Biological and ecological aspects of the distribution of *Sepia australis* (Cephalopoda: Sepiidae) off the south coast of southern Africa *

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During the South Coast Biomass Survey in 1988, 49,4 kg (6336 individuals) of *Sepia australis* were caught between Cape Agulhas and Algoa Bay. A biomass index of 803 t of *S. australis* was calculated for the area at that time. Largest catches were taken between about 20°E and 22°E, in waters of 10–11°C and 50–150 m depth. The overall sex ratio was 2M : 3F and mean individual mass was 6,47 g for males and 8,67 g for females. The largest animals were a mature male of 58 mm mantle length and a maturing female of 65 mm mantle length. Most of the animals trawled off the South Coast were maturing or fully mature in early winter and very few immature animals were found. Differences in mean mantle length and maturity stage of the animals in different areas were found to be correlated most strongly with water temperature but also with depth and longitude. Largest numbers and mean sizes of mature animals caught suggest that the main spawning grounds off the South Coast may be in deeper water on the western side of the Agulhas Bank. To the east the deeper water is warmer and the animals there may be at a disadvantage, as optimum temperatures and depths for spawning do not coincide.

Gedurende die Suidkus-Biomassa-opname in 1988 is altesaam 49,4 kg (6336 individue) *Sepia australis* gevang. n' Biomassa-indeks van 803 t *S. australis* is toe vir die gebied bereken. Die grootste vangste is tussen 20°O en 22°O in water van 10–11°C, op 'n diepte van 50–150 m, gemaak. Die algemene geslagsverhouding was 2M : 3V en die gemiddelde enkele massa was 6,47 g vir manlike en 8,67 g vir vroulike diere. Die grootste diere was 'n ryp mannetjie met 'n mantellengte van 58 mm en 'n deels ryp wyfie met 'n mantellengte van 65 mm. Die meeste diere aan die Suidkus was òf ryp òf deels ryp in die vroeë winter en baie min onryp diere is gevind. Verskille in gemiddelde mantellengte en stadium van rypheid in verskillende gebiede was mees konsekwent met watertemperatuur gekorreleer maar ook met diepte en lengteligging. Die grootste getalle en gemiddelde groottes van ryp diere dui daarop dat die hoof teelgebiede aan die Suidkus meer Wes, in dieper water, mag wees. Ooswaarts is die dieper water warmer wat die diere mag benadeel aangesien die optimum-temperature en -diepte vir teling nie saamval nie.

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Sepia australis is a southern African cuttlefish species occurring from Namibia to the Transkei (Roeleveld 1972; Sanchez & Villanueva 1989). Further afield, there is one other doubtful record from the Red Sea (Rochebrune 1884). The abundance of stranded shells of *Sepia australis* on the beaches led to a first estimate of this species as 'one of the commonest Sepiidae along the coast of the western Cape' (Roeleveld 1972: 231). Since then the species has frequently been collected during the Sea Fisheries Institute's routine biomass surveys off the west and south coasts of South Africa. These surveys are aimed primarily at the determination of biomass indices for the two Cape hakes, *Merluccius capensis* and *M. paradoxus*, which form the basis of a large commercial fishery. However, the small mesh size used to catch all sizes of hake also catches a broad spectrum of other benthic and nekto-benthic species.

As a relatively small animal, *Sepia australis* had not received much attention beyond a scant estimate of catch weight in earlier surveys. This cruise record provides a snapshot of the *S. australis* population against which changes in population structure and abundance at another time or in another region may be compared. The aim of this study is to obtain an estimate of the distribution and population structure (mainly size and maturity) of *S. australis* on the south coast of southern Africa, with an assessment of the relationships of these factors with water temperature, depth and longitude. The reports of *S. australis* from recent West Coast surveys, following a rather different approach, are presented elsewhere (Lipinski, Roeleveld & Augustyn 1991, 1992).

To our knowledge there exists no examination of distribution in the field in relation to environmental conditions for any species of *Sepia*, despite many years of study (primarily of *Sepia officinalis*) in the North Atlantic and Mediterranean (e.g. Mangold-Wirz 1963; Boucaud-Camou 1991) and extensive experiments in aquaria (e.g. Richard 1967, 1970; Boletzky 1983, 1989).

Material and Methods

Sepia australis was collected as part of the routine trawling for hake during the South Coast Biomass Survey of the F.R.S. *Africana* from 10 May to 3 June 1988. Virtually the entire catch of *S. australis* was preserved. The survey covered the Agulhas Bank between 20°E and 27°E, corresponding with International Commission for South-east Atlantic Fisheries (ICSEAF) Subarea 2.

Sampling was by means of a 180 foot (±55 m) German Otter Trawl with an effective mesh size in the codend of 27,5 mm. The catchability of *S. australis* is believed to be low with this gear but it does provide a consistent measure of abundance for this species (Augustyn, Lipinski & Roeleveld in press). The trawl was fished on the sea bed, usually for 30 min, during daylight in stratified semi-random squares (ICSEAF 1984; Payne, Augustyn & Leslie 1985). The survey area was divided into four depth strata (<50, 50–100, 100–150 and 150–500 m). During the 1988 South Coast Survey most of the stations trawled were in the 50–100 and 100–150 m depth strata, owing to the bathymetry of the sampling area, the distribution of untrawlable rocky ground and the size of the ship.

The entire catch of *Sepia australis* for each station was weighed and subsamples were taken for the determination of individual mass, dorsal mantle length (ML, in mm), sex and maturity stage and for inclusion in feeding studies (Lipinski unpubl). Simple maturity stages were used (as described by Roeleveld & Liltved 1985), intended primarily to distinguish between immature and fully mature animals: Stage I — immature (gonad and accessory reproductive glands small, undeveloped); Stage II — maturing (gonad and accessory glands partially developed but spermatophores/mature eggs absent); and Stage III — fully mature (mature eggs present in ovary, spermatophores present in Needham's sac, in penis or on hectocotylus).

The relationships between sex and mean ML with depth, temperature and longitude were assessed separately for each sex and maturity stage using multiple regression (Genstat 5 Committee 1987). As samples of immature animals were very small, only maturity Stages II and III were included in the regression analyses. Stations from 20°00′–20°59′E and 21°00′–22°59′E were grouped into longitudinal classes 20° and 21°+22°E, respectively. The data were untransformed and there were no zero values in the matrix.

Results

Distribution

In May/June 1988 *S. australis* was taken in 73 of the 91 successful trawls between Cape Agulhas and Port Elizabeth. Almost all of these 73 stations were in the 50–100 and

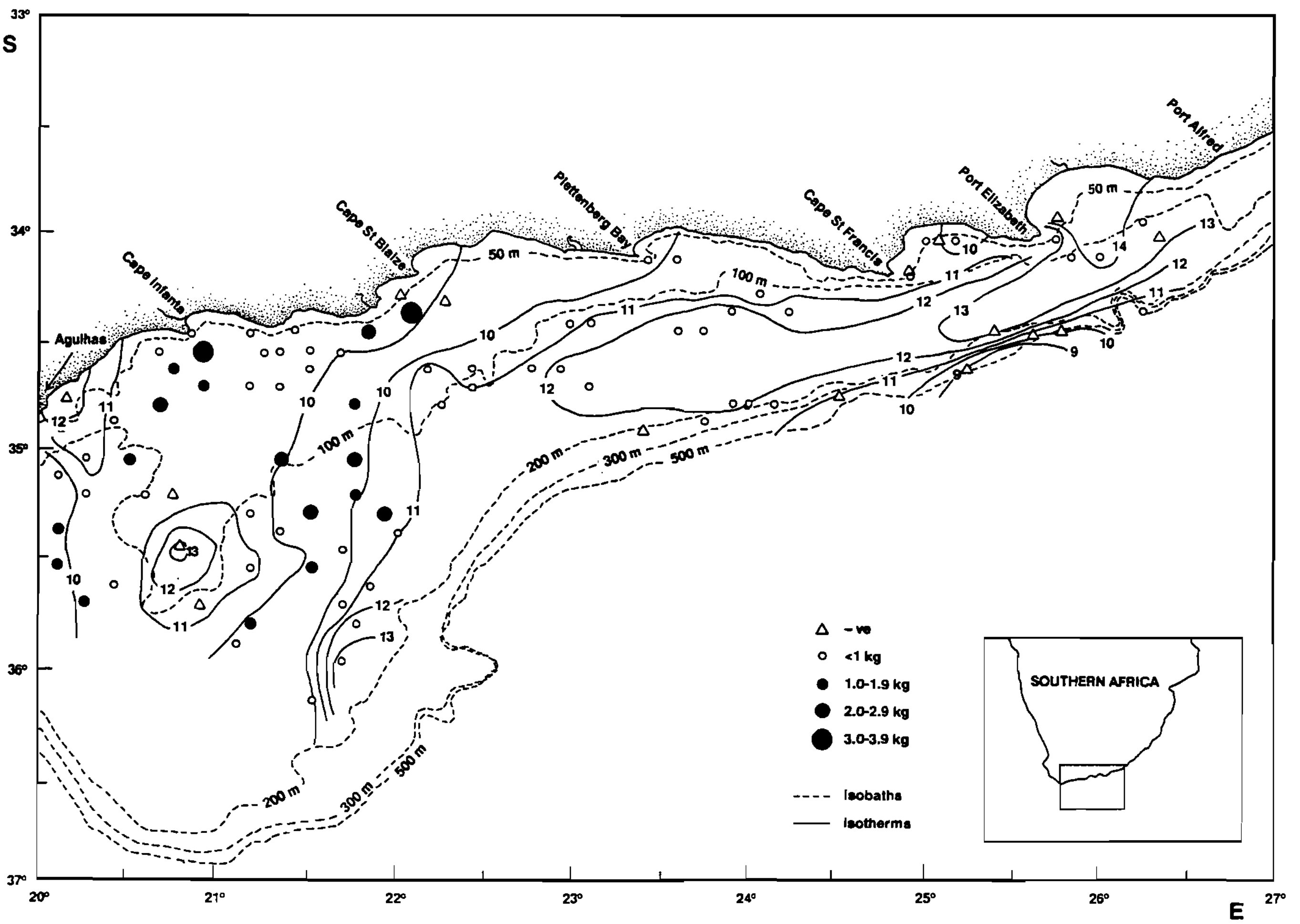

Figure 1 Distribution and abundance of *Sepia australis* on the South Coast of southern Africa compared with the temperature regime at the bottom in May/June 1988. Open triangles indicate trawls that were negative for *S. australis*.

100–150 m depth strata, only a few trawls being taken shallower or deeper (Figures 1 & 2). Successful trawls that were negative for *S. australis* were in less than 45 or more than 227 m, or east of 23°E, or near a ring of warm water over the centre of the Agulhas Bank (Figure 1).

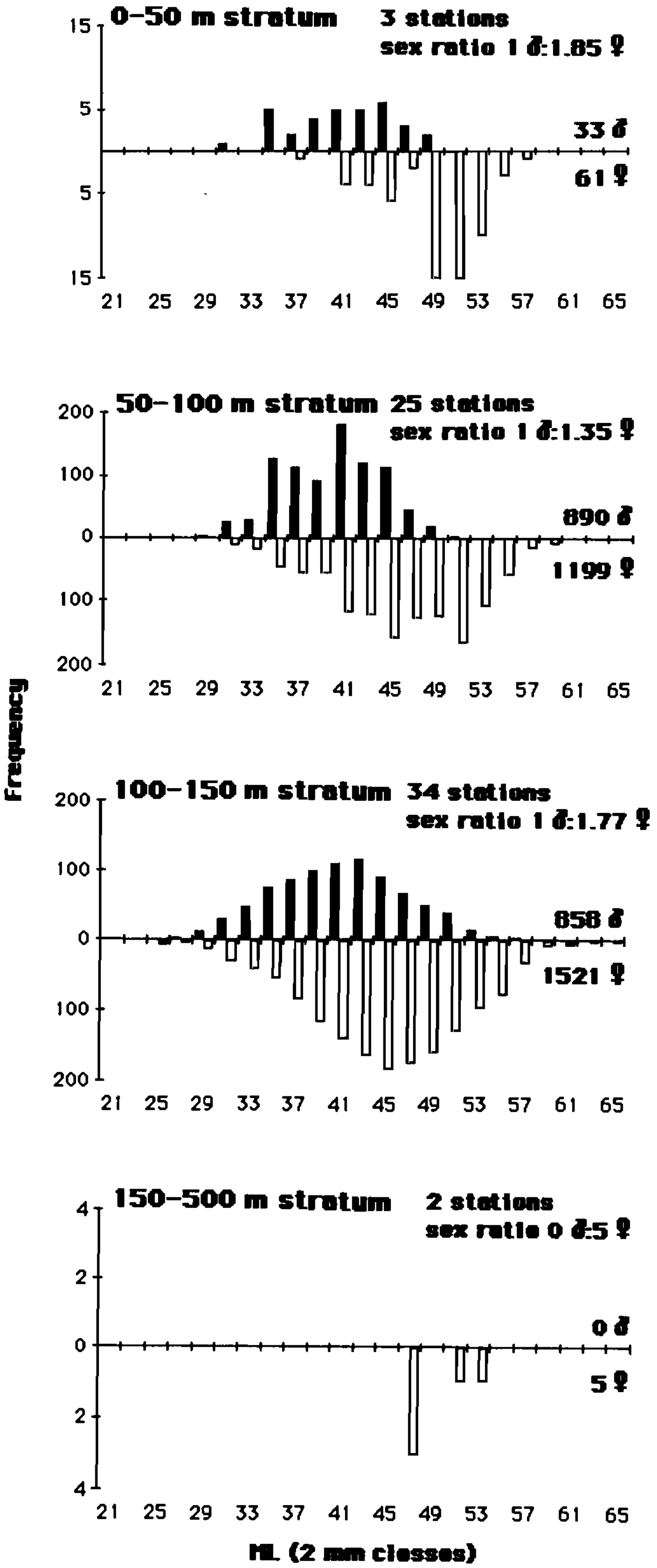

Figure 2 Sex ratio of *Sepia australis* and length frequency distribution by sex, compared by depth strata; South Coast of southern Africa May/June 1988.

Largest catches were taken on the widest part of the Agulhas Bank, between Cape Agulhas and Cape St. Blaize in waters of 10–11°C and 50–150 m depth (Figure 1). The two largest catches, each over 3 kg, were taken in 10,4–10,5°C and 60–70 m depth, fairly close to shore between Cape Infanta and Cape St. Blaize (at 34°33′S, 20°57′E in 71 m and at 34°21′S, 22°05′E in 62 m; Figure 1).

A total of 49,4 kg of *Sepia australis* was caught during the cruise and a biomass index of 803 t was calculated for *S. australis* in the area at the time surveyed (Augustyn *et al.* in press). Individuals of *S. australis* are small but females attain a somewhat larger size than do males. A length frequency diagram showed no marked difference in size range by depth for either sex (Figure 2). On this cruise females generally outnumbered males and the overall male to female sex ratio was 2 : 3 (Table 1). The average individual mass was 6,47 g for males and 8,67 g for females, giving an overall mean individual mass of 7,79 g (sexes combined). This mean mass was used to estimate a total number of 6336 individuals collected during the cruise. The largest specimens were taken at 35°31′S, 20°05′E in 151 m and 35°40′S, 20°20′E in 148 m and were a mature male of 58 mm mantle length and a partially mature female of 65 mm ML.

Variation by depth and maturity stage

In early winter 1988 on the South Coast very few animals caught of either sex were completely immature. The numbers of males at Stages II and III were similar, whereas females were mostly at Stage II, even some of the largest (Table 1).

Males at Stage I were found only in deeper water. Maturing males were of similar numbers in 50–100 m and 100–150 m but mature males were more numerous in deeper water (Table 1).

For females at Stage I the numbers increased with depth and they were most numerous at 100–150 m. About 70% of all females were maturing and occurred in about equal numbers in the two middle depth strata sampled. Mature females were also about equally abundant in the two middle strata. Only small numbers of animals of either sex at Stages II and III were found shallower than 50 m (Table 1), but sampling there was less intense (Figure 1).

Mean sizes by depth and longitude

An examination of length frequency distribution for each sex, divided into maturity stages, by depth and from east to west, showed a large overlap in ML between maturity stages for both sexes and some of the largest females were still at Stage II (Figure 3). Figure 3 also showed a trend of increasing modal mantle length eastwards. This trend was checked by grouping the stations in the main fishing area and depth strata by degree squares (20°, 21° and 22°E) and by depth strata. The mean ML for each maturity stage of both sexes for each block (Table 2) were compared for significant differences by *t* test (Table 3). Variance for the different categories was very similar, except for males at Stage I; the last group was excluded from the comparison.

The trend of increasing mean ML with longitude was statistically significant between stations grouped in 20°E

Table 1 Maturation stages of *Sepia australis* in May/June 1988 compared by depth strata sampled

Depth stratum	Stage I	Stage II	Stage III	Σ	
Males					
0–50 m					
n	0	2	6		
%		25,0	75,0		
ML mean		41,0	43,2		
range		40–42	38–47		
50–100 m					
n	0	53	64		
%		45,3	54,7		
ML mean		38,5	41,6		
range		28–48	30–49		
100–150 m					
n	5	55	83		
%	3,5	38,5	58,0		
ML mean	27,4	36,1	43,8		
range	25–30	27–46	34–55		
Females					
0–50 m					
n	0	8	3		
%		72,7	27,3		
ML mean		45,5	51,3		
range		41–50	50–52		
50–100 m					
n	5	144	41		
%	2,6	75,8	21,6		
ML mean	31,8	44,8	48,9		
range	27–38	34–60	40–57		
100–150 m					
n	29	138	44		
%	13,7	65,4	20,9		
ML mean	33,4	44,5	50,0		
range	25–43	31–65	40–57		
All depths combined					
Males					
Σ*n*	5	110	153	268	39,41%
mean ML	27,4	37,3	42,9	40,3	
Females					
Σ*n*	34	290	88	412	60,59%
mean ML	33,2	44,7	49,5	44,8	
Total sample	M+F				
ΣΣ*n*	680				
mean ML	43,0				

Σ = total; ΣΣ = grand total

Table 2 Mean mantle length by sex and maturity stage for *Sepia australis* in the two main depth strata, with stations grouped by °E (see Figure 3 for numbers of stations per category; a few more easterly and shallower stations omitted)

		20°E		21°E		22°E	
		n	mean ML	*n*	mean ML	*n*	mean ML
♂I	50–100 m	0		0		0	
	100–150 m	3	27,3	2	27,5		
♂II	50–100 m	22	35,8	19	39,8	12	41,5
	100–150 m	31	34,8	24	37,8		
♂III	50–100 m	28	39,3	23	43,3	13	43,4
	100–150 m	43	44,9	40	42,6		
Σ ♂	50–100 m	50	37,8	42	41,7	25	42,5
	100–150 m	77	40,2	66	40,4		
ΣΣ ♂	50–150 m	127	39,2	108	40,9	25	42,5
♀I	50–100 m	2	29,5	3	33,3	0	
	100–150 m	14	32,9	15	33,9		
♀II	50–100 m	57	42,0	73	46,3	15	47,5
	100–150 m	59	44,7	79	44,5		
♀III	50–100 m	19	46,3	11	51,4	10	50,9
	100–150 m	20	52,0	24	48,5		
Σ ♀	50–100 m	78	42,7	87	46,5	25	48,9
	100–150 m	93	44,5	118	43,9		
ΣΣ ♀	50–150 m	171	43,7	205	45,0	25	48,9
sex ratio,	50–100 m	1 : 1,6		1 : 2,1		1 : 1,0	
♂ : ♀	100–150 m	1 : 1,2		1 : 1,8			

and 21°E for maturity Stages II and III of both sexes in the 50–100 m depth stratum (Table 3). In deeper water of 100–150 m the mean mantle lengths of males at Stages II and III and females at Stage III (but not at Stage II) were also significantly different between 20°E and 21°E (Table 3). The difference in mean ML was not significant between 21°E and 22°E for either sex at any maturity stage in 50–100 m; there were no data available for the 100–150 m stratum at 22°E. Stage I animals showed no significant trend in mean ML, but samples were small for females and even smaller for males.

Multiple regression

Results of the regression analyses for maturity Stage I were not significant. Results for maturity Stages II and III are presented in Tables 4 and 5.

For maturity Stage II, the regression equation predicting mean mantle length from depth and longitude is: ML = 35,0 + 7,2 (if female) + 1,5 (if depth 100–150 m) + 4,6 (if longitude 21° or 22°E) – 3,8 (if depth 100–150 m and longitude 21° or 22°E). This regression equation explains 34,8% of the variance in mantle length.

For maturity Stage III the equation is: ML = 39,4 + 6,9 (if female) + 5,6 (if depth 100–150 m) + 4,3 (if longitude 21° or 22°E) – 7,0 (if depth 100–150 m and longitude 21° or 22°E). This equation explains 44,4% of the variance in mantle length.

The trends in mean ML with bottom water temperature followed a reverse pattern to those with depth and longitude (Table 4, Figure 4). The relationship between ML and temperature (with sex as a covariate) is modelled by the following regression equations: for maturity Stage II, ML = 53,4 + 7,3 (if female) – 1,6 × T°C (28,9% of variance explained); for maturity Stage III, ML = 74,4 + 6,6 (if female) – 3,1 × T°C (37,5% of variance explained).

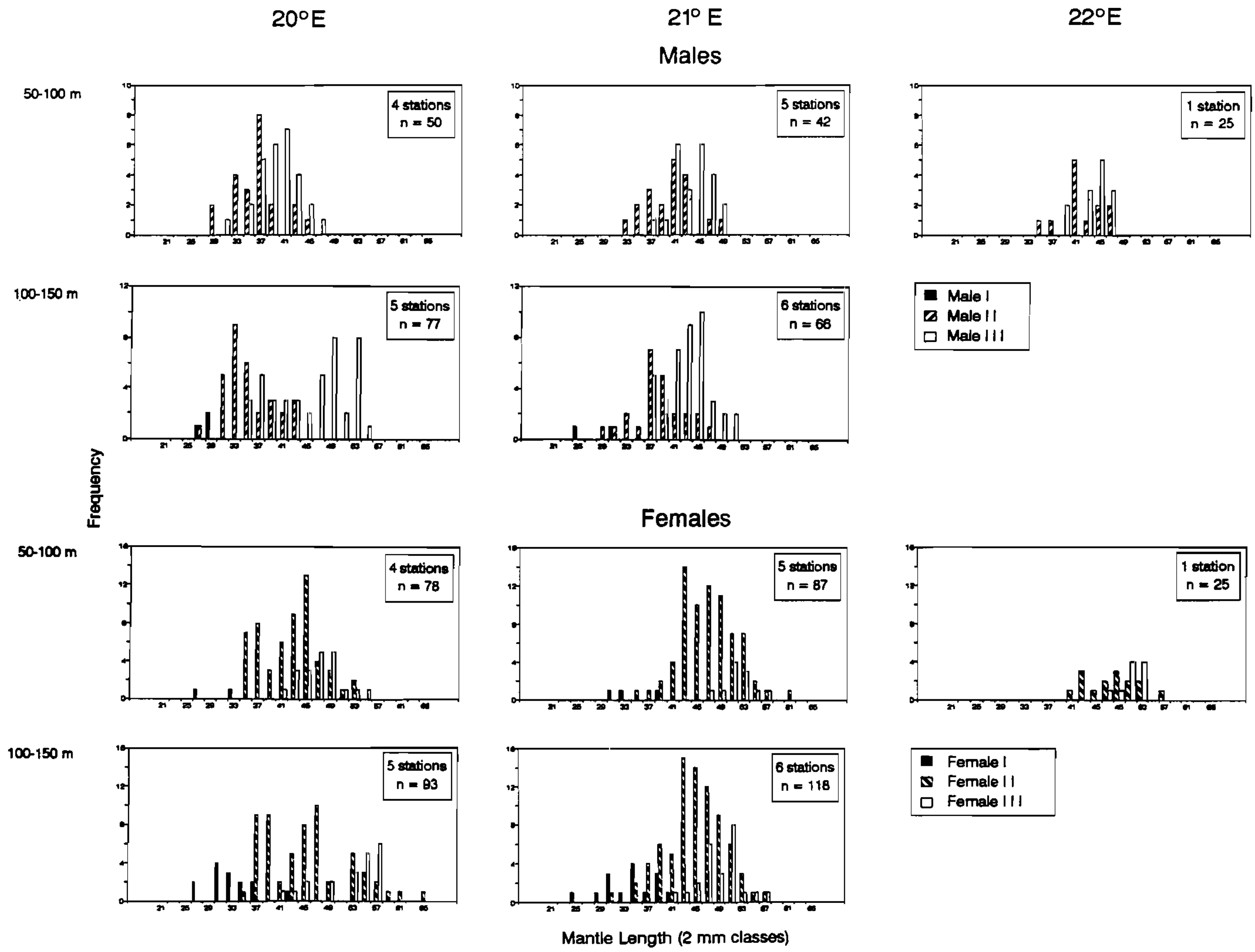

Figure 3 Population structure of *Sepia australis* — length frequency distribution of maturity stages, from west to east, compared for 50–100 m and 100–150 m depth strata. Stations grouped by one degree longitude, South Coast of southern Africa, May/June 1988.

Table 3 Comparison by *t* test of mean mantle lengths from Table 2 by longitude

		20°E vs 21°E		21°E vs 22°E
		50–100 m	100–150 m	50–100 m
♂II	*t* value	3,274	2,561	1,214
	degrees of freedom	39	53	29
	significance	< 0,01	< 0,05	n.s.
♂III	*t* value	4,207	2,072	0,115
	degrees of freedom	49	81	34
	significance	< 0,001	< 0,05	n.s.
♀I	*t* value	1,059	0,637	
	degrees of freedom	3	27	
	significance	n.s.	n.s.	
♀II	*t* value	5,290	0,202	0,922
	degrees of freedom	128	136	86
	significance	< 0,001	n.s.	n.s.
♀III	*t* value	3,889	2,584	0,423
	degrees of freedom	28	42	19
	significance	< 0,001	< 0,05	n.s.

n.s. = not statistically significant

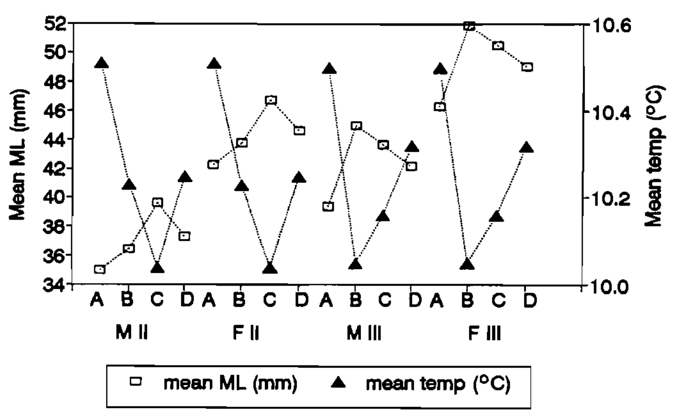

Figure 4 Predicted mean mantle length (from regression analysis; open symbol) and observed mean bottom temperature (solid symbol) by sex and maturity stage for *Sepia australis* in the two main depth strata, with stations grouped by °E. A: 20°E, 50–100 m; B: 20°E, 100–150 m; C: 21°+22°E, 50–100 m; D: 21°+22°E, 100–150 m. See Table 4 for comments on variation in mean temperature.

Models are not given for the relationships of sex with depth or with longitude as these were not significant.

Table 4 Results of regression analysis: predicted mean mantle length (and standard error) and observed bottom temperature (and standard error) — by sex and maturity stage for *Sepia australis* in the two main depth strata, with stations grouped by °E. Variance accounted for was 34,8 % for both sexes at maturity Stage II and 44,4% for both sexes at Stage III. Differences in mean temperature for the same longitude and depth stratum are due to the method of data handling by GENSTAT for different numbers of animals in various maturity stages (GENSTAT 5 Committee 1987)

		20°E			21°+22°E	
		ML mean (*s.e.*)	T°C mean (*s.e.*)		ML mean (*s.e.*)	T°C mean (*s.e.*)
50–100 m	M II	35,0 (0,7)	10,51 (0,02)	M II	39,6 (0,6)	10,04 (0,02)
		$p < 0{,}001$			$p < 0{,}001$	
	F II	42,3 (0,6)	10,51 (0,02)	F II	46,8 (0,5)	10,04 (0,02)
		$p < 0{,}001$			$p < 0{,}001$	
	M III	39,4 (0,7)	10,50 (0,02)	M III	43,7 (0,6)	10,16 (0,03)
		$p < 0{,}001$			$p < 0{,}001$	
	F III	46,3 (0,7)	10,50 (0,02)	F III	50,5 (0,7)	10,16 (0,03)
		$p < 0{,}001$			$p < 0{,}001$	
100–150 m	M II	36,5 (0,6)	10,23 (0,05)	M II	37,3 (0,7)	10,25 (0,05)
		p = 0,052			p = 0,052	
	F II	43,8 (0,6)	10,23 (0,05)	F H	44,6 (0,5)	10,25 (0,05)
		$p < 0{,}001$			$p < 0{,}001$	
	M III	45,0 (0,6)	10,05 (0,05)	M III	42,2 (0,6)	10,32 (0,07)
		$p < 0{,}001$			$p < 0{,}001$	
	F III	51,9 (0,7)	10,05 (0,05)	F III	49,1 (0,6)	10,32 (0,07)
		$p < 0{,}001$			$p < 0{,}001$	

p = probability of regression not being significant

Table 5 Results of regression analyses of *Sepia australis*. Estimates of regression parameters, their standard errors and the probability that they are zero for the two models: a. ML = constant (mean ML) + sex + depth + longitude + depth × longitude; b. ML = constant (mean ML) + sex + temperature. (*s.e.* = standard error, *p* = probability of regression not being significant)

	Maturity Stage II			Maturity Stage III		
	regression coefficient	*s.e.*	*p*	regression coefficient	*s.e.*	*p*
a. mean ML (constant)	35,04	0,70	< 0,001	39,37	0,65	< 0,001
sex = female	7,23	0,57	< 0,001	6,88	0,57	< 0,001
depth = 100–150 m	1,50	0,77	= 0,052	5,61	0,81	< 0,001
longitude = 21° or 22°E	4,58	0,73	< 0,001	4,29	0,82	< 0,001
depth = 100–150 m and longitude = 21° or 22°E	–3,77	1,03	< 0,001	–7,03	1,11	< 0,001
% variance accounted for	34,8			44,4		
b. mean ML (constant)	53,43	6,66	< 0,001	74,35	7,10	< 0,001
sex = female	7,31	0,59	< 0,001	6,58	0,60	< 0,001
temperature	–1,57	0,65	< 0,001	–3,07	0,69	< 0,001
% variance accounted for	28,9			37,5		

Predicted values for mean ML calculated from the formulae for each sex, maturity stage, mean bottom temperature, depth stratum and longitude are presented in Table 4. Standard errors and probabilities for the regression coefficients are presented in Table 5. Results of the regression analyses showed several trends. At 20°E fully mature animals (Stage III) of both sexes had a significantly higher mean ML in deeper water. The same trend was shown by maturing animals (Stage II) but was weaker. In the more easterly stations (21°+22°E) this trend in mean ML was reversed, though less strong, with larger animals found in shallower water. The increasing mean ML with depth at 20°E was inversely correlated with temperature, as was the increasing mean ML with latitude, with larger mean MLs found in colder water, except for Stage II males in deeper water, where there was no significant difference in either mean ML or temperature with longitude.

Predicted mean MLs were (inversely) correlated with mean bottom temperature but not with depth nor latitude (Figure 4). Both sexes behaved in the same manner but mature animals differed from those at Stage II. Because of the different distributions of Stage II and III animals, the mean temperature and mean ML at 100–150 m predicted for Stage II was virtually the same at 20°E and 21°+22°E. For Stage III, however, there was a difference in both mean temperature and mean ML for the same depth and the correlation of mean ML with temperature held true, whereas that of mean ML with longitude did not.

Discussion

The large numbers and widespread distribution of *S. australis* caught during the South Coast Biomass Survey indicate that this species is common off the South Coast, primarily in the colder waters of the western part (Figure 1), with maximum abundance at 60–160 m (Figure 2). Only relatively small catches were taken on the eastern Agulhas Bank in May/June 1988, when a tongue of warm water extended over the Bank from the Agulhas Current and a warm water ring was present over the middle of the Bank.

The explanation for the unequal sex ratio found (Figure 2 and Table 2) is not clear but possibly indicates stressful conditions. Females were considerably more numerous (overall sex ratio of 2M : 3F) than off the West Coast, where females were only slightly more numerous than males and mature animals were considerably larger (Lipinski *et al.* 1992), perhaps in response to more suitable conditions. A similar preponderance of females has been recorded for *S. officinalis* (1M : 1,2F, calculated from data of Guerra & Castro 1988) in a presumably stressful estuarine environment (since cephalopods are sensitive to decreased salinity), whereas in the Gulf of Tunis the same species had a 1 : 1 sex ratio and its genotypic distribution was considered to be in equilibrium (Ezzedine-Najai 1984: 104–106).

Differences in distribution and mean mantle lengths of animals at different maturity stages were found to be correlated with water temperature, depth and longitude (Tables 2–5, Figures 2–4). The variation in mean mantle length was most strongly correlated with temperature; variations in mean ML with depth and longitude were less consistent but could be explained in terms of a combination of these with mean water temperatures.

Both sexes behaved in a similar manner with regard to depth, bottom temperature and longitude but there was a difference between maturity Stages II and III. Stage II animals had larger mean mantle lengths in deeper water at 20°E, when water temperature was lower, but at 21°+22°E the mean mantle length was larger and the water temperature lower in shallower water (50–100 m versus 100–150 m), confirming the stronger correlation of mean mantle length with water temperature.

The larger numbers and mean mantle lengths of fully mature animals at 100–150 m (Tables 2 and 4) suggest that *Sepia australis* prefers to spawn in deeper water. This is in agreement with information from the West Coast (Lipinski unpublished). Off the South Coast, however, deeper water further east is warmer, owing to the influence of the Agulhas Current, and in this region *S. australis* spawns in shallower water at a smaller size. These animals are perhaps at a disadvantage, as preferred depth and temperature for spawning do not coincide. The fecundity of the more eastern animals would also be lower, as it has been shown that fecundity is related to mantle length in *Sepia* (Boletzky 1983, 1987) and consequently smaller animals produce fewer eggs.

The less favourable nature of more eastern waters for spawning of *S. australis* is borne out by the decreasing abundance eastwards and indeed only sporadic individual records of *S. australis* are known east of Port Elizabeth, though it has been recorded as far east as the Transkei (Roeleveld 1972). The presence of colder upwelled waters on the Agulhas Bank and closer inshore eastwards in late summer (March) has been established by Shannon (1985, figure 35).

It is possible that *Sepia australis* is primarily a West Coast species, as suggested by the higher abundance and larger mean size there (Lipinski *et al.* 1992) and the animals on the South Coast may be approaching the limits of their distribution range. The preference of *Sepia australis* for cold water in southern African waters casts further doubt on the validity of the record of *S. australis* from the Red Sea (Rochebrune 1884), based on two poorly preserved females now in a poor state of conservation (Adam 1959: 149). The occurrence of *Sepia australis* in the Red Sea should be considered doubtful.

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