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A NOTE ON REDUCED ROCK LOBSTER GROWTH RATES AND RELATED ENVIRONMENTAL ANOMALIES IN THE SOUTHERN BENGUELA, 1988-1995

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A series of environmental perturbations in the southern Benguela upwelling system off the Cape west coast has had dramatic effects on the productivity of the rock lobster *Jasus lalandii*, a keystone predator of the nearshore ecosystem. Reduced lobster growth rates adversely affected annual recruitment to the legal size range, and Total Allowable Catches were drastically reduced during the early 1990s. The widespread nature of the reduction in lobster growth rates indicate a large-scale environmental perturbation. Productivity changes in the southern Benguela, associated with the anomalous *El Niño* years of 1990-1993, are believed to be the main cause of the phenomenon.

After an initial, localized decline in rock lobster *Jasus lalandii* growth rates recorded during male moulting in November 1988, reductions in lobster growth became a coastwide phenomenon during subsequent seasons. The period between 1990 and 1993 became known as *El Niño* years, during which time severe droughts were experienced over most parts of southern Africa, indicative of widespread anomalies in weather patterns associated with a prolonged *El Niño* – Southern Oscillation (ENSO) event in the Pacific Ocean. In the southern Benguela, the most obvious signature of this ENSO was the reduced frequency and intensity of southerly, upwelling-inducing winds, with a concomitant increase in westerly winds.

This study attempts to relate the reduction in lobster growth and productivity to environmental factors which prevailed in the southern Benguela during the late 1980s and early 1990s. The reduction in growth had a severe effect on the production and yields from the lobster resource. As shown in Table I, the Total Allowable Catch (*TAC*) could not be filled in the 1989/90 and 1990/91 seasons, and a series of major reductions in *TAC* took place during ensuing years, with serious impacts on the economics of the fishery. This situation was not alleviated by a reduction in the minimum size limit from 89 to 75 mm carapace length in 1993 (Castilla *et al.* 1994, Cockcroft and Payne 1997).

Table I: *TAC*s and landings of *Jasus lalandii* on the Cape west coast, 1988–1996

Season	*TAC* (tons)	Landings (tons)
1988/89	4 000	4 000
1989/90	3 900	3 491
1990/91	3 790	2 996
1991/92	2 400	2 480
1992/93	2 200	2 176
1993/94	2 200	2 177
1994/95	2 000	1 958
1995/96	1 500	1 518

The reason for the collapse in productivity of the Cape west coast rock lobster resource, which began in 1988 and continued throughout the early 1990s, is still not thoroughly understood. This paper documents the series of events associated with this phenomenon, information that may provide a better understanding of the role of the environment in influencing possible future anomalous changes in the growth rate and productivity of rock lobster.

CHRONOLOGICAL SUMMARY OF EVENTS IN THE SOUTHERN BENGUELA, 1988–1995

Shannon *et al.* (1992) first drew attention to a series of environmental anomalies in the Benguela system during the late 1980s and early 1990s. They highlighted a number of dramatic changes in various marine resources during that period, but they lacked the necessary data to link pelagic and benthic ecosystem changes quantitatively. The following summarizes the events in the Benguela system from 1988 to 1995, thereby updating the account of Shannon *et al.* (1992).

1988. Growth increments of male rock lobsters moulting in November/December 1988 declined notably at Elands Bay and Donkins Bay (Fig. 1), but not on the fishing grounds farther south (Table II).

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Table II: Annual growth increments (negative moult increments included) for two size-classes of male *Jasus lalandii* in four areas on the east coast of South Africa (modified from Goosen and Cockcroft 1995 and Cockcroft and Goosen 1995)

Moulting season (November)	Growth increment (mm) per size-class					
	70.0–79.9 (mm)			80.0–89.9 (mm)		
	n	Mean	*SD*	*n*	Mean	*SD*
Cape Peninsula (Olifantsbos)						
1968				54	2.9	1.96
1969	54	4.3	1.52	75	3.7	1.98
1970	12	4.7	1.67	17	3.4	1.37
1971				16	3.4	1.55
1982				197	3.3	1.98
1986				10	1.7	1.25
1987				88	2.2	1.51
1988				122	1.8	1.76
1989				96	2.2	1.75
1990				42	1.3	1.61
1991				149	0.9	1.55
1992	177	2.2	1.45	295	1.1	1.17
1993	67	1.3	1.55	74	0.8	1.63
1994	63	1.8	1.93	53	1.4	1.90
1995	99	1.7	1.11	49	1.0	1.16
Dassen Island						
1969	20	5.3	1.38	53	4.4	1.56
1970	35	4.1	1.90	34	4.6	1.86
1971	29	5.9	2.30	51	5.7	2.08
1980				458	3.7	2.03
1983				87	3.4	1.92
1987				47	4.3	1.59
1988				54	4.6	1.62
1989				55	3.0	2.32
1990				36	1.4	1.42
1991				63	0.7	1.16
1992	79	1.8	1.60	92	1.1	1.76
1993	37	3.6	2.45	53	2.5	2.01
1994	91	2.8	1.99	43	2.5	1.57
1995	41	3.8	1.80	34	3.6	2.20
Elands Bay						
1975				53	5.3	1.97
1976				28	4.2	1.64
1981				221	4.7	1.83
1982				28	4.7	1.72
1987				9	4.8	3.19
1988				33	3.6	1.73
1989				14	2.1	2.46
1990				15	0.9	1.41
1991				107	3.3	1.77
1992	36	2.5	2.06	139	2.1	2.20
1994	76	3.0	2.01	94	2.2	1.42
1995	97	2.7	2.30	35	1.4	1.80
Port Nolloth (Obeep Bay)						
1987	38	2.5	1.75	72	1.4	1.58
1988	26	2.7	1.57	41	1.7	1.53
1989	18	1.8	2.20	21	1.4	1.66
1990	56	0.5	1.10	66	0.3	0.95
1991	31	1.2	1.96	56	0.3	1.86
1992	31	1.2	1.65	57	0.9	1.31
1993	58	1.1	1.78	147	1.1	1.53
1994	53	0.3	0.94	47	0.2	0.93
1995	55	1.2	1.25	66	1.1	1.35

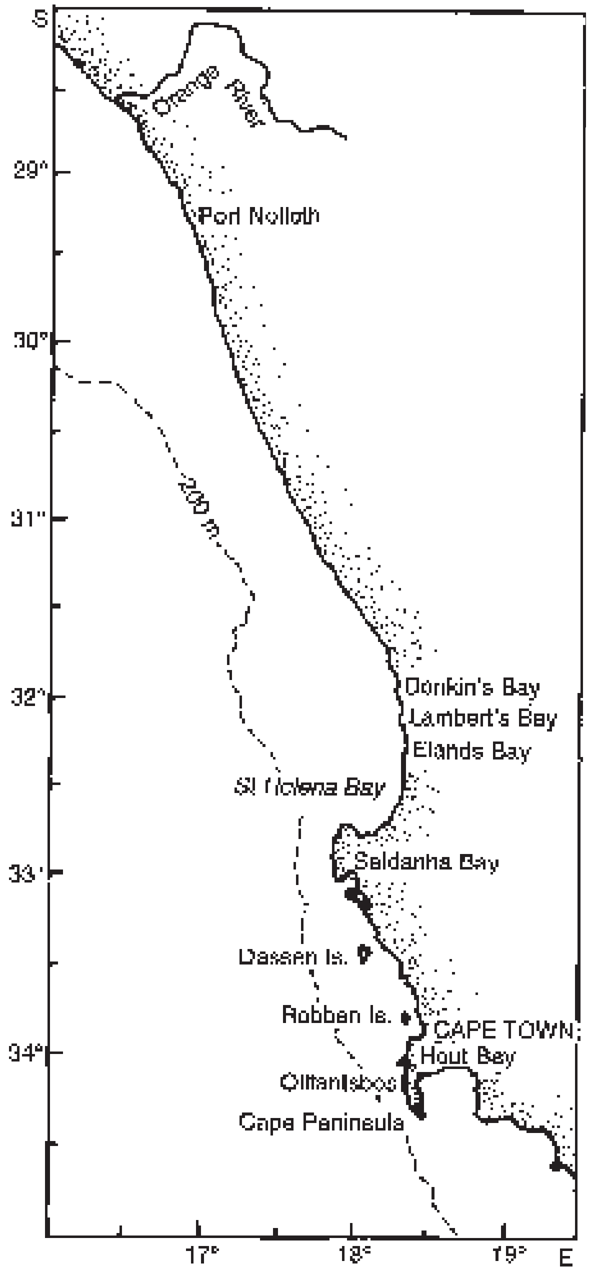

Fig. 1: The west coast of South Africa showing the places and localities mentioned in the text

Shelf waters cooled markedly in 1988, and anomalous environmental conditions in the pelagic environment were reflected in the low anchovy oil yields recorded for that year (Anon. 1991, Schülein *et al.* 1995).

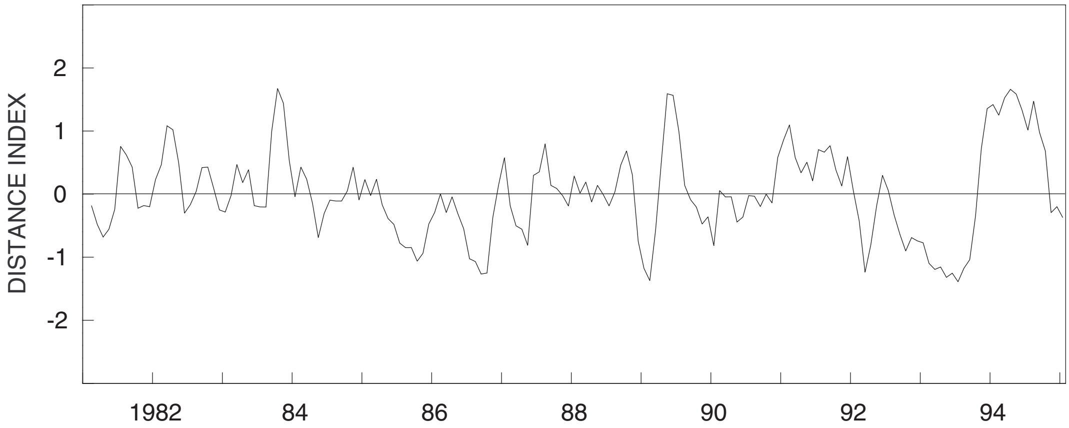

Fig. 2: Monthly average position of the 16°C isotherm (distance from the coast) at 31°S, off the west coast of South Africa. Data have been normalized and smoothed with a three-month running mean

1989. Although shelf waters remained cool in January and February, there were surface intrusions of very warm water along the Cape west coast, illustrated by a retraction in the offshore position of the 16°C isotherm at 31°S (Fig. 2). During that period, surface waters were oligotrophic, with very low values of chlorophyll-*a* content. By June, it was apparent that anchovy *Engraulis capensis* recruitment had failed, and growth rates of 0-year olds were slower than in 1986. Anchovy oil content was also low (Schülein *et al.* 1995), reflecting poor feeding conditions in the pelagic zone. A sharp reduction in male lobster growth rates at moulting in November/ December 1989 was recorded at Donkins Bay, Elands Bay and Dassen Island fishing grounds in the north (Table II), whereas farther south, along the Cape Peninsula, lobster growth rates remained unaffected.

1990. The year marked the start of a period in which the Benguela system was affected by the anomalies associated with the ENSO event in the Pacific (Fig. 3). The most obvious signal in the southern Benguela was the reduction in southerly, upwelling-inducing winds and concomitant increase in westerly winds (Fig. 4). Also, summer (November-March) atmospheric pressures were lower than average between 1990/91 and 1992/93 (Fig. 5). It is note-

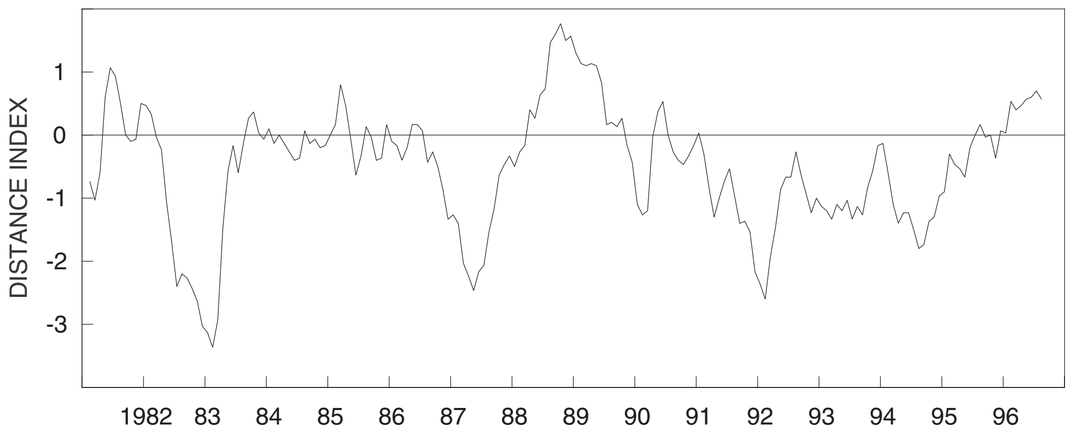

Fig. 3: Monthly Southern Oscillation Index values from 1981 to 1996, smoothed with a three-month running mean. Data obtained from the Climate Analysis Center, NOAA, USA

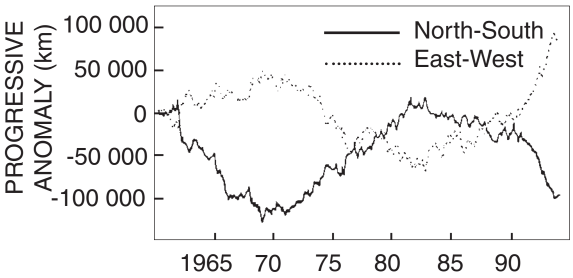

Fig. 4: Progressive North-South and East-West wind displacement anomalies, computed from the Cape Point lighthouse wind data, 1960–1993

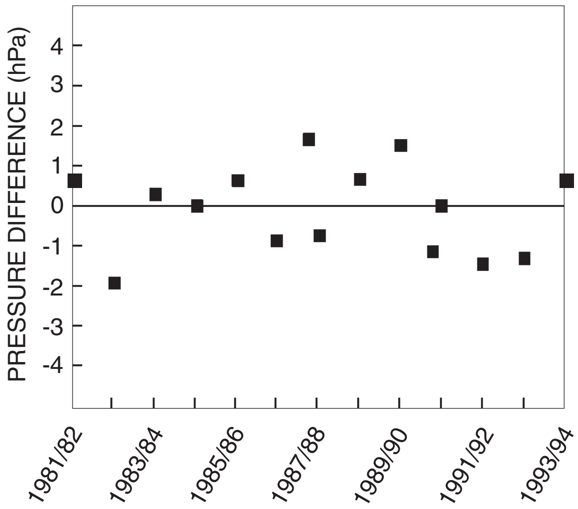

Fig. 5: Sea level atmopheric pressure difference, measured southwards from Cape Agulhas (35°S, 20°E) to 40°S, 20°E. Data are presented for summer only (November-March) for the period 1981–1994. Positive indices indicate predominantly southerly and easterly winds and negative values indicate predominantly northerly and westerly winds. Redrawn from Agenbag (1996)

worthy that the index also indicated the 1982/83 and 1986/87 ENSO anomalies (Fig. 5). The summer of 1989/90 was characterized by a high incidence of red tides, which included the toxic dinoflagellate *Gonyaulax catanella* that causes paralytic shellfish poisoning. Early autumn storms, especially in April 1990, caused large wash-outs and mortalities of black mussels, which had probably been weakened by exposure to toxic red tides during the preceding summer and autumn. Farther north, in Namaqualand, heavy winter rains, driven by north-westerly gales, caused extensive flooding of the Berg River and the rivers entering Lambert's Bay and Elands Bay (Verlorenvlei). Evidence of extensive silting and sanding-over of shallow reefs was observed during diving surveys along that coastline during December 1990.

By May 1990, anchovy recruitment was again exceptionally poor. At the moulting of males in November/December 1990, lobster growth rates were extremely low on all fishing grounds along the West Coast, extending even as far south as the Cape Peninsula and the adjoining rock lobster sanctuary at Hout Bay (Tables II, III). Shelf waters were still unusually cold during 1990, which was reflected in a prolongation of the normal incubation period (the berried lobster phase; normally from June to late October) of female lobsters. However, in 1990/91 females were still in berry during December and some even into January 1991. Brood sizes of females were also smaller in 1990, coincident with the retarded growth rates of males recorded in November/December of that year (Melville-Smith *et al.* 1995).

It is noteworthy that, during diving surveys in 1990 and 1991, high densities of newly-settled lobsters were observed on the inshore reefs (PCG pers. obs.). This phenomenon may have been related to enhanced onshore transport of offshore surface waters as a result of persistent westerly winds. Such conditions would be expected to concentrate late-stage phyllosoma larvae at the shelf-break and facilitate the cross-shelf migration of the puerulus stage, thereby enhancing recruitment.

1991. The ENSO-related anomalous conditions persisted during 1991, with many red tides being recorded between January and May, when westerly winds dominated (SFRI unpublished data). Shelf waters remained cool. A diving survey conducted at Dassen Island during February 1991 indicated that the previously abundant population of ribbed mussels *Aulacomya ater* there had been largely annihilated, probably as a result of adverse environmental conditions such as red tides and storms of the previous year. Mussel biomass at depths shallower than 20 m was about an order of magnitude lower than that recorded during earlier surveys in 1971. Fishermen reported that lobsters were caught at greater depths than normal during the 1990/91 fishing season, suggesting that the deeper areas were still relatively well oxygenated, even during autumn, enabling the lobsters to forage in deeper, less productive depths. Growth rates of male lobsters remained extremely low at the November/December 1991 moulting, a feature once again preceded by below average female brood sizes recorded during June 1991 (Melville-Smith *et al.* 1995). The coastwide

Table III: Mean growth increments for six size-classes of male *Jasus lalandii* at the Hout Bay Sanctuary, 1984–1995

Moulting season (November)	Growth increment (mm) per size-class											
	70–79 (mm)		80–89 (mm)		90–99 (mm)		100–109 (mm)		110–119 (mm)		120–129 (mm)	
	Mean	*n*	Mean	*n*	Mean	*n*	Mean	*n*	Mean	*n*	Mean	*n*
1984			4.7	17	4.5	52	4.1	47	3.0	14		
1985	3.8	11	4.2	23	3.9	16	2.3	15	1.4	61	0.5	43
1986			3.7	3	1.9	56	0.8	59	0.2	46	–1.0	3
1987			5.0	41	3.6	250	1.9	182	0.8	40	0.0	3
1988			3.6	7	3.4	54	1.3	43				
1989			3.4	10	2.6	16	1.0	3				
1990			0.3	3	0.4	23	0.3	6				
1991			1.8	22	1.4	73	1.4	10				
1992	2.0	50	1.7	170	1.3	90	0.5	2				
1993	2.0	30	1.4	48	1.1	20						
1994	4.2	72	3.2	130	2.7	37						
1995	3.5	63	3.3	180	2.2	71						

reduction in lobster growth rates indicated a widespread anomaly in the southern Benguela system, as postulated by Shannon *et al*. (1992). However, despite a much reduced adult population of anchovy recorded during November 1990, anchovy recruitment recovered during 1991.

1992. The ENSO event and associated anomalous westerly winds persisted in the southern Benguela system. Growth rates of male lobsters remained low on all West Coast fishing grounds (Table II). The slow growth rates of males were coincident with below-average brood sizes in females spawning during winter (Melville-Smith *et al*. 1995).

1993. The ENSO event terminated towards the end of the year and strong, south-easterly, upwelling-favourable winds resumed in the summer of 1993/94. However, growth of male lobsters at the November/December 1993 moult remained low (Table II).

1994. Despite the resumption of more normal southerly wind conditions in the summer of 1993/94, during February 1994 the winds slacked off abruptly and light onshore winds prevailed. These wind conditions were responsible for concentrating an extensive red tide along hundreds of kilometres of coastline. Subsequent decay of the bloom caused severe oxygen depletion, which resulted in the mortality of approximated 1 500 tons of fish and 60 tons of lobsters in St Helena Bay (Matthews and Pitcher 1996). This so-called "black-tide" event in March 1994 was the first of its kind recorded in South Africa. Anoxic conditions were associated with the formation of hydrogen sulphide, which is highly toxic to marine life. The impact of this event on the benthic environment and its subsequent recovery is under investigation.

The summer of 1994/95 again showed a fairly high incidence of upwelling, and the first sign of a possible improvement in male lobster growth rates was evident in the Hout Bay sanctuary area, where the mean moult increment of males increased in November 1994 (Table III). Elsewhere, growth rates still remained depressed (Table II).

1995. Catches of rock lobsters began to improve during the 1995/96 season, both along the Cape west coast and farther north in Namibian waters. The summer of 1995/96 was characterized by a high incidence of southerly to south-easterly winds, which commenced as early as September/October 1995 and continued intermittently until at least April 1996.

Growth rates of rock lobsters in the Hout Bay sanctuary were once again high relative to the average growth during the 1990–1993 *El Niño* years (Table III). Average growth in 1995/96 increased at Dassen Island and Port Nolloth, but remained low at Elands Bay and at Olifantsbos in the Cape Peninsula.

DISCUSSION

Given the strong correlation between the reduction in male rock lobster moult increments and brood sizes of females recorded during the period 1987–1992 (Melville-Smith *et al*. 1995), it is likely that the underlying cause of the slower growth rate in rock lobster was related to a diminished food supply and/or a decline in food quality. Food energy requirements affect both moult increments and female brood sizes in *J. lalandii* (Beyers and Goosen 1987, Melville-Smith *et al*. 1995, Pollock 1995). Therefore, it is not surprising that both indices of production declined simultaneously. What is unexpected, however, is the protracted nature and the widespread extent of the reduction, which suggests that the phenomenon was a result of a large-scale environmental perturbation in the Benguela system.

A plausible explanation for the reduction in rock lobster growth rate is a collapse of their most important food source, the ribbed mussel *A. ater*, which would effectively force them to switch to alternative, less abundant and/or less nutritious food sources. *J. lalandii* are omnivorous, but primarily carnivorous (Pollock 1979), and they can subsist on a wide variety of food items (Barkai *et al*. 1996). They are also able to survive lengthy periods of starvation (Cockcroft and Goosen 1995). It is noteworthy that those authors reported that between 13 and 25% of tagged male lobsters recaptured between 1990 and 1993 exhibited a shrinkage in body size. This phenomenon highlights the severity of the dietary deficiency, supporting the belief that a large, overall decline in the benthic productivity of the southern Benguela system may have had a detrimental impact on the health of the West Coast lobster resource.

This hypothesis does not explain why lobster growth rates started to decline as early as 1988, before the observed mortality of mussels in 1990. It is noteworthy that shelf waters cooled markedly in 1988, and anomalous conditions in the pelagic environment were reflected in the low anchovy oil yields and reduced anchovy recruitment reported for 1989 (Shannon *et al.* 1992). Although several studies have highlighted the importance of kelp bed detritus in fueling the energy requirements of detritivores and filter-feeders in the intertidal zone of the West Coast (Bustamente and Branch 1980), there is published (Pollock 1976, Field *et al.* 1980) as well as much anecdotal evidence that the large biomass of filter-feeders (especially ribbed mussel *Aulacomya ater*) in depths of 10–50 m on the West Coast rely largely on the rich phytoplankton-based food supply. This would imply that pelagic productivity in parts of the southern Benguela began to decline as early as 1988, but decreased still further and became more widespread during the 1990–1993 *El Niño* event. Shannon *et al.* (1992) noted low primary production in the southern Benguela in1988 and 1989.

Another possible explanation for the poor feeding conditions and subsequent reduction in lobster growth rates after 1989 is the effect of toxic dinoflagellate blooms on the physiology of mussels and other benthic filter-feeders. Toxicity of such important food items during summer and autumn, when lobsters lay down their food reserves (Cockroft and Goosen 1995), could have a detrimental effect on their growth-at-moulting later in the year. It is tempting to speculate that toxic red tides may be an important factor responsible for some of the interannual fluctuations in growth rates of the Cape west coast lobster during past decades.

Only when primary productivity in the Benguela system can be adequately assessed in a quantative manner, for example, by means the SeaWiFs ocean colour sensor, will it be possible to test the hypotheses presented here.

The present occurrences of high densities of small lobsters (possibly as a result of enhanced puerulus settlement during the *El Niño* years) feeding on newly settled mussels and other sessile organisms may impede the recovery to normal growth in the lobsters. This effect would likely be most pronounced in areas such as Elands Bay, and Olifantsbos in the Cape Peninsula, where the densities of sublegal lobsters are particularly high. If that is the case, the fishery will likely remain depressed until those lobsters have grown into the legal size range. Given that it takes approximately 7–8 years for males to reach the legal minimum size limit of 75 mm carapace length, the 1990–1993 year-classes would attain legal size by between 1997 and 2000.

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LITERATURE CITED

AGENBAG, J. J. 1996 — Pacific ENSO events reflected in meteorological and oceanographic perturbations in the southern Benguela system. *S. Afr. J. Sci.* **92**: 243–247.

ANON. 1991 — An investigation into the causes of the recent fluctuations in pelagic fish stocks off South Africa. Unpublished Report, Sea Fisheries Research Institute, South Africa: 8 pp. + 18 Figures (mimeo).

BARKAI, A., DAVIS, C. L. and S. TUGWELL 1996 — Prey selection by the South African Cape rock lobster *Jasus lalandii*: ecological and physiological approaches. *Bull. mar. Sci.* **58**: 1–8.

BEYERS, C. J. DE B. and P. C. GOOSEN 1987 — Variations in fecundity and size at sexual maturity of female rock lobster *Jasus lalandii* in the southern Benguela ecosystem. In *The Benguela and Comparable Ecosystems*. Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 513–521.

BUSTAMANTE, R. H. and G. M. BRANCH 1996 — The dependence

of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. *J. expl mar. Biol. Ecol.* **196**: 1–28.
CASTILLA, J. C., BRANCH, G. M. and A. BARKAI 1994 — Exploitation of two critical predators: the gastropod *Concholepas concholepas* and the rock lobster *Jasus lalandii*. In *Rocky Shores*: *Exploitation in Chile and South Africa.* Siegfried,W. R. (Ed). Berlin; Springer: 101–130.
COCKCROFT, A. C. and P. C. GOOSEN 1995 — Shrinkage at moulting in the rock lobster *Jasus lalandii* and associated changes in reproductive parameters. *S. Afr. J. mar. Sci.* **16**: 195–203.
COCKCROFT, A. C. and A. I. L. PAYNE 1997 — Cautious fisheries management in South Africa: the fisheries for rock lobster. *ICES Doc.* **C.M.1997/N:03**: 14 pp. (mimeo).
FIELD, J. G., GRIFFITHS, C. L., GRIFFITHS, R. J., JARMAN, N.[G.], ZOUTENDYK, P., VELIMIROV, B. and A. BOWES 1980 — Variation in the structure and biomass of kelp communities along the south-west Cape coast. *Trans. R. Soc. S. Afr.* **44**(2): 145–203.
GOOSEN, P. C. and A. C. COCKCROFT 1995 — Mean annual growth increments for male West Coast rock lobster *Jasus lalandii*, 1969-1993. *S. Afr. J. mar. Sci.* **16**: 377–386.
MATTHEWS, S. G. and G. C. PITCHER 1996 — Worst recorded marine mortality on the South African coast. In *Harmful and Toxic Algal Blooms*. Yasumoto, T., Oshima, Y. and Y. Fukuyo (Eds). Paris; UNESCO: 89–92.
MELVILLE-SMITH, R., GOOSEN, P. C. and T. J. STEWART 1995 — The spiny lobster *Jasus lalandii* (H. Milne Edwards, 1837) off the South African coast: inter-annual variations in male growth and female fecundity. *Crustaceana* **68**(2): 174–183.
POLLOCK, D. E. 1976 — The influence of environmental factors on the growth rates of rock lobster *Jasus lalandii* (H. Milne-Edwards) in the Western Cape. SANCOR/ECOR/LSSA/NPES 1st Interdisciplinary Conference on Marine and Freshwater Research in South Africa. Port Elizabeth, July 1976. *Symp. S. Afr. Coun. scient. ind. Res.* **S122** (Fiche 18): B13–D6.
POLLOCK, D. E. 1979 — Predator-prey relationships between the rock lobster *Jasus lalandii* and the mussel *Aulacomya ater* at Robben Island on the Cape west coast of Africa. *Mar. Biol.* **52**(4): 347–356.
POLLOCK, D. E. 1995 — Changes in maturation ages and sizes in crustacean and fish populations. *S. Afr. J. mar. Sci*. **15**: 99–105.
SCHÜLEIN, F. H., BOYD, A. J. and L. G. UNDERHILL 1995 — Oil-to-meal ratios of pelagic fish taken from the northern and the southern Benguela systems: seasonal patterns and temporal trends, 1951–1993. *S. Afr. J. mar. Sci.* **15**: 61–82.
SHANNON, L. V., CRAWFORD, R. J. M., POLLOCK, D. E., HUTCHINGS, L., BOYD, A. J., TAUNTON-CLARK, J., BADENHORST, A., MELVILLE-SMITH, R., AUGUSTYN, C. J., COCHRANE, K. L., HAMPTON, I., NELSON, G., JAPP, D. W. and R. J. Q. TARR 1992 — The 1980s – a decade of change in the Benguela ecosystem. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 271–296.