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First Study on the Ecology of *Sepia australis* in the Southern Benguela Ecosystem

by

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Abstract. *Sepia australis* is most abundant in the eastern South Atlantic between Luderitz and St. Helena Bay (about 27–33°S in 100–200 m). There seems to be no link between the variation in abundance of *S. australis* and that of its most important predator, the shallow-water Cape hake, *Merluccius capensis*. The variations in abundance of *S. australis* and one of its most important prey species, the stomatopod crustacean *Pterygosquilla armata capensis*, show simultaneous changes, suggesting that both species respond to the same environmental factors.

Mantle length, total weight, gonad weight, and sex ratio of *Sepia australis* vary from year to year and by region off the west coast of southern Africa. Animals from the south coast (eastward of Cape Point) were very different: length-weight relationships were found to be similar in slope and intercept for both sexes and within each sex between years and regions off the west coast, but different for the south coast.

INTRODUCTION

Sepia australis is one of the most common sepiids in the Benguela ecosystem of southern Africa (in this instance from Luderitz to Agulhas Bank, Figure 1; for definitions and geographic boundaries see SHANNON, 1985). It is particularly abundant off the west coast of southern Africa (Figure 1), as indicated by its frequent occurrence in bottom trawls (SANCHEZ & VILLANUEVA, 1989, 1991; LIPINSKI *et al.*, 1991) and the abundance of its cuttlebones on some of the South African beaches (ROELEVELD, 1972: 231). *Sepia australis* is a small cephalopod with a maximum dorsal mantle length (ML) slightly above 80 mm. Little is known about this species other than its systematic position and distribution range; its importance in the ecosystem is only now being assessed (LIPINSKI *et al.*, 1991, and unpublished data; Roeleveld *et al.*, unpublished data). The species has a known distribution range in southern African waters from southern Namibia (ca. 27° S) to about Rame Head (31°30′S 29°20′E) on the south coast (ADAM & REES, 1966:145; ROELEVELD, 1972:228; SANCHEZ & VILLANUEVA, 1989, 1991; LIPINSKI *et al.*, 1991; Roeleveld *et al.*, unpublished data) and has also been reported from the Red Sea (a single doubtful record in ROCHEBRUNE [1884] repeated by ADAM [1942, 1959]). Its known vertical distribution is 2–457 m (ADAM & REES, 1966:145) but it occurs primarily in the upper 200 m (ROELEVELD, 1972:

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277). The species was reported from southern Namibia only recently, with a center of abundance at 28–30°S in 75–250 m of water and a second, smaller center at 27°S in 150–300 m; its absence off northern Namibia was attributed to the anoxic conditions and narrow continental shelf (SANCHEZ & VILLANUEVA, 1989).

Sepia australis has been caught by the R/S *Africana* in the course of regular biomass surveys conducted by the Sea Fisheries Research Institute off both the west coast and the south coast of South Africa. In 1986 the abundance of *S. australis* was merely estimated for catch records but during the latter part of the survey in January 1987 this species was found to form a significant part of the diet of the shallow-water Cape hake (*Merluccius capensis*) (LIPINSKI *et al.*, in press). Since then, catch data for *S. australis* have been more carefully monitored (Augustyn *et al.*, unpublished data) and extensive biological data, part of which form the basis for this study, have been collected. There is no fisheries-related data base, however, because this species is not fished commercially.

Sepia australis has recently been found widely distributed along the south coast of southern Africa (east of Cape Point; Figure 1). It was shown to be an important species on the Agulhas Bank (Roeleveld *et al.*, unpublished data), where it was found to be primarily a cold-water species, most abundant at bottom-water temperatures of 10–11°C. This agrees with the observation that the abundance of *S. australis* is higher off the west coast than off the south coast (Augustyn *et al.*, unpublished data).

This study presents a first assessment of the biology of *Sepia australis* off the west coast of South Africa, in the southern Benguela ecosystem (Orange River to Cape Agulhas). The distribution, abundance, length/weight relationship, distribution of maturity stages, mean gonad weights, and sex ratio of *S. australis* are described for the first two detailed surveys of the species, in the northern region in 1987 and all three regions in 1988 (Figure 1). Results of the feeding analysis of these samples are described elsewhere (LIPINSKI *et al.*, 1991).

MATERIALS AND METHODS

The biomass surveys of the Sea Fisheries Research Institute are conducted by the R/S *Africana*, usually twice yearly off the west coast of South Africa and once yearly off the south coast. The west coast survey encompasses the southern Benguela ecosystem and extends from the Orange River mouth (ca. 29°S 16°E) to the Agulhas Bank (Figure 1). The south coast survey extends from Cape Agulhas (20°E) to Port Alfred (27°E) (Figure 1). These surveys consist primarily of half-hour bottom trawls during daylight, made in 1.5 × 1.5 m squares selected by the stratified semirandom method (ICSEAF, 1984; PAYNE *et al.*, 1985) and are continuing.

All specimens were collected with a 54-m German otter trawl with 1500-kg polyvalent doors, sampling on the seabed in depths of 50–500 m. Effective mesh size in the cod end was 27.5 mm (using a pilchard liner). For each trawl, all components of the catch were sorted and weighed; key species such as hake, kingklip, monkfish, and squid were measured and subjected to biological analyses (length, weight, sex, maturity stage, stomach contents, *etc.*).

Sepia australis catch data have been recorded in the course of these biomass surveys since 1986, in depths to 345 m, though data for the first year (January and July 1986) are only estimates and should be treated with caution. The actual weight of *S. australis* caught was recorded from the latter part of the survey (the northern region) in January 1987 and in all subsequent surveys. Almost all *S. australis* catches were made in the 0–209 m depth stratum, and only these data were further analyzed.

Two species that show important interaction with *Sepia australis* are the shallow-water Cape hake (*Merluccius capensis*), one of the sepiid's main predators, and the stomatopod crustacean *Pterygosquilla armata capensis*, one of its two main prey species (LIPINSKI *et al.*, 1991). Only limited information is available for the other main prey species of *S. australis*, the sternoptychid lightfish *Maurolicus muelleri* (HULLEY & PROSCH, 1987; ARMSTRONG & PROSCH, 1991).

The shallow-water Cape hake (*Merluccius capensis*) is not only one of the most important species in the Benguela ecosystem (both ecologically and commercially) but also one of the most important predators in the 0–209 m depth zone between northern Namibia and Cape Columbine (PAYNE *et al.*, 1985, 1986, 1987, 1988, 1989). The geographical distribution of *M. capensis* overlaps that of *Sepia australis* in the area investigated (PAYNE *et al.*, 1985, 1986, 1987, 1988, 1989) and *S. australis* is both a competitor and a prey item of the shallow-water hake. *Sepia australis* also forms a link in the food chain between the mesopelagic *Maurolicus muelleri*, which is consumed by small- and medium-sized hake only (PAYNE *et al.*, 1987), and large hake, which take *S. australis* but not *M. muelleri* (LIPINSKI *et al.*, 1991).

Relatively good data are available on the abundance of the stomatopod *Pterygosquilla armata capensis* (GRIFFITHS & BLAINE, 1988; ABELLO & MACPHERSON, 1990). Therefore, we attempted to compare the abundance of *Sepia australis* with that of *Merluccius capensis* and of *P. armata capensis* caught in the same depth stratum (0–209 m). The abundance indices (as catch per standardized trawl) for *S. australis, M. capensis,* and *P. a. capensis* were back-calculated for all R/S *Africana* benthic biomass surveys (both west coast and south coast) for the years 1986–1990. The abundance of *S. australis* before January 1987 was roughly estimated (see above). Data from January 1989 were incomplete and are not included; during the latter survey, the data collected for *S. australis* and *P. a. capensis* were inadequate, because only 16 trawls could be made in the 0–209 m depth zone. *Pterygosquilla a. capensis* was not caught in any of the three south coast biomass surveys discussed here.

For each survey the mean catch per trawl was calculated for all three species under consideration (Table 1). The

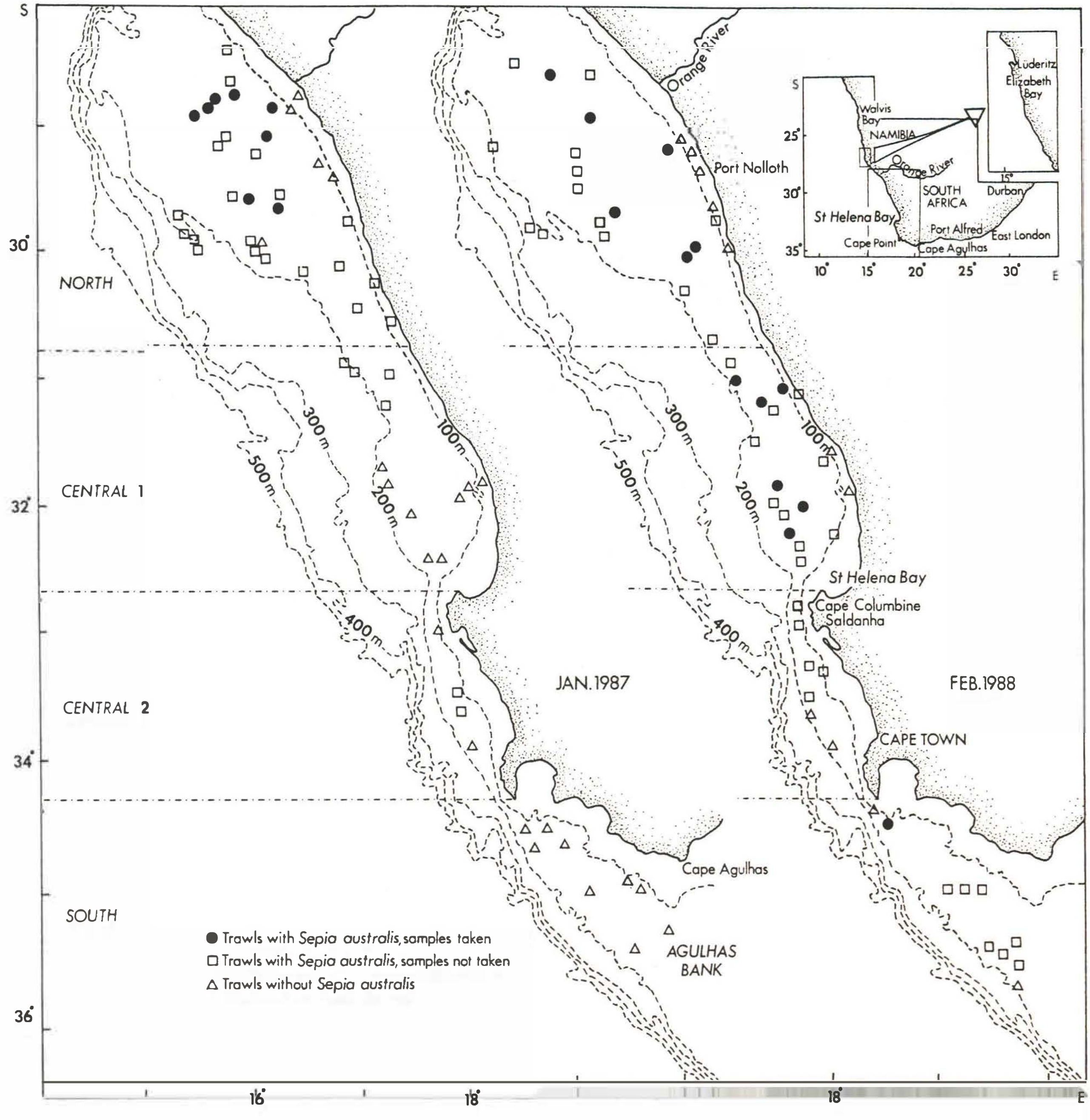

Figure 1

South African west coast biomass survey sampling area, from the Orange River mouth to Cape Agulhas, and localities of stations from which *Sepia australis* samples were collected for biological analysis 22–28 January 1987 and 5–23 February 1988 (closed circles). Stations at which *S. australis* was collected were grouped into northern, central (1 and 2), and southern regions, bounded by broken lines.

mean number of animals per trawl was calculated from the mean individual weight for each species. For *Sepia australis* the mean individual weight was 20.4 g, calculated from regional means for 1987 and 1988 (Table 2). For *Pterygosquilla a. capensis* the mean weight was 11.9 g, calculated from data of GRIFFITHS & BLAINE (1988). The actual number and total weight of hake for each trawl were determined as part of the routine procedure in these surveys (PAYNE *et al.*, 1985).

The biological analysis is based on specimens collected in the northern region between 22 and 28 January 1987 (Figure 1 left, closed circles: 129 specimens from 9 stations)

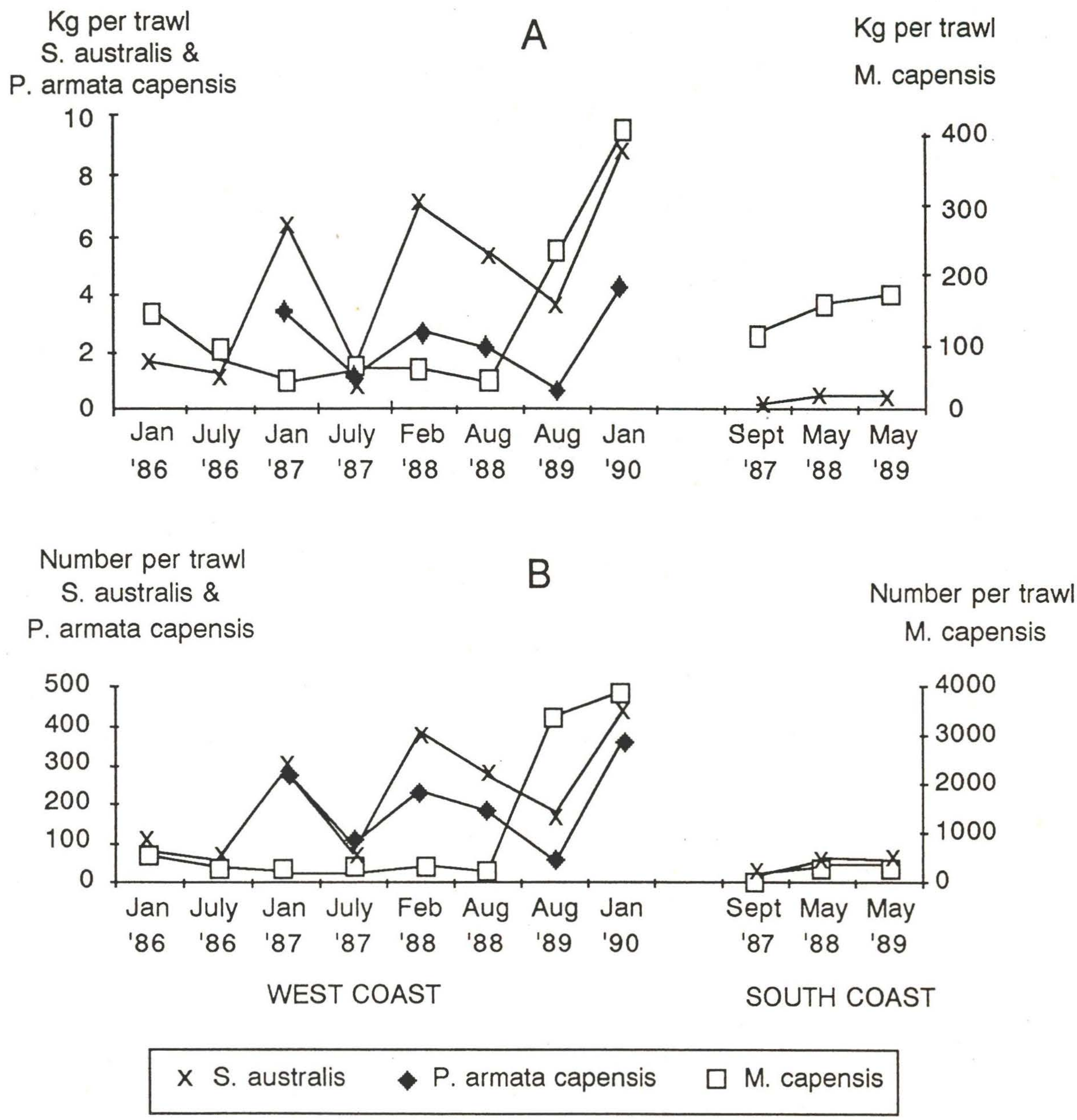

Figure 2

Abundance of *Sepia australis, Merluccius capensis,* and *Pterygosquilla armata capensis* in southern African waters. Abundance in mean kg/trawl (A) and in mean number of individuals/trawl (B) for each survey off the west coast (see text), sampled in summer (January–February) and winter (July–August) and south coast (see text) in spring or autumn (September or May) in 1986–1990. Data for *P. armata capensis* were not collected in 1986; this species was absent in south coast surveys. Variance is not given to simplify the drawings; it does not affect the comparisons of relative abundance.

and throughout the survey between 5 and 23 February 1988 (Figure 1 right, closed circles: 1150 specimens from 12 stations). These stations may conveniently be grouped into the northern, central 1, central 2, and southern regions, as indicated in Figure 1. The boundary between the northern and central 1 regions is arbitrary. There are no profound oceanographic differences between these regions. On the other hand, the oceanography and shelf morphology of the two central regions differ substantially (SHANNON, 1985), and the borderline between them at Cape Columbine reflects real differences. Unfortunately, no samples of *Sepia australis* were collected in the central 2 region.

Table 1

Indices of abundance (weight and numbers) for *Sepia australis*, *Merluccius capensis*, and *Pterygosquilla armata capensis* in 0–209 m. Results of groundfish surveys on R/S *Africana* in the years 1986–1990 (see also Figure 1).

			S. australis				*M. capensis*				*P. armata capensis*			
Survey area	Month and year	No. of trawls	kg	kg/trawl	No.**	No./trawl	kg	kg/trawl	No.**	No./trawl	kg	kg/trawl	No.**	No./trawl
West coast	Jan. 1986	51	85.5*	1.7	4191	82	7272.5	142.6	28,722	563	197.6	3.9	16,605	326
	July 1986	43	50.8*	1.2	2488	58	3037.7	70.6	13,129	305	46.1	1.1	3874	90
	Jan. 1987	59	387.4	6.6	16,917	287	3649.1	61.8	10,736	182	202.5	3.4	17,017	288
	July 1987	35	53.5	1.5	2622	75	1961.4	56.0	7292	208	41.0	1.2	3445	98
	Feb. 1988	57	411.2	7.2	23,893	419	3443.3	60.4	20,415	358	160.1	2.8	13,451	236
	Aug. 1988	44	245.5	5.6	12,036	274	1703.1	38.7	8668	197	95.2	2.2	8001	182
	Aug. 1989	50	181.4	3.6	8890	178	10,742.2	214.8	172,280	3446	32.2	0.6	2705	54
	Jan. 1990	50	451.6	9.0	22,138	443	19,465.4	389.3	197,594	3952	219.8	4.4	18,473	369
South coast	Sep. 1987	81	12.1	0.2	1553	19	8765.2	108.2	15,205	188	0	0	0	0
	May 1988	87	42.6	0.5	5468	63	12,877.8	148.0	30,389	349	0	0	0	0
	May 1989	62	25.9	0.4	3321	54	10.059.3	162.2	22,040	355	0	0	0	0
West coast regions														
Northern region	Jan. 1987-N	26	382.7	14.7	16,712	643	1270.4	48.9	2207	85	47.0	1.8	3950	152
Northern region	Feb. 1988-N	22	254.2	11.6	14,099	643	1063.1	48.2	1274	58	41.0	2.2	3445	181
Central region	Feb. 1988-C	18	150.3	8.3	7441	413	1201.7	66.8	15,740	874	115.7	8.3	9723	694
Southern region	Feb. 1988-S	9	4.3	0.5	319	35	672.5	74.7	2060	229	0.0	0.0	0	0

* Based on estimate for individual trawls.
** Numbers calculated from mean weights of individual samples.

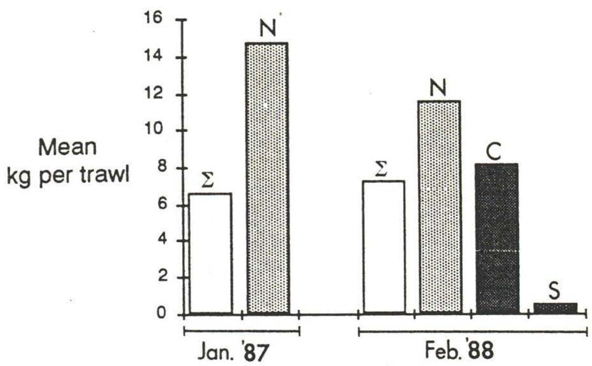

Figure 3

Comparison of abundance of *Sepia australis* off the west coast by region and for the entire survey in each of two summer surveys (1987 and 1988). Sigma—all trawls in the entire survey (up to 209 m); N, C, S—all trawls in northern, central 1, and southern regions, respectively (up to 209 m).

The borderline between the central 2 and southern regions lies at Cape Point (Figure 2). Oceanographically the southern region belongs to the south coast, and the borderline between these regions also reflects real differences (SHANNON, 1985).

Subsamples of *Sepia australis* for biological analysis were frozen immediately after capture and processed in the laboratory. Subsamples contained up to several hundred individuals taken randomly from the sample (*i.e.*, the whole catch per station per species). Biological analysis consisted of determination of dorsal mantle length (to the nearest millimeter), sex and maturity stage (according to a simplified version [ROELEVELD & LILTVED, 1985] of the universal maturity scale for squids [LIPINSKI, 1979]), total weight, gonad weight, and weight of stomach contents (results of stomach contents analysis were presented by LIPINSKI *et al.*, 1991).

RESULTS

Abundance

The most northerly station at which *Sepia australis* was caught during the west coast biomass surveys was at 27°58.8′S, 14°57.6′E (R/S *Africana* station E46, 190 m, 24 January 1989). During these surveys the species was found at a maximum depth of 345 m, the depth range of main abundance being 140–190 m. Mean catches per trawl of *S. australis* from nine west coast surveys and three south coast surveys in South African waters (Figure 2A, B) show considerable fluctuation, particularly off the west coast. The abundance off the south coast is more regular (Lipinski, unpublished data) but also much lower, by an order of magnitude, than off the west coast (Table 1). *Sepia australis* was generally more abundant in summer than in winter except in 1988 (Figure 2A, B). This general pattern was confirmed by the results of biomass calculations (Augustyn *et al.*, unpublished data).

In comparison with the shallow-water hake (*Merluccius capensis*), the most important fish species in the ecosystem in the 0–209 m depth stratum, the abundance of *Sepia australis* was sometimes higher, as regards to numbers (Figure 2B), since *S. australis* is small and *M. capensis* attains a large size. Compared with the stomatopod *Pterygosquilla armata capensis,* one of its most important prey species, *S. australis* was more abundant both by weight and by numbers (Figure 2A, B).

A comparison of variations in the abundance of *Sepia australis, Merluccius capensis* and *Pterygosquilla a. capensis* show interesting trends (Figure 2A, B) that will be checked when a longer time series has accumulated. Available data

Table 2

Sepia australis mean mantle lengths (ML), total weights (TW), with standard deviations (SD), and sex ratio, by year and region off the west coast (see Figure 1).

Area Month, year	Northern Jan. 1987	Northern Feb. 1988	Central Feb. 1988	Southern Feb. 1988	Total
Males (M)					
n	58	167	299	41	565
mean ML ± SD	61.24 ± 6.46	53.56 ± 6.60	55.52 ± 7.01	50.02 ± 4.17	
mean TW ± SD	20.49 ± 5.02	15.49 ± 4.88	17.17 ± 5.34	11.63 ± 2.27	
Females (F)					
n	71	234	373	38	716
mean ML ± SD	65.61 ± 7.78	58.37 ± 7.82	60.43 ± 9.13	54.82 ± 4.96	
mean TW ± SD	24.86 ± 7.15	19.84 ± 6.50	22.62 ± 8.34	15.33 ± 4.26	
Sexes combined					
n	129	401	672	79	1281
mean ML ± SD	63.64 ± 7.51	56.37 ± 7.65	58.25 ± 8.60	52.33 ± 5.14	
mean TW ± SD	22.90 ± 6.63	18.03 ± 6.20	20.20 ± 7.66	13.41 ± 3.84	
Sex ratio, M:F	1:1.22	1:1.40	1:1.25	1:0.93	1:1.27

Table 3

Comparison by *t*-test of *Sepia australis* mean mantle length (ML) and total weight (TW) from Table 2, independent samples by year and region off the west coast (see Figure 1). df, degrees of freedom; *P*, the probability that the regions do not differ significantly.

	Northern Jan. 1987 vs. Northern Feb. 1988			Northern Jan. 1987 vs. Central Feb. 1988			Northern Jan. 1987 vs. Southern Feb. 1988			Northern Feb. 1988 vs. Central Feb. 1988			Northern Feb. 1988 vs. Southern Feb. 1988			Central Feb. 1988 vs. Southern Feb. 1988		
	t	df	*P*	*t*	df	*P*	*t*	df	*P*	*t*	df	*P*	*t*	df	*P*	*t*	df	*P*
Males																		
mean ML	7.68	223	<0.005	5.76	355	<0.001	9.77	97	<0.001	2.95	464	<0.01	3.27	206	<0.001	4.90	338	<0.001
mean TW	6.67	223	<0.005	4.37	355	<0.001	10.55	97	<0.001	3.36	464	<0.001	4.93	206	<0.001	6.56	338	<0.001
Females																		
mean ML	6.84	303	<0.005	4.48	442	<0.001	7.74	107	<0.001	2.86	605	<0.01	2.71	270	<0.01	3.73	409	<0.001
mean TW	5.57	303	<0.005	2.12	442	<0.05	7.48	107	<0.001	4.34	605	<0.001	4.13	270	<0.001	5.31	409	<0.001
Sexes combined																		
mean ML	9.43	528	<0.005	6.65	799	<0.001	11.80	206	<0.001	3.61	1071	<0.001	4.50	478	<0.001	5.99	749	<0.001
mean TW	7.63	528	<0.005	3.74	799	<0.001	11.58	206	<0.001	4.81	1071	<0.001	6.38	478	<0.001	7.76	749	<0.001

(Figure 2A, B) suggest that variation in hake abundance is not linked to those of *S. australis* or *P. a. capensis*; when the last mentioned two species are scarce, hake can apparently switch easily to other prey species. Nor does the abundance of *S. australis* seem to be influenced by that of hake. On the other hand, changes in the numbers of *P. a. capensis* seem to run parallel with those of *S. australis*.

In both 1987 and 1988, the abundance of *Sepia australis* off the west coast varied greatly among regions (Figure 3). In the southern region the mean catch per trawl was similar to those off the rest of the south coast (Table 1), whereas in the central 1 and northern regions the abundance was much higher (Figure 3), especially in the northern region.

To explore further the relationship between the abundance of *Sepia australis* and that of hake and stomatopods, the number of times that increases and decreases in occurrences were in the same or opposite directions (Figure 2A, B) was counted. The results were as follows:

		Sepia australis increase	*Sepia australis* decrease	
Hake	increase	2	1	$P = 0.5$
	decrease	1	2	
Stomatopods	increase	3	0	$P = 0.05$
	decrease	0	3	

The Fisher Exact Probability Test for a 2 × 2 contingency table was used to examine these relationships. For hake the relationship was not significant ($P = 0.50$) but it was significant for stomatopods ($P = 0.05$).

Population Structure

In all surveys, female *Sepia australis* were larger and heavier than males and hence showed greater variation about the mean (*i.e.*, larger standard deviation). Dorsal mantle length (ML) and total weight showed large variations from year to year (Tables 2, 3). In the northern region, differences of 7.27 mm in mean ML and 4.87 g in mean weight (both sexes combined) were recorded in successive years for the same season. Within one year (1988) the ML and total weight of *S. australis* in the central 1 region were significantly greater than in the northern and southern regions (Table 3).

The length-weight relationships (Figure 4) were found to be similar for both sexes and within each sex between years and regions, except in the southern region in 1988. The length-weight relationships for *Sepia australis* in the southern region had a somewhat different intercept and slope for both males (4.6×10^{-3} g and 2.00 g mm^{-1}, respectively) and females (1.3×10^{-3} g and 2.34 g mm^{-1}) than in the northern and central 1 regions in both years (males: 1.1–1.3 × 10^{-3} g and 2.36–2.38 g mm^{-1}; females: 0.76–0.91 × 10^{-3} g and 2.44–2.48 g mm^{-1}, respectively). The animals in the southern region were also smaller than in the other regions (see above). The lower correlation coefficients in the southern region are probably due primarily to the smaller sample size.

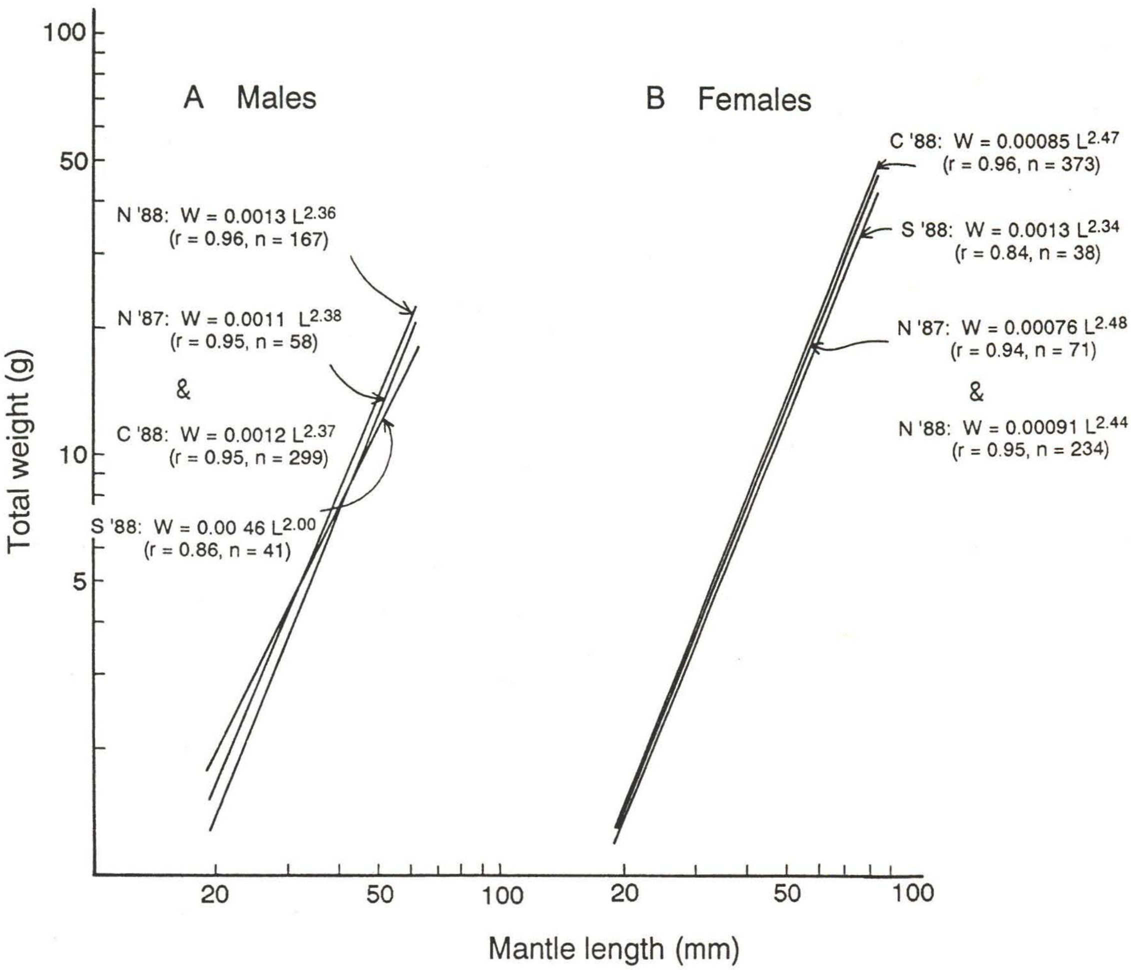

Figure 4

Sepia australis length-weight relationships by year and by region off the west coast in summer 1987 and 1988: Male (A) and female (B) regression lines are virtually the same but have been plotted separately to facilitate comparison among regions; appended to the regression lines are the values for each slope and intercept in the relationship $W = aL^b$ and the correlation coefficient (r) and sample size (n). N, C, S—north, central 1, and southern region, respectively; W is weight in g; L is length in mm.

The distribution of maturity stages varied between years and regions (Figure 5). In the northern region in January 1987, most of the males (56.9%) and females (73.2%) were mature, whereas in February 1988 most animals were completely immature (56.9% and 77.8%, respectively). Mature and maturing males and females were generally bigger than immature animals and there were always slightly more females present than males, except in the southern region, where most of the animals were immature and the sex ratio was about 1:1 (Table 2). In the central 1 region the proportion between mature and immature males was close to parity; there were, however, considerably more immature females.

Mean gonad weights for the different sexes and maturity stages are presented in Figure 6. In the northern region in January 1987, the mean gonad weight for maturity stages II and III was about the same and considerably bigger than for stage I in both sexes. In February 1988, the mean gonad weight showed a more regular increase in weight from stage I to III in both sexes in all three regions, although the mean gonad weight for stage II was somewhat higher in the central 1 region and there were no fully mature animals of either sex in the southern region. This is in agreement with the observation that in the northern region most of the animals were fully mature or almost so in 1987, whereas in 1988 the animals with the most developed reproductive systems were in the central region, where most of the males and almost half the females were fully mature and stage II animals had somewhat larger gonads (Figures 5, 6).

DISCUSSION

Abundance

Our results confirm that the northern boundary of the distribution range of *Sepia australis* off the west coast of

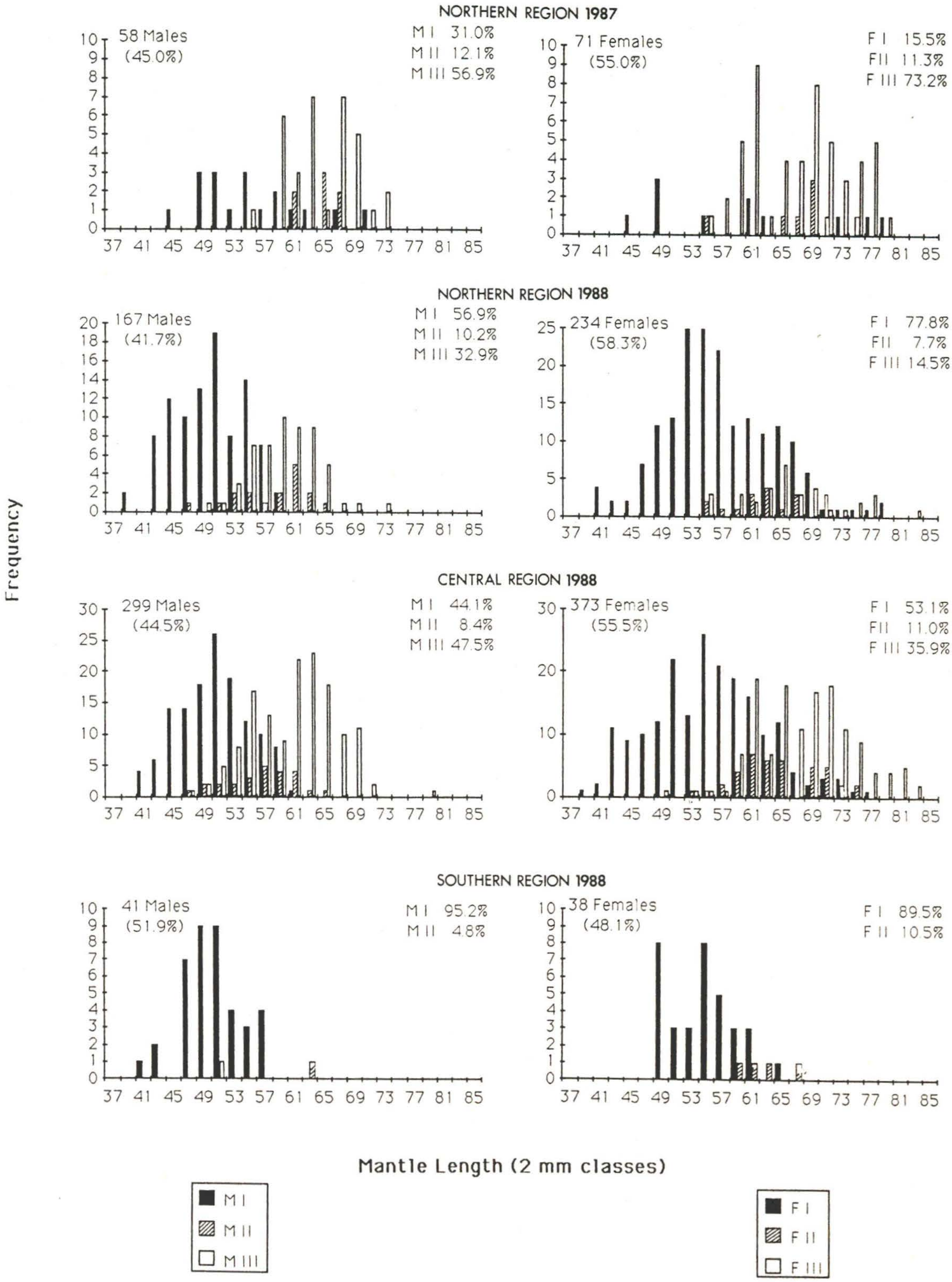

Figure 5

Sepia australis maturity stages: frequency of occurrence compared in successive years off the west coast in summer (1987–1988) in the northern region and by region in 1988. Sample size and percentage of each sex are indicated for each region. M—males; F—females.

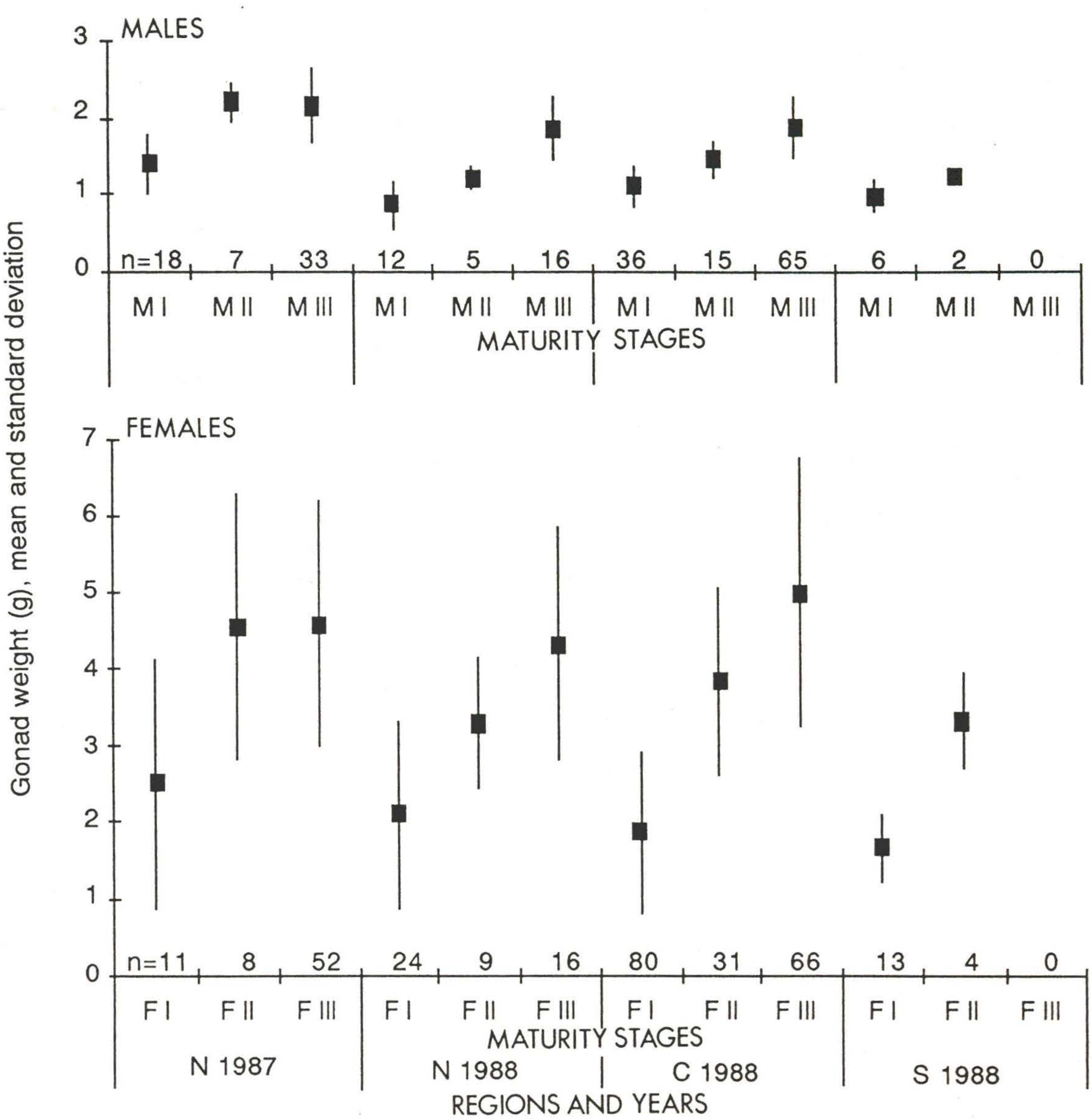

Figure 6

Mean gonad weight and standard deviation for *Sepia australis* by maturity stage and by region in summer 1987 and 1988, off the west coast of southern Africa.

southern Africa lies close to 27°00′S in Namibian waters, as established by SANCHEZ & VILLANUEVA (1989). They reported fairly high concentrations of this species, but the units of measure (individuals per mile) are unfortunately not comparable with those presented here. However, their report of a consistently high abundance of *S. australis* is in accordance with our observations of its great abundance and importance in the Benguela ecosystem (Figure 2; LIPINSKI *et al.*, 1991). The main concentrations of *S. australis* are located between St. Helena Bay and Elizabeth Bay, south of Luderitz (SANCHEZ & VILLANUEVA, 1989, 1991; Augustyn *et al.*, unpublished data; our data). Its distribution seems to be fairly uniform in the 100–209 m depth zone (our data; Augustyn *et al.*, unpublished data; SANCHEZ & VILLANUEVA, 1989, 1991).

The white-chinned petrel (*Procellaria aequinoctialis*) seems to be an important consumer of *Sepia australis*, as most of the Sepioidea reported from the gizzards and stomachs of these birds by JACKSON (1988) probably belonged to this species (Lipinski, unpublished data). The white-chinned petrels, however, most probably scavenge dead *S. australis* from the sea surface (LIPINSKI & JACKSON, 1989) and therefore the abundance of the birds does not influence the abundance of *S. australis*.

The Cape hake is the most important predator of *Sepia australis* identified to date (LIPINSKI *et al.*, in press); yet

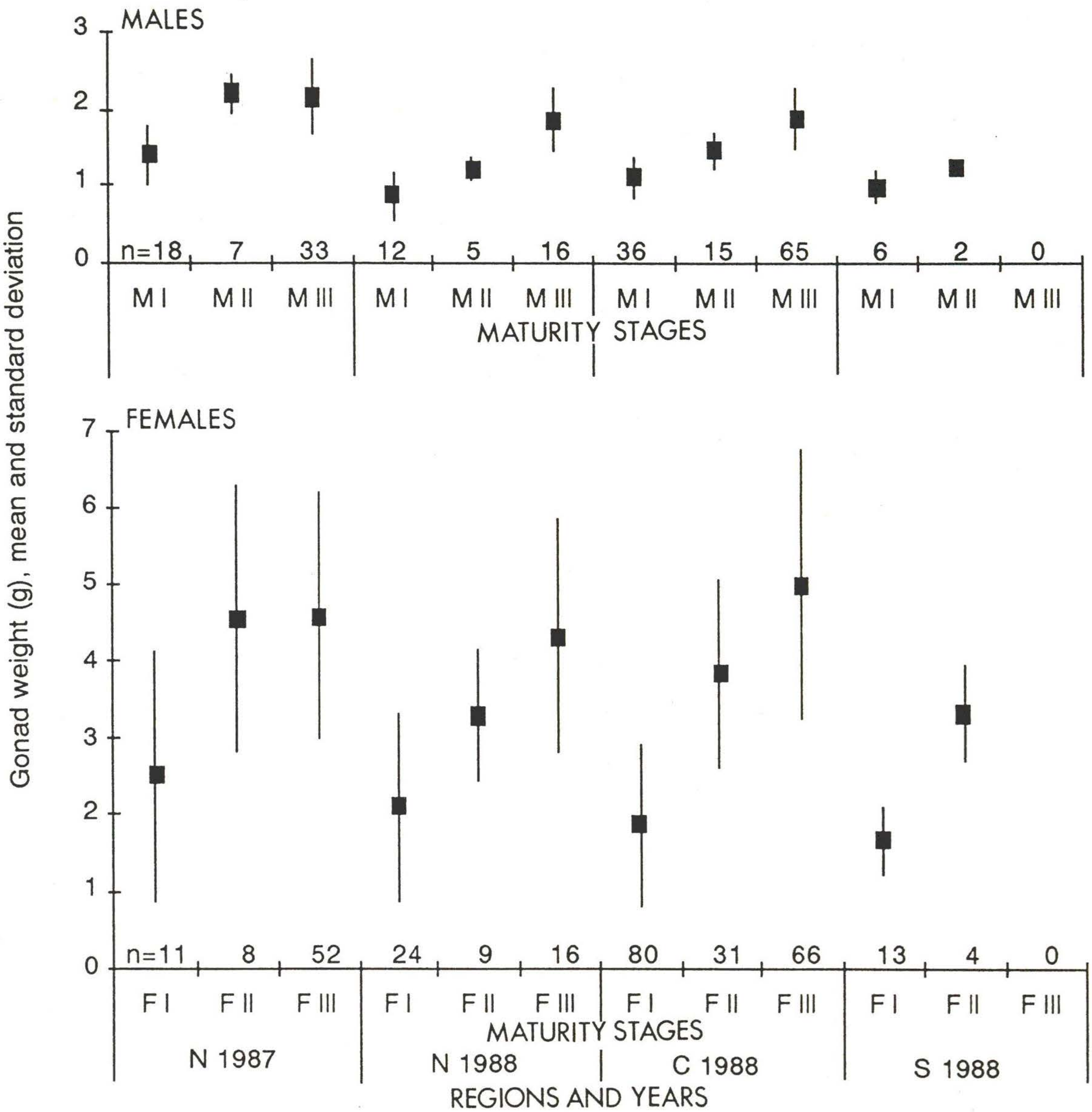

Figure 6

Mean gonad weight and standard deviation for *Sepia australis* by maturity stage and by region in summer 1987 and 1988, off the west coast of southern Africa.

southern Africa lies close to 27°00'S in Namibian waters, as established by SANCHEZ & VILLANUEVA (1989). They reported fairly high concentrations of this species, but the units of measure (individuals per mile) are unfortunately not comparable with those presented here. However, their report of a consistently high abundance of *S. australis* is in accordance with our observations of its great abundance and importance in the Benguela ecosystem (Figure 2; LIPINSKI *et al.*, 1991). The main concentrations of *S. australis* are located between St. Helena Bay and Elizabeth Bay, south of Luderitz (SANCHEZ & VILLANUEVA, 1989, 1991; Augustyn *et al.*, unpublished data; our data). Its distribution seems to be fairly uniform in the 100–209 m depth zone (our data; Augustyn *et al.*, unpublished data; SANCHEZ & VILLANUEVA, 1989, 1991).

The white-chinned petrel (*Procellaria aequinoctialis*) seems to be an important consumer of *Sepia australis,* as most of the Sepioidea reported from the gizzards and stomachs of these birds by JACKSON (1988) probably belonged to this species (Lipinski, unpublished data). The white-chinned petrels, however, most probably scavenge dead *S. australis* from the sea surface (LIPINSKI & JACKSON, 1989) and therefore the abundance of the birds does not influence the abundance of *S. australis.*

The Cape hake is the most important predator of *Sepia australis* identified to date (LIPINSKI *et al.*, in press); yet there seems to be no link between the changes in abundance of these two species (Figure 2A, B). On the other hand, existing data show parallel changes in abundance for *S. australis* and *Pterygosquilla a. capensis* for at least six trawl surveys (see results of Fisher's Exact Probability Test), which suggests that these two species may respond similarly to biological or environmental factors, or some combination of these. It is unlikely that these changes reflect predator-prey interactions because there is no time lag (Figure 2A, B), as predicted by the classical Lotka-Volterra model and its more sophisticated modifications (*e.g.*, BEGON & MORTIMER, 1981:119–128).

The interaction between *Sepia australis* and its other important prey species, the lightfish *Maurolicus muelleri*, cannot be assessed at present. Data for *M. muelleri* are scarce and difficult to interpret (M. Armstrong, personal communication). It would seem, however, that the lightfish also shows seasonal (summer-winter) fluctuations; concentrations in summer have a higher density, especially in the Cape Columbine area (ARMSTRONG & PROSCH, 1991).

The trends in the abundance of *Sepia australis* reported here are essentially in agreement with the biomass estimates found by Augustyn *et al.* (unpublished data). In addition, there were regional differences (Figure 3A, B), and catches (kg/trawl) were much higher in the northern and central regions than the overall mean value for the entire survey (Table 1).

This assessment of abundance for *Sepia australis* is almost certainly an underestimate of total *S. australis* biomass, because of the sepiid's small size, and the relatively large mesh size in the cod end. The catchability coefficient of *S. australis* must be very different from that of hake, the main target species in the biomass surveys. This suggests that the abundance of *S. australis* is far greater than reported here and by Augustyn *et al.* (unpublished data).

Population Structure

Both length and weight of *Sepia australis* seem to vary from year to year in the central 1 and northern regions. Animals from the southern region are, however, very different (Table 2): they are much smaller and show less variation (smaller standard deviations). This is in agreement with the data for the south coast (at a different time of year, May 1988), where most of the *S. australis* were sexually maturing or mature (Roeleveld *et al.*, unpublished data).

For the squid *Todarodes pacificus*, the length-weight relationship has been found to be an important indicator of stock conditions (biological characteristics and stock identity) in various areas and different years (MURATA, 1978). The length-weight relationships in *Sepia australis* were found to be similar in slope and intercept for both sexes and within each sex between years and regions, except in the southern region in 1988 (Figure 4). This similarity (especially between sexes) agrees with observations of ROELEVELD (1972:278) and SANCHEZ & VILLANUEVA (1991), and was also reported by BELLO (1988) for *S. orbignyana* and *S. elegans* in the southern Adriatic Sea. This similarity, however, may well have been the result of the relatively uniform size within the samples investigated as well as the small data sets available.

The analysis of maturity stages revealed considerable variation between years and regions. The general characteristics of the animals from the southern region in 1988 most resemble those of animals off the south coast (Roeleveld *et al.*, unpublished data) but differ in maturity. Most of the *Sepia australis* off the south coast in May 1988 were either maturing or fully mature (Roeleveld *et al.*, unpublished data); near Cape Point (34°18′S, 18°30′E) in February 1988, most of the specimens were immature (Figure 5). This difference in maturity may be attributed to the three-month time difference.

On the other hand, animals from the southern region differed considerably from those of the northern and central region in abundance, sex ratio, mean length and weight, length-weight relationship, and distribution of maturity stages. All these biological differences indicate that *Sepia australis* off the south coast may belong to a separate population.

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