

The ecology of *Sepia australis* (Cephalopoda: Sepiidae) along the south coast of South Africa

Mandisile Mqoqi, Marek R. Lipiński, and Anne G. V. Salvanes

Mqoqi, M., Lipiński, M. R., and Salvanes, A. G. V. 2007. The ecology of *Sepia australis* (Cephalopoda: Sepiidae) along the south coast of South Africa. – ICES Journal of Marine Science, 64: 945–955.

The influence of abiotic factors (depth, region, temperature, salinity, and oxygen) on the abundance of the cuttlefish *Sepia australis* was investigated using data from bottom-trawl stations occupied in April/May (austral winter) 1988 and August/September (austral spring) 2001 off South Africa's south coast. April/May survey data for 1999, 2003, and 2004, and August/September data for 2003 and 2004 were used to assess regional or depth-related patterns in abundance. Temperature differences in the two years mainly analysed influenced distribution and abundance significantly. Abundance increased eastwards in 2001 presumably because of a high-temperature anomaly stretching westwards (i.e. limiting the species abundance to the west), whereas abundance increased westwards in the more typical winters of 1988, 1999, 2003, and 2004. Abundance increased with depth in spring 2001, 2003, and 2004. Smaller sizes of mature males may indicate that they mature earlier than females. The main prey of all size groups and maturity stages was crustaceans, and there were no size- or maturity-related changes in diet. It appears that *S. australis* is an opportunistic feeder dependent on whatever prey of appropriate size is abundant at any time. However, the data show an array of patterns, some likely to be the result of biological flexibility in response to a changing environment. Other patterns are part of more stable, well-balanced ecological characteristics of the species.

Keywords: cuttlefish, diet composition, distribution and abundance, ecology.

Received 6 October 2006; accepted 25 March 2007; advance access publication 7 June 2007.

M. Mqoqi and M. R. Lipiński: Department of Environmental Affairs and Tourism, Marine and Coastal Management, Private Bag X2, Rogge Bay, Cape Town 8012, South Africa. Anne G. V. Salvanes: Department of Fisheries and Marine Biology, University of Bergen, Bergen N-5020, Norway. Correspondence to M. R. Lipiński: tel: +27 21 4023148; fax: +27 21 4023639; e-mail: lipinski@deat.gov.za.

Introduction

Sepia australis Quoy and Gaimard, 1832, occurs from southern Namibia (31°48'S 29°21'E) on southern Africa's west coast, south around Cape Agulhas (35°55'S 20°00'E), and east to Transkei (31°30'S 29°20'E) (Figure 1; Roeleveld, 1972; Jereb and Roper, 2005). Records farther east are doubtful. It is distributed from 45 to 345 m deep with greatest abundance between 60 and 190 m (Jereb and Roper, 2005). Lipiński *et al.* (1992b) suggested that the species is primarily one of southern Africa's west coast, because of its greater mean size there relative to the situation on the south coast (a statement confirmed by Roeleveld *et al.*, 1993). *S. australis* is a small cuttlefish with maximum mantle length (ML) of 85 mm (Lipiński *et al.*, 1992b). Sepiids are semelparous spawners with lifespans varying from a few months to 3 y, according to the adult size and in relation to temperature and food availability (Boletzky, 1983). They grow fast in warm waters, maturing smaller than congeners living in cool (temperate) waters. Off southern Africa's west coast, *S. australis* spawns in deepwater (Lipiński *et al.*, 1992b; Roeleveld *et al.*, 1993), but on the south coast spawning is in shallower water at a smaller animal size, presumably because water temperatures are warmer as a result of the influence there of the Agulhas Current (Roeleveld *et al.*, 1993).

S. australis feeds on hyperbenthic and pelagic crustaceans (Lipiński *et al.*, 1991; Sánchez and Villanueva, 1991) and

lightfish *Maurolicus muelleri* (Lipiński *et al.*, 1991), and is itself preyed upon by several fish species, including the commercially important Cape hake *Merluccius capensis* and *M. paradoxus* (Payne *et al.*, 1987; Lipiński *et al.*, 1992a). *S. australis* is the most abundant of more than 20 sepiids in the southern African ecosystem (Roeleveld, 1972, 1998; Sánchez and Villanueva, 1989, 1991). It is not currently exploited commercially, but has potential to be fished (Augustyn *et al.*, 1995; Jereb and Roper, 2005); further research on factors such as the sustainability of the fishery is needed (Lipiński, 1992). *S. elegans*, slightly larger than *S. australis* with a maximum ML of 90 mm compared with the 85 mm of *S. australis*, is commercially exploited in the Mediterranean Sea and northeast Atlantic (Jereb and Roper, 2005). Knowledge of general ecology, including feeding, is infinitely better for *S. officinalis* (Castro and Guerra, 1990; Dickel *et al.*, 2006; Guerra, 2006) than for most congeners. The feeding ecology of *S. australis* is only known from the west coast of southern Africa. Also, virtually nothing is known about *S. australis* diet in relation to environmental change. The aims of this study were therefore: (i) to assess the seasonal changes in population structure and abundance by investigating relationships between the abundance of *S. australis* over ranges of environmental factors (temperature, oxygen, and salinity); (ii) to investigate whether the composition of the diet of *S. australis* differs by sex, depth, size category, and

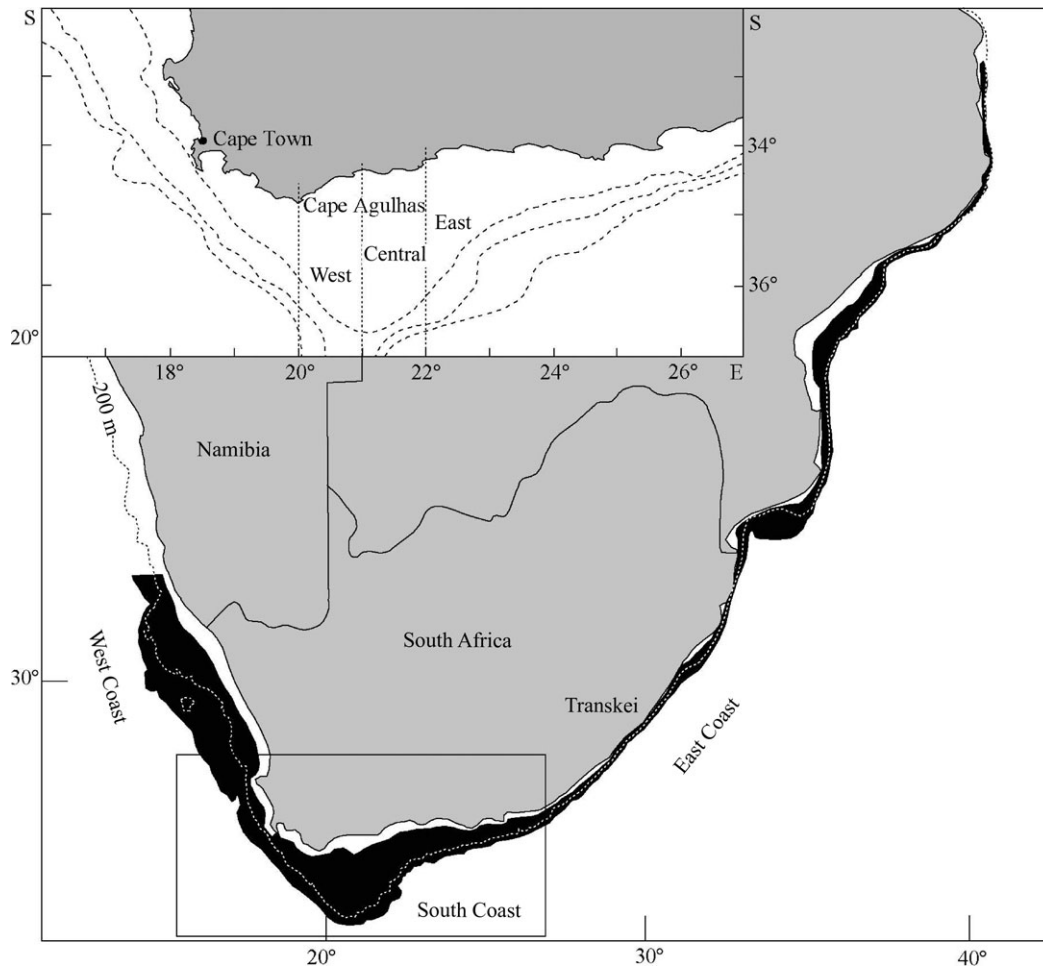


Figure 1. The known distribution of *S. australis* (black shading) and the regions compared during our analysis of *S. australis* along South Africa's south coast. The trawl surveys are carried out between Cape Agulhas and 27°E (right border of the inset). Depth contours in the insert are 200, 500, and 1000 m.

maturity stage by assessing the percentage mass and frequency of occurrence of various prey items; and (iii) to test whether diet is related to environmental variables (oxygen, temperature, and salinity).

Material and methods

Data

Since 1983, bottom-trawl surveys have been carried out regularly off the west and south coasts of South Africa from FRS "Africana" (Figure 1). The main objective of these surveys was to assess the abundance of Cape hake and other demersal species. The methods used and the areas surveyed were described in detail by Badenhorst and Smale (1991). Briefly, a 180-A German bottom trawl was towed for 30 min at each station during daylight according to a stratified semi-random design. The mesh size of the codend (27.5 mm) was small enough to retain *S. australis* as a bycatch. The depth covered by the surveys ranged from 50 to 500 m.

Samples of *S. australis* for abundance estimation, and biological and diet analysis were collected in winter (April/May) 1988 and spring (August/September) 2001. Further, winter (April/May) survey data for 1999, 2003, and 2004, and spring (August/September) data for 2003 and 2004 were used to assess regional

or depth changes in abundance. Samples were frozen on board, and biological measurements [dorsal ML, sex, maturity stage, total weight (TW), and gonad weight (GW)] were undertaken ashore, in the laboratory. The ML was measured to the nearest millimetre (mm) and weights were measured in grammes (g). A three-scale maturity stage (described by Roeleveld and Liltved, 1985), intended primarily to distinguish between immature and fully mature animals, was used. During the 1988 cruise, 680 cuttlefish were measured, and the stomachs of 186 were retained (the other 494 stomachs were empty). In 2001, 605 cuttlefish were measured, and 333 stomachs were retained (the other 272 stomachs were empty). The mean weight of individual cuttlefish in each trawled area was used to estimate the number of individuals in the total catch. Stations which had no catch of *S. australis* were included in the analysis. Catch data were transformed by means of a $\log(y + 1)$ function. Prey type and species were identified to the lowest possible taxon from diagnostic structures such as heads, eyes, pereopods, uropods, otoliths, and suckers viewed under a dissecting microscope at 16 \times magnification.

Frequency of occurrence and percentage mass by prey type in individual stomachs were the indices used to compare components of prey. Frequency of occurrence represented the percentage of *S. australis* that had taken a specific prey, and percentage

weight was the proportion of the prey species or taxon in relation to the total stomach weight of an individual cuttlefish. Numerical frequency could not be used because prey items were too digested to be counted. Prey types present were identified and categorized. A volumetric method was used to quantify the relative mass of categories (Wootton, 1998); it estimates the volume of each food category and relative importance is expressed as a percentage of the total. The percentage of each food category in each stomach was used to calculate the mass of that prey category from the total stomach content mass.

Depth, bottom temperature, bottom oxygen concentration, and bottom salinity were measured by means of a conductivity, temperature, depth (CTD) probe and rosette sampler, which was deployed after each trawl at the end position of the trawl station.

Data were categorized by region and longitude. The whole south coast was subdivided into three regions: west (20°00'–20°59'E), central (21°00'–22°59'E), and east (23°00'–26°59'E) (Figure 1). No biological measurements were taken in the east in 1988. Male and female data were divided by depth ranges of ≤100 m (shallow) and >100 m (deep). Size categories for both sexes were small (≤40 mm ML) and large (>40 mm ML). In order to compare temperature regimes between the two years analysed, two categories were used. In 1988 “cold” (8–10°C) and “warm” (10.1–12°C) temperatures were chosen, but in 2001, “cold” was considered to be 8–12°C and “warm” was 12.1–16°C. The ranges differed because the temperature range was narrower in 1988 (8–12°C) than in 2001 (8–16°C). The oxygen categories chosen were 0–3 ml l⁻¹ (low), 3–5 ml l⁻¹ (medium), and >5 ml l⁻¹ (high), for both years. The range of salinity in both years was narrow, so no categories were used.

Data analysis

Abundance, diet, and environmental variables

Dummy regressions were used to test the relationships between log-transformed abundances, prey composition, and environmental variables (depth, oxygen, temperature, and salinity). The results were analysed by fitting general linear models (multiple regressions) to the data, for which categorized variables were encoded as dummy variables and therefore recast analysis of variance (ANOVA) as the regression (Hamilton, 1992). The regression coefficients were used to deduce significance. Beta coefficients in general are the distances between the dummy variable and the reference category. The reference category was omitted in the model. A positive beta coefficient means that the dummy variable scored higher on the response variable than the reference category, or if negative, then lower.

Diet similarities by age, sex, and depth

Comparisons of diet similarity between different groups, by sex and depth were carried out in order to calculate the degree of overlap between the categories. The competition index (Pianka, 1974) was used to calculate diet overlap:

$$\alpha_{jk} = \alpha_{kj} = \frac{\sum_{i=1}^n p_{ij} p_{ik}}{\sqrt{\sum_{i=1}^n p_{ij}^2 p_{ik}^2}}$$

The notations p_{ij} and p_{ik} are percentages by mass of the i th prey group in the stomach content of groups j and k , and $\alpha_{jk} = \alpha_{kj}$ is the dietary overlap index between groups. The index was used as the resource overlap measure, but not as a measure of

competition. The range is between 0 (where there is no overlap) and 1 (when the proportion is similar for all groups). The following ranges were used: 0–0.3, low overlap; 0.31–0.6, medium overlap; and 0.61–1, high overlap, as utilized by Salvanes and Nordeide (1993) in their study of dietary overlap among fish. As diet similarity values depend on the level of aggregation of prey, absolute values were not used to compare diet similarities (Salvanes and Nordeide, 1993). The extent of pooling of prey data influences both the absolute values of the index and the significance level of statistical tests when the groups are compared (Salvanes and Nordeide, 1993). As the outcome of the test is determined by how the data sets are pooled, we decided against using statistical tests. A two-factor ANOVA (Zar, 2000) was used to test for differences in diet between sexes and regions.

Results

Abundance and size trends

In winter (1988, 1999, 2003, and 2004), *S. australis* abundance increased from east to west, but in spring 2001 the greatest abundance was in the east (Tables 1 and 2). Abundance increased with depth in spring 2001, 2003, and 2004, but there was no depth effect in any of the winters sampled (Table 2). In 1988, with data from all regions combined, the mean ML of female *S. australis* was 46.4 mm (range 25–65 mm, s.e. = 0.64, $n = 117$), and that of males was 41.5 mm (range 28–55 mm, s.e. = 0.74, $n = 69$). The spatial (west, central, east) frequency distributions are shown in Figure 2a. Again for pooled data from all regions, female mean ML in 2001 was 42.8 mm (range 31–57 mm, s.e. = 0.28, $n = 221$), and male mean ML was 40 mm (range 28–51 mm, s.e. = 0.43, $n = 112$). Distributions in each region are shown in Figure 2b.

The differences in ML between males and females in the west in 1988 were not significant ($t = 1.84$, d.f. = 78, $p = 0.068$), but they were highly significant in all regions in 2001 ($F = 18.9$, d.f. = 321, $p < 0.001$). Generally, there were no regional differences in ML between sexes except for females in the east in 2001, where females were larger ($t = -3.15$, d.f. = 144, $p = 0.002$).

Regional differences in ML, TW, and GW by sex and depth were significant in both 1988 and 2001 (ANOVA, Appendix, $p < 0.001$). ML was smallest in the west (Tukey test, $p < 0.01$) and increased with depth. In 1988, the ML of cuttlefish caught shallower than 100 m tended to be larger in the central region than in the west (Tukey test, $p = 0.015$).

Table 1. Estimated coefficients from dummy variable regression of log-transformed abundance (kg 30 min⁻¹) of response variables in relation to explanatory variables for male and female *S. australis* in 1988 and 2001. West, dummy for west region; Central, dummy for central region; East, reference, and F , F -statistic.

Parameter	Females 1988	Males 1988	Females 2001	Males 2001
Constant	-28.59	-18.07	-141.35	-118.79
Central	-0.23	-0.2	0.28	0.27
West	0.41	0.41	-0.60*	-0.53*
Depth (m)	0	0	0.008*	0.007*
d.f.	6 (79)	6 (79)	6 (57)	6 (57)
F	3.76**	3.77**	4.49***	4.68***

* $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$.

Table 2. Regression coefficients explaining abundance ($\text{kg } 30 \text{ min}^{-1}$) of *S. australis* in relation to depth and region for 1999, 2003, and 2004. Constant, intercept, West, dummy for west region; East, reference, and *F*, *F*-statistic.

Parameter	April/May 1999	April/May 2003	April/May 2004	August/September 2004	August/September 2004
Cruise	C152	C177	C191	C182	C200
Constant	1.88***	1.286***	2.58***	1.41***	-0.226
Depth	0.008	0.0027	-0.001	0.01*	0.012**
West	1.59***	0.917***	0.808*	0.348	0.793
d.f.	2 (54)	2 (61)	2 (43)	2 (60)	2 (67)
<i>F</i>	11.7***	5.20**	2.328	2.93*	11.75***

* $p < 0.05$; ** $p < 0.01$; and *** $p < 0.001$.

GW relative to body weight in winter of 1988 was 13 and 7% for females and males, respectively. GW differed significantly between females (GW = 1.12 g) and males (GW = 0.46 g) in 1988 ($t = 5.4$, d.f. = 78, $p < 0.001$). In spring 2001, GWs relative to body weights were 4 and 7% for females and males, respectively. Overall in 2001, GW differed significantly ($t = 4.2$, d.f. = 94, $p < 0.001$) between sexes. Males tended to have larger gonads (GW = 0.46 g) than females (GW = 0.34 g).

In 1988, female *S. australis* had larger gonads ($F = 12$, d.f. = 178, $p = 0.011$) at lower temperatures than at higher temperatures. Gonads were largest in the west (0.92 g) than in the central region (0.73 g) (Tukey test, $p = 0.049$) and temperatures were low. Indeed, GW increased with decreasing temperature in the west. In spring 2001 too, GW was greater at low than at high water temperature. The interaction of region and temperature was significant ($F = 5.9$, d.f. = 321, $p = 0.003$), suggesting that the effect of temperature differed between regions. There were no differences in GW between regions at high temperature ($F = 1.97$, d.f. = 321, $p = 0.14$). *Sepia* had larger gonads (GW = 0.54 g) at low temperatures in the west than in the east (GW = 0.37 g, Tukey test, $p = 0.002$). GW also differed between males in the west (0.56 g) and east (0.43 g) (Tukey test, $p = 0.003$), but that situation did not apply to females.

Males tended to mature earlier than females in both 1988 and 2001 (Figure 3). Maturity patterns were similar in both years, with most females at maturity stage 2 and males at stage 3. In 2001, there was more maturity differentiation than in 1988, clearly a seasonal pattern (Figure 3).

Diet analyses

Stomach content mass relative to body mass

In both years and for both sexes, stomach content mass constituted some 2% of total body mass. The mass of stomach contents relative to total body mass in 1988 did not differ between males and females or between regions (Figure 4a). However, no stomachs were collected in the east in 1988.

Females and males had similar stomach content mass relative to body mass in 2001 (ANOVA, $p = 0.69$, Table 3), but there were significant differences between regions ($p < 0.001$). Differences occurred between the west and the central regions (Tukey test, $p < 0.001$), and between the central region and the east (Tukey test, $p = 0.008$; Figure 4b). The mean mass of stomach contents relative to the total body mass of the sexes combined showed that cuttlefish in the west had taken more food ($\hat{x} = 0.019$ g) relative to their body mass than those in the east ($\hat{x} = 0.016$ g) and far more than those in the central region ($\hat{x} = 0.001$ g).

Frequency of occurrence of prey types by region and year

In 1988, 68% of females and 75% of males had empty stomachs; in 2001 the values were 57 and 47%, respectively. The percentage of empty stomachs decreased later in the day (Table 4).

Food was mainly crustaceans (mysids, megalopae, euphausiids, and hyperiids), cephalopods, and fish. Crustaceans tended to be well digested, making species identification difficult, often impossible. Of the prey that it was possible to identify, mysids, megalopae,

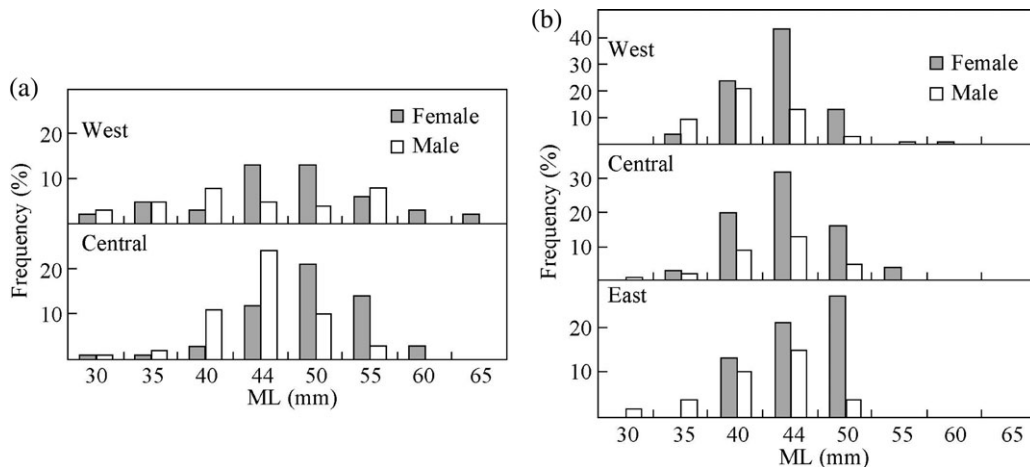


Figure 2. Frequency distribution of MLs (mm) for female and male *S. australis* in (a) 1988 and (b) 2001.

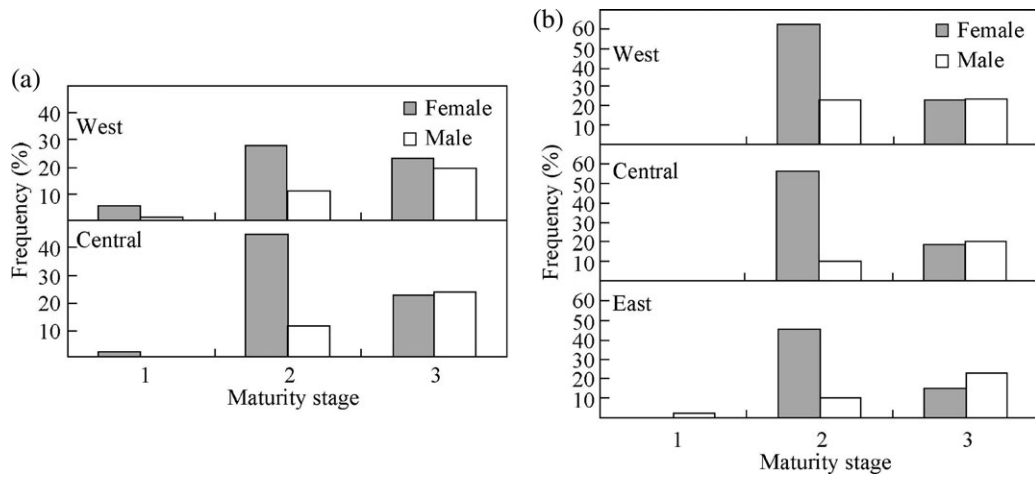


Figure 3. Frequency distribution of maturity stages of *S. australis* by regions of South Africa's south coast in (a) 1988, and (b) 2001.

and euphausiids dominated in 1988. Euphausiids were eaten more frequently in 1988 than in 2001 and more in the west than elsewhere. In 2001, megalopae were the dominant prey type in all regions in terms of frequency of occurrence (Table 5).

The only cephalopod identified in the diet was identified as *S. australis*, in both years. The incidence of cannibalism was greatest in the east, more than double that in the other two regions. Fish occurrence ranged between 5% and 13%, indicating its lesser

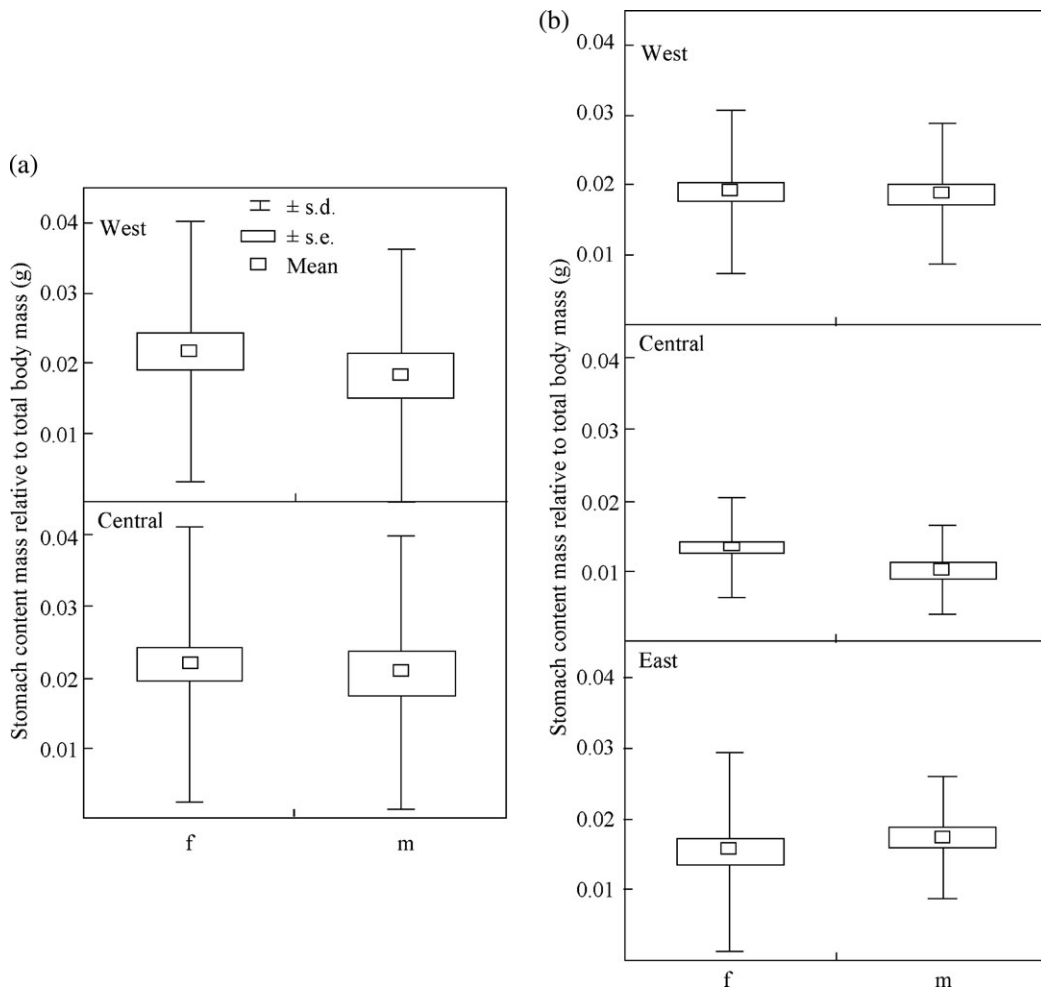


Figure 4. Mass of stomach contents relative to total body mass (g) by sex and region for *S. australis* caught between (a) 11 May and 2 June 1988, and (b) 31 August and 25 September 2001. m, male; f, female.

Table 3. Summary of stomach content mass relative to total body mass (g) in 2001 for *S. australis*.

Parameter	d.f. effect	d.f. error	F	p-value
Region	2	327	11.29	<0.001
Sex	1	327	0.16	0.69
Sex and region	2	327	1.4	0.25

Table 4. Percentage of empty stomachs in the morning (08:00–13:00) and afternoon (13:00–18:00) in 1988 and 2001. Values in parenthesis are the total sample sizes.

Time and year	Female	Male	Number of trawls
Morning 1988	74 (213)	80 (139)	11
Afternoon 1988	63 (199)	71 (129)	11
Morning 2001	60 (169)	49 (70)	8
Afternoon 2001	54 (230)	46 (136)	11

importance as food than crustaceans. The fish species eaten in 1988, identified from the otoliths, were white-spotted lanternfish (*Lampadena speculigera*), tonguesole (*Cynoglossus zanzibarensis*), dragonet (*Paracallionymus costatus*), and Cape hake *M. capensis*. In 2001, the fish species identified were *P. costatus*, *M. capensis*, and Cape conger (*Conger wilsoni*).

Percentage mass of prey type by region and year

In 1988, the percentage mass of prey was dominated by euphausiids (52%), megalopae (20%), and unidentifiable prey (16%) in the west (Figure 5). In the central region, the dominant prey items by mass were euphausiids (36%), mysids (25%), and unidentifiable prey (22%). Percentage mass was dominated by unidentifiable prey types (about 50%) in all three regions in 2001.

The average bottom temperature was greater in 2001 (12.3°C) and this might have speeded up digestion, so reducing the possibility of identifying prey. In the west and the central region, the dominant identifiable prey type was crustacean megalopae, which constituted >30% of the percentage mass (Figure 5). In the east, cannibalism was clearly rife (19%), because the dominant identifiable prey item was *S. australis*.

Diet similarity and overlap by sex, depth, region, and year

In the west in 1988, the diet was similar at like depths for both males and females, but different when compared between depths (Table 6). At depths >100 m, males fed mainly on euphausiids (>80%), whereas in shallower water mysids and megalopae dominated the prey. Females in deeper water consumed mostly euphausiids (>60%), and in shallower water took mainly megalopae (>60%). In the central region in 1988, the diets of males and females were similar within and between depths (Table 6). In the west and the central region in 2001, males and females tended to have a similar diet by depth and overlap was moderate in the east (Table 7). Females had the most diverse prey composition, so the modest overlap of diet in the east may be due at least partly to the slightly different diet of the two sexes.

The diet of females was less similar between depths (Table 7). In shallower water the diet was mainly megalopae (>70%), and in deeper water the food tended to be finely macerated possibly because of a longer time for digestion before the cuttlefish were caught. Euphausiids were the most important identifiable prey in deeper water. The diet of males in the east differed between

Table 5. Percentage frequency of occurrence of various prey types in 1988 and 2001 from stomach contents of *S. australis* on South Africa's south coast. *n* is the number of stomachs examined.

Prey	West 1988	Central 1988	West 2001	Central 2001	East 2001
Euphausiid	27.5	16.0	7.6	3.8	4.2
Mysid	32.5	55.7	4.5	5.7	11.5
Megalopae	30	26.4	30.3	31.4	16.7
Unknown	80	94.3	81.1	78.1	86.5
Fish	5	10.4	6.8	6.7	12.5
Cephalopod	2.5	2.8	1.5	0.0	7.3
Hyperiid	0	0.0	0.0	5.7	1.0
<i>n</i>	80	106	132	105	96

depths. In shallow water they fed mainly on euphausiids, whereas in the deeper the food was generally unidentifiable (>78%).

In 1988, the diet of males and females across the study area was similar, in shallower and deeper water. In 2001, the diet of males in shallower water in the east tended to differ from that of other regions. There was a moderate diet overlap between females in shallower water in the west and those in the same depth range in the central region and the east. Year-on-year comparisons between the data for 1988 and 2001 revealed low (males) or modest (females) overlap in the diet of cuttlefish in deeper water (Table 8). The low diet overlap for males was an annual occurrence within the study area and years for cuttlefish caught deeper than 100 m (Table 8).

Overall, the diet was similar between large and small cuttlefish in all regions in 1988 and 2001. In the central region, the diet at all maturity stages was similar both for males and for females. In the west, males tended to take different prey when they were at maturity stages 2 and 3. At maturity stage 3, the cuttlefish tended to consume more euphausiids (>80%) and perhaps a more diverse prey spectrum than when they were at stage 2. Diet overlap between sexes at maturity stage 2 was moderate. Females at maturity stage 2 had a diverse diet dominated by euphausiids and megalopae, whereas males had a greater proportion of unidentifiable prey.

In 2001, the diet of cuttlefish at all maturity stages was similar, as revealed by the high indices of overlap for all regions (Table 8).

Diet and the environment

In the west in 1988, more euphausiids were consumed (Table 9), and mysid prey was scarcer. Additionally, females relied more on megalopae than males for prey. Lesser quantities of fish were eaten in the west, and this prey type decreased with declining oxygen concentration. There were no differences by sex in the quantity eaten relative to total body mass (Table 9).

In 2001, the quantity of euphausiids consumed decreased with increasing depth, whereas the quantity of mysids eaten increased with increasing depth (Table 9). More megalopae were eaten in the west, the quantity increased with increasing oxygen concentration, and females consumed more megalopae and fish than males. Cannibalism was most intense in the east. The quantity of hyperiids eaten decreased with increasing depth, but increased towards east. Stomach content mass relative to total body mass was greater in the west and rose with increasing depth in 2001 (Table 9).

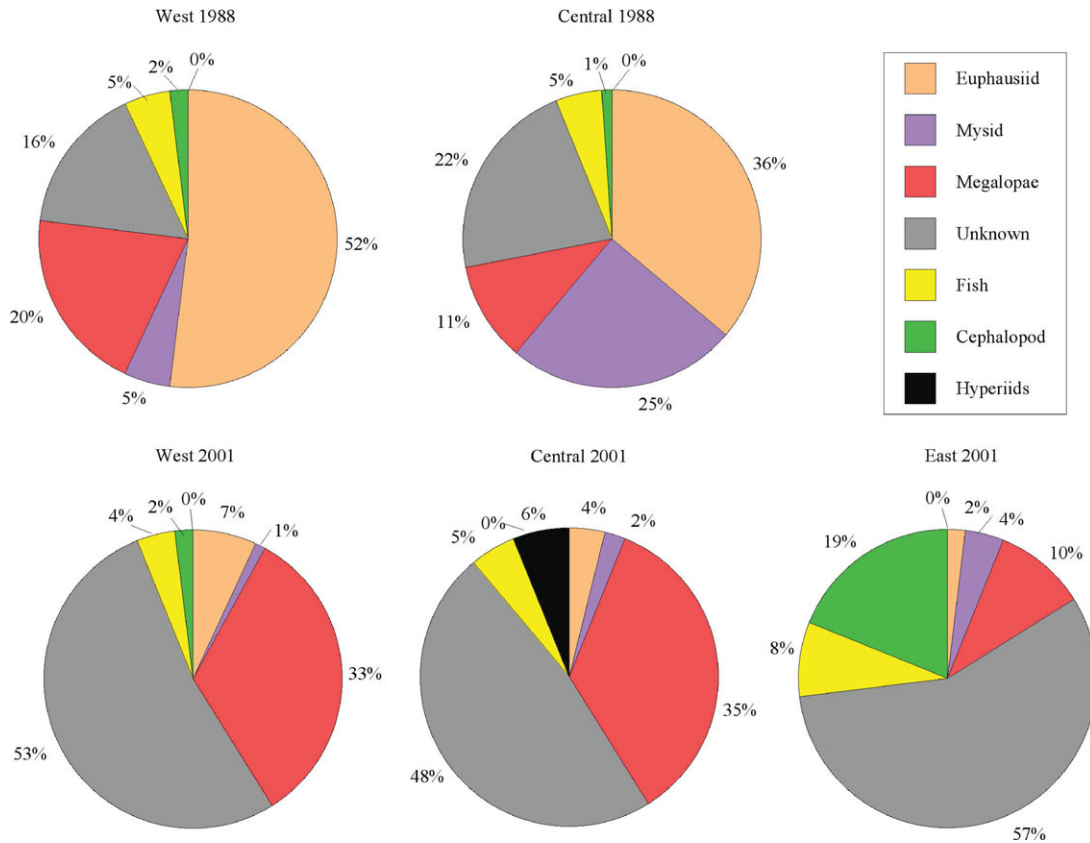


Figure 5. Percentage mass of prey items in May/June 1988 (above) and August/September 2001 (below) from stomach contents of *S. australis* on the south coast of South Africa.

Overall, it appears from the results that feeding trends can be reversed in certain years depending on the stage of the life cycle, biology, and the environment, the latter presumably influencing prey availability.

Discussion

During our austral winter surveys, cuttlefish abundance increased from east to west (Tables 1 and 2), as shown by positive regression coefficients for the west. However, abundance increased in an eastward direction during spring surveys (Tables 1 and 2), as shown by negative regression coefficients. The temperature differences between regions are likely to have influenced the distribution

pattern in spring 2001. Higher temperatures (13.8°C) then may have accelerated reproduction and postspawning mortality of larger *Sepia*, yielding the lesser abundance in the west and overall a smaller mean ML. Higher temperatures do induce early reproduction in *Sepia* (Boletzky, 1983). Forsythe (1993) noted that small changes (e.g. 1°C change per month) can significantly change the population characteristics of cephalopods. The greater abundance in the east in spring 2001 at slightly lower temperature (10.8°C) would then be the result of the presence of large numbers of prespawning *S. australis*. This is also supported by the increase in the ML and GW from west to east. Circulation patterns on South Africa’s south coast are likely to be the major cause of the

Table 6. Indices of diet overlap based on percentage mass of prey groups of male and female *S. australis* by region in 1988. Top panel, west; bottom panel, central region. Black squares, high overlap (>0.6); grey squares, moderate overlap (0.31–0.6); white squares, low overlap (<0.3); and None, no comparison possible.

Sex and depth, m	Males < 100	Males > 100	Females < 100	Females > 100
Males < 100				None
Males > 100			None	
Females < 100				
Females > 100				
Males < 100				None
Males > 100			None	
Females < 100				
Females > 100				

Table 7. Indices of diet overlap based on percentage mass of prey groups of male and female *S. australis* by region in 2001. Top panel, west; middle panel, central region, bottom panel, east. Black squares, high overlap (>0.6); grey squares, moderate overlap (0.31–0.6); white squares, low overlap (<0.3); and None, no comparison possible.

Sex and depth, m	Males < 100	Males > 100	Females < 100	Females > 100
Males < 100		■	■	None
Males > 100			None	■
Females < 100				■
Females > 100				■
Males < 100		■	■	None
Males > 100			None	■
Females < 100				■
Females > 100				■
Males < 100		□	■	None
Males > 100			None	■
Females < 100				■
Females > 100				■

different temperatures in the three regions in 2001 (Shannon, 1985). In spring 2001, 2003, and 2004, cuttlefish abundance increased with increasing depth, showing the preference of the species for cooler water.

Earlier maturation of males than females is common in animals (Wootton, 1998), and was also found in *S. australis* in Namibia (Sánchez and Villanueva, 1991), for *S. officinalis* (Boletzky, 1983), and for *S. dollfusi* and *S. pharaonis* (Gabr et al., 1998). Earlier maturity and a longer duration of reproductive activity of males probably contributes to a high rate of genetic exchange within the population. Most cuttlefish in the present study were either maturing or fully mature during winter 1988 and also in spring 2001 (Figure 3b), indicating a prolonged spawning period. Boletzky (1983) noted that temperature and light influence the body size of *Sepia* at maturity; early gonad growth (though not maturation) results in overall somatic growth and depends on temperature. High light intensity slows down gonad maturation, whereas it stimulates mating and spawning in mature animals (Boletzky, 1983). Lipiński et al. (1992b) found that >50% of *S. australis* were mature in summer 1987 on South Africa’s west coast.

The diet of *S. australis* on South Africa’s south coast was mainly crustaceans (euphausiids, mysids, and megalopae). However, little is known about the general benthic ecology of crustaceans of the South African region (Meyer and Smale, 1991). Food found in stomachs generally reflects the last meal of an animal. Some food categories are easily digested and difficult to detect, but hard parts such as otoliths can be retained in stomachs for longer, so to use such material as indicators of the last meal is

likely unreliable. The problem with such structures is knowing the time they have been in the stomach, but to our knowledge there is no information in the literature on this subject.

In 1988, 72% of the stomachs were empty, whereas in 2001, the value was less, 52% (Table 4). It is possible that the lower bottom temperature in 1988 (10.1°C over all regions) may have reduced activity and metabolic rate, leading to there being a greater percentage of empty stomachs than in 2001, when the mean temperature was higher (12.3°C). Compared with 1988, the stomach contents were much better digested in 2001. We speculate that the higher mean bottom temperature increased the rate of digestion in 2001. Generally, prey digestion rate increases with increasing temperature (Salvanes et al., 1995; Knutsen and Salvanes, 1999). Quintela and Andrade (2002a, b) stated that the rate of gastric evacuation increased for *S. officinalis* at higher temperatures, and, drawing on the literature, concluded that rates of activity and metabolic rates of cuttlefish are directly related to temperature.

In our study, *S. australis* had more food relative to body mass in the west than in the other regions. This may suggest greater prey abundance in the west than elsewhere. The dominant prey, euphausiids and mysids, were seemingly consumed more often in 1988 than in 2001. Sánchez and Villanueva (1989) also noted that euphausiids were the most important prey of *S. australis* in Namibian waters. Clearly, the amount consumed will increase with the density of the traditionally utilized prey (Wootton, 1998).

There were no significant differences by sex in the quantity eaten, similar to the situation for *S. officinalis* and *S. elegans* (Castro and Guerra, 1990). For related species, however, differences in consumption by sex have been reported, e.g. Bello and

Table 8. Indices of diet overlap based on percentage masses of prey groups within and between years 1988 and 2001) for male and female *S. australis* in the same regions at different depth ranges. Black squares, high overlap (>0.6); grey squares, moderate overlap (0.31–0.6); white squares, low overlap (<0.3); and None, no comparison possible.

Depth, m	Sex	West and central 1988	West and central 2001	West and east 2001	Central and east 2001	West 1988 and 2001	Central 1988 and 2001
<100	F	■	■	■	■	■	■
>100	F	■	■	■	■	■	■
<100	M	■	■	■	■	■	■
>100	M	■	■	■	■	■	■

Table 9. Estimated coefficients from dummy variable regressions of prey mass (g) as response variables as a function of environmental variables for (top panel) 1988, and (bottom panel) 2001. West, dummy for west; male, dummy for male; RSTW, relative stomach content mass; BT, bottom temperature (°C); BS, bottom salinity; BO, bottom oxygen (ml l⁻¹); Depth, sampling depth; and *F*, *F*-statistic.

Factors	Euphausiids	Mysids	Megalopae	Fish	Cephalopods	Hyperiid	RSTW
1988							
Constant	42.0296	-23.2446	-17.1303	9.9827	-4.18		-0.9409
West	0.12**	-0.047**	0.0081	-0.021**	-0.0027		0.0053
Male	0.0065	-0.0060	0.031**	0.008†	0.0003		0.0049†
Depth	0.0006	0.0004†	-0.0002	0.0002	0.0000		0.0001†
BT	-0.0001	-0.0573	-0.0573	0.0253	-0.0135		-0.0121
BS	-1.2102	0.6827	0.5085	-0.2911	0.1241		0.0300
BO	0.076**	-0.0114	-0.0126	-0.019c	-0.0049		0.006†
d.f.	6 (179)	6 (179)	6 (179)	6 (179)	6 (179)		6 (179)
<i>F</i>	11.49	2.59	4.08	2.94	0.90		7.58
<i>p</i>	<0.001	0.02	<0.001	0.009	0.49		<0.001
2001							
Constant	0.169**	-0.0216	-0.2406*	0.0300	-0.0472	0.0202	-0.055**
West	-0.0024	-0.0001	0.03c	-0.0050	-0.0098	-0.0053*	0.0063**
Central	-0.0005	-0.0003	0.0092	-0.0029	-0.016†	0.0017	0.0001
Male	0.0023	-0.0010	0.019**	0.006†	0.0064	0.0020	0.0007
Depth	-0.0002*	0.0001**	0.0001	-0.0001	0.0001	-0.0001*	0.0001**
BT	-0.0001	0.002*	0.0006	-0.0001	-0.0012	-0.0003	0.0017**
BS	-0.0004	-0.0002	-0.0005	0.0012	0.0016	0.0000	0.001d
BO	-0.025***	-0.0024	0.048***	-0.01*	0.0019	-0.0004	-0.0006
d.f.	7 (323)	7 (323)	7 (323)	7 (323)	7 (323)	7 (323)	7 (323)
<i>F</i>	3.82	2.617	6.66	1.74	2.39	3.27	5.68
<i>p</i>	<0.001	0.012	<0.001	0.10	0.021	0.002	<0.001

No superscript, $p > 0.1$; † $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

Piscitelli (2000) found that female *S. orbignyana* (also a relatively small species, up to 120 mm ML) ingested more food than males at a given size; they suggested that a longer size of tentacles in females than in males gave the former a competitive advantage. Quintela and Andrade (2002a) suggested that the greater demand for energy in terms of ovary maturation may cause female *S. officinalis* to consume more food than males.

The percentage of empty stomachs decreased from morning to evening in *S. australis* (Table 4), suggestive of increased feeding activity in the evening and consistent with the findings of Castro and Guerra (1989), who reported that feeding activity of *S. officinalis* increases after sunset. However, Quintela and Andrade (2002a) found a different temperature-dependent feeding pattern for *S. officinalis*. When temperatures were low (winter), the weight fullness index (WFI) was high at sunset and sunrise, but when temperatures were warmer (summer) there were no differences in WFI throughout the day (Quintela and Andrade, 2002a). Our results for *S. australis* are likely related to the behaviour of its main prey (euphausiids and mysids), both of which are more active at night, probably influencing prey encounter rates and their proportion in the diet. Southern African euphausiids are known to swarm (aggregate), but mechanisms for their aggregations have not yet been identified (Pillar *et al.*, 1992; Gibbons, 1999). Mysids also aggregate (Meyer and Smale, 1991; Gibbons, 1999), but little research has been done on this group in South Africa to date. The larger sizes of euphausiids than other mesozooplankton (e.g. copepods) make them more susceptible to predation by larger predators (Pillar *et al.*,

1992). *S. australis*, like other sepiids, feed throughout their life cycle, as shown by the presence of food in all maturity stages.

The results of this study, in terms of diet of *S. australis*, differ from those for South Africa's west coast, where Lipiński *et al.* (1991) reported that the diet, by frequency of occurrence, consisted mainly of lanternfish, lightfish (*Maurolucus muelleri*), and stomatopods (*Pterygosquilla armata capensis*) in January 1987 and February 1988. Fish were clearly of less importance as prey in the current study. Guerra (1985) noted that crustaceans, in terms of percentage occurrence (65 and 80%) dominated the diet of *S. officinalis* and *S. elegans*, respectively.

Ecological interactions

Cannibalism in *S. australis* was low (2.8%), comparable with the results of other studies on sepiids (Guerra, 1985; Sánchez and Villanueva, 1989; Lipiński *et al.*, 1991). However, cannibalism was more pronounced in the east (7.3%) in 2001 than elsewhere (1.5%), perhaps suggestive of greater overlap in abundance of small and large *Sepia* in the east. Also, a relative scarcity of other prey species may have influenced the level of cannibalism. Fish increased in the diet towards the east, a finding that, along with those of cannibalism and the relative uniformity of prey composition between sexes at similar depth, reflects the opportunistic nature of *S. australis* feeding, as for other cephalopods (Lipiński, 1992).

The diet of cephalopods usually changes as they grow because of morphological changes such as increased beak gape and sensory capability (Mangold, 1987). Prey size generally depends

on the mouth gape of the predator, meaning that larger predators ingest larger and more diverse prey than smaller ones simply because of the larger gape (Wootton, 1998). Also, as animals get older and larger their experience in capturing different prey types increases. In this study, there were no substantial differences in the diet of small (ML ≤ 14 mm) and large (ML > 14 mm) *S. australis*, similar to the situation in *S. officinalis* (Castro and Guerra, 1989).

Mangold (1987) pointed out that juvenile *Sepia* fed exclusively on crustaceans, whereas adults take fish and cephalopods as well. In this study, however, very few juvenile *S. australis* were caught, probably because of net selectivity, so we were unable to compare the diets of juveniles and adults. It has been recorded before that surveys such as this tend not to catch juvenile cephalopods, so improved technology is necessary for more information to be collected on the behaviour and distribution of early life stages (Anon., 2002). However, Pinczon du Sel *et al.* (2000) found that diet varied between different age groups in both type and size of prey species captured by *S. officinalis* off France. They stated that amphipods were the main prey in the first three months of the year and then fish dominated, although crustaceans again dominated the diet of cuttlefish migrating inshore. We caught very few *S. australis* at maturity stage 1, but there was a high diet overlap between cuttlefish of maturity stages 2 and 3.

We conclude that *S. australis* is an opportunistic feeder, its diet highly dependent on whatever prey is abundant, so influenced by the environment at any time. This statement also applies to other sepiids, notably the best researched member of the group, *S. officinalis* (Guerra, 2006). However, we believe that the terms “opportunistic feeder”, “trophic opportunist”, or “generalist predator” in the case of cephalopods, should be reviewed and perhaps totally revised. Individualistic prey preference has been documented for adult *S. officinalis* by Dickel *et al.* (2006). Abundance in a predator’s environment *per se* does not mean that a certain animal will be taken frequently as prey. An energetic advantage (with many constraints attached) is crucial in prey selection, especially for energetically expensive budgets. We believe that this issue warrants study; there is seemingly sufficient published evidence to address it through a comprehensive review of the literature.

Environmental characteristics such as topography, season, temperature, and currents influence distribution patterns (of predator and prey) and diets. Different prey types differ in their life cycles, with specific periods of reproduction and greater abundance when environmental conditions are favourable. Some prey types are also associated with certain habitats that favour their survival and successful reproduction. On the basis of our data, it is difficult to separate the cause and effect for each factor. The substratum over which the cuttlefish were caught was mainly muddy clay, small gravel sand, silty sand, and clay in varying proportions in the west, and gravelly sand and muddy sand in the central region (Le Clus *et al.*, 1996). Prey populations will differ according to substratum type and depth, so seasonal migrations between shallow and deeper waters will bring sepiids into contact with different substrata (Boletzky, 1983) and prey types.

As shown by the high diet overlap indices (Table 8), the diet of *S. australis* was similar throughout our study regions in each survey, though slightly different in winter 1988 and spring 2001. We therefore assume that prey distribution was similar throughout our study area. The quantity of food increased with depth in 1988, and in both years, the quantity of mysids eaten increased with

depth. Mysids are generally benthopelagic and display diurnal vertical migration, by daylight staying close to the seabed (Gibbons, 1999). Such a distribution is similar to that of *S. australis*, so it is not surprising that the two taxa interact greatly as predator and prey when the mysids are particularly abundant.

We note that stomach content mass relative to total mass was higher in the west and increased with temperature, salinity, and depth in 2001. Increased temperature likely results in increased feeding activity, but the greater stomach mass relative to body mass we found in deeper water is likely the result of cuttlefish foraging in the upper water column at night and descending to depth by day, when they were caught. Finally, we note that, as an opportunistic feeder, *S. australis* seemed to take more food in the west of our study area, where environmental productivity is high, supporting large populations of zooplankton such as euphausiids (Gibbons, 1999).

In conclusion, we note that some of the patterns revealed by this work likely stem from normal biological flexibility in response to a changing environment (e.g. abundance, average ML and TW, food composition). Other patterns, however, may represent the more stable, well balanced ecological characteristics of the species (e.g. earlier maturation of males than females, well known in cephalopods, deepwater spawning, and hence larger gonads with increasing depth and decreasing temperature; the greater importance of the western region in terms of the distribution of the species).

Acknowledgements

MM was supported at the University of Bergen by NORAD (the Norwegian Agency for Development) and the South African Department of Environmental Affairs and Tourism (DEAT). We thank Malcolm Smale for assisting in identification of prey otoliths, and Jeremy David, Stan Pillar, and two anonymous reviewers for comments that helped us improve the manuscript.

References

- Anon. 2002. Report of the Working Group on Cephalopod Fisheries and Life History. ICES Document CM 2002/G: 04.
- Augustyn, C. J., Lipiński, M. R., and Roeleveld, M. A. C. 1995. Distribution and abundance of Sepioidea off South Africa. *South African Journal of Marine Science*, 16: 69–83.
- Badenhorst, A., and Smale, M. J. 1991. The distribution and abundance of seven commercial trawlfish from the Cape south coast of South Africa, 1986–1990. *South African Journal of Marine Science*, 11: 377–393.
- Bello, G., and Piscitelli, G. 2000. Effect of sex on tentacular club development and relationships with feeding efficiency and growth in *Sepia orbignyana* (Cephalopoda, Sepiidae). *Ophelia*, 53: 113–118.
- Boletzky, S. von. 1983. *Sepia officinalis*. In *Cephalopod Life Cycles*, 1, pp. 31–52. Ed. by P. R. Boyle. Academic Press, London.
- Castro, B. G., and Guerra, A. 1989. Feeding pattern of *Sepia officinalis* (Cephalopoda: Sepioidae) in the Ria De Vigo (NW Spain). *Journal of the Marine Biological Association of the UK*, 69: 545–553.
- Castro, B. G., and Guerra, A. 1990. The diet of *Sepia officinalis* (Linnaeus, 1758) and *Sepia elegans* (D’Orbigny, 1835) (Cephalopoda: Sepioidea) from the Ria de Vigo (NW Spain). *Scientia Marina*, 54: 375–388.
- Dickel, L., Darmailacq, A. S., Poirier, R., Agin, V., Bellanger, C., and Chichery, R. 2006. Behavioural and neural maturation in the cuttlefish *Sepia officinalis*. In *The Cuttlefish Sepia officinalis*, 56, pp. 89–95. Ed. by N. Koueta, J. P. Andrade, and S. von Boletzky. *Vie et Milieu*, 56(2).

- Forsythe, J. W. 1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. *In* Recent Advances in Fisheries Biology, pp. 133–143. Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokyo University Press, Tokyo.
- Gabr, H. R., Hanlon, R. T., Hanafy, M. H., and El-etreby, S. G. 1998. Maturation, fecundity and seasonality of reproduction of two commercially valuable cuttlefish, *Sepia pharaonis* and *S. dollfusi*, in the Suez Canal. *Fisheries Research*, 36: 99–115.
- Gibbons, M. J. 1999. An Introduction to the Zooplankton of the Benguela Current Region. National Book Printers, Cape Town.
- Guerra, A. 1985. Food of the cuttlefish *Sepia officinalis* and *Sepia elegans* in the Ria de Vigo (NW Spain) (Mollusca: Cephalopoda). *Journal of Zoology London (A)*, 207: 511–519.
- Guerra, A. 2006. Ecology of *Sepia officinalis*. *In* The Cuttlefish *Sepia officinalis*, 56, pp. 97–107. Ed. by N. Koueta, J. P. Andrade, and S. von. Boletzky. *Vie et Milieu*, 56(2).
- Hamilton, L. C. 1992. Regression with Graphics. A Second Course in Applied Statistics. Duxbury Press, Belmont, CA.
- Jereb, P., and Roper, C. F. E. 2005. Cephalopods of the World. An Annotated and Illustrated Catalogue of Cephalopod Species Known to Date. 1. Chambered nautilus and sepioids (Nautilidae, Sepiidae, Sepiolidae, Sepiadariidae, Idiosepiidae and Spirulidae). FAO Species Catalogue for Fishery Purposes, 4. 262 pp.
- Knutsen, I., and Salvanes, A. G. V. 1999. Temperature dependent digestion handling time in juvenile cod and possible consequences for prey choice. *Marine Ecology Progress Series*, 181: 61–79.
- Le Clus, F., Hennig, H. F.-K. O., and Rogers, J. 1996. Bathymetry and sediment type effects on catch rates of *Austroglossus pectoralis* (Soleidae) on the inner central Agulhas Bank. *South African Journal of Marine Science*, 17: 79–92.
- Lipiński, M. R. 1992. Cephalopods and the Benguela ecosystem: trophic relationships and impact. *South African Journal of Marine Science*, 12: 791–802.
- Lipiński, M. R., Payne, A. I. L., and Rose, B. 1992a. The importance of cephalopods as prey for hake and other groundfish in South African waters. *South African Journal of Marine Science*, 12: 651–662.
- Lipiński, M. R., Roeleveld, M. A. C., and Augustyn, C. J. 1991. Feeding studies on *Sepia australis* with an assessment of its significance in the Benguela ecosystem. *In* La Seiche/The Cuttlefish, pp. 117–129. Ed. by E. Boucaud-Camou. University Press, Caen (Proceedings of the First International Symposium on the Cuttlefish *Sepia*, Caen, June 1989).
- Lipiński, M. R., Roeleveld, M. A. C., and Augustyn, C. J. 1992b. First study on the ecology of *Sepia australis* in the southern Benguela ecosystem. *Veliger*, 35: 384–395.
- Mangold, K. 1987. Reproduction. *In* Cephalopod Life Cycles, 2, pp. 157–200. Ed. by P. R. Boyle. Academic Press, London.
- Meyer, M., and Smale, M. J. 1991. Predation patterns of demersal teleosts from the Cape south and west coasts of South Africa. 2. Benthic and epibenthic predators. *South African Journal of Marine Science*, 11: 409–442.
- Payne, A. I. L., Rose, B., and Leslie, R. W. 1987. Feeding of hake and a first attempt at determining their trophic role in the South African west coast marine environment. *South African Journal of Marine Science*, 5: 471–501.
- Pianka, E. 1974. Niche overlap and diffuse competition. *Proceedings of the US National Academy of Sciences*, 71: 2141–2145.
- Pillar, S. C., Stuart, V., Barange, M., and Gibbons, M. J. 1992. Community structure and trophic ecology of euphausiids in the Benguela ecosystem. *South African Journal of Marine Science*, 12: 393–409.
- Pinczon du sel, G., Blanc, A., and Daguzan, J. 2000. The diet of the cuttlefish *Sepia officinalis* (Mollusca: Cephalopoda) during its life cycle in the northern Bay of Biscay (France). *Aquatic Sciences*, 62: 167–178.
- Quintela, J., and Andrade, J. P. 2002a. Diel feeding rhythms, daily ration and gastric evacuation rates of *Sepia officinalis* in Ria Formosa lagoon (South Portugal). *Bulletin of Marine Science*, 71: 665–680.
- Quintela, J., and Andrade, J. P. 2002b. Effects of temperature on gastric evacuation rates in *Sepia officinalis* in laboratory conditions. *Bulletin of Marine Science*, 71: 681–689.
- Roeleveld, M. A. 1972. A review of Sepiidae (Cephalopoda) of southern Africa. *Annals of the South African Museum*, 59: 193–313.
- Roeleveld, M. A. C. 1998. The status and importance of cephalopod systematics in southern Africa. *South African Journal of Marine Science*, 20: 1–16.
- Roeleveld, M. A., and Liltved, W. R. 1985. A new species of *Sepia* (Cephalopoda: Sepiidae) from South Africa. *Annals of the South African Museum*, 96: 1–18.
- Roeleveld, M. A., Lipiński, M. R., and van der Merwe, M. G. 1993. Biological and ecological aspects of the distribution of *Sepia australis* (Cephalopoda: Sepiidae) off the south coast of southern Africa. *South African Journal of Zoology*, 28: 99–106.
- Salvanes, A. G. V., Aksnes, D. L., and Giske, J. 1995. A surface-dependent gastric evacuation model for fish. *Journal of Fish Biology*, 47: 679–695.
- Salvanes, A. G. V., and Nordeide, J. T. 1993. Dominating sublittoral fish species in the west Norwegian fjord and their trophic links to cod (*Gadus morhua*). *Sarsia*, 78: 221–234.
- Sánchez, P., and Villanueva, R. 1989. Distribution and abundance of three species of cephalopod sepiids in Namibian waters. *Collection of Scientific Papers International Commission for the Southeast Atlantic Fisheries*, 16: 151–160.
- Sánchez, P., and Villanueva, R. 1991. Morphometrics and some aspects of biology of *Sepia australis* in Namibian waters. *In* La Seiche/The Cuttlefish, pp. 105–115. Ed. by E. Boucaud-Camou. University Press, Caen (Proceedings of the First International Symposium on the Cuttlefish *Sepia*, Caen, June 1989).
- Shannon, L. V. 1985. The Benguela ecosystem. 1. Evolution of the Benguela, physical features and processes. *Oceanography and Marine Biology. An Annual Review*, 23: 105–182.
- Wootton, R. J. 1998. Feeding. *In* Ecology of Teleost Fish, 2nd edn, pp. 27–63. Kluwer Academic, London.
- Zar, J. H. 2000. Biostatistical Analysis, 4th edn. Prentice Hall, New Jersey.

Appendix

Summary of ANOVA results for the effect of region, sex, and depth on ML, TW, and GW of *S. australis* in 1988 and 2001.

Factor	d.f.	F	p
1988			
ML	178	13.229	0.000
TW	178	16.096	0.000
GW	178	12.168	0.001
2001			
ML	321	18.914	0.000
TW	321	20.294	0.000
GW	321	13.959	0.000

doi:10.1093/icesjms/fsm064