

GROWTH OF SPINY LOBSTER *PALINURUS GILCHRISTI* (DECAPODA: PALINURIDAE) OFF SOUTH AFRICA

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Growth of spiny lobster *Palinurus gilchristi* was investigated on four traditional lobster fishing grounds, Agulhas Bank, St Francis, Port Elizabeth and Port Alfred, using tagging data. Of 11 144 individuals tagged in six tagging sessions between 1988 and 1993, 1 031 (9.25 %) were recaptured by May 1995. Most *P. gilchristi* moult once annually, between December and February. Moulting frequency decreases with increasing length, as do annual growth increments and moult increments. Males grow marginally faster than females. Annual growth increments at Port Alfred were significantly smaller than at Agulhas Bank, St Francis and Port Elizabeth, but growth did not differ significantly between the last three areas. Growth models based on moult increment-at-size and intermoult period-at-size gave realistic descriptions of growth, but Von Bertalanffy L_{∞} parameters underestimated observed maximum carapace lengths. It is suggested that regional variations in the growth of *P. gilchristi* result from intraspecific competition for food, which is greatest on narrow shelf regions.

The deep-water spiny lobster *Palinurus gilchristi* is one of five species of the genus *Palinurus*, all of which are of present or potential commercial interest (Holthuis 1991). Of the five species, only *P. gilchristi* and *P. delagoae* occur off south-east Africa, whereas *P. elephas*, *P. mauritanicus* and *P. charlestoni* are found in the north-eastern Atlantic and Mediterranean (Berry and Plante 1973, Holthuis 1991). *P. gilchristi* is restricted to South Africa's southern coast, on rocky substrata between Cape Point and East London (Fig. 1) at depths between 55 and 360 m (Holthuis 1991).

A longline trap-fishery for *P. gilchristi* has been in operation since 1974. Intensive exploitation during the first years of the fishery led to declining catches and catch rates (Pollock and Augustyn 1982), but since 1984, a total allowable catch (TAC) has been enforced. Assessment of the resource and establishment of an appropriate TAC are currently achieved by surplus production modelling. However, size-based models have been suggested as an improved assessment method. Estimates of growth-at-size are an essential component of size-based models.

Estimating growth in lobsters is difficult under field conditions because all features that can be used to determine the age of individuals are lost at moulting (Campbell 1983). Tagging and recapturing provide an approach in which two easily obtainable measurements, namely the size increase between tagging and recapture and the time spent at large, can be used to determine growth rates (Aiken 1980). This paper aims to determine the growth rates of *P. gilchristi* in different fishing areas by the use of tag-recapture data. Moulting season is determined, and annual growth-at-size, moult increment-at-size and moult frequency

are estimated and used to develop models of growth for each area.

MATERIAL AND METHODS

Tagging was conducted on board commercial fishing vessels, usually towards the end of each fishing season (May – September) so that newly tagged lobsters had time to disperse before fishing effort increased at the beginning of the next season in October. Plastic T-bar internal anchor tags (Hallprint TBA-1 tags) were inserted into the abdominal muscle of each lobster, dorso-laterally between the posterior edge of the carapace and the first abdominal segment, or between the first and second abdominal segments. Tag number, position and depth of release, carapace length (CL) and sex were recorded for each lobster before it was released on the fishing grounds. Tagged lobsters caught in traps by commercial vessels were returned, together with details of the position, depth and date of recapture.

Tagging took place on four traditional lobster fishing grounds: Agulhas Bank (Cape Point – Mossel Bay), St Francis (Mossel Bay – St Francis Bay), Port Elizabeth (St Francis Bay – Bird Island) and Port Alfred (Bird Island – East London, Fig. 1). These four areas were defined at the start of the fishery in the 1970s and were used in previous studies of *P. gilchristi* (Pollock and Augustyn 1982, Groeneveld 1993, Groeneveld and Melville-Smith 1994, Groeneveld and Rossouw 1995).

Lobsters that move from one fishing area to another during their period at large were attributed to the area in which they were tagged. Because few *P. gil-*

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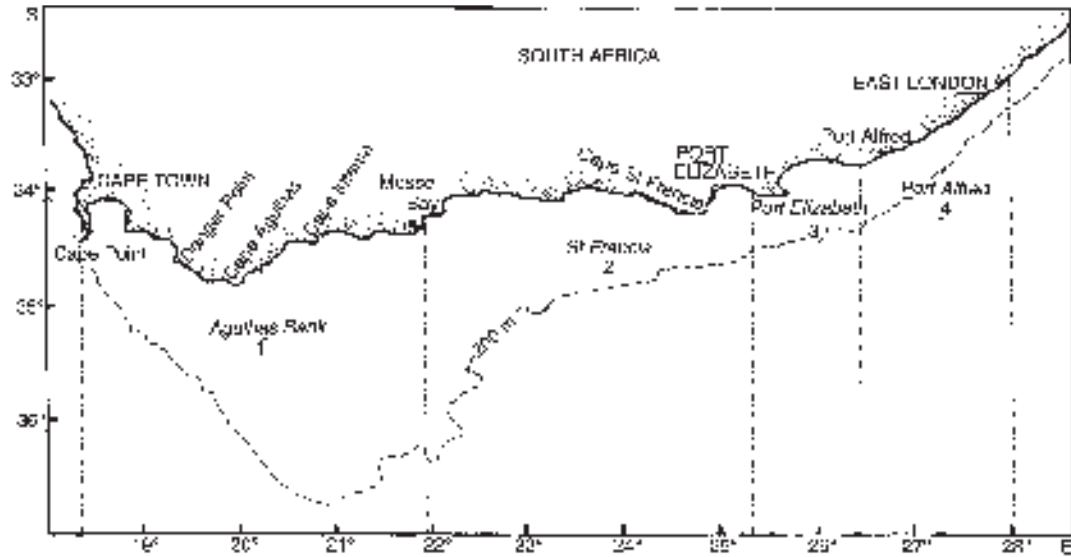


Fig. 1: The south coast of South Africa, showing the four commercial rock-lobster fishing grounds: Agulhas Bank, St Francis, Port Elizabeth and Port Alfred

christi move far from their point of tagging within one year (Sea Fisheries Research Institute [SFRI] unpublished data), it was assumed that the tagged lobsters under study remained in the area where they were tagged.

Moulting season (the season in which the highest proportion of lobsters moult) was estimated according to the method described by McKoy and Esterman (1981). For each tagging date, growth increments of recaptured animals were plotted against the number of days at large. Along this time-scale, seasonality in moulting can be identified by comparing the numbers of rock lobsters that have increased in size with the numbers that have not.

Annual growth-at-size, i.e. the increase in *CL* (mm) per year for an individual of a certain size, was determined according to the "anniversary method" of Hancock and Edwards (1967). Using this method, all growth increments of lobsters recaptured on or near the anniversary date of tagging were used, regardless of the number of moults. Linear regressions of annual growth as a function of *CL* were calculated for each area and gender using a least-squares fit. Trends were compared using either analysis of covariance or *t*-tests (Zar 1984). When no geographical difference was found, data were pooled and combined regressions were calculated.

Moult increment-at-size, i.e. the increase in *CL* (mm) per moult for an individual of a certain size, was de-

termined after selecting animals that had moulted only once. Selection criteria were a noticeable increase in *CL* and a time at large that did not span more than one moulting season. It was assumed that negative growth did not occur, and that an increment of zero indicated that no moulting had taken place. Linear regressions of moult increment as a function of *CL* were calculated using a least-squares fit and were compared between areas using *t*-tests.

The number of times that lobsters of a certain size moult per year, i.e. annual moult frequency, was estimated according to the two methods described by Annala and Bycroft (1988): first, by dividing the ave-

Table 1: Date of each tagging experiment for the four study areas, and the numbers of *P. gilchristi* tagged and recaptured for which growth data were available. Recapture data up to 1 May 1995

Locality	Month tagged	Number tagged	Number recaptured	% recaptured
Agulhas Bank	May 1988	1 997	176	8.81
St Francis	May 1990	1 499	213	14.21
Port Elizabeth	Aug. 1990	1 797	233	12.97
Agulhas Bank	Feb. 1992	941	117	12.43
Port Alfred	Jun. 1992	2 035	220	10.81
Agulhas Bank	May 1993	2 875	72	2.50
Total		11 144	1 031	9.25

Table II: Date and numbers of recaptures of male and female *P. gilchristi* in the first year after tagging, and the frequency of moulting for the four study areas and areas combined

Month tagged	Month recaptured	Males		Females	
		Number recaptured	% moulted	Number recaptured	% moulted
<i>Agulhas Bank</i>					
May 1988	Jun. – Nov. 1988	0	–	0	–
	Dec. 1988 – Feb. 1989	5	60	3	67
	Mar. 1989	1	100	3	67
	Apr. – May 1989	5	60	0	–
<i>Agulhas Bank</i>					
Feb. 1992	Mar. 1992	1	0	0	–
	Apr. – Sep. 1992	0	–	0	–
	Oct. – Nov. 1992	12	100	10	100
	Dec. 1992 – Feb. 1993	42	100	36	100
<i>Agulhas Bank</i>					
May 1993	Jun. – Aug. 1993	0	–	0	–
	Sep. – Nov. 1993	7	14	4	0
	Dec. 1993 – Mar. 1994	0	–	0	–
	Apr. – May 1994	2	100	2	100
<i>St Francis</i>					
May 1990	Jun. – Sep. 1990	6	17	5	0
	Oct. – Nov. 1990	16	13	13	15
	Dec. 1990 – Feb. 1991	13	77	15	60
	Mar. 1991	7	100	6	67
	Apr. – May 1991	11	91	11	73
<i>Port Elizabeth</i>					
Aug. 1990	Sep. – Nov. 1990	71	4	19	0
	Dec. 1990 – Feb. 1991	9	78	1	100
	Mar. 1991	1	100	0	–
	Apr. – Jun. 1991	12	83	12	75
<i>Port Alfred</i>					
Jun. 1992	Jul. – Nov. 1992	0	–	1	0
	Dec. 1992 – Jan. 1993	0	–	0	–
	Feb. 1993	75	87	64	58
	Mar. 1993	3	100	0	–
	Apr. 1993	14	71	15	67
<i>All data combined</i>					
	Tag date – Nov.	113	17	52	23
	Dec. – Feb.	144	88	119	71
	Mar.	12	100	9	67

range annual growth per 5-mm length interval by the mean moult increment in that interval; second, by dividing predictions of annual growth (obtained from the preceding analyses) by predictions of moult increment. Moult frequency was inverted to provide the intermoult period (the number of months between moults), which could be used in growth models based on moult increment and intermoult period.

Growth models for *P. gilchristi* were based on the assumption that juveniles recruited to the fishery at a *CL* of 50 mm, the smallest *CL* found in commercial

catches. Models were constructed by combining the regressions of moult increment with intermoult period (Botsford 1985). This formed a complete description of growth after recruitment for the region from the Agulhas Bank to Port Elizabeth, and for Port Alfred. In the models, *CL* at each moult after recruitment at 50 mm is given by the equation

$$CL_{n+1} = CL_n + m_n \quad (1)$$

where CL_n is the carapace length at moult n , and m_n

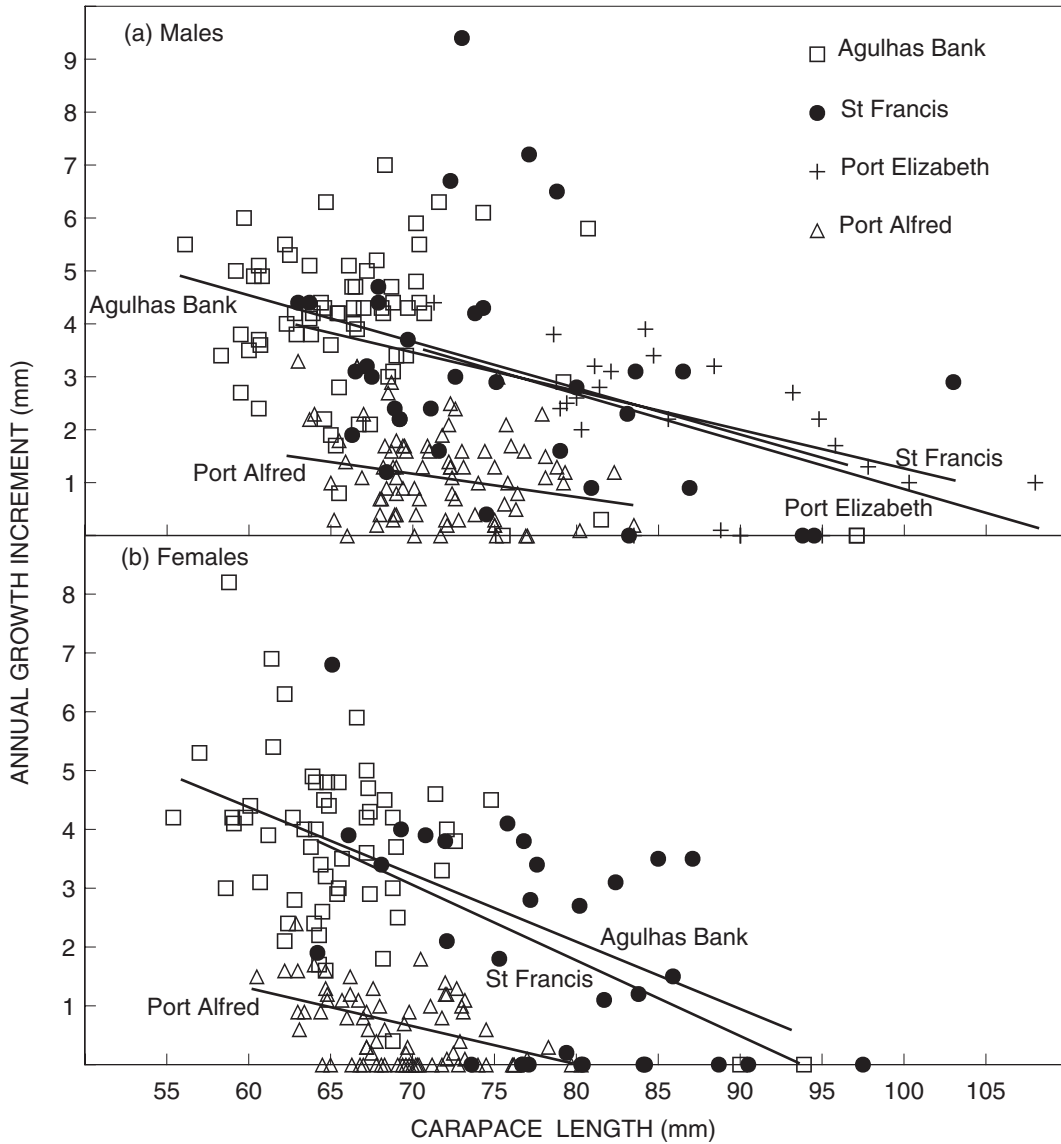


Fig. 2: Relationships between annual growth increments and carapace length for (a) male and (b) female *P. gilchristi* at the Agulhas Bank, St Francis, Port Elizabeth and Port Alfred fishing grounds

is the moult increment corresponding to CL_n , calculated from the linear regression of moult increment ($m_n = \alpha + \beta CL_n$). The time period t_{n+1} needed to reach CL_{n+1} is calculated from the equation

$$t_{n+1} = t_n + P_n \quad (2)$$

where P_n is the intermoult period derived from

$$P_n = m_n / a_n \quad (3)$$

where a_n is calculated from the linear regression of annual increment-at-size ($a_n = \gamma + \lambda CL_n$).

Table III: Proportions of small and large *P. gilchristi* that moulted in two-month intervals in the first year after tagging

Number of months after tagging	Recapture per size-class			
	Small (< 70 mm pre-moult <i>CL</i>)		Large (> 70 mm pre-moult <i>CL</i>)	
	Number recaptured	% moulted	Number recaptured	% moulted
1–2	1	0	14	0
3–4	1	0	31	9
5–6	11	0	24	25
7–8	8	75	75	32
9–10	106	85	98	70
11–12	91	88	68	76

In addition to these growth models, L_{∞} (mm *CL*) and K ($\cdot\text{year}^{-1}$) data for the generalized form of the Von Bertalanffy growth function

$$L_t = L_{\infty} (1 - e^{-Kt})$$

are presented for males and females from each study area. These data were derived from annual growth-at-size regressions.

RESULTS

Of 11 144 lobsters tagged during six tagging sessions between May 1988 and May 1993, 1 031 (9.25%) were recaptured by May 1995 (Table I).

Table II summarizes information used to estimate moulting season. On the Agulhas Bank, most lobsters that were tagged in May 1988 and recaptured between December 1988 and February 1989 had increased in size, having presumably moulted. Only a small percentage of those tagged in May 1993 and recaptured in November that year had moulted, but all those recaptured in April and May of the following year had moulted. These findings suggest that most lobsters on the Agulhas Bank moult between December and February.

At St Francis, few lobsters tagged in May 1990 and recaptured before December 1990 had moulted, but most of those recaptured between December 1990 and February 1991 had moulted. Similarly, few lobsters tagged at Port Elizabeth in August 1990 and recaptured before December that year had moulted, but most individuals recaptured between December 1990 and February 1991 had moulted. Therefore, most lobsters at St Francis and Port Elizabeth moult between December and February, but some may moult at other times of the year.

At Port Alfred, lobsters tagged in June 1992 were

recaptured between February and April 1993, and most had moulted. This suggests that most lobsters at Port Alfred moult between July and February. There is some evidence, based on a single animal recaptured between June and November, to suggest that the moulting season at Port Alfred may also be between December and February.

Small (<70 mm pre-moult *CL*) lobsters moult more frequently than large (>70 mm pre-moult *CL*) lobsters ($p < 0.05$, for the hypothesis that equal proportions moult within one year of tagging, Table III). The February 1992 sample on the Agulhas Bank indicated that small lobsters start to moult earlier in summer than do large lobsters; all lobsters (of which 92% were <70 mm *CL*) caught in October and November 1992 had already moulted (Table II).

All regressions of annual growth as a function of *CL* were significant ($p < 0.05$), except for females at Port Elizabeth, where the sample size was small, and males at St Francis ($p < 0.01$, Table IV). An analysis of covariance comparing annual growth between areas indicated that growth in males and in females differed between areas. However, if the Port Alfred data are omitted from the analysis, the annual growth in males and in females did not differ significantly between Agulhas Bank, St Francis and Port Elizabeth. When pooling the data from those three areas, the regression analysis indicated that the annual growth in male and in female lobsters at Port Alfred was significantly less than in the other study areas (Fig. 2). In all areas, males grew slightly faster (but not significantly) per year than females.

For the determination of moult increment and moult frequency as a function of *CL*, data from Agulhas Bank, St Francis and Port Elizabeth were combined. The growth regressions indicated that annual growth in these three areas was similar.

All regressions of moult increment as a function of *CL* (Table IV) were significant ($p < 0.05$), with moult increments decreasing with increasing size. Moult

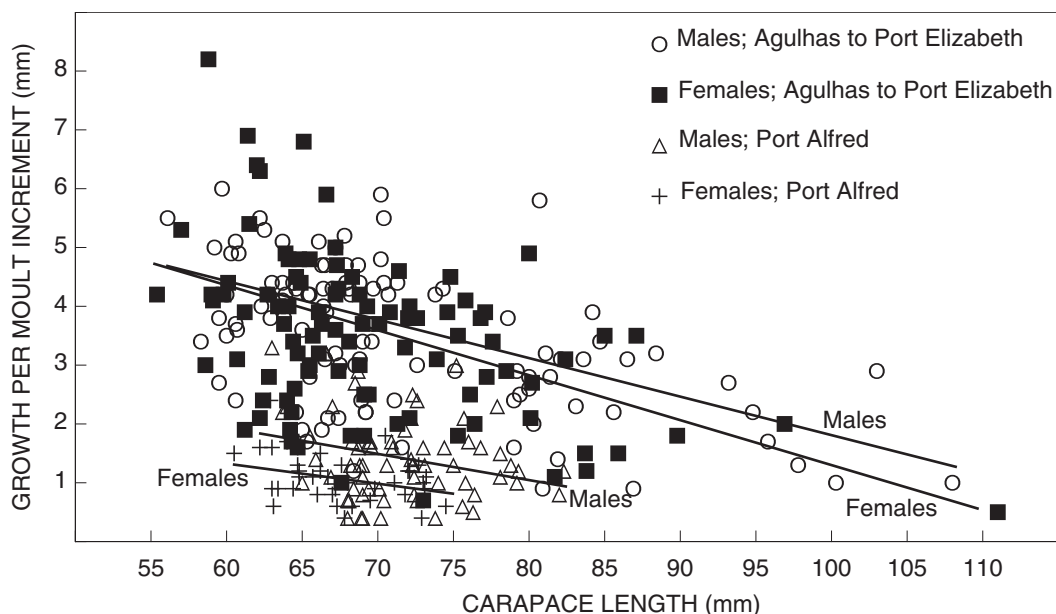


Fig. 3: Relationships between moult increments and carapace length for male and female *P. gilchristi* between Agulhas Bank and Port Elizabeth and at Port Alfred

increments for both males and females between Agulhas Bank and Port Elizabeth were significantly larger than at Port Alfred (Fig. 3). There was no significant difference in moult increment between males and females

in either the region between Agulhas Bank and Port Elizabeth or at Port Alfred.

Both methods used to estimate the annual number of moults for an individual of a certain size showed that

Table IV: Regression statistics for the annual growth and moult increment relationships for male and female *P. gilchristi* at Agulhas Bank, St Francis, Port Elizabeth and Port Alfred, and between Agulhas Bank and Port Elizabeth

Locality	Sex	Number of days at large	Relationship ($y = a + b CL$)	r^2	SE of y	SE of b	n	p
<i>Annual increment-at-size</i>								
Agulhas Bank	Male	244 – 404	$y = 9.738 - 0.0864 CL$	0.17	1.423	0.024	67	< 0.001
St Francis	Male	211 – 428	$y = 8.501 - 0.0721 CL$	0.10	2.023	0.037	35	< 0.1
Port Elizabeth	Male	172 – 433	$y = 10.08 - 0.0919 CL$	0.33	1.144	0.028	24	< 0.005
Port Alfred	Male	232 – 307	$y = 4.854 - 0.0512 CL$	0.07	0.853	0.021	84	< 0.025
Agulhas Bank – Port Elizabeth	Male	172 – 433	$y = 9.786 - 0.0880 CL$	0.29	1.547	0.012	126	< 0.001
Agulhas Bank	Female	254 – 424	$y = 11.26 - 0.1146 CL$	0.24	1.325	0.028	57	< 0.001
St Francis	Female	258 – 427	$y = 12.52 - 0.1339 CL$	0.35	1.508	0.033	32	< 0.001
Port Elizabeth	Female	409 – 426	$y = 3.949 - 0.0145 CL$	0.02	0.913	0.039	9	> 0.25*
Port Alfred	Female	231 – 307	$y = 5.832 - 0.0763 CL$	0.24	0.593	0.016	75	< 0.001
Agulhas Bank – Port Elizabeth	Female	254 – 427	$y = 11.61 - 0.1208 CL$	0.41	1.361	0.015	98	< 0.001
<i>Moult increment-at-size</i>								
Agulhas Bank to Port Elizabeth	Male	137 – 433	$y = 7.974 - 0.0628 CL$	0.29	1.054	0.009	106	< 0.001
Port Alfred	Male	232 – 508	$y = 4.365 - 0.0407 CL$	0.06	0.713	0.020	68	< 0.05
Agulhas Bank to Port Elizabeth	Female	165 – 427	$y = 8.441 - 0.0715 CL$	0.21	1.255	0.014	97	< 0.001
Port Alfred	Female	231 – 304	$y = 3.625 - 0.0373 CL$	0.12	0.395	0.017	39	< 0.05

CL = Carapace length (mm)

* = Not significant

Table V: Annual moult frequency of male and female *P. gilchristi*, estimated by dividing the average annual growth increment by the moult increment per 5-mm length interval (Method 1), and by dividing the predicted annual growth by the predicted moult increment (Method 2)

Length interval (mm)	Number of moults per year			
	Agulhas Bank, St Francis and Port Elizabeth		Port Alfred	
	Males	Females	Males	Females
<i>Method 1</i>				
50 – 54	–	–	–	–
55 – 59	1.00	1.00	–	–
60 – 64	1.02	0.97	1.00	0.91
65 – 69	1.02	1.03	0.89	0.48
70 – 74	1.13	1.06	0.83	0.47
75 – 79	1.23	0.67	0.71	–
80 – 84	0.84	0.43	0.50	–
85 – 89	0.81	0.79	–	–
90 – 94	0.33	–	–	–
95 – 99	0.40	–	–	–
100 – 104	0.84	–	–	–
105 – 109	–	–	–	–
<i>Method 2</i>				
50 – 54	1.11	1.14	0.98	1.15
55 – 59	1.09	1.10	0.96	1.04
60 – 64	1.07	1.05	0.93	0.91
65 – 69	1.04	0.99	0.88	0.73
70 – 74	1.01	0.92	0.84	0.49
75 – 79	0.98	0.83	0.77	0.14
80 – 84	0.93	0.72	0.68	–
85 – 89	0.87	0.57	0.55	–
90 – 94	0.80	0.37	0.35	–
95 – 99	0.71	0.08	–	–
100 – 104	0.58	–	–	–
105 – 109	0.40	–	–	–

P. gilchristi from the Agulhas Bank to Port Elizabeth region moulted more frequently than those at Port Alfred. In all regions, moult frequencies decreased with increasing size (Table V). Small individuals (50 – 70 mm *CL*) between the Agulhas Bank and Port Elizabeth generally moulted more than once per year. For larger lobsters, females moulted progressively less frequently than males. Small individuals (50 – 60 mm *CL*) at Port Alfred moulted annually. However, as *CL* increased, moult frequency decreased sharply, particularly for lobsters >75 mm, which sometimes had growth increments too small (<1 mm) to measure (Table V).

Predictions of lobster size-at-age after recruitment (Table VI) indicate slower growth at Port Alfred than between Agulhas Bank and Port Elizabeth, as a result of smaller moult increments. Females grew slower than males because of smaller moult increments and longer intermoult periods, the latter becoming more

apparent after 5 – 6 moults. The model predicts theoretical maximum lengths of 127 mm (males) and 119 mm (females) for the region between Agulhas Bank and Port Elizabeth and 107 mm (males) and 97 mm (females) at Port Alfred. These are consistent with maximum observed lengths of approximately 130 mm in the larger, combined region and 110 mm at Port Alfred (pers. obs.).

The theoretical maximum lengths (L_{∞}) of the Von Bertalanffy growth function for males and females (Table VII) were considerably smaller than those observed in the commercial fishery (SFRI unpublished data). The growth coefficients (*K*) were larger for lobsters from Agulhas Bank to Port Elizabeth than at Port Alfred.

DISCUSSION

Estimates of various aspects of lobster growth, such as annual growth, moult increment and moulting frequency, are subject to the limitations of tag-recapture data, and certain assumptions need to be made. In this study, a positive increment in *CL* was assumed to be the sole indicator that moulting had taken place. In rock lobsters, moulting may occur without growth, and even with body shrinkage (Conan 1985, Cockcroft and Goosen 1995). Therefore, some animals may moult without detection. Consequently, the intermoult periods computed in the present growth models are likely overestimated, especially in the larger size-classes where moult increments are often too small to detect (see Table VI).

The parameters of the Von Bertalanffy growth functions were determined from annual growth increments-at-size. This eliminated the need to combine moult increments with intermoult periods and to use an increase in *CL* as an indication of moulting. That the predicted maximum lengths (L_{∞}) were considerably smaller than the lobsters sampled is likely a result of the zero increments recorded in many of the larger lobsters, when increments were too small to detect.

Female *P. gilchristi* grew progressively slower than males for a given length after reaching 65 – 69 mm *CL* at Port Alfred and 70 – 74 mm in the region between Agulhas Bank and Port Elizabeth (Table VI). It is around this length that females attain sexual maturity and start reproducing; in the combined region they attained sexual maturity at a larger *CL* (63 – 71 mm) than at Port Alfred (59 – 62 mm, Groeneveld and Melville-Smith 1994). In many crustaceans, female growth decreases at the onset of maturity (Hartnoll 1985, Lipcius 1985), which seems to be the case for *P. gilchristi*. The present study indicates

Table VI: Prediction in the size (CL_n)-at-age (t_n) after recruitment of male and female *P. gilchristi* for the region between Agulhas Bank and Port Elizabeth and for Port Alfred. P_n and m_n denote intermoult period- and moult increment-at-age respectively

Recruitment (R) and number of moults	Males				Females			
	t_n (months)	CL_n (mm)	m_n (mm·moult ⁻¹)	P_n (months)	t_n (months)	CL_n (mm)	m_n (mm·moult ⁻¹)	P_n (months)
<i>Agulhas Bank, St Francis and Port Elizabeth</i>								
R	0	50.00	4.83	10.8	0	50.00	4.87	10.4
1	10.8	54.83	4.53	11.0	10.4	54.87	4.52	10.9
2	21.8	59.36	4.25	11.2	21.3	59.38	4.20	11.3
3	33.0	63.61	3.98	11.4	32.6	63.58	3.89	11.9
4	44.4	67.59	3.73	11.6	44.5	67.47	3.62	12.5
5	56.0	71.32	3.50	12.0	57.0	71.09	3.36	13.3
6	68.0	74.81	3.28	12.2	70.3	74.45	3.12	14.3
7	80.2	78.09	3.07	12.6	84.6	77.57	2.89	15.5
8	92.8	81.16	2.88	13.1	100.1	80.46	2.69	17.1
9	105.9	84.04	2.70	13.4	117.2	83.15	2.50	19.1
10	119.3	86.73	2.53	14.2	136.3	85.65	2.32	22.0
11	133.5	89.26	2.37	14.6	158.3	87.96	2.15	26.2
12	148.1	91.63	2.22	15.4	184.5	90.11	2.00	33.1
13	163.5	93.85	2.08	16.4	217.6	92.11	1.85	46.1
14	179.9	95.93	1.95	17.4	263.7	93.97	1.72	79.8
15	197.3	97.87	1.83	18.7	343.5	95.69	1.60	378.5
16	217.6	99.71	1.71	20.3		97.29	1.48	
17	239.8	101.42	1.60	22.2		98.77	1.38	
18	264.8	103.02	1.50	25.0		100.15	1.28	
19	293.4	104.52	1.41	28.6		101.43	1.19	
20	327.7	105.94	1.32	34.3		102.62	1.10	
<i>Port Alfred</i>								
R	0	50.00	2.33	12.2	0	50.00	1.76	10.5
1	12.2	52.33	2.24	12.3	10.5	51.76	1.69	10.8
2	24.5	54.57	2.14	12.5	21.3	53.45	1.63	11.2
3	37.0	56.71	2.06	12.7	32.5	55.09	1.57	11.6
4	49.7	58.77	1.97	12.8	44.1	56.66	1.51	12.0
5	62.5	60.74	1.89	13.0	56.1	58.17	1.46	12.5
6	75.5	62.63	1.82	13.2	68.6	59.62	1.40	13.1
7	88.7	64.45	1.74	13.4	81.7	61.02	1.35	13.8
8	102.1	66.19	1.67	13.7	95.5	62.37	1.30	14.5
9	115.8	67.86	1.60	13.9	110.0	63.67	1.25	15.4
10	129.7	69.46	1.54	14.2	125.4	64.92	1.20	16.4
11	143.9	71.00	1.48	14.5	141.8	66.12	1.16	17.7
12	158.4	72.48	1.42	14.9	159.5	67.28	1.12	19.2
13	173.7	73.89	1.36	15.2	178.7	68.40	1.07	21.0
14	188.9	75.25	1.30	15.6	199.7	69.47	1.03	23.4
15	204.5	76.55	1.25	16.0	223.1	70.51	1.00	26.4
16	220.5	77.80	1.20	16.5	249.5	71.50	0.96	30.5
17	237.0	79.00	1.15	17.0	280.0	72.46	0.92	36.5
18	254.0	80.15	1.10	17.6	316.5	73.38	0.89	45.7
19	271.6	81.25	1.06	18.3	362.2	74.27	0.85	62.1
20	289.9	82.31	1.01	19.0	424.3	75.12	0.82	98.7

that the relatively slower growth in mature females is because of their longer intermoult periods and smaller moult increments.

A greater number of animals moulted during summer (December – February) than in other months. Intermoult periods ranged between 10.4 months and several years (Table VI). Therefore, frequent moulting should occur outside the summer moulting season. Small lobsters moult more often than large lobsters, probably

in early summer and again later in the season. This higher moult frequency and large moult increments result in rapid growth. Reproductively active female lobsters are believed to moult once annually, during summer and outside the winter egg-bearing season (Groeneveld and Rossouw 1995). Large females (>85 mm CL) may bear eggs more than once per year (Groeneveld and Rossouw 1995) and are likely to moult fewer than once per year.

Table VII: Values of the parameters of the Von Bertalanffy growth equation estimated for male and female *P. gilchristi* between Agulhas Bank and Port Elizabeth and at Port Alfred

Locality	Value		
	Sex	L_{∞} (mm)	K (year ⁻¹)
Agulhas Bank to Port Elizabeth	Male	111.20	0.092
Agulhas Bank to Port Elizabeth	Female	96.11	0.129
Port Alfred	Male	95.75	0.050
Port Alfred	Female	78.50	0.065

Comparing the present annual growth estimates with those determined by Pollock and Augustyn (1982) from tag recaptures between 1974 and 1978 (Table VIII), current growth appears to be slower than in the earlier

between Agulhas Bank and Port Elizabeth. In addition, the average size (Pollock and Augustyn 1982, Groeneveld and Rossouw 1995) and the size at sexual maturity (Groeneveld and Melville-Smith 1994) are smaller at Port Alfred than between Agulhas Bank and Port Elizabeth. Many studies (see Pollock 1995) have shown a positive relationship between growth and size at maturity.

Studies on palinurid species suggest that food availability is an important factor in determining growth rates (Newman and Pollock 1974, Chittleborough 1976, Pollock 1979, 1982, 1991, McKoy and Esterman 1981, Pollock and Beyers 1981). Temperature, photoperiod, oxygen, crowding and loss of limbs have also been shown to influence growth in lobsters (Chittleborough 1975). Groeneveld (1993) suggested that regional variations in the average size and size at sexual

Table VIII: Annual growth increments for male and female *P. gilchristi* between Agulhas Bank and Port Elizabeth and at Port Alfred. Increments in parenthesis are from Pollock and Augustyn (1982)

Carapace length (mm)	Annual growth increment (mm·year ⁻¹)			
	Agulhas Bank to Port Elizabeth		Port Alfred	
	Male	Female	Male	Female
65	4.1 (5.0*)	3.8	1.5 (1.7)	0.9 (1.3)
75	3.2	2.6	1.0 (1.4)	0.1 (0.7)
85	2.3	1.3	0.5	0
95	1.4 (1.0*)	0.1	0	0
105	0.5 (1.0*)	0.0 (0*)	0	0

* From Rocky Bank, west of the Agulhas Bank fishing grounds

study. In the only direct regional comparison (for males of 65 mm *CL*), the declines are similar, i.e. 18% between Agulhas Bank and Port Elizabeth and 12% at Port Alfred. It should be noted that the earlier study was limited to particular size-classes and was based on small sample sizes. Also, annual fluctuations in growth rates are common in local lobster populations (Melville-Smith *et al.* 1995).

Both the present study and that of Pollock and Augustyn (1982) indicate that the growth rate of *P. gilchristi* at Port Alfred is significantly slower than

maturity of *P. gilchristi* were possibly linked to differences in food availability and the relative proximity of the Agulhas Current. It was suggested that strong bottom currents at Port Alfred, where the Agulhas Current flows close inshore (Schumann 1987), may limit lobster foraging efficiency (Groeneveld and Melville-Smith 1994), or that potential food may be entrained and removed from that region by the Current (Groeneveld 1993). However, between the Agulhas Bank and Port Elizabeth the core of the Agulhas Current flows farther offshore, limiting the effect of

Table IX: Commercial catch-per-unit-effort, expressed as the numbers of *P. gilchristi* caught per trap for the four study areas

Season	Catch-per-unit-effort by locality				Source
	Agulhas Bank	St Francis	Port Elizabeth	Port Alfred	
1977/78	1.02	0.92	0.92	1.88	Pollock and Augustyn (1982)
1992/93	1.33	0.87	0.74	1.78	SFRI unpublished data
1993/94	0.88	0.82	0.84	1.10	SFRI unpublished data
1994/95	1.06	0.69	0.79	1.20	SFRI unpublished data

bottom currents on food availability and foraging conditions of *P. gilchristi*. Also, possible density-dependent mechanisms may be involved, considering the narrow width of the continental shelf off Port Alfred, which would result in increased intraspecific competition for food in that area. Catch-per-unit-effort of lobsters, expressed as numbers caught per trap, is higher at Port Alfred than in any of the other study areas (Table IX).

Regional variations in the average size of another South-East African *Palinurus* species, *P. delagoae*, follows a similar pattern to that of *P. gilchristi*. Small *P. delagoae* occur on narrow continental shelf areas, whereas larger *P. delagoae* are found on wider shelf areas (Cockcroft *et al.* 1995). Like *P. gilchristi*, juvenile *P. delagoae* are believed to recruit to the fishing grounds by migrating up the continental slope from greater depths (Cockcroft *et al.* 1995). It is likely that similar physical and density-dependent mechanisms operate on both species.

In conclusion, it is postulated that the regional variation in the growth of *P. gilchristi* on the South Coast is a result of density-dependence. There is increased intraspecific competition for limited food resources in areas where the population density is greater as a result of limited space on narrow shelf areas. Growth rates in lobsters are also slower in those areas, reflected in their smaller average size (Pollock and Augustyn 1982, Groeneveld and Rossouw 1995) and size at sexual maturity (Groeneveld and Melville-Smith 1994). Strong bottom currents off Port Alfred may further influence growth rates by affecting food availability and foraging conditions. Future research to investigate the environmental factors responsible for regional growth variations should focus on both *P. gilchristi* and *P. delagoae*, as similar mechanisms probably operate on both species.

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