peak through which it can reasonably be assumed that the growth curve must pass. Using ELEFAN 1B, a narrow search is then performed using as fixed values the initial estimates of L_∞ and of the starting point. This results in a first estimate of the growth coefficient, K.

(iv) The ELEFAN 2A program is then run, using the first estimates of K and L_∞. This yields a first estimate of Z, the total mortality coefficient and, if an estimate of the natural mortality rate is available, first estimates of the probabilities of capture of the smallest size classes (within the selection curve) can be calculated.

(v) The observed frequencies of the smallest size groups in the monthly samples are/can then be corrected by dividing the observed frequencies by the probabilities of retention of successive size classes.

(vi) The corrected data are then restructured (ELEFAN 1A), the most conspicuous peak identified (the starting point or SP) and a 'response surface' generated for that starting point and a range of values of K and L_∞ which bracket the first estimates. This will result in one or more combinations of the K and L_∞ which give the largest ratios of the 'estimated sum of peaks' to the 'available sum of peaks' (E_{max}/A).

(vii) The 'starting point' is then allowed to vary for the current estimates of K and L_∞ to see if the E_{max}/A ratio can be improved and, thereafter, a final response surface generated for a narrow range of values of K and L_∞, yielding final estimates of the growth parameters.

(viii) A growth curve is then calculated and superimposed on the restructured length frequency data to verify the fit.

(ix) Once the growth parameters are available the mortality rate is estimated, using the ELEFAN 2A program to generate length-converted catch curves for each sex, species and area. The option in which the samples are converted to percentage frequencies, weighted by the square roots of the sample size and, if there are gaps in the data, weighted in respect of the interval between samples, has been routinely chosen. Trials showed that provided the sampling has been adequate, the results are remarkably insensitive to the weighting mode used.

(x) The ELEFAN 2A program also generates estimates of the mean size of first capture (L_c) and sizes at which they are fully selected (L') together with the probabilities of retention of successive size classes.

It is emphasised that it is not possible simply to run the ELEFAN 1B program and blindly accept the answers which are generated. The program does nothing more than fit the best von Bertalanffy growth curve to a set of length frequency data. If the sampling program has been inadequate or selective, the result might be erroneous. As a general case the program should not be used if no modal progression is apparent to the eye. Clearly more weight can be ascribed to growth curves which are based on large samples and which pass through all or most 'peaks' and avoid most 'troughs'. Mortality analyses were done separately for the island groups, as the fisheries are known to differ in their rate of exploitation, the fishery being more intensive at Tongatapu, the site of the Tongan capital city of Nuku'alofa.

Results

The parameter estimates are summarised in Table 3. As in any other form of analysis, the estimates are only as good as the samples and as a general rule are improved by large sample sizes. The monthly size frequency distributions, fitted growth curves and length-converted catch curves are shown in Figures 1 to 8.

Table 3: Summary of estimates of growth and mortality rates for *Panulirus penicillatus* and *Panulirus longipes* in Tongatapu and Ha'apai, Tonga

Growth parameters (all areas)	*Panulirus penicillatus* Male	*Panulirus penicillatus* Female	*Panulirus longipes* Male	*Panulirus longipes* Female
Asymptotic carapace length(CL_∞)	179.00	128.00	133.00	118.00
Asymptotic weight(W_∞)g	3718.00	1467.00	1884.00	1356.00
Growth coefficient (K)	0.27	0.32	0.31	0.42
Ø'	3.94	3.72	3.74	3.77
Ø	1.82	1.63	1.69	1.72
Mortality and recruitment				
M	0.284*	0.244*	(0.23**)	(0.23**)
M/K	1.05	0.76	(0.73)	(0.55)
Tongatapu				
Z	1.66	1.33	1.19	1.41
L_c	77.00	62.00	41.00	42.00
L'	(82.50)	72.50	47.50	47.50
F	1.38	1.09	0.96	1.18
E	0.83	0.82	0.81	0.84
Ha'apai				
Z	0.75	0.88	0.61	(0.89)
L_c	70.00	67.00	52.00	(49.00)
L'	82.50	77.50	57.50	(52.50)
F	0.47	0.64	0.38	(0.66)
E	0.62	0.72	0.62	(0.74)

* from Ebert & Ford (1986)
** from Phillips et al. (1980) for *Panulirus cygnus*

Note: Values in brackets are approximations and should not be regarded as definitive. Lengths in mm, weights in g.

Growth parameters

Panulirus penicillatus

Males:
The Wetherall plot produced first estimates of L_∞ = 178 mm (Z/K = 2.195) at Ha'apai but gave a non-significant regression for the data from Tonga. Analysis of the Tongatapu data yielded estimates of L_∞ = 179 mm and K = 0.27 (SP = 57.5 mm November, E_{max}/A = 233). This is a relatively low E/A value but the curve does fit the major peaks (Fig. 1). It is possible that there is some seasonality in the growth curve, with diminished growth in the cooler months (June–September), but the data are not sufficiently good to substantiate this.

Data for Ha'apai gave low E/A ratios for combinations of L_∞ and K, bracketing the values of K and L_∞ found for Tongatapu. E_{max}/A was only 133 for K = 0.28 and L_∞ = 179 mm. These values are close to the estimates for Tongatapu.

Females:
The analysis produced estimates of K = 0.32, L_∞ = 128 mm (SP = 48 mm in September, E_{max}/A = 326). The progression of recruits from 37.5 mm in May through to the following January is particularly clear (Fig. 2).

No modal progression could be seen in the data for Ha'apai and the E/A ratio was close to zero for the combination of K and L_∞ found for Tongatapu.

Panulirus longipes

Males:
The standard analytical protocol produced estimates of K = 0.31, L_∞ = 133 mm (SP 42.5 mm in September, E_{max}/A = 569) for samples taken in Tongatapu. The relatively high value of E_{max}/A gives much credence to the estimate. Figure 3 shows the fit of the calculated growth curve. The sample from Ha'apai was too small (N = 300) to warrant analysis.

Females:
Estimates of K = 0.42 and L_∞ = 118 mm (SP = 40 mm in August, E_{max}/A = 434) were produced by the usual routine. Figure 4 shows a moderately good fit of the calculated growth curve to the monthly peaks, but with some conspicuous peaks missed around 62.5 mm in September to November. The sample from Ha'apai was too small (N = 289) for analysis.

Mortality and recruitment parameters

Parameters estimated for *P. penicillatus* and *P. longipes* at Tongatapu and Ha'apai are summarised in Table 3.

It must be borne in mind that the size frequencies that have been recorded are a combination of the results of selective action by the spear-fishermen and may also be influenced by decisions concerning which size groups will be offered in the market place at Nuku'alofa in Tongatapu or which would be purchased by the fish dealers in Ha'apai. The selective action of the fishermen would be manifested by selective spearing of the largest lobsters, but the perception of what is large would be expected to change towards smaller sizes in a heavily exploited fishery. It is also possible that behavioural traits, such as movement of larger lobsters into deeper water, could affect the catchability of different size groups. Finally, a number of different year-classes are represented in the catches and any marked deviations away from a steady rate of recruitment would be manifested as departures of the right-hand arm of the catch curves from linearity.

The real test of the validity of the length-converted catch curve is the degree of scatter of the points on the right hand limb. Points in the larger size classes which are based on less than five specimens are ignored (Brey and Pauly, 1986).

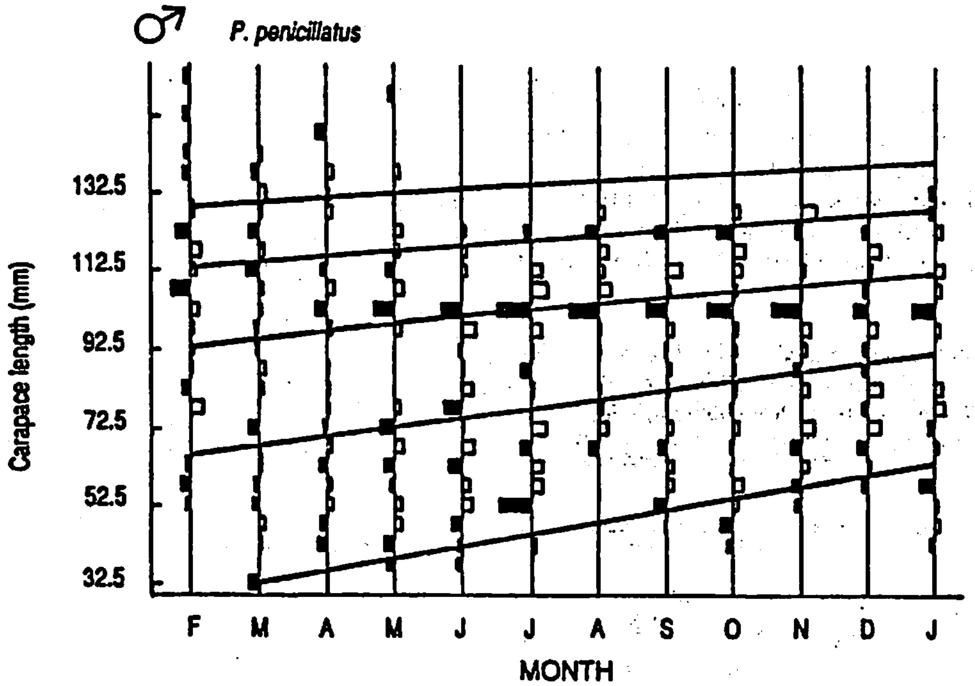

Figure 1. Restrictured size frequency distributions and fitted von Bertalanffy growth curves for male *Panulirus penicillatus* at Tongatapu. L_∞ = 179 mm, K = 0.27, SP = 57.5 mm in November, E_{max}/A = 233

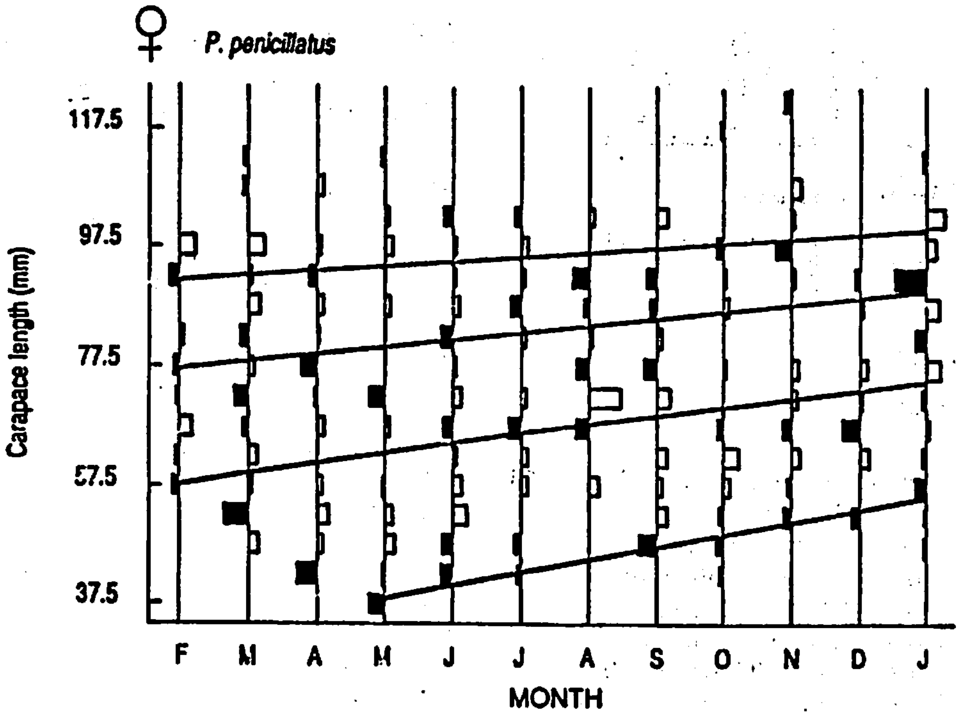

Figure 2. Restructured size frequency distribution and fitted von Bertalanffy growth curves for female *Panulirus penicillatus* at Tongatapu. L_∞ = 128 mm, K = 0.32, SP = 48 mm in September, E_{max}/A = 326

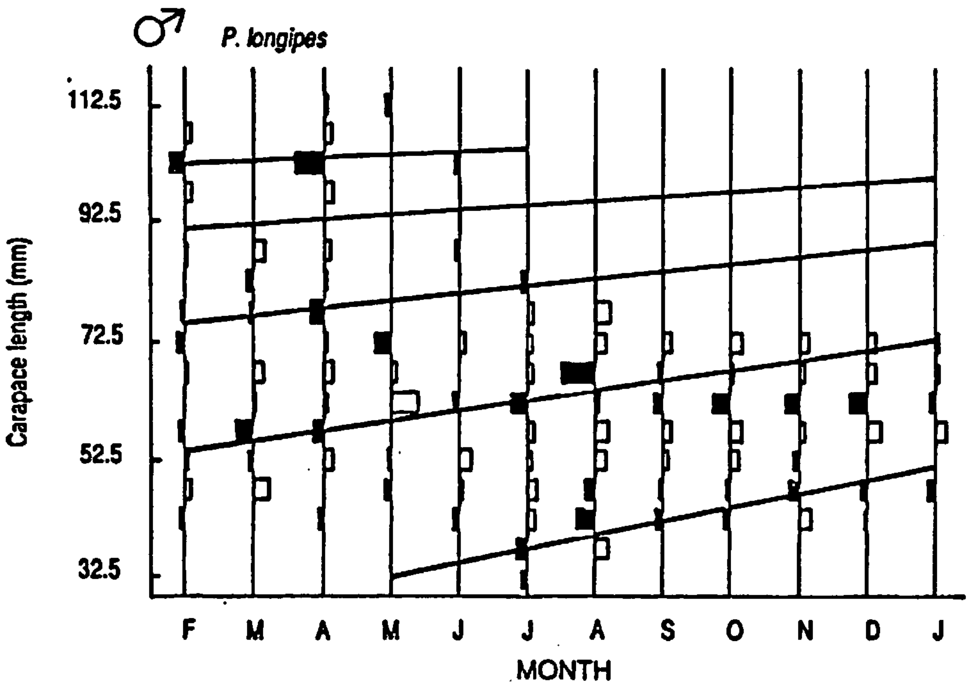

Figure 3. Restructured size frequency distributions and fitted von Bertalanffy growth curves for male *Panulirus longipes* at Tongatapu. L_∞ = 133 mm, K = 0.31, SP = 42.5 mm in September, E_{max}/A - 569

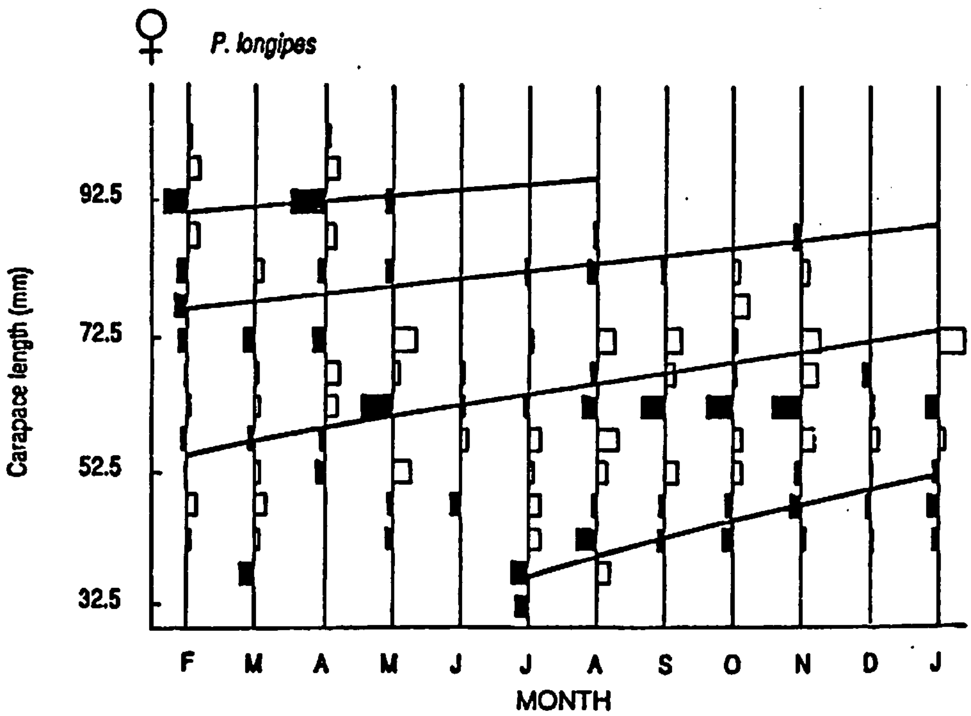

Figure 4. Restructured size frequency districutions and fitted von Bertalanffy growth curves for female *Panulirus longipes* at Tongatapu. L_∞ = 118 mm, K = 0.42, SP = 40 mm in August, E_{max}/A = 434

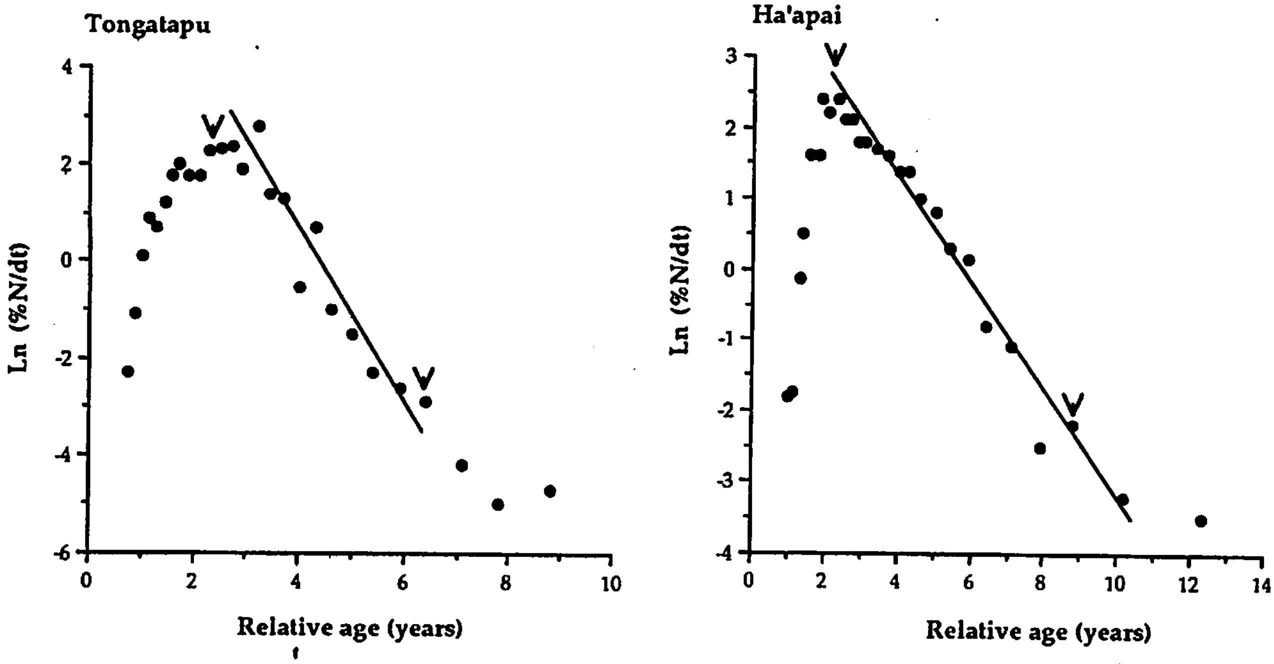

Figure 5. Length-converted catch curves for estimation of total mortality rate (Z) of male *Panulirus penicillatus* at Tongatapu and Ha'apai. The portion of the curve delineated by arrows was used in the calculation of total mortality.

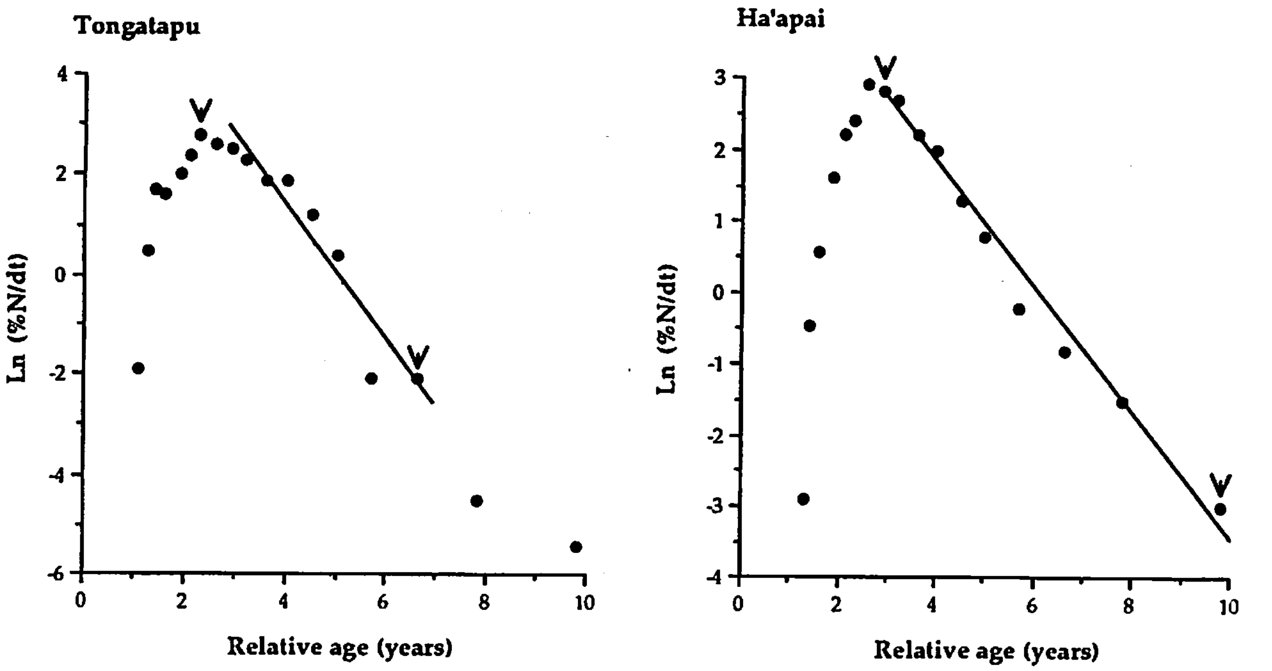

Figure 6. Length-converted catch curves for estimation of total mortality rate (Z) of female *Panulirus penicillatus* at Tongatapu and Ha'apai. The portion of the curve delineated by arrows was used in the calculation of total mortality.

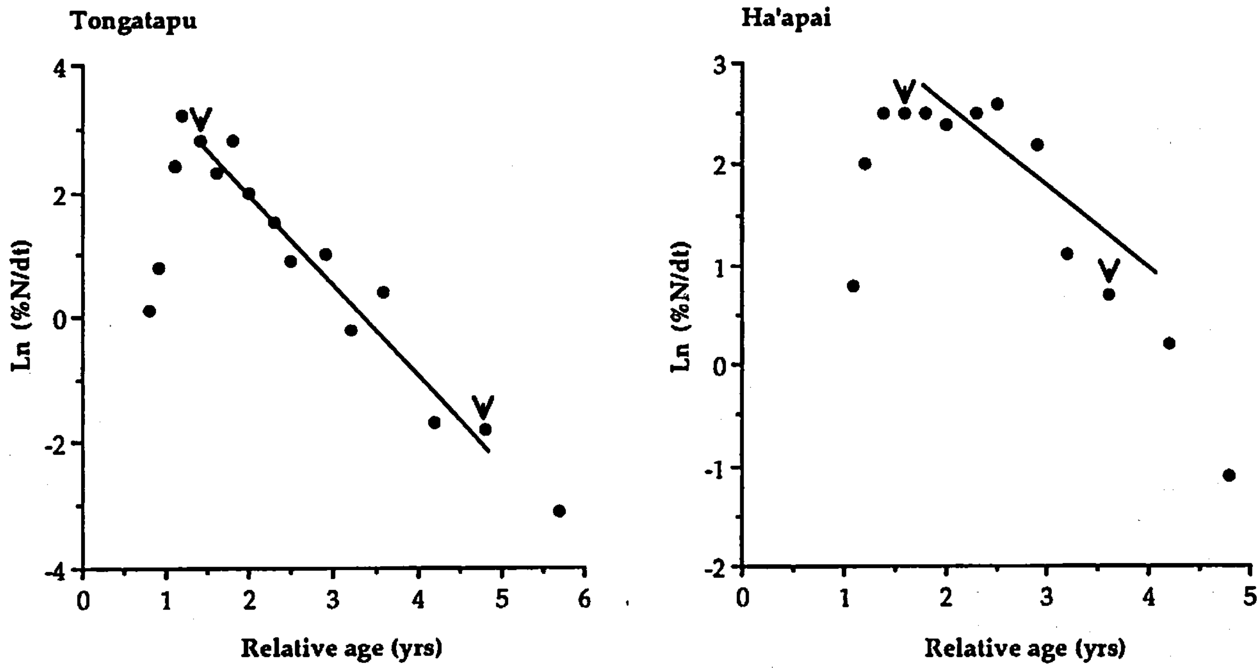

Figure 7. Length-converted catch curves for estimation of total mortality rate (Z) of male *Panulirus longipes* at Tongatapu and Ha'apai. The portion of the curve delineated by arrows was used in the calculation of total mortality.

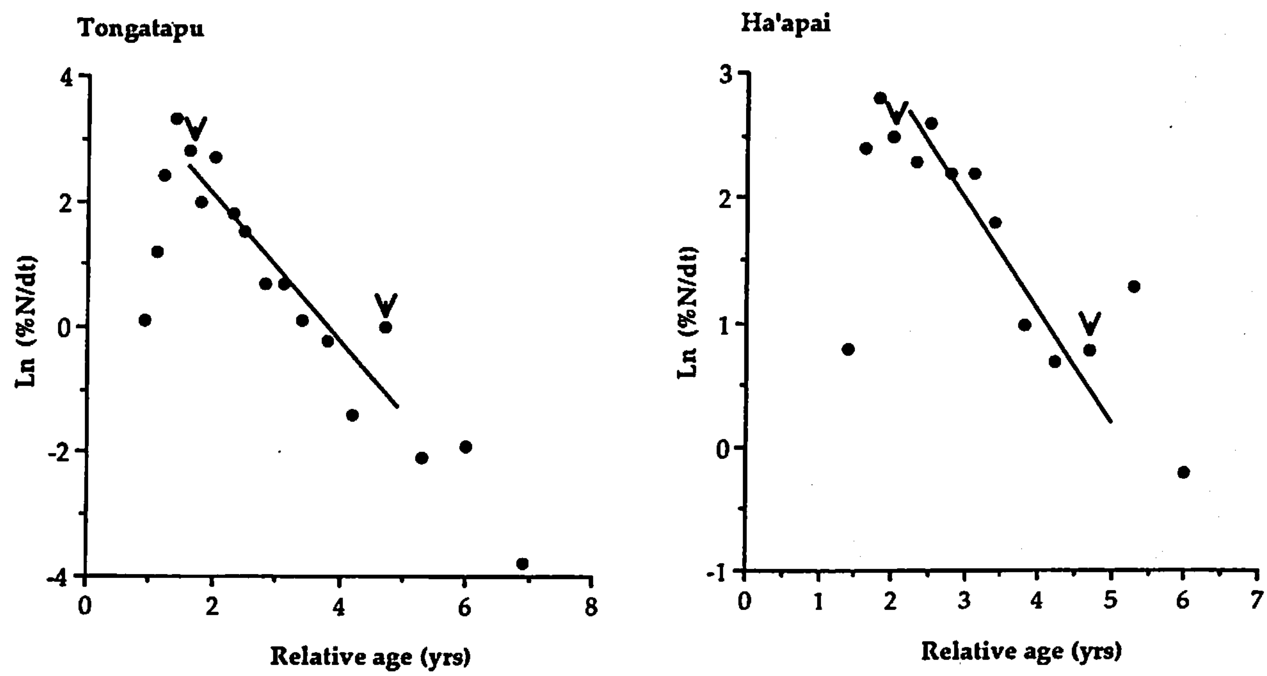

Figure 8. Length-converted catch curves for estimation of total mortality rate (Z) of female *Panulirus longipes* at Tongatapu and Ha'apai. The portion of the curve delineated by arrows was used in the calculation of total mortality.

Panulirus penicillatus

Figures 5 and 6 show length-converted catch curves for males and females at Tongatapu and Ha'apai. The results suggest that the mortality rate for males is somewhat higher than for females and is much greater in Tongatapu than in Ha'apai.

Males:
For male *P. penicillatus* at Tongatapu the left-hand limb of the catch curve (Fig. 5) ascends to a plateau at 82.5–92.5 mm L whereas for Ha'apai the curve descends linearly from 82.5 mm. As it could be expected that the length at full recruitment (L') would be larger at Ha'apai (because the lobsters are actually selected by divers), it is reasonable to believe that L' = 82.5 mm CL at Tongatapu, and that any peaks at larger sizes are artefacts resulting from the sampling or from variation in recruitment. A regression based on the size range 87.5–147.5 mm gives an estimate of Z = 1.66 for male *P. penicillatus* at Tongatapu. A similar regression for the Ha'apai male stock based on the range between 82.5–167.5 mm gives Z = 0.75.

At Tongatapu males are recruited at a mean size, L_c, of 77 mm whereas at Ha'apai the estimate is L_c = 70. The estimates of L_c are rather sensitive to the frequencies in the successive length groups and to the estimated natural mortality rate and therefore should be regarded as generalisations.

Females:
As was the case with male *P. penicillatus*, the catch curve is more sharply peaked for the Ha'apai stocks (Fig. 6), suggesting full recruitment at L' = 77.5 mm, whereas the Tongatapu stocks had a L' = 72.5 mm.

A regression covering the range 72.5–112.5 mm L for the Tongatapu stock yields estimates of Z = 1.33 and L_c = 62 mm, while for the Ha'apai stock over the range 77.5–122.5 mm, estimates were Z = 0.88 and L_c = 67 mm.

Panulirus longipes

Large samples of this species were available for Tongatapu (Table 1) but for the Ha'apai Islands the recorded catches were very low. The reasons for this difference are not known.

Males:
From the length-converted catch curve for this species at Tongatapu (Fig. 7), it appears that the males are fully recruited to the fishery at L' = 47.5 mm. A length-converted catch curve regressed over the length range 52.5–102.5 mm yields an estimate of Z = 1.19 and L_c = 41 mm.

For the small sample from Ha'apai, the males appear to be fully recruited by L' = 57.5 mm and a regression of the catch curve regressed over the range 62.5–102.5 mm yields an estimate of Z = 0.61 and L_c = 52 mm.

Females:
The length-converted catch curve for Tongatapu indicates full recruitment, L', at 47.5 mm (Fig. 8) and a regression over the range 52.5–102.5 mm yields estimates of Z = 1.41 and L_c = 42 mm.

The small sample from Ha'apai gives a length-converted catch curve which is almost horizontal between CL of 42.5–67.5 mm, and then declines sharply. The samples are strongly biased towards the situation in May and June when almost half of the total sample was measured. Using entirely unweighted samples to remove any bias towards these months had no appreciable effect. A regression over the range 57.5–92.5 mm CL yields preliminary estimates of Z = 0.89 and L_c = 49 mm.

Yield per recruit and rate of exploitation

Figures 9 and 10 show yield-per-recruit curves and computations for the two species based on the population and fishery parameters which are summarised in Table 3.

For each species the curves selected for illustration include one curve representing the current size at first capture at Tongatapu, one curve showing the maximum yield per recruit which could be attained at current levels of fishing effort, but with a change in the size at first capture, and several other representative curves.

Panulirus penicillatus

Males:
Figure 9 shows that the Tongatapu fishery is being subjected to growth overfishing and the harvest could be substantially increased by raising the size at first capture to 127.5 mm CL. Larger or similar harvests could be taken by half the current fishing effort. Any increase in effort at Ha'apai will result in decreased landings.

Females:
As is the case for males, the fishery would benefit from a substantial increase in the size at first capture and a decrease in the fishing effort (Fig. 9). The optimum L_c is around 95 mm CL. Harvests off Ha'apai will decrease if effort is increased.

Panulirus longipes

Males:
Harvests could be doubled by increasing L_c to 100 mm CL. A halving of fishing effort would have no appreciable effect on yield/recruit when L_c = 100 mm and would increase harvests substantially at the current Lc = 41 mm (Fig. 10). The Ha'apai fishery is fully exploited at current levels of F and Lc.

Females:
The situation is the same as for males. Figure 10 shows that the optimum L_c = 95 mm.

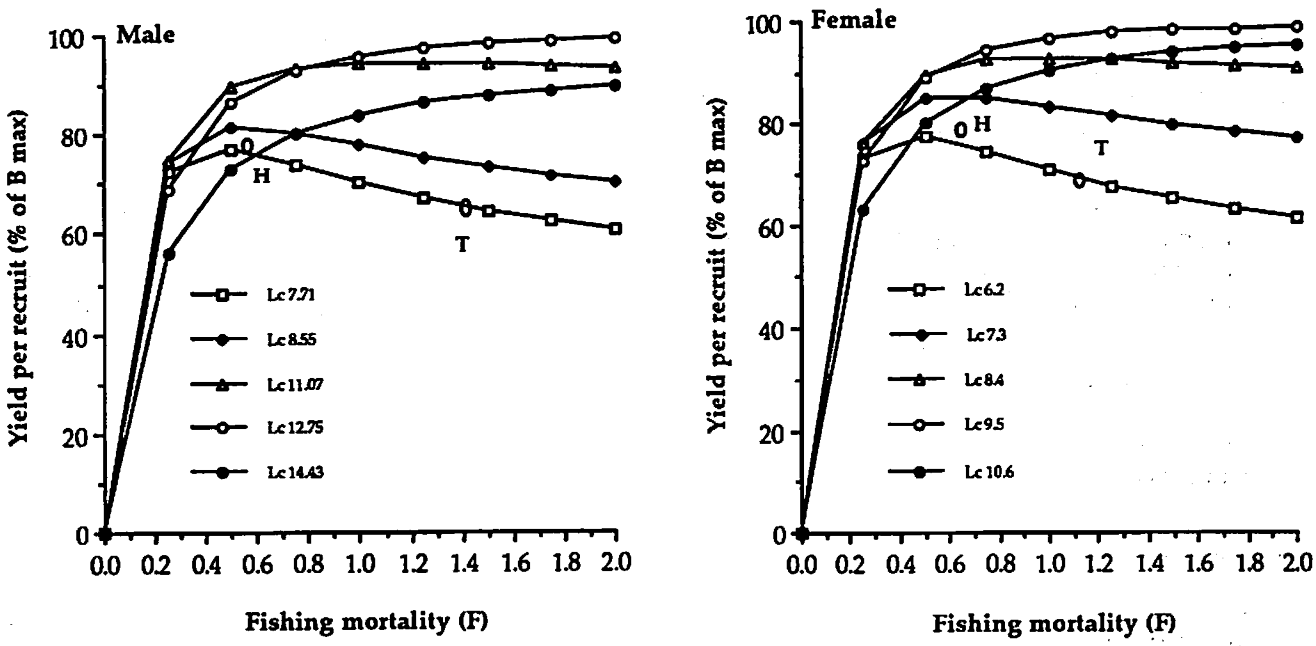

Figure 9. Yield per recruit of male and female *Panulirus penicillatus*, relative to fishing mortality, F, expressed as percentage of maximum biomass of a cohort, for five sizes at first capture. T and H indicate points representative of the status of the Tongatapu and Ha'apai fisheries in 1985/86.

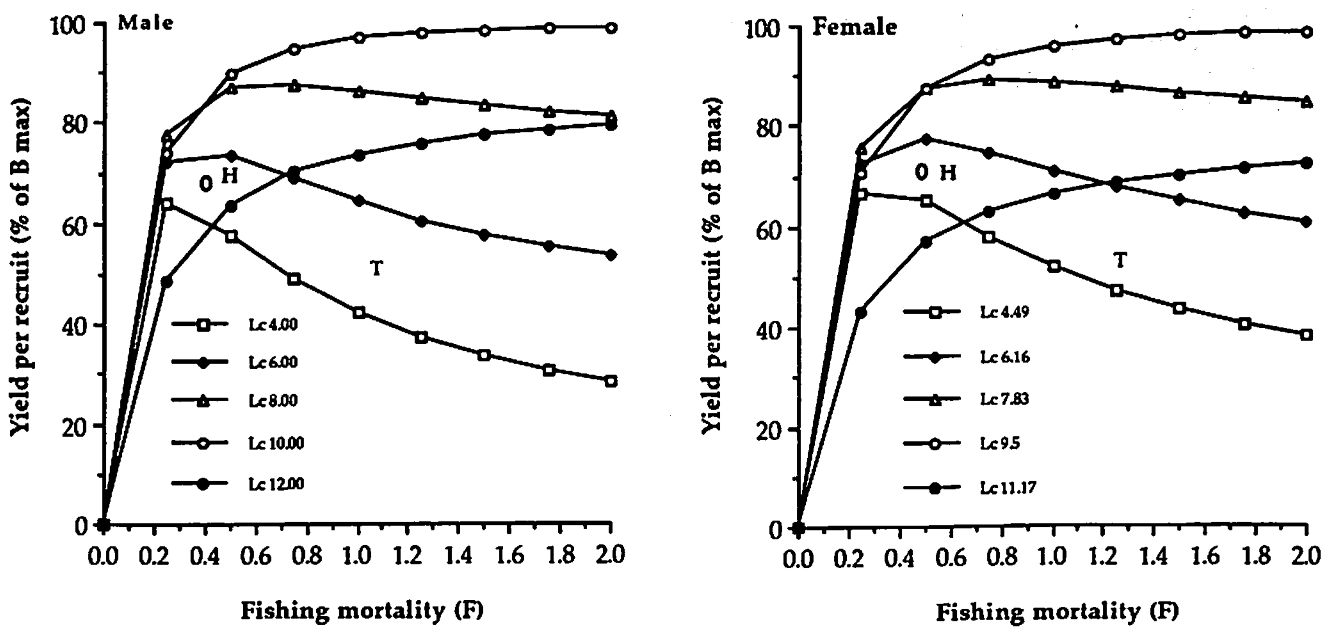

Figure 10. Yield per recruit of male and female *Panulirus longipes*, relative to fishing mortality, F, expressed as percentage of maximum biomass of a cohort, for five sizes at first capture. T and H indicate points representative of the status of the Tongatapu and Ha'apai fisheries in 1985/86.

Management options

The optimum values of L_c are 127.5 mm and 95 mm respectively for male and female *P. penicillatus* and 100 mm and 95 mm for male and female *P. longipes*. These are substantially greater than the current L_cs for all species. Imposition of a minimum size regulation combined with mandatory possession of a standard gauge, as suggested by Zann (1984), is an obvious solution. If marketing requirements dictate smaller L_cs it must be recognised that this will be at the price of lower landings.

It is suggested that minimum size regulations be phased in over three years, with the immediate imposition of a 75 mm size limit, increased to 85 mm in the second year and to 95 mm in the third year.

Measures to reduce fishing effort need to be considered within the framework of the entire nearshore fisheries situation. It is obvious that increases in fishing effort will result in no increases, or even in decreases, in harvests.

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