The biomass and ecology of chokka squid *Loligo vulgaris reynaudii* off the West Coast of South Africa

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Migration, stock size and ecology of chokka squid *Loligo vulgaris reynaudii* off the West Coast of South Africa were studied and their relationship to other regions compared by analysis of distributional, biomass, and size composition, and biological data collected from biannual research cruises from 1983–1987. Biomass was lower than on the South Coast, higher in summer than in winter and declined over the duration of the study. The distribution of squid was generally continuous from the east up to between Cape Point and Cape Columbine. North of Cape Columbine it was more sporadic and occurred only occasionally in the far north (north of 31°S). Depth distribution, at up to 350 m, was much greater than on the S. Coast where an insignificant percentage of the biomass occurs over 200 m. The size composition was unimodal compared to a polymodal distribution on the S. Coast, and mean and modal sizes were smaller. Maturity rates and gonado-somatic indices were also much lower. The percentage of feeding squid was, however, considerably higher. These findings, together with distributional and commercial catch data, showed that cyclic immigration and emigration occurs between the two areas, probably to enable subadult squid to exploit the good foraging opportunities on the W. Coast. A multiple correlation analysis and regression model showed that catches were correlated with a combination of bottom depth, bottom temperatures and bottom oxygen levels. Bottom temperatures of below 8°C and bottom oxygen levels of below 3,5 $\mathrm{ml.l^{-1}}$ appeared to represent important limiting factors in the distribution.

Trekgewoontes, stapelgrootte en die ekologie van die tjokka *Loligo vulgaris reynaudii* aan die Weskus van Suid-Afrika is bestudeer en verwantskappe met ander gebiede vergelyk aan die hand van ontleding van verspreidings-, biomassa-, grootteverspreidings- en biologiese data wat twee maal jaarliks tussen 1983 en 1987 versamel is. Biomassa was laer as aan die Suidkus, hoër in die somer as gedurende die winter en biomassaskattings het tydens die studie gedaal. Die verspreiding van tjokka was oor die algemeen aaneenlopend vanaf die ooste tot tussen Kaappunt en Kaap Columbine. Noord van Kaap Columbine was dit meer sporadies, en het slegs af en toe in die verre noorde (noord van 31°S) voorgekom. Diepteverspreiding was tot 350 m, heelwat dieper as aan die Suidkus waar 'n onbeduidende persentasie van die biomassa dieper as 200 m voorkom. Die grootteverspreiding was unimodaal vergeleke met 'n polimodale verspreiding aan die Suidkus, en gemiddelde en modale groottes was kleiner. Die mate van geslagsrypheid en gonadosomatiese indekse was ook baie laer. Voedingstempos was egter heelwat hoër. Hierdie bevindings, tesame met verspreidings- en vangsdata, het daarop gedui dat daar 'n sikliese immigrasie en emigrasie tussen die twee gebiede plaasvind, waarskynlik sodat voorvolwasse pylinkvis die goeie voedingspotensiaal aan die Weskus kan benut. 'n Meerveranderlike korrelasie-analise en regressiemodel het bewys dat vangste gekorreleerd was met 'n kombinasie van bodemdiepte, bodemtemperatuur en bodemsuurstofvlakke. Bodemtemperatuur onder 8°C en bodemsuurstofvlakke onder 3,5 $\mathrm{ml.l^{-1}}$ is blykbaar belangrike fakore wat beperkend inwerk op verspreiding.

Total annual landings of *Loligo vulgaris reynaudii* have averaged about 5 000 t since 1983 (catch statistics from Sea Fisheries Research Institute). This species has been utilized as a by-catch by the bottom-trawling industry for many years but since 1985 directed fishing by means of handline jigging has supplanted trawling as the primary source of production. Total annual catches peaked in 1989 when almost 11 000 t were taken, 90% of this by jigging. Export of frozen squid from this fishery has been a valuable source of foreign exchange to South Africa. A substantial infrastructure of fishing vessels, factory installations and jobs has developed. In order to minimize the risk of overfishing, efforts towards better stock management have increased. This has resulted in several research projects being carried out since 1980, viz. biomass surveys of the S. Coast (Hatanaka, Sato, Augustyn, Payne & Leslie 1983; Uozumi, Hatanaka, Sato, Augustyn, Payne & Leslie 1984; Uozumi, Hatanaka, Payne & Augustyn 1985), biological studies in False Bay, the offshore S. Coast and the inshore S.E. Coast of South Africa (Augustyn 1989, 1990) and systematics (Augustyn 1988). Lipiński (1987) has studied feeding off the S. Coast and Sauer (1991), aspects of the inshore spawning population biology.

The main area of occurrence of chokka squid is between Cape Point in the west and Port Alfred in the east (Augustyn 1986, 1988), but it occurs to the west of Cape Point and up the W. Coast at least as far as southern Namibia. Augustyn (1990) showed that seasonal changes in abundance occur on the S. Coast in the inshore areas and that these are probably related to spawning migrations. During routine hake biomass surveys, it has been possible to examine the distribution and assess the relative abundance of chokka squid bi-annually in midsummer and midwinter since July 1983 on the W. Coast shelf between the Orange River and Cape Agulhas by SFRI's R.S. *Africana*.

Payne, Augustyn & Leslie (1985, 1986) and Payne, Leslie & Augustyn (1987, 1988) have reported on the W. Coast stock status of several demersal fish species and chokka squid based on these biomass surveys. In this paper it is attempted (i) to explain interannual and seasonal variations in the distribution and abundance, size composition, maturation status and feeding of chokka squid on the shelf between

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the Orange River and Cape Agulhas and (ii) to relate these parameters to those of the population occurring further east.

Methods

Results presented in this paper originated from nine surveys between June 1983 and July 1987. A total of 742 bottom trawl stations (345 in summer and 397 in winter) for biomass assessment were carried out between the Orange River and Cape Agulhas (Figure 1).

The West Coast surveys are aimed primarily at estimating the biomass of deep and shallow-water Cape hake (*Merluccius capensis* and *M. paradoxus*) across the normal depth range of their occurrence (0–500 m). In practice, the vessel is limited to a minimum trawling depth of about 20 m. Moreover, the rocky nature of a large part of the inshore grounds, particularly in the south, makes trawling difficult in depths shallower than 100 m. Being restricted to coastal areas and continental shelves, loliginid squids generally occur at maximum depths of 200–400 m (Voss 1967; Roper, Sweeney & Nauen 1984). *L. vulgaris reynaudii* occurs in very low numbers deeper than 300 m. These restrictions on sampling and distribution meant that length frequency and biological analyses were limited to the 100–200 and 200–300 m depth ranges.

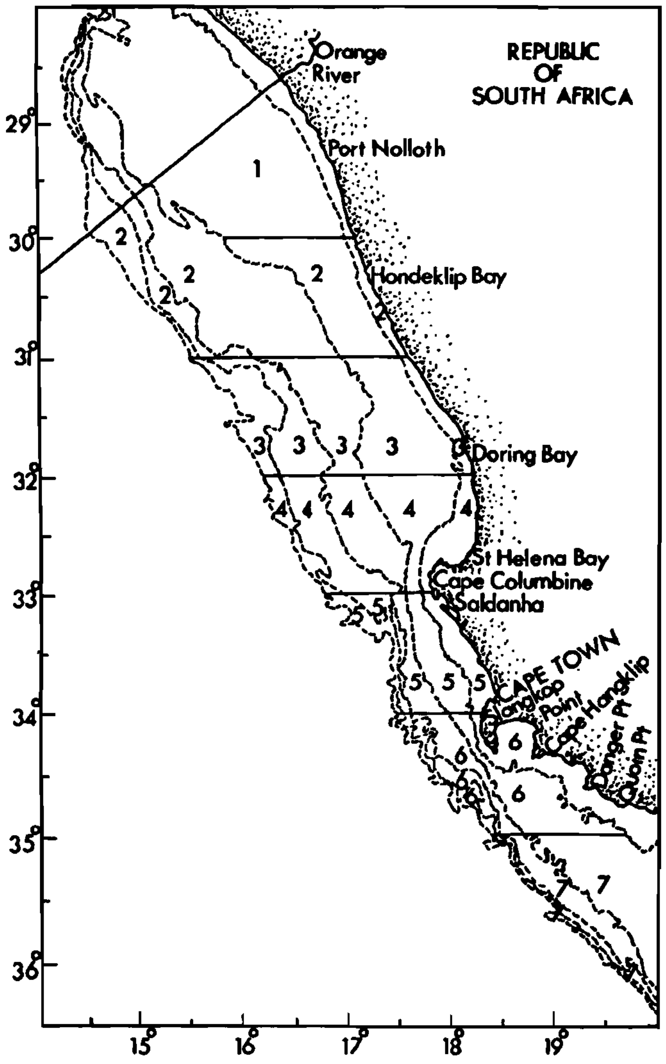

Figure 1 The study area off the West Coast of South Africa. Depth and latitudinal strata are delineated respectively by 100 m interval contour lines and 10 latitudinal boundaries. The latitudinal strata are numbered 1–7 from North to South.

The gear used in the surveys has been described by Payne *et al.* (1985), and is similar to that used by some vessels in the trawling industry (Engelhardt 1987). Catches were limited to daylight to avoid variability caused by vertical migration at night, which occurs in many species. This subject has been discussed by Summers (1969) and Serchuk & Rathjen (1974).

The biomass index is determined using the stratified random sampling method, which has been described in detail by Payne *et al.* (1985). The method has been applied to assess the biomass of squid in other fisheries, e.g. *Illex illecebrosus* off the east coast of Canada (Rowell, Young, Poulard & Robin 1985) and *Loligo pealei* off the eastern USA (Serchuk & Rathjen 1974). The distance between the wings of the net was estimated directly by two 50 kHz echo-sounder transducers mounted vertically on the wings and firing inward. The method gives a consistent estimate of the mouth opening, so a reasonably accurate estimation of swept area can be made.

For the present surveys squid biomass was calculated on two levels: by depth range and by stratum. Figure 1 shows how the strata were drawn up along depth range and latitudinal boundaries. For biomass estimates within depth ranges where no trawling was possible, results from adjacent trawlable areas within the same depth range were extrapolated. For instance, no trawls shallower than 100 m were possible in the southern part of the grid, owing to the rocky nature of the grounds. These areas were excluded from the surveyed area but included in the area for which biomass estimates were made, because chokka squid are known to occur there (Augustyn 1989). Some of the smallest sub-strata were merged with adjacent larger ones, e.g. the northernmost two sub-strata in the 200–300 m, 300–400 m and 400–500 m depth ranges were combined.

To establish distribution, squid catches at the position of each randomly selected station were plotted on a map of the study area. Relative abundance was represented by contour lines.

Environmental data were collected at most trawl stations with a Conductivity, Temperature and Depth (CTD) probe. Several variables which were thought possibly to influence squid catches were included in a SAS statistical package correlation procedure from which Pearson correlation coefficients were obtained (SAS Institute Inc. 1985). The variables were: time of day, bottom depth (m), bottom temperature (°C), bottom oxygen ($ml.l^{-1}$) and bottom salinity (‰). A transformation of the catch data by a log(catch+1) function improved the normality of the catch distribution considerably and gave better correlations. The bottom depth data were transformed by a cubic function to linearize them, as the distribution of catches by depth indicated such a relationship. All stations deeper than 350 m, i.e. outside the normal depth range distribution of chokka squid, were excluded from the analysis. Results were also compared on a seasonal basis. Time appeared to have the lowest correlation with catch of all the factors considered, and was excluded from the subsequent *r*-square and Mallows' C_p statistical analyses. Finally, both time and bottom salinity

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were excluded from the multiple regression analysis in which a model with the variables depth, bottom temperature and bottom oxygen was constructed. C_p is a criterion for selecting a model from a set of models consisting of all the possible combinations of p variables. If C_p is graphed with p, the model is recommended where C_p first approaches p (SAS Institute Inc. 1985).

To obtain the size composition of squid, the catches were first separated by sex and the length frequency measurements (in 10-mm intervals) carried out on an electronic measuring board linked to a Data General DG10 desktop computer. A FORTRAN computer programme summarized the length frequency data by depth range and latitudinal stratum.

A biological sample consisting of a size range of up to ten squid of each sex was usually selected from the catch. The biological analysis, the same as that used on the S. Coast, has been described by Augustyn (1989).

The reproductive state of the population as a whole was assessed on each survey by three different criteria: maturity stage analysis, examination of the gonad weight and mantle length relationship, and calculation of two gonado-somatic indices (GSI1 and GSI2). The latter were: gonad length divided by dorsal mantle length (GSI1 = 100GL/DML) and gonad weight divided by total wet weight (GSI2 = 100GW/TWW). These indices represent the relative development of gonads for a particular population, and enable direct comparisons between seasons, areas etc. Gonado-somatic indices have been used in other molluscs (e.g. Newman 1967) and in other squid species by e.g. Worms (1983) in *L. vulgaris vulgaris*. In the latter case, the whole genital tract was weighed. In the present study, gonad length was measured as the testes length in males and the nidamental gland length in females, to the nearest millimetre. Gonad weight (to the nearest 0,1 g) was taken as testes weight in males and ovary weight in females.

Stomach contents were examined on board. At times it was possible to identify prey to species level in fresh samples, but most often prey could be classified only broadly in categories such as fish, cephalopods or crustaceans. Occasionally, even these categories were not distinguishable and the well-digested contents of stomachs had to be classified as Unidentified. Any otoliths found in stomachs were kept for later identification, which gave more precise information in some cases. Each component of the stomach contents was weighed to the nearest 0,1 g to calculate the percentage contribution by weight to the diet.

Results

Biomass and density

Biomass indices determined between July 1983 and June 1987 are shown in Figure 2. The highest value measured was 11 434 ± 3 851 t in summer 1984 and the lowest 304 ± 98 t in winter 1984.

No clear seasonal pattern in biomass trends has emerged. Until January 1985, there appeared to be a varying pattern of high biomass in summer and low biomass in winter in some years, but this trend was upset by the high estimate in July 1985. After that there was a general decline in the total biomass index from just under 10 000 t to just over 1 000 t in June 1987.

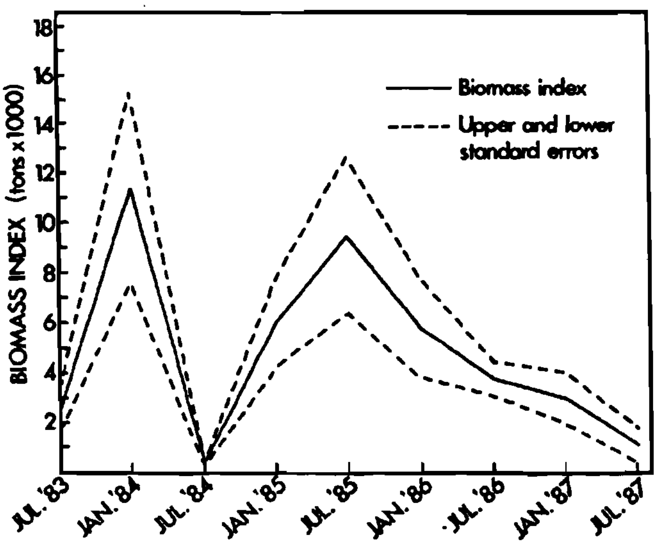

Figure 2 Fluctuation in *Loligo vulgaris reynaudii* biomass indices for the study area, determined from nine summer and winter surveys between July 1983 and June 1987.

Except for a few hauls, chokka squid were taken in only two of the five depth strata covered during the surveys, namely the 100–200 and 200–300-m ranges. Not many hauls shallower than 100 m could be done in the south. This is radically different from the situation on the S. Coast, where three surveys since 1986 (unpublished data) have revealed that less than 2% of the biomass is located deeper than 200 m but between 42 and 66% occurs at depths shallower than 100 m. In the latter area, all depth ranges could be sampled adequately, so it is clear that the results were a consequence of the squid distribution rather than gear limitations.

Annual and seasonal biomass indices and densities in the two depth ranges and seven latitudinal ranges are graphically represented in Figure 3. The seven latitudinal ranges are numbered from north to south in one-degree intervals between 29 and 36°S (see also Figure 1). The biomass index for each depth range and for the total area, as well as squid densities in kg.mile^{-2} are given. The biomass in the > 300 m zone was insignificant, so the data from this zone are not described.

Besides the two surveys in winter 1985 and summer 1987, the highest biomass was located in the 100–200 m depth zone. This still applies when these biomass indices are converted to densities per square nautical mile, but Student's *t* tests showed that differences in mean densities in the two depth ranges shown in Figure 3 were not statistically significant in either season. Densities varied in individual depth ranges between as low as 6 kg.mile^{-2} to 825 kg.mile^{-2} in 200–300 m in winter 1984 and winter 1985 respectively. For the whole area they varied between 9 and 336 kg.mile^{-2} in the winter and summer of 1984 respectively. Biomass, and therefore mean densities, were higher in summer (6 556 t or 193 kg.mile^{-2}) than in winter (3 691 t or 109 kg.mile^{-2}). A Student's *t* test on the means again showed this difference not to be significant, because of high variability.

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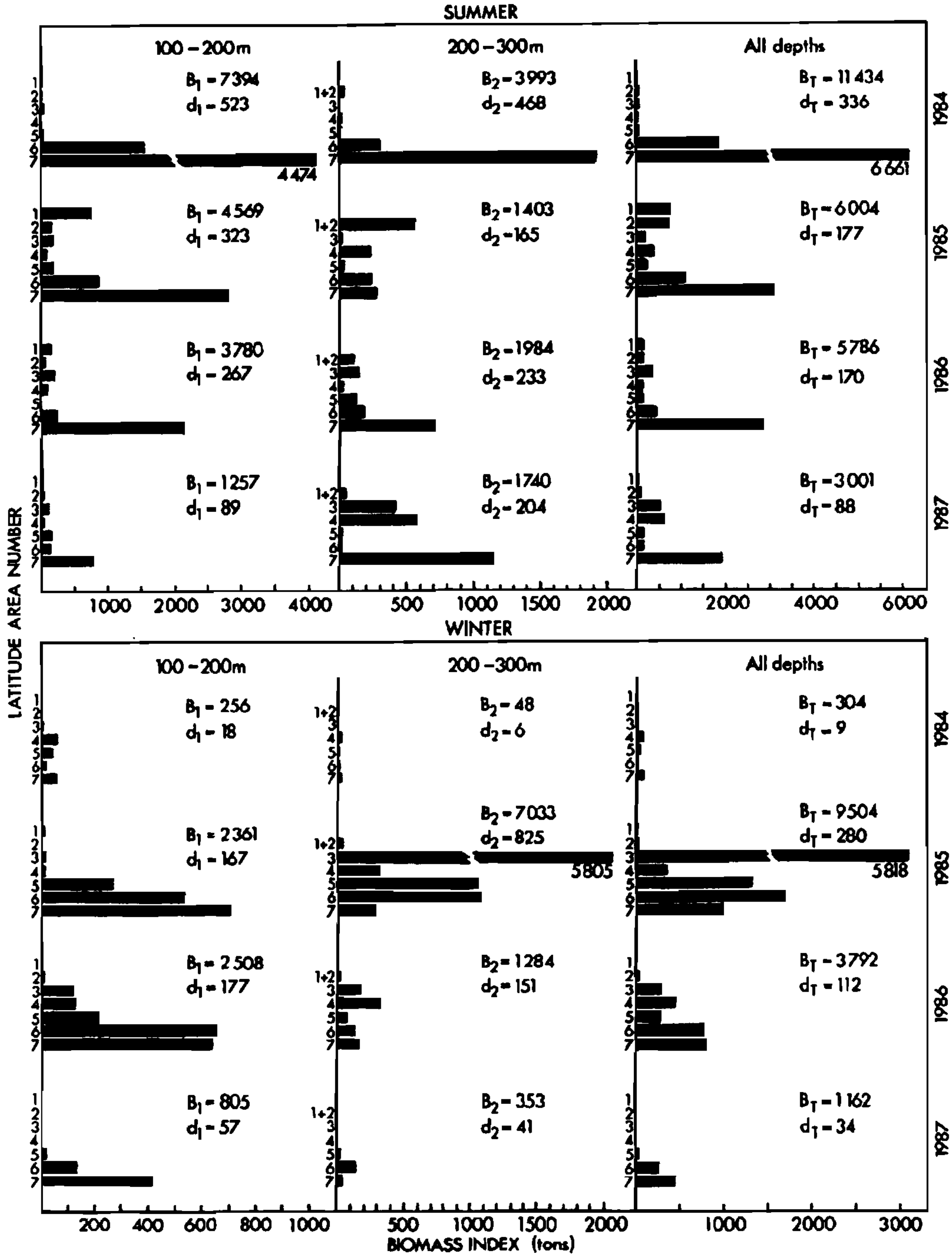

Figure 3 Seasonal and annual *Loligo vulgaris reynaudii* biomass indices in seven latitudinal ranges (1–7 on the y-axis), in two depth ranges and all depths, 1984–1987. Biomass (tons) and density (kg.mile^{-2}) in 100–200 m (B_1 and d_1), in 200–300 m (B_2 and d_2) and total biomass and density (B_T and d_T) are given for each survey.

In most years the highest biomass was found in the most southerly strata (6 and 7, south of 34°S), particularly in summer. Biomass in the most northerly strata (latitudinal strata 1 and 2, north of 31°S) was, except in summer 1985, extremely low. Between 31 and 33°S (strata 3 and 4) the biomass varied somewhat but was usually higher than in the northerly strata, particularly in winter. In winter 1985, for instance, there was a large concentration in area 3 (between 31 and 32°S) in 200–300 m.

Distribution and Movements

Maps of the summer and winter distributions of squid during each survey, represented by density contour lines plotted from catches at each station, are presented in Figure 4 and 5 respectively.

These data do not show consistent seasonal differences in the distribution of chokka squid. The July 1985 distribution, for instance, was similar to that in January 1986. In July 1987 the distribution was rather similar to that in January 1984, i.e. concentrated almost entirely in the south. The level of biomass during the former survey was, however, much lower.

Generally, the distribution is continuous from the east up to between Cape Point and Cape Columbine. Further to the west and north, occurrences are more sporadic.

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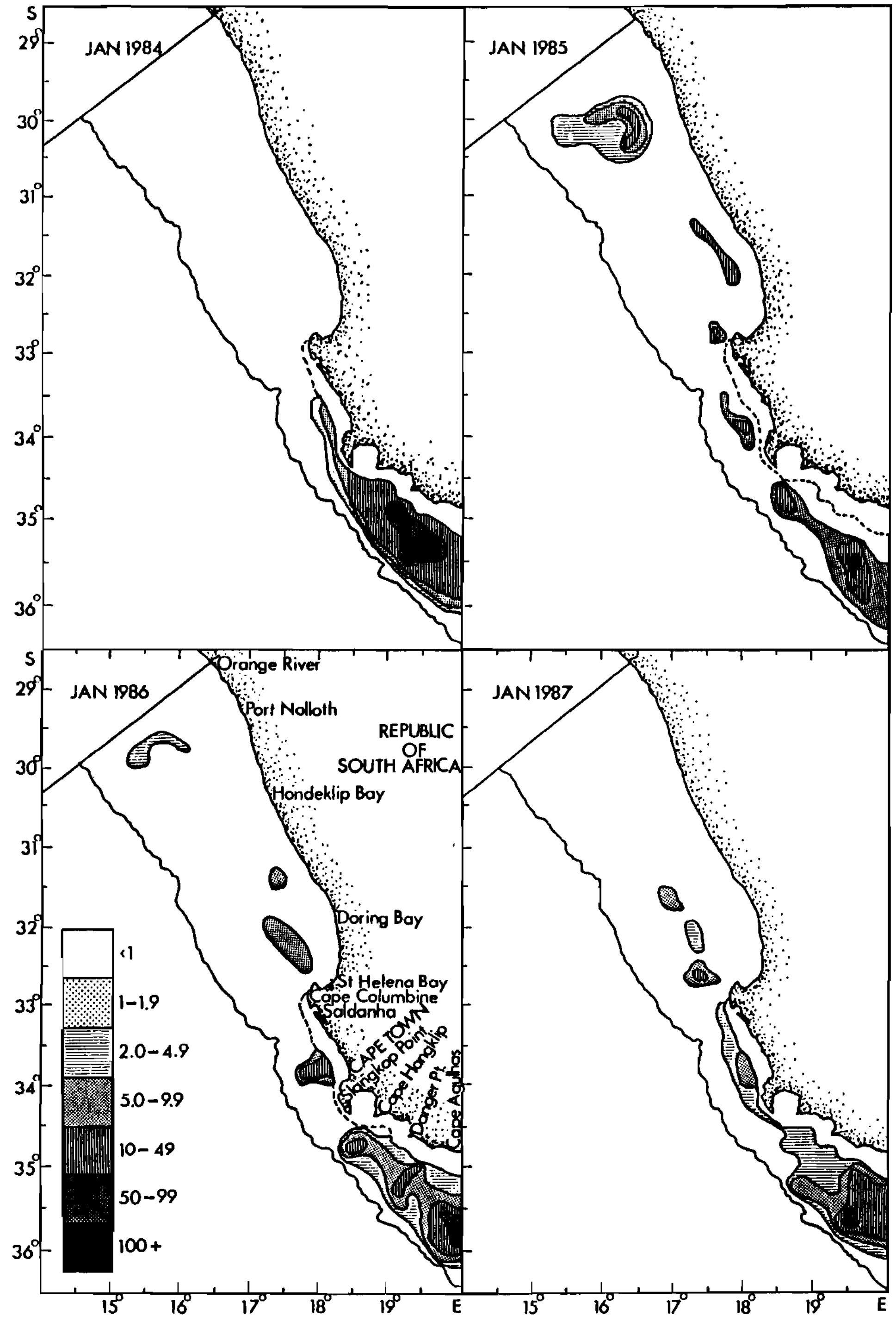

Figure 4 The summer distribution of *Loligo vulgaris reynaudii* off the West Coast of South Africa in terms of catch in kg.h^{-1}, represented by contour lines, 1984–1987.

Environmental factors affecting catches and distribution

Mean catches at various levels of the environmental parameters considered are presented in Figures 6 to 9. Variances were large, so these figures provide only descriptive trends in catches.

Figure 6 shows mean catches in 2-h intervals during daylight. In both seasons mean catches were variable throughout the mornings; in summer mean catches picked up after noon, in winter they appeared to drop off.

Figure 7 shows mean catches in 50-m intervals up to 350 m and greater. In both summer and winter, catches peaked in the 151–200 m depth range. They declined rapidly in greater depths, dropping to an insignificant level below 300 m. Results from the S. Coast (Augustyn 1989) were similar, with catches peaking in 130–180 m in summer and 170–190 m in winter.

Figures 8 and 9 give mean catches in 1°C bottom temperature intervals and 0,5 ml.l^{-1} oxygen level intervals respectively. There were very distinct threshold levels of both bottom temperature and bottom oxygen concentration below which mean squid catches dropped off very rapidly. These levels were at about 8°C and 3,5 ml.l^{-1}. This trend was

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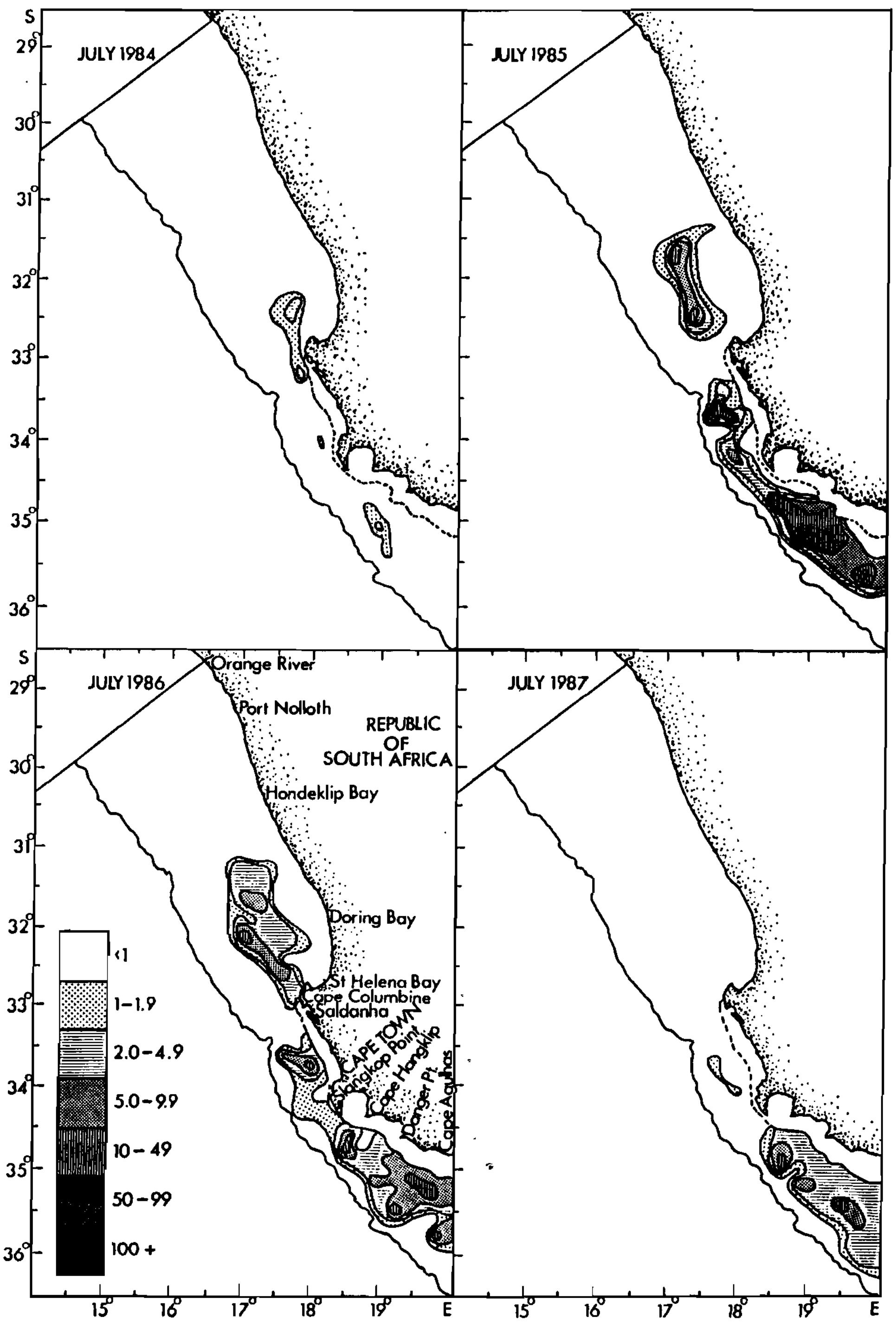

Figure 5 The winter distribution of *Loligo vulgaris reynaudii* off the West Coast of South Africa in terms of catch in kg.h^{-1}, represented by contour lines, 1984–1987.

more marked in summer than in winter but this was not tested statistically.

The Pearson correlation coefficients calculated between the transformed squid catches and each of the five parameters: bottom depth, bottom temperature, bottom oxygen, bottom salinity and time of day are presented in Table 1, together with those for the two seasons. Bottom oxygen was most strongly correlated with squid catches on a seasonal basis and when all data were combined. Bottom temperature and, to a lesser extent, bottom salinity, were also correlated significantly. Time of day and bottom depth were not significantly correlated. Time of day was the least correlated, and was therefore excluded from the C_p and multiple regression analyses which followed. The C_p analysis (Table 2) showed that the most applicable model was that which included depth, bottom temperature and bottom oxygen, but excluded bottom salinity. This can be seen in the overall (All Data) analysis where C_p first approaches p at this combination of factors. A multiple regression model was therefore constructed using these three variables only (Table 3).

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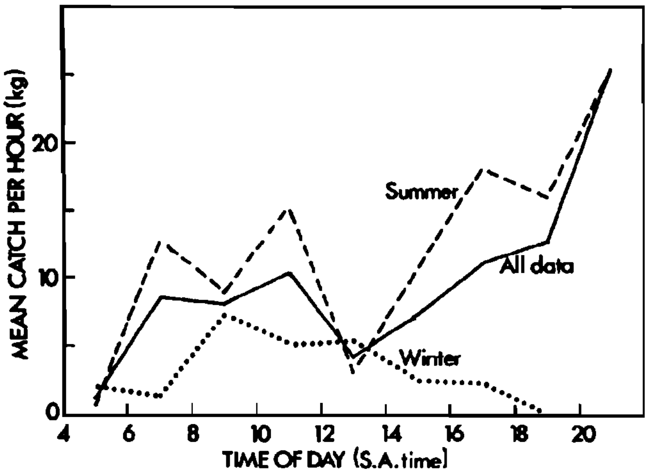

Figure 6 Mean catches (kg.h^{-1}) of *Loligo vulgaris reynaudii* in 2-h intervals during summer, winter and both seasons (all data).

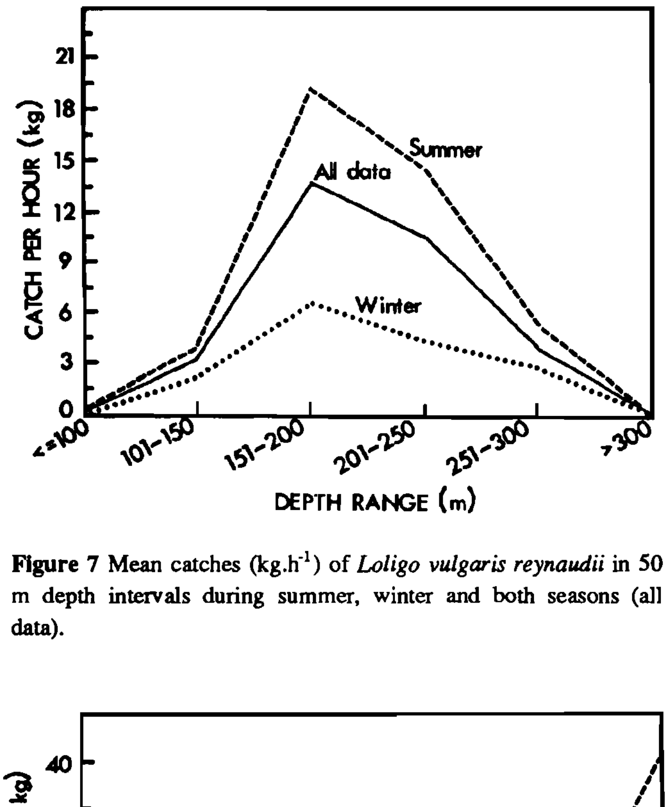

Figure 7 Mean catches (kg.h^{-1}) of *Loligo vulgaris reynaudii* in 50 m depth intervals during summer, winter and both seasons (all data).

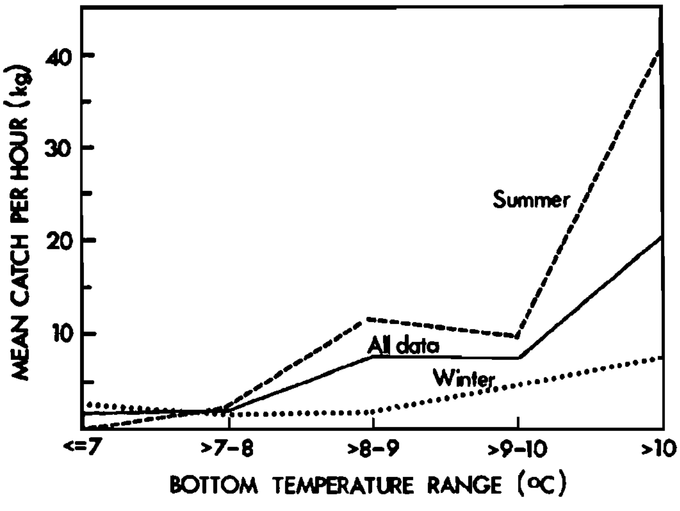

Figure 8 Mean catches (kg.h^{-1}) of *Loligo vulgaris reynaudii* in 1° temperature intervals during summer, winter and both seasons (all data).

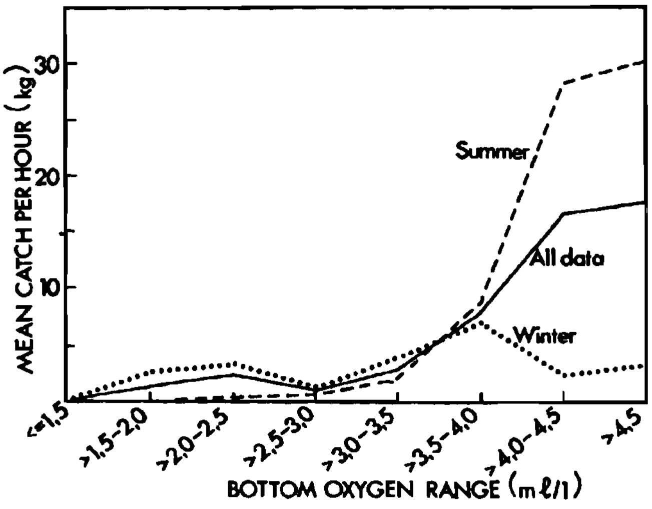

Figure 9 Mean catches (kg.h^{-1}) of *Loligo vulgaris reynaudii* in 0,5 ml O_2.l^{-1} intervals during summer, winter and both seasons (all data).

Size composition

The size distributions of male and female squid are presented in Figure 10 which allows comparison between summer and winter surveys. The mean and modal lengths are summarized in Table 4.

The most striking feature of these size distributions is that they are generally unimodal. The only clear exceptions were females in winter 1985 and winter 1986 which were weakly bimodal. All the length frequency data collected from the S. Coast to date have shown bimodal or polymodal distributions, with cohorts of juveniles, subadults and/or mature adults being discernable (Augustyn 1989). In contrast, the W. Coast distribution has consisted almost entirely of a single cohort of mostly immature and maturing squid (subadults). In both sexes the mean size and modal lengths were larger in summer than in winter. Male modes were around 180–190 mm in summer and 110–150 mm in winter, and

Table 1 Pearson correlation coefficients (bold type), significance levels, and number of observations for *Loligo vulgaris reynaudii* catches vs. depth, bottom temperature (BT), bottom oxygen (BO), bottom salinity (BS) and time of day. 'All data' means both summer and winter data were combined

	Depth	BT	BO	BS	Time
All data	**-0,017** $p > 0,05$ 437	**0,189** $p < 0,001$ 330	**0,338** $p < 0,001$ 287	**0,175** $p < 0,01$ 326	**-0,004** $p > 0,05$ 430
Summer	**0,016** $p > 0,05$ 245	**0,232** $p < 0,01$ 173	**0,450** $p < 0,001$ 140	**0,191** $p < 0,05$ 169	**0,015** $p > 0,05$ 241
Winter	**-0,047** $p > 0,05$ 192	**0,171** $p < 0,05$ 157	**0,183** $p < 0,05$ 147	**0,165** $p < 0,05$ 157	**-0,064** $p > 0,05$ 189

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Table 2 R-squared and Mallows' C_p statistics for regression models representing various combinations of the variables depth, bottom salinity (BS), bottom oxygen (BO) and bottom temperature (BT); p is the number of variables included in each model

		All data		Summer		Winter	
p	Variables	R^2	C_p	R^2	C_p	R^2	C_p
1	Depth	0,007	76,30	0,006	68,98	0,011	19,46
	BS	0,012	74,67	0,022	65,85	0,014	19,11
	BO	0,047	62,53	0,073	55,91	0,031	16,37
	BT	0,105	42,41	0,191	32,95	0,037	15,43
2	Depth BS	0,015	75,88	0,022	67,83	0,018	20,34
	Depth BT	0,049	64,03	0,081	56,23	0,037	17,42
	BT BS	0,052	62,83	0,089	54,72	0,040	17,37
	BO BS	0,138	33,00	0,199	33,18	0,070	12,06
	Depth BO	0,195	13,39	0,267	20,07	0,097	7,78
	BT BO	0,200	11,41	0,286	16,42	0,114	5,07
3	Depth BT BS	0,054	64,30	0,099	54,88	0,037	19,36
	Depth BO BS	0,201	12,93	0,296	16,46	0,114	6,99
	BT BO BS	0,204	12,29	0,297	16,28	0,120	5,98
	Depth BT BO	0,228	3,90	0,324	10,92	0,138	3,23
4	Depth BT BO BS	0,230	5,00	0,365	5,00	0,139	5,00

females 150–160 and 130–150 mm in summer and winter respectively.

The variation in mean and modal sizes was much smaller in summer than in winter, particularly in females. Males were also less variable than females in winter. The higher variation in the female size composition resulted from the presence of additional cohorts of either larger or smaller females, or both, as in the winter of 1986.

When the depth range size composition is examined

Table 3 F-values, significance levels and parameter estimates for the multiple regression model with dependent variable squid catch and independent variables depth, bottom temperature (BT) and bottom oxygen (BO). The squid catch data were transformed by means of a log(y+1) transformation

	All data	Summer	Winter
F-value	**27,58**	**18,86**	**7,39**
Sign.	$p < 0{,}001$	$p < 0{,}001$	$p < 0{,}001$
Summarized R^2	**0,234**	**0,307**	**0,138**
Parameter estimates			
Intercept	**-3,080**	**-2,804**	**-2,261**
Sign.	$p > 0{,}01$	$p < 0{,}001$	$p > 0{,}05$
Depth	**-0,005**	**-0,006**	**-0,003**
Sign.	$p < 0{,}01$	$p < 0{,}01$	$p > 0{,}05$
BT	**0,300**	**0,217**	**0,258**
Sign.	$p < 0{,}01$	$p < 0{,}001$	$p < 0{,}05$
BO	**0,624**	**0,863**	**0,387**
Sign.	$p < 0{,}001$	$p < 0{,}001$	$p < 0{,}001$

Table 4 Summary of mean and modal (bold type) dorsal mantle lengths (in mm) of *Loligo vulgaris reynaudii* from eight summer and winter surveys from 1984–87

	♂				♀			
	Summer		Winter		Summer		Winter	
Year	Mean	Mode	Mean	Mode	Mean	Mode	Mean	Mode
1984	173	**145, 185**	149	**145**	147	**125, 145**	139	**135**
1985	189	**185**	132	**115**	166	**165**	105	**75, 135**
1986	188	**185**	160	**155**	156	**155**	140	**85, 135, 185**
1987	181	**185**	167	**155**	149	**155**	146	**155**

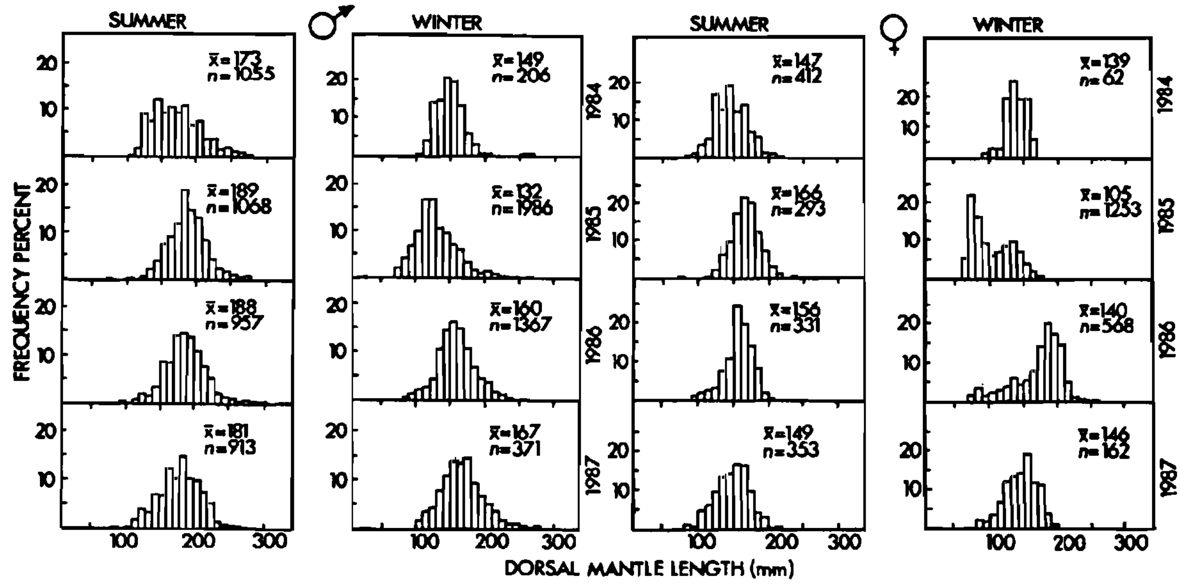

Figure 10 Seasonal size composition in male and female *Loligo vulgaris reynaudii*, 1984–87. Mean sizes ($\bar{x}$) and number of squid sampled (n) are given.

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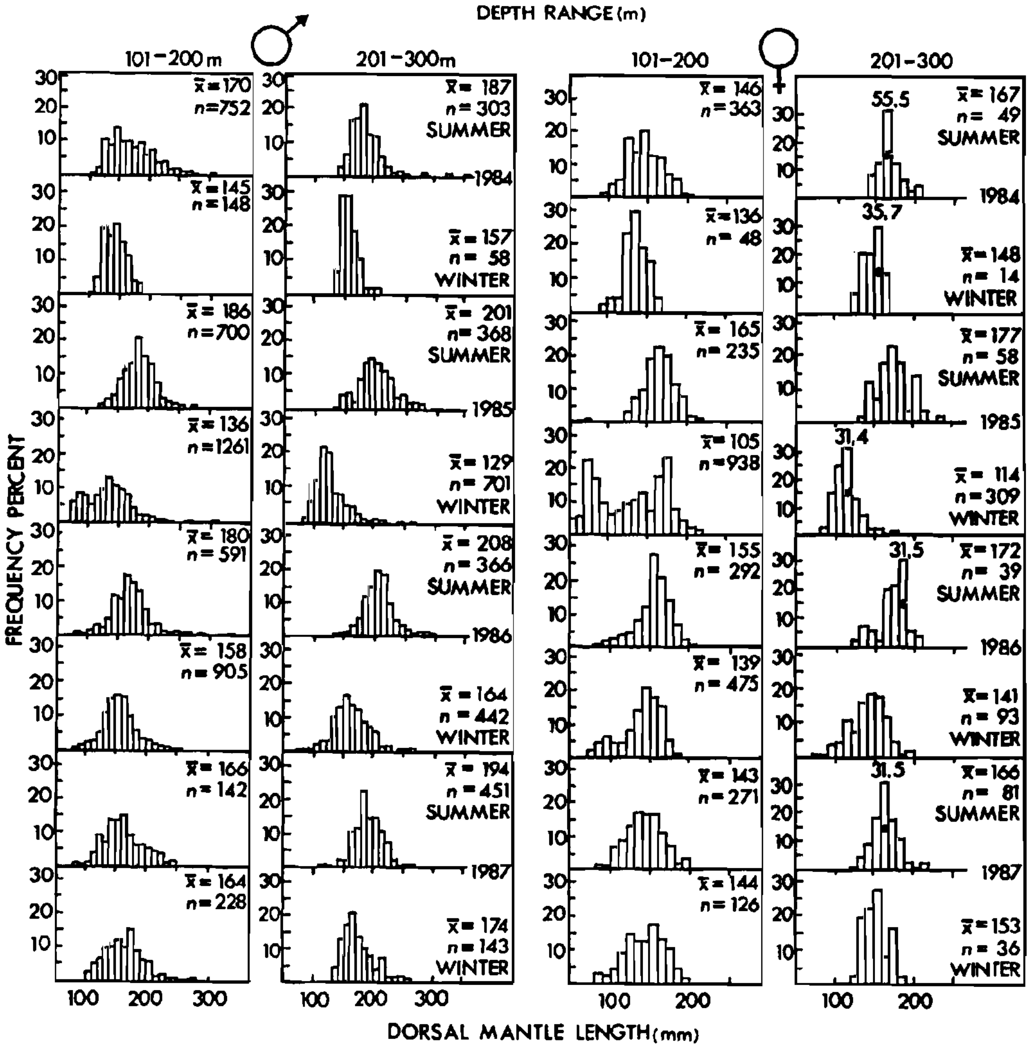

Figure 11 *Loligo vulgaris reynaudii* size composition in 100–200 and 200–300 m depth ranges, 1984–87. Mean sizes ($\bar{x}$) and number of squid sampled (n) are given.

(Figure 11) mean sizes are in general slightly larger in the 201–300 m depth range than in the 101–200 m range, in both sexes. In some instances, cohorts of small squid become obvious when the length frequency data are split between the two depth ranges, e.g. summer and winter 1985 in males and in summer 1986 in females. The depth location of the two female juvenile cohorts in the winters of 1985 and 1986 can be traced to the shallower range in both cases.

Reproductive biology

Sexual maturity

Table 5 gives the number and percentage of each of the three maturity stages for each survey and for each sex. The summarized values for summer and winter cruises, as well as an overall distribution of maturity stages (Total in Table 5) are also presented. The percentage of immature (i.e. stage 1) males varied between 33 and 82% with a mean of 69%, that of maturing (stage 2) males between 9 and 43% (mean 20%), and that of mature (stage 3) males between 5 and 23% (mean 11%). In females these figures were 53–82 (mean 70), 8–23 (mean 16) and 0–26 (mean 13)% for stages 1, 2 and 3 respectively. The maturing and mature percentages are much lower than those from S. Coast biomass surveys (Augustyn 1989). There the overall percentage of immature animals at sizes over 100 mm did not exceed 30%. On the other hand the percentage of mature and maturing animals was never lower than 70% and sometimes as high as 90%.

The maturity stage distribution appeared to differ markedly between summer and winter, with a higher percentage of animals being mature in winter, particularly among females. This was tested in both sexes by a contingency table analysis. The classification of stages in the two seasons was found to be independent in both males (at $p < 0,01$) and females (at $p < 0,001$). Notwithstanding the variation between individual surveys, the distribution of maturity stages in the two sexes was very similar in both seasons and overall.

The maturity stage distribution per size class of male and female squid is represented graphically in Figure 12. As is to be expected, there was an increasing percentage of maturing and mature squid in the larger size classes, but this increase was much lower than was found farther to the east on the S. Coast (Augustyn 1989).

The size composition and maturity data therefore show not only lower levels of maturity in the western part of the

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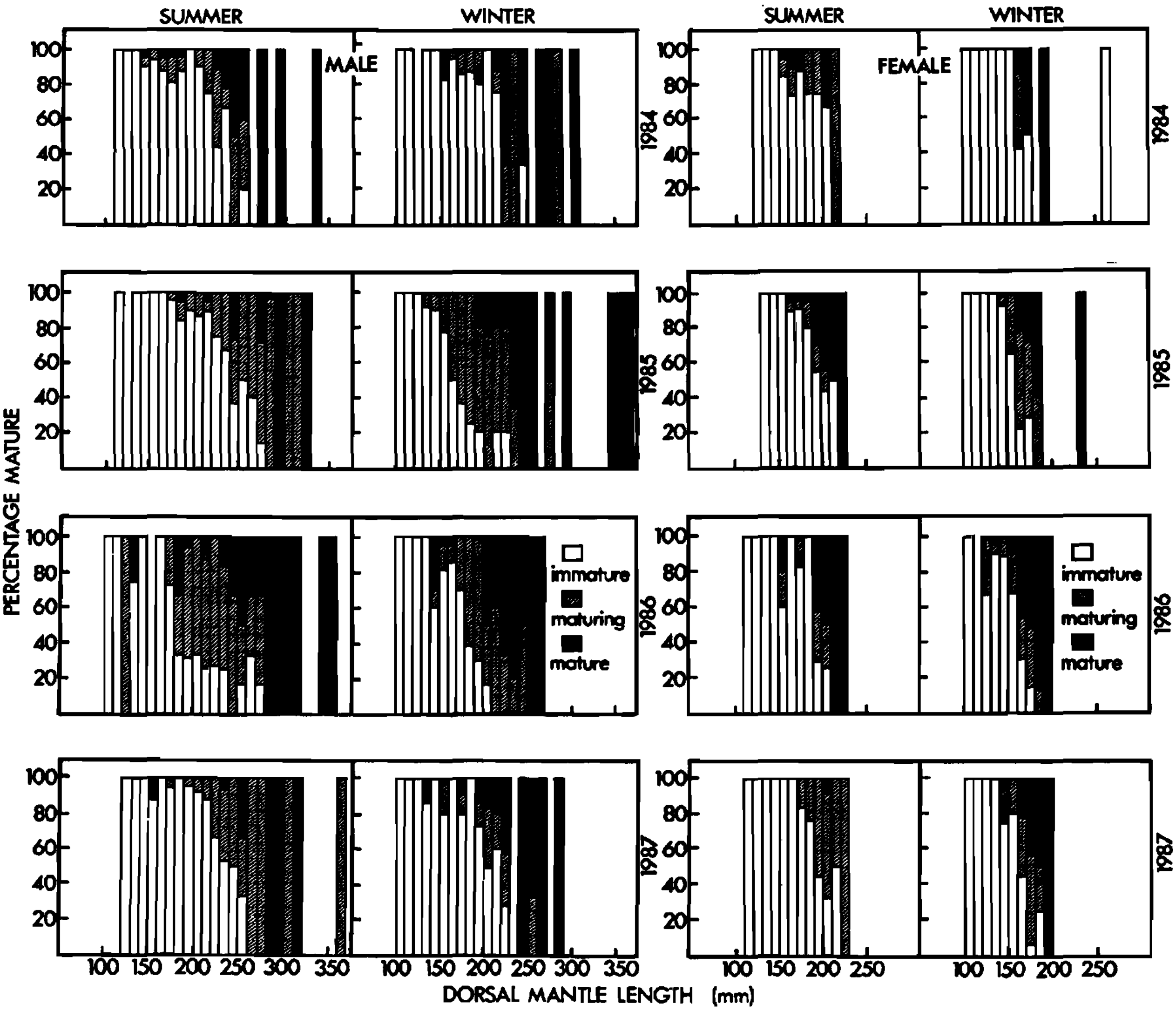

Figure 12 Proportions of immature, maturing and mature male and female *Loligo vulgaris reynaudii* in 10 mm size classes.

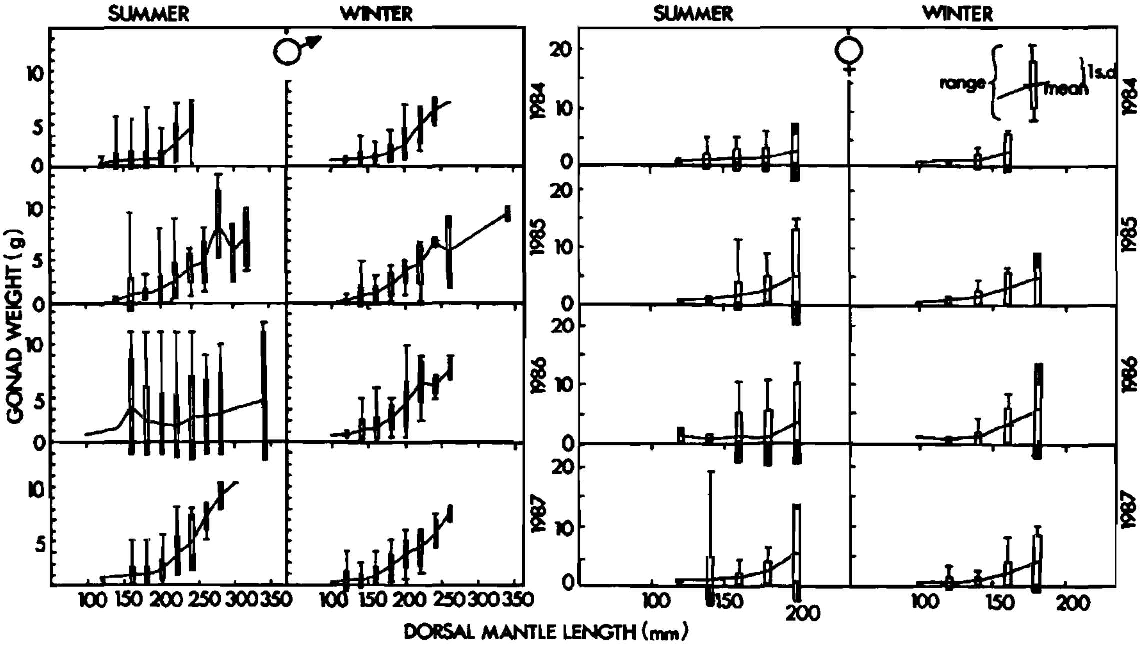

Figure 13 Mean gonad weight per 20 mm size class in male and female *Loligo vulgaris reynaudii*. Gonad weight ranges and standard deviations are also indicated.

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Table 5 Numbers and percentages (in bold type) of immature (stage 1), maturing (stage 2), mature (stage 3) and maturing + mature (stage 2 + 3) male and female *Loligo vulgaris reynaudii* in eight summer and winter surveys from 1984–87. Summarized values for summer, winter and total (both seasons) are also given

		Maturity stage							
		♂				♀			
Survey		1	2	3	2+3	1	2	3	2+3
1984									
Summer	No.	216	31	17	48	66	9	5	14
	%	**82**	**12**	**6**	**18**	**82**	**11**	**6**	**17**
Winter	No.	91	10	12	22	25	3	3	6
	%	**81**	**9**	**11**	**19**	**81**	**10**	**10**	**19**
1985									
Summer	No.	144	34	12	46	89	9	15	34
	%	**76**	**18**	**6**	**24**	**79**	**8**	**13**	**21**
Winter	No.	52	35	15	50	60	17	8	25
	%	**51**	**34**	**15**	**49**	**71**	**20**	**9**	**29**
1986									
Summer	No.	40	52	28	80	40	6	10	16
	%	**33**	**43**	**23**	**67**	**71**	**11**	**18**	**29**
Winter	No.	88	51	30	81	77	27	36	63
	%	**52**	**30**	**18**	**48**	**55**	**19**	**26**	**45**
1987									
Summer	No.	140	29	9	38	110	29	1	30
	%	**79**	**16**	**5**	**21**	**79**	**21**	**1**	**21**
Winter	No.	87	12	16	28	39	17	18	35
	%	**76**	**10**	**14**	**24**	**53**	**23**	**24**	**47**
Summer	No.	540	146	66	212	305	53	31	84
	%	**72**	**19**	**9**	**28**	**78**	**14**	**8**	**22**
Winter	No.	318	108	73	181	201	64	65	129
	%	**64**	**22**	**15**	**36**	**61**	**19**	**20**	**39**
Total	No.	858	254	139	393	506	117	96	213
	%	**69**	**20**	**11**	**31**	**70**	**16**	**13**	**30**

chokka squid distribution because of the prevalence of smaller size classes, but also lower levels of maturity in equivalent size classes. This is true of both sexes.

This trend is confirmed when the mean gonad weight per size class data is examined (Figure 13), particularly in females. Whereas mean gonad weights on individual surveys on the W. Coast in female 180 and 200 mm size classes were between approximately 1 and 6 g, they were between 7 and 15 g for corresponding size classes on the S. Coast in 1980/82 (Augustyn 1989). In males at 220 and 240 mm (a size at which large groups were present in both areas), the mean gonad weights were between 1,5 and 6 g on the W. Coast, compared with between 4 and 6 g on the S. Coast.

Gonado-somatic indices

The two gonado-somatic indices, GSI1 and GSI2 calculated for each survey, are presented in Table 6.

In individual surveys GSI1 varied between 24,1 and 32,5% in males and 16,3 and 23,9% in females with overall means of 27,9 and 18,9% in males and females respectively. The summer means were 27,6 and 17,6% in males and females respectively, compared with 28,4 and 20,3% in winter. A Student's *t* test confirmed that no significant differences existed between summer and winter means in either sex for this index.

GSI2 varied between 0,64 and 1,64% in males and between 0,43 and 1,92% in females. Summer means were 0,84 and 0,77% and winter means 1,26 and 1,62% in males and females respectively. Student's *t* tests showed that the gonads of both sexes were significantly heavier but not longer in winter than in summer. The difference between the seasons found in GSI2 is consistent with the higher rates of mature and maturing + mature squid in winter. This confirms that GSI2 is a more sensitive indicator of sexual development than GSI1 over the size ranges examined.

Sex ratios

Tables 7, 8 and 9 present squid sex ratio analyses by cruise, depth range and latitudinal stratum,. summarized also by season and all data combined. Table 7 shows that males were very highly significantly ($p < 0{,}001$) in the majority during every survey at ratios of between 1,45 : 1 (July 1985) and 3,32 : 1 (July 1984). The bias towards males was greater in summer than in winter: 2,51 vs. 1,74. This result was, however, influenced greatly by the large July 1985

Table 6 Mean dorsal mantle lengths (DML), total wet weight (TWW), gonad lengths (GL) and gonad weights (GW) together with two gonado-somatic indices calculated from these parameters and expressed as percentages, GSI1 = GL/DML and GSI2 = GW/TWW

Survey	Sex	Mean DML (mm)	Mean TWW (g)	Mean GL (mm)	Mean GW (g)	GSI1 (%)	GSI2 (%)
1984							
Summer	M	170	138	41	0,88	24,1	0,64
	F	153	102	25	0,44	16,3	0,43
Winter	M	166	129	47	1,43	28,3	1,11
	F	138	86	33	1,44	23,9	1,63
1985							
Summer	M	198	198	56	1,54	28,3	0,78
	F	166	128	28	1,62	16,9	1,27
Winter	M	167	132	45	1,72	26,9	1,30
	F	136	77	24	1,35	17,6	1,75
1986							
Summer	M	209	198	68	1,95	32,5	0,99
	F	163	133	35	0,77	21,5	0,58
Winter	M	172	135	48	2,21	27,9	1,64
	F	144	89	30	1,71	20,8	1,92
1987							
Summer	M	194	176	52	1,94	26,8	1,10
	F	163	113	27	1,46	16,6	1,29
Winter	M	171	140	51	1,58	29,8	1,13
	F	146	99	29	1,29	19,9	1,30
Means							
Summer	M	193	178	54	1,58	27,6	0,84
	F	161	119	29	1,47	17,6	0,77
Winter	M	169	134	48	1,74	28,4	1,26
	F	141	88	29	1,45	20,3	1,62
Total	M	181	156	51	1,66	27,9	1,01
	F	151	103	29	1,26	18,9	0,99

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Table 7 Numbers of male and female *Loligo vulgaris reynaudii,* sex ratios and computed chi-squared values in eight summer and winter surveys from 1984-87, and summarized values for summer, winter and both seasons (Total)

Survey	Males	Females	Ratio	χ^2
1984				
Summer	2 225	989	2,25	475
Winter	206	62	3,32	77,4
1985				
Summer	1 641	497	3,30	612
Winter	4 066	2 798	1,45	234
1986				
Summer	1 494	670	2,23	314
Winter	1 673	609	2,75	496
1987				
Summer	1 039	394	2,64	290
Winter	403	179	2,25	86,2
Summer	6 399	2 550	2,51	1 655
Winter	6 348	3 648	1,74	729
Total	12 747	6 198	2,06	2 263

Table 8 Numbers of male and female *Loligo vulgaris reynaudii,* sex ratios and computed chi-squared values in two depth ranges in eight summer and winter West Coast surveys from 1984–87. Summer, winter and total sex ratios are summarized

	Depth range							
	101–200 m				201–300 m			
Survey	M	F	R	χ^2	M	F	R	χ^2
1984								
Summer	1922	940	2,04	337	303	49	6,18	183
Winter	148	48	3,08	51,0	58	14	4,14	26,9
1985								
Summer	1273	439	2,9	406	368	58	6,34	226
Winter	1493	1302	1,15	13,1	2549	1490	1,71	278
1986								
Summer	1058	616	1,72	117	436	54	8,07	298
Winter	1089	501	2,17	217	584	108	5,41	327
1987								
Summer	474	285	1,66	47,1	565	109	5,18	309
Winter	260	143	1,82	34,0	143	36	3,97	64,0
Summer	4727	2280	2,07	854	1672	270	6,19	1012
Winter	2990	1994	1,50	199	3334	1648	2,02	571
Total	7717	4274	1,81	989	5006	1918	2,61	1377

Table 9 Numbers of male and female *Loligo vulgaris reynaudii,* sex ratios (bold type), and chi-squared values in seven latitudinal strata off the West Coast of South Africa. Strata 1 through 7 represent latitudes 29/30°S through 35/36°S

	Latitudinal stratum no.						
Survey	1	2	3	4	5	6	7
1984							
Summer						650:282	575:707
						2,30	**2,23**
						145,3	330,2
Winter						58:14	148:48
						4,14	**3,08**
						26,9	51,02
1985							
Summer	116:51	35:14	25:7	76:11	68:105	406:67	906:242
	2,27	**2,5**	**3,57**	**6,91**	**0,65**	**6,06**	**3,74**
	25,3	9,0	10,1	48,6	7,91	243,0	384,1
Winter		81:20	389:115	118:15	1351:812	1276:864	827:966
		4,05	**3,38**	**7,87**	**1,66**	**1,48**	**0,86**
		36,8	149,0	79,8	134,3	79,3	10,8
1986							
Summer	12:1		38:6			152:107	1292:556
	12,0		**6,33**			**1,42**	**2,32**
	9,31		23,3			7,82	293,1
Winter			123:13	323:26	253:97	403:172	571:301
			9,46	**12,42**	**2,61**	**2,34**	**1,90**
			88,97	252,8	69,5	92,8	83,6
1987							
Summer		4:0	99:19	240:55	65:42	73:54	558:224
			5,21	**4,36**	**1,55**	**1,35**	**2,49**
			54,24	225,4	4,94	2,84	142,7
Winter					17:1	157:58	229:120
					17,0	**2,71**	**1,91**
					14,22	45,59	34,04
Summer	128:52	39:14	162:32	316:66	133:147	1281:510	4331:1729
	2,46	**2,79**	**5,06**	**4,79**	**0,90**	**2,51**	**2,50**
	32,1	11,8	87,1	163,6	0,70	331,9	1117
Winter		81:20	512:128	441:41	1621:910	1894:1108	1775:1435
		4,05	**4,00**	**10,76**	**1,78**	**1,71**	**1,24**
		36,84	230,4	332,0	199,7	205,8	36,01
Total	128:52	120:34	674:160	757:107	1754:1057	3175:1618	6106:3164
	2,46	**3,53**	**4,21**	**7,07**	**1,66**	**1,96**	**1,93**
	32,09	48,03	316,8	489,0	172,8	505,8	933,7

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sample which had an anomalously low ratio of males : females of 1,45 : 1. If mean values for the two seasons are calculated from the ratios for each survey, there is a still greater bias towards males in summer, but the difference is much smaller and not statistically significant. In the overall analysis, there were more than twice as many males as females at 2,06 : 1. This value is even higher if the mean of the ratios for each survey is taken: 2,52 : 1. Table 8 shows that the sex ratio is even more biased in the deeper depth zone (201–300 m) than shallower (101–200 m). On every survey except July 1985, the ratio was 4 : 1 or greater with 8,07 : 1 being recorded in January 1986. This bias towards males in deep water is much greater in summer than in winter.

Table 9 shows a drastic change in the sex ratio from a bias of about 2 : 1 in favour of males to a much greater bias between the northern and southern halves of the study area, i.e. at about Cape Columbine. This was the case in both summer and winter and also overall. It is best illustrated by a direct comparison of the sex ratios in areas 4 and 5, i.e. at this interface: in summer the ratio changed from 0,9 to 4,79 : 1, in winter from 1,78 to 10,76, and overall from 1,66 to 7,07.

Feeding

Out of 1629 stomachs examined, 1135 or 69,7%, were empty. Table 10 gives the overall composition of all the components identified. Of stomachs containing food, three major groups could be identified, namely fish, cephalopods and crustaceans. These contributed 71,5; 1,4 and 27,5% by frequency of occurrence respectively. Of the fish, 208 out of a total of 344, or about 60%, could not be identified. Of those that could be identified, anchovy *Engraulis capensis* (30,6%) and dragonettes *Paracallionymus costatus* (29,3%) made up the major portions. Lightfish *Maurolicus muelleri* (18,4%), lanternfish *Lampanyctodes hectoris* (8,8%) and juvenile Cape hake *Merluccius capensis* (5,4%) made minor contributions. Other species were other myctophids, round herring *Etrumeus whiteheadi*, rattails *Coelorhynchus fasciatus* and saury *Scomberesox saurus scomberoides*. Cephalopods were found in only seven stomachs, with unidentified squid (probably the same species) being the most frequently encountered. Crustaceans were found in 129 stomachs but 30% of these could not be identified. Of those that could be identified, euphausiids (35,7%) followed by decapod larvae (32,7%) were the most common. Amphipods and isopods also occurred in lesser quantities.

The contribution of each component by weight is also given in Table 10. By weight, fish constituted an even more important part of the diet (85%). Anchovy constituted over 20% by weight of all the non-empty stomachs, 56% of all identified fish and 43% of all identified components, i.e. excluding the unidentified category.

A comparison of the diet in summer and winter (Table 11) shows that the percentage of crustaceans eaten is much higher in winter, but the contribution of fish is lower. The consumption of anchovy was similar in terms of percentage of diet by weight in the two seasons, but occurred more frequently in winter. Myctophids were found only in winter, while lanternfish and lightfish were more prevalent in winter. These results may be biased to some extent, however, by the large difference in the percentage of unidentified fish, which totalled over 55% by weight in summer, compared with only 38% by weight in winter.

Table 10 The diet of *Loligo vulgaris reynaudii* off the West Coast of South Africa from stomach contents analyses

			Non-empty stomachs	
Classification group	Frequency (n)	% Frequency	Frequency %	% by weight
Empty	1135	69,7	–	–
Non-empty	494	30,3	–	–
Unidentified	**16**	**1,0**	**3,2**	**1,4**
Unidentified fish	208	12,8	42,1	49,3
Merluccius sp.	8	0,5	1,6	1,0
Paracallionymus costatus	43	2,6	8,7	6,1
Myctophidae	3	0,2	0,6	0,5
Lampanyctodes hectoris	13	0,1	2,6	1,1
Etrumeus whiteheadi	4	0,2	0,8	2,2
Maurolicus muelleri	27	1,7	5,5	3,8
Coelorhynchus fasciatus	1	0,1	0,2	0,2
Engraulis capensis	45	2,8	9,1	20,2
Scomberesox saurus scomberoides	1	0,1	0,2	0,8
Total fish	**344**	**21,7**	**71,5**	**85,0**
Unidentified cephalopods	1	0,1	0,2	0,1
Squids	5	0,3	1,0	1,0
Sepiids	1	0,1	0,2	0,1
Total cephalopods	**5**	**0,4**	**1,4**	**1,2**
Unidentified crustaceans	38	2,3	7,7	3,0
Euphausiiacae	35	2,1	7,1	1,5
Amphipoda	19	1,2	3,9	3,2
Decapoda (megalopae larvae)	32	2,0	6,5	3,5
Isopoda	12	0,7	2,4	1,6
Total crustaceans	**129**	**8,4**	**27,5**	**12,7**
Total	1629			

Discussion

In common with many other species of squid, e.g. *L. pealei* (Summers 1969), *L. opalescens* (Hurley 1978) and *L. plei* and *L. braziliensis* (Juanico 1981), *Loligo vulgaris reynaudii* forms schools. The consequent patchy spatial distribution leads to high variances around mean catch calculations from random sampling. Nevertheless, the trends of peak catches in the 151–200 m depth range, at bottom temperatures over 8°C, and at bottom oxygen levels over 3,5 $ml.l^{-1}$ are fairly clear-cut, particularly in summer. This is confirmed by the high significance of the parameters in the regression models and the high correlation coefficients for these variables with catches. Summers (1969) found that *L. pealei* was also restricted to bottom temperatures higher than 8°C. This was confirmed by Whitaker (1978), Lange (1980) and Macy (1980). In species with a more pelagic mode of living, such as *Todarodes pacificus*, high densities are often found near offshore frontal zones and in areas where a high degree of

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Table 11 The seasonal diet of *Loligo vulgaris reynaudii* off the West Coast of South Africa from stomach contents analyses

	Summer			Winter		
Classification group	Freq.	Freq. %	% by weight	Freq.	Freq. %	% by weight
Unidentified	**16**	**6,0**	**2,1**	**0**	**0**	**0**
Unidentified fish	134	50,4	55,1	74	32,5	38,2
Merluccius sp.	1	0,4	0,2	7	3,1	2,5
Paracallionymus costatus	18	6,8	6,0	25	11,0	6,3
Myctophidae	0	0	0	3	1,3	1,4
Lampanyctodes hectoris	1	0,4	0,2	7	3,1	2,5
Etrumeus whiteheadi	1	0,4	1,0	3	1,3	4,5
Maurolicus muelleri	7	2,6	3,0	20	8,8	5,3
Coelorhynchus fasciatus	1	0,4	0,2	0	0	0
Engraulis capensis	19	7,1	19,8	26	11,4	21,0
Scomberesox saurus scomberoides	1	0,4	0,8	0	0	0
Total fish	**182**	**68,8**	**86,3**	**162**	**74,6**	**81,8**
Unidentified cephalopods	0	0	0	1	0,4	0,2
Squids	3	1,1	0,8	2	0,9	0,6
Sepiids	0	0	0,0	1	0,4	0,3
Total cephalopods	**3**	**1,1**	**0,8**	**2**	**1,8**	**1,1**
Unidentified crustaceans	32	12,0	4,2	6	2,6	0,7
Euphausiaciae	12	4,5	1,4	23	10,1	1,7
Amphipoda	5	1,9	1,3	14	6,1	6,7
Decapoda (megalopae larvae)	7	2,6	0,7	25	11,0	8,0
Isopoda	12	4,5	2,4	0	0	0,0
Total crustaceans	**65**	**25,6**	**10,0**	**64**	**29,8**	**17,1**
Total	266			228		

mixing occurs. They apparently feed on plankton near thermoclines (Kasahara 1978). In contrast, most loliginids live near the bottom during the day (Roper & Young 1975). Research trawl catches, as in the present and other studies (e.g. Augustyn 1989), suggest that *L. vulgaris reynaudii* subadults spend daytime feeding close to the bottom and the temperature *v.* catch data do not suggest a strong association with thermoclines.

Temperature preferences may change at transitional stages of the life cycle. Whereas temperatures above 8°C are important in governing the distribution in the offshore subadult phase, they seldom fall as low as this in areas where mature adults occur, such as in False Bay. Augustyn (1989) found that research catches there were influenced by a combination of water temperatures and south-easterly winds, and were generally low when temperatures dropped below 17°C. Sauer (1991), working in the inshore spawning grounds in the Eastern Cape, has recently found catches of mature squid to be correlated with sea temperatures, that upwelling events influence catches and that catches were low outside of the 11–21°C range.

Some species of cephalopods (mainly those occurring in shallow waters and estuaries) such as *Sepia officinalis* (Guerra & Castro 1988) and *Lolliguncula brevis* (Dragovich & Kelly 1963; Hendrix, Hulet & Greenberg 1981) have been shown to be tolerant of low salinities. Others, such as *Sepia australis* and *Sepia hieronis* occur in relatively restricted salinity regimes (Augustyn, Lipiński & Roeleveld, in press). Salinity has been examined as a factor affecting distribution by Tinbergen & Verwey (1945) in *L. vulgaris vulgaris*, without the use of statistical methods. They found that this species was restricted to coastal waters with salinities of 30–36‰ off the Netherlands. *L. pealei* does not normally occur in salinities below 32‰ (Hixon 1980). In the present study, catches showed no correlation with salinity, but the range of salinities encountered was very limited, so the effect of more extreme salinities could not be tested in *L. vulgaris reynaudii*. Low salinity could well be an important restrictive factor in inshore areas, particularly near river mouths.

Although the effect of the time of day was not linearly correlated with catches, the relationship showed some similarities to results obtained elsewhere. The winter pattern (Figure 6) is similar to that found by Hurley (1980) for *Illex illecebrosus* in the N.W. Atlantic, where the best catches were made between dawn and noon. Porębski (1970) found that catches of *L. vulgaris vulgaris* in shallow waters (< 110 m) off N.W. Africa were best between 07h00 and 10h00 and between 14h00 and 18h00. Midday catches were poor. These findings were very similar to those reported by Augustyn (1989) for the S. Coast.

The biomass index calculated from the W. Coast surveys (Orange River to Cape Agulhas) shows that biomass is lower than on the S. Coast (Cape Agulhas to Port Alfred).

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This is so despite a slightly smaller shelf area (0–500 m) on the S. Coast of about 29 000 nautical mile^2 compared to some 34 000 nautical mile^2 on the W. Coast. Densities from the S. Coast biomass surveys in 1980–82 (Augustyn 1989) were much higher at between 600 and 3500 kg.mile^{-2} in individual strata in summer and between 200 and 1800 kg.mile^{-2} in winter. Comparable estimates of biomass on the S. Coast in spring (September 1986 and September 1987) were 14 000 ± 3 100 t and 11 500 ± 1 700 t respectively. The closest estimates in time to these on the W. Coast, in July 1986, January 1987 and June 1987 were 3 800 ± 700 t, 3 000 ± 1 000 t and 1 200 ± 400 t. The latitudinal biomass estimates and the distribution of catches show that while it occurs sporadically up the W. Coast as far north as Port Nolloth and may be locally abundant anywhere south of this at times, the largest concentrations are usually found to the south-east of the Cape Peninsula. The rocky nature of the ground in the south of the study area unfortunately does not allow the biomass of squid in depths shallower than 100 m to be assessed directly. Estimates by extrapolation from areas further north may lead to an underestimate of overall biomass. However, this is a constant factor and year to year comparisons may be made keeping this drawback in mind. In general, biomass is higher in the 100–200-m zone than in 200–300 m. This is confirmed by the peak in catches found in 150–200 m in the catch analyses (Figure 7).

The lower biomass in the west coupled with its continuous distribution to the east indicate that the W. Coast population of *L. vulgaris reynaudii* is a westerly extension of the main population concentrations to the east of Cape Agulhas. The biomass, distributional, size composition and reproductive data from the present study show, however, that the population characteristics of chokka squid in this western extent of its distribution differ substantially from those further east, as described by Augustyn (1989). Reductions in the winter population may sometimes be more drastic than occur further east, e.g. in July 1984. The size distribution is also much narrower, and gonadal development is not as far advanced.

There has been evidence of limited spawning in areas such as False Bay and the eastern side of Danger Point. Egg capsules are occasionally attached to anchor ropes or hooked with jigs, and have been seen by SCUBA divers (pers. obs.). A single record of squid eggs at Robben Island, near Cape Town has been reported (Augustyn 1990). There are, however, no known major spawning areas in the study area. Juveniles as small as 20 mm are regularly taken and a cohort of 40–60 mm is often present on the S. Coast, but not on the W. Coast. Here the smallest squid taken have been around 70 mm and no regular juvenile cohort below 100 mm is discernable. There has been only one exception, in July 1985, when a strong juvenile cohort at 70–80 mm was detected. There is usually only one major cohort in the area, consisting mostly of juveniles and subadults (maturity stage 1 and 2). The wide size range of roughly 100 to 300 mm in males and 100–220 mm in females, however, indicates some overlapping of broods. This overlap probably partly results from an extended breeding season and the presence of some remnants of the previous year-class in the larger sizes, but there are too few of the latter to represent a distinct mode or peak in the size distribution. In both sexes this single cohort is at a somewhat larger size in summer than in the preceding winter. Large, mature females of over 230 mm and males over 300 mm, common in the east where they may be represented by discrete cohorts, are rare on the W. Coast.

Compared to farther east, a lower percentage of mature and maturing animals, slower development of gonads relative to body size, and lower overall gonado-somatic indices are found on the W. Coast. This shows that squid over the entire size spectrum are not as reproductively advanced as farther east. Higher maturity rates and gonad somatic indices in winter indicate that maturation is further advanced than in summer.

Given the above evidence from biomass, size composition and maturity data, it is suggested that there is an ongoing, but varying in intensity, immigration and emigration cycle in the area by juveniles and small subadults from, and by larger subadults to, the spawning areas in the east, i.e. to the east of Plettenberg Bay. The timing, duration and intensity of immigration determine the biomass at any given time in the area. When the surveys take place in January (summer), the population may in some years already have declined somewhat following the influx which occurs some time before September or October, when trawler catches normally peak (Augustyn 1989). The major part of the population with males at about 180–190 mm and females at 150–160 mm probably leaves the W. Coast and migrates back to the spawning areas (where they hatched a year or more earlier) soon after the summer survey and the W. Coast stock is often low by the time the winter survey takes place in July. This group probably reaches the S.E. Coast by late spring or early summer at a somewhat larger size. The biomass is therefore not necessarily at a peak on the W. Coast in January when the summer survey is carried out. This emigration from the west causes a major decline in the biomass there until the next influx of subadults. Occasionally, as in July 1985, immigration occurs sooner than usual, resulting in a higher than normal winter biomass.

The influx of squid from the east does not appear to be purely seasonal; there is no consistency in their summer and winter distributions, and it is likely that other factors are also important. Local abundances may depend on the presence of food organisms and/or favourable environmental conditions, such as bottom temperatures and oxygen levels. Complete depletion of the population, as in July 1984, may be caused by particularly unfavourable conditions, may merely represent a phase of the immigration/emigration cycle when the resident population abundance is low, or may be the result of a combination of these causes. Tinbergen & Verwey (1945) describe a similar coastwise migration in *L. vulgaris vulgaris* from the south into the North Sea in spring; this is an apparent breeding migration to the shallow waters off the Dutch coast. The location of the winter population of the latter species is uncertain, but this may be off Portugal (an area possibly analogous to the W. Coast in the present study).

Summers (1969) describes the winter population of *L. pealei* in the mid-Atlantic Bight as an onshore-offshore and biannual coastwise migration. The northern limit of its distribution is 600 km south of its summer range limit, which is strongly influenced by temperature. In *L. vulgaris reynaudii*, there is no consistent difference in the summer

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and winter range limits on the W Coast. The CTD data collected during this study showed that factors limiting distribution, such as bottom temperature and oxygen levels, are not critically different between the two seasons. Bottom temperatures above 8°C and oxygen levels above 3,5 $ml.l^{-1}$ are still common in winter. However, the radically different depth distribution of the population between the S. and W. Coasts indicates an onshore-offshore component to the migration cycle, i.e. from inshore S. Coast to offshore W. Coast and *vice versa*. Whereas there may be some uncertainty about the inshore W. Coast region owing to few samples, the area deeper than 200 m has been well sampled in both regions.

The very high and consistent bias towards males in the sex ratios is an intriguing aspect of the reproductive biology. In a population where several age classes are present and where breeding occurs, as on the S. Coast (Augustyn 1989), this could be explained by the differential migration pattern of the sexes offshore of the spawning areas, and by the survival of some males beyond a single breeding season. There is a high bias in favour of males in the spawning areas in November/December, but a female majority offshore of the breeding areas (Augustyn 1990). In the western part of the S. Coast, there was a bias in favour of males (Augustyn 1989) and in the present study on the W. Coast this bias is even greater and is particularly prevalent in deeper water. It also increases in a northerly direction, is more marked in summer and peaks in the Cape Columbine area of the W. Coast.

The bias towards males on the W. Coast cannot be due largely to a differential post-breeding mortality between the sexes, because there is no obvious older size class component. Both sexes were nearly always caught in individual trawls, so there is no question of a general areal segregation. However, school segregation cannot be excluded completely, because more than one school may be sampled in the course of a half-hour trawl. Some individual trawls have shown very marked segregation, e.g. in January 1985, 37 : 1 and 51 : 4 in favour of males and 7 : 42 in favour of females. It is possible that sexual segregation in individual schools may to some extent be based on size. Hurley (1978) found that schools of *L. opalescens* attracted to night lights were very uniform in size, despite the general size range being quite wide. School segregation does not, however, explain the general bias towards one sex, because one would still expect overall parity in such a large area. Unfortunately, the 0–100-m zone could not be sampled much in the south, but even in this region, the sex ratios encountered inshore have favoured males, e.g. in False Bay (Augustyn 1989).

A severe bias towards males exists in the western region as a whole, and it must be assumed that males are more prominent in both the eastward and westward migrations than females. Given the information available, there is no ready explanation for this phenomenon. Hixon, Gillespie & Griffin (1980) examined sexual segregation in *Ommastrephes pteropus*. They found a significant bias in the sex ratio, school segregation between the sexes, and similar sizes schooling together. They concluded that the deviation from parity may have resulted from spatial and seasonal differences in distribution of shoals. In a laboratory study of shoaling behaviour Hurley (1978) found that *L. opalescens* tended to shoal in schools composed of individuals of uniform size.

While the distribution of chokka squid may be limited to some extent by the environmental factors mentioned earlier, some force must be driving the very considerable migrations from the shallow inshore waters on the S. Coast to deeper, colder waters often hundreds of kilometres westward. That factor is most likely to be the richer feeding grounds in the vicinity of the highly productive upwelling areas in the west. Augustyn (1989) showed that on the S. Coast the fish : crustacean ratio was dependent on the size of the squid. Squid larger than 150 mm consumed a larger proportion of fish than did those smaller than 150 mm, so diet requirements obviously change to fish as the squid grow larger. Because of the difficulty of working with squid stomachs, and the consequently low proportion of items that can be identified with certainty, it is difficult to make general statements about the diet on the W. Coast, but it does appear that both anchovy and dragonettes are important in the fish diet. These are both species which are less common in the diet on the inshore S. Coast and the squid may be exploiting their availability to the west of Cape Agulhas. Lipiński (1987) found that the two main identifiable fish species in the diet of *L. vulgaris reynaudii* off St Francis Bay were *Bregmaceros* sp. and hake *Merluccius capensis*.

A likely influential factor affecting the migration of squid is the sea current patterns off the S. Coast, including the Agulhas current. Once juveniles have moved far enough offshore, their westward migration may be aided by the prevailing flow in that direction. A detailed analysis of current patterns and the influence they could exert on various components of the population are, however, beyond the scope of the present study.

The return migration to the east may be prompted by the need for more sheltered habitat and more suitable topography and/or bottom types necessary for spawning (Augustyn 1990).

The trawler by-catch from the W. Coast, and to some extent the squid jigged between False Bay and Cape Agulhas (the latter in the summer months, November to March), represent a small catch but a relatively valuable income to the fishing community. The availability of squid, particularly inshore, is much more sporadic than further east, because the population strength depends on migration from the east. Squid regularly appear inshore from spring through summer in the east, but their presence is much more sporadic in the west in e.g. False Bay and the Danger Point area. However, the seasonal abundance of squid on the W. Coast may give some indication of the state of the stock as a whole and of recruitment strength of subadults. The W. Coast squid are obviously only part of the stock that exploits the food resources of the region, but trends in squid stocks on the W. Coast, as seen from annual biomass estimates and from trawler catches and CPUE, have often been accompanied by similar trends in these parameters on the S. Coast (Augustyn 1989 and SFRI, unpublished data). These trends may sometimes be somewhat obscured by complicating factors such as the effect of the environment on regional availability and distribution, but generally they appear to be valid. Moreover, a relatively young component of the population is being measured, so a low biomass estimate on the W. Coast may function as an early warning sign of impending adult stock depletion in the east.

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