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J. Mar. Biol. Ass. U.K. (2003), **83**, 535–541
Printed in the United Kingdom

Population biology of *Octopus vulgaris* on the temperate south-eastern coast of South Africa

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Population structure and biology of *Octopus vulgaris* was investigated along the south-eastern coast of South Africa. Samples were collected inter- and sub-tidally as a precursor to the establishment of an experimental octopus fishery in the region. In total, 300 (intertidal) and 147 (subtidal) *O. vulgaris* were collected over a two year period. Females were found to dominate the intertidal area (sex ratio 2:1), while no difference was found subtidally (sex ratio 1:1). Of those collected intertidally, immature females were most prevalent while males ranged from immature to mature. Mature females were only found subtidally. A marked size difference was apparent, with the subtidal octopus being substantially larger. Although brooding females were found throughout the year, numbers peaked in summer. Individual fecundity ranged between 42,000–790,000 eggs. The total number of eggs produced and the number of eggs per egg string were correlated to female size. Diet did not vary greatly between the inter- and sub-tidal areas, with the main prey items being crustaceans, teleosts and octopus. It appears that the immature females use the intertidal area to feed and grow, before migrating to deeper areas to mature and spawn.

INTRODUCTION

Octopus vulgaris Cuvier 1797 is one of the most intensely studied cephalopod species in the world (Mangold, 1997), with research concentrated in the Mediterranean Sea and on the north-west African coast (Mangold & Boletzky, 1973; Guerra, 1979; Hatanaka, 1979; Caverivière et al., 2002). This species was previously believed to have a global distribution, however it is now considered to occur in the Mediterranean and the eastern Atlantic only, but forms part of a larger cosmopolitan species complex (Mangold, 1998). It has been suggested that the South African *O. vulgaris* is a separate species (Roeleveld, 1998), however this has not been verified.

The distribution of *O. vulgaris* in southern Africa ranges from Luderitz on the west coast of Namibia, to approximately Durban on the east coast of South Africa (Smale et al., 1993). Limited biological research has been conducted on the subtropical east coast (Smale & Buchan, 1981) and the cold temperate south-western coast (Smith, 1999) of South Africa. Biological and ecological data on *O. vulgaris* on the warm temperate south-eastern coast is lacking, although an isolated laboratory study on mussel predation by *O. vulgaris* has been carried out (McQuaid, 1994). These three areas differ vastly in oceanographic climate, species diversity and zoogeography (Branch et al., 1994). Differences in water temperature and prey availability have been shown to influence octopus growth rates and size (Forsythe & Hanlon, 1988; Forsythe, 1993).

The intertidal *O. vulgaris* stock along the South African coast is exploited by both recreational and subsistence fishermen, with the level of exploitation varying between the different regions (Clark et al., 2002). The octopus stock in the subtidal area is currently unexploited. This study was initiated to provide biological and ecological information on *O. vulgaris* along the warm temperate coast of South Africa, which would supplement existing data for other regions. This baseline information will be used in the development of a proposed octopus fishery around the South African coast. The aim of this study was to describe the population structure, biology and distribution of *O. vulgaris* over both intertidal and subtidal areas.

MATERIALS AND METHODS

Study area

Intertidal collections were conducted around Algoa Bay, a large log-spiral bay situated on the south-east coast of South Africa (Schumann et al., 1987). The collection sites, consisted mainly of rocky substrata, and were located around Cape Recife the headland at the western end of Algoa Bay (Figure 1). Subtidal sites were located on various reefs in Algoa Bay, St Francis Bay and Tsitsikamma National Park (a marine reserve) (Figure 1). A description of both the intertidal areas and subtidal reefs are given in Table 1. The water temperature in the study area is warm but fluctuating (12–24°C) during summer but colder and more stable (14–18°C) during winter months (Beckley, 1988). The temperature fluctuations in summer are induced by localized upwelling, caused by prevalent easterly winds.

Sampling techniques

Intertidal collections were conducted during spring low tides from January 1999 to February 2000. Total monthly

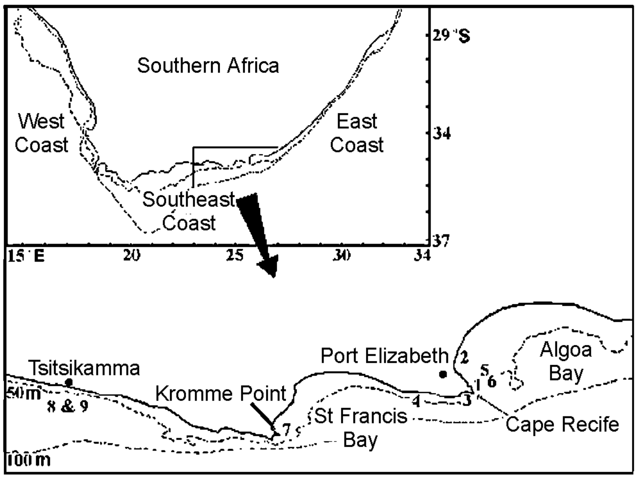

Figure 1. Geographical location of octopus collection sites along the south-east coast of South Africa.

Table 1. *Descriptions of the intertidal and subtidal collection sites of* Octopus vulgaris.

Site	Intertidal Area description
Algoa Bay	1&2 Sheltered low profile rock. 3&4 Exposed high profile rock.
Site	**Subtidal Reef description**
Algoa Bay	5 Medium to high profile, dense invertebrate cover, depth: 5–20 m. 6 Low profile, sparse invertebrate cover, interspersed sand, depth: 15–20 m.
St Francis Bay	7 Boulder reef, seaweed cover, few invertebrates, depth: <8 m.
T.N. Marine Park	8 High profile, dense invertebrate cover, depth: 15–30 m. 9 Tidal gully, sparse invertebrate cover, interspersed sand, depth: <12 m.

effort was calculated from two people searching a set area, in a set time of two hours. Searches were conducted for approximately three days a month. Collections were done during daylight hours (morning), with a few collections at night. A comparative study however, showed that den sites were located more effectively during the day.

Subtidal samples were collected during the day, through SCUBA (Self Contained Underwater Breathing Apparatus) diving, from June 1999 to November 2000. Octopuses were removed from their dens by squirting a mild dilution of copper sulphate ($CuSo_4$) an irritant, or chloroform an anaesthetic, into the den. Specimens were euthanased in a 3% ethanol–seawater solution and frozen for later biological analysis.

Exposed (Sites 3, 4) and sheltered (Sites 1, 2) intertidal areas were compared over a six-month period, to investigate octopus densities. Effort was calculated from two people searching a set area, in a set time of two hours.

Biological data collection

Total mass (TM), total length (TL), dorsal mantle length (DML), head width (HW), and gonad mass (GM) were recorded from thawed samples. The gonadosomatic index (GSI) was determined by gonad mass as a percentage of total mass. Sex was determined by the presence of the spermatophoric groove and heterocotylus on the third right arm of the males (Mangold, 1983). Female maturity was categorized according to Mangold (1987). Stage 1 (immature) when the ovary is small and white, Stage 2 (maturing) when the ovary is larger and the oviducal glands are off-white in colour, Stage 3 (mature) when loose oocytes are present in the ovary and Stage 4 (spent) when the ovary is flaccid with few loose oocytes present. Males were classified as sexually mature on the presence of spermatophores in Needham's sac. Egg counts were done from egg strings collected from the dens. The total number of egg strings collected was counted and measured. The total number of eggs per string was determined from a sub sample and extrapolated to determine the total number of eggs per female. Beaks were removed, soaked in freshwater for 3–7 days after which they were rinsed and preserved in 10% formaldehyde. The diet was assessed by analysing stomach contents and den remains. Contents from the crop and stomach were removed, weighed and preserved in 10% formaldehyde. Teleosts were identified to the lowest taxon possible, at least to family level, through otoliths and eggs found in the gut contents. Den remains were collected and preserved in 10% formaldehyde for later analysis. Gonads were removed and weighed.

Statistical analysis

Morphometric and egg number–female mass (TM) relationships were analysed with GraphPad Prism® and Statistica (StatSoft®) software using linear and non-linear, least square regression line or best fit curve. The chi-square (χ^2) test was used to determine sex ratios (Zar, 1984). Seasonal data (mean mass, GSI) were tested for normality and homogeneity of variance, transformed where necessary and tested using a one-way analysis of variance (Statistica, StatSoft®). Den volume and octopus size were correlated using the Spearman rank correlation in GraphPad Prism® software. No significant difference for any of the measured parameters was found between the subtidal sites, or between the intertidal sites, data were therefore lumped for analyses.

RESULTS

Density and distribution

A comparison between the exposed (Sites 3, 4) and sheltered (Sites 1, 2) areas showed that octopus were more abundant on low profile rocky areas on the sheltered sites. A mean number of octopus/hour of 3.4 ± 0.9 SD were collected for the sheltered sites, compared to 0.5 ± 0.2 SD for the exposed sites. The distribution of octopus within an area in both the intertidal and subtidal regions was patchy and clumped.

A total of 300 octopuses weighing 125.68 kg were removed from the intertidal area within one year. Intertidal

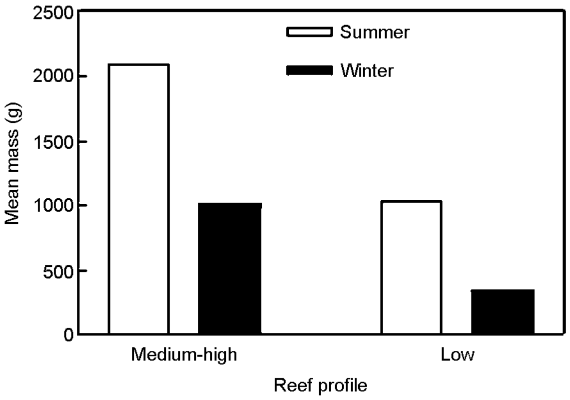

Figure 2. Summer and winter mean mass for *Octopus vulgaris* found on two reef profiles.

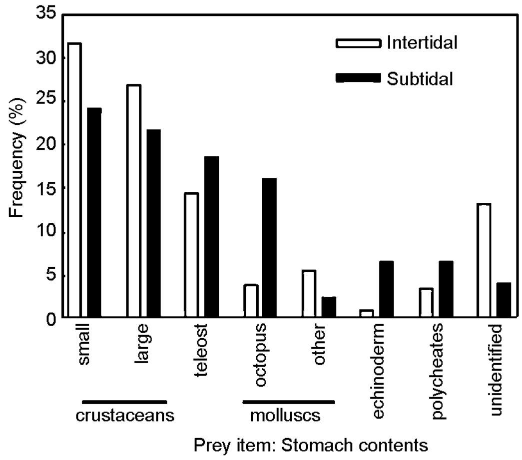

Figure 3. The frequency of main prey items identified from the stomach contents of *Octopus vulgaris* collected on the south-east coast of South Africa.

densities were relatively low and ranged between 0.02–1 octopus/100 m^2 (mean 0.28 ± 0.08 SE), with density decreasing in the following year (personal observation). The effort for collecting 1 kg of octopus was approximately 1 h search time per person. A total of 147 octopuses weighing 168.34 kg were collected from the subtidal area at a search time of 1h 20 min for 1.1 kg octopus.

Significant size differences were noted in octopuses occurring in the different subtidal habitats sampled. The mean mass (1553.84 g ±225.63 SE) of octopuses found on medium to high profile reef, with dense invertebrate cover, was significantly ($P<0.05$) larger than the mean mass (534.12 g ±131.38 SE) of octopuses found on flat profile reef, with sparse cover. This difference was also apparent in the seasonal mean mass comparison for the different reef types (Figure 2). Brooding females were more prevalent on medium profile boulder reef (N=7) than on high profile reef (N=2). Loose boulder reef offered particularly good den habitat compared to solid structure high profile reef (personal observation).

Den use and diet

During intertidal collections 75% of the octopuses were found in dens and only 25% were found exposed in rock pools. The den volume (cm^3) positively correlated ($r=0.83$, $P<0.0001$) to octopus size, the larger the size the larger the den volume. Two different den types were observed, small octopus (342.5 g ± 249.0 g SD) generally occupied holes sunk perpendicular into the substrate, while larger sized octopus (580.6 g ± 542.3 g SD) excavated dens beneath rocks and ledges. Of the specimens collected, 47% of intertidal (N=141) and 41.5% of subtidal (N=61) octopus had prey remains in the gut. Prey remains were only present at 11.92% of intertidal and 9.23% of subtidal dens. No distinct middens were found at the dens either intertidal or subtidally. The main prey items from the stomach content analysis were crustaceans, teleosts and octopus (Figure 3). Octopus was identified as *O. vulgaris* from beaks and partially digested flesh. Molluscs were most prevalent in the den remains, with the dominance in bivalves attributed mainly to one species, *Venus vericosa* (Figure 4). Teleosts found in the diet, were identified to family level (Figure 5). Small sized (<300 g) octopuses were found to eat Blenniidae and Gobiidae eggs attached to rock surfaces.

Population biology

Sex ratio

Females were found to dominate the intertidal area (2:1 female to male ratio, $P>0.05$), while there was no

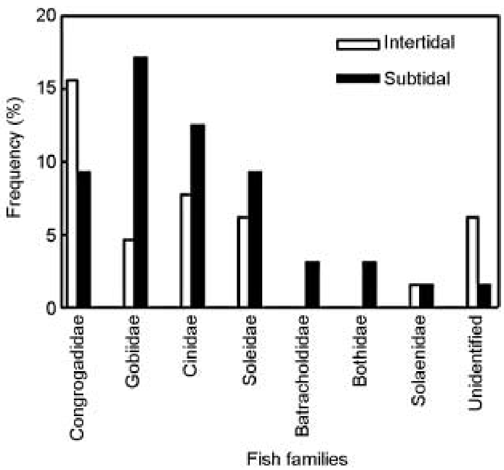

Figure 4. The frequency of occurrence of main prey items from the den remains of *Octopus vulgaris* collected on the south-east coast of South Africa.

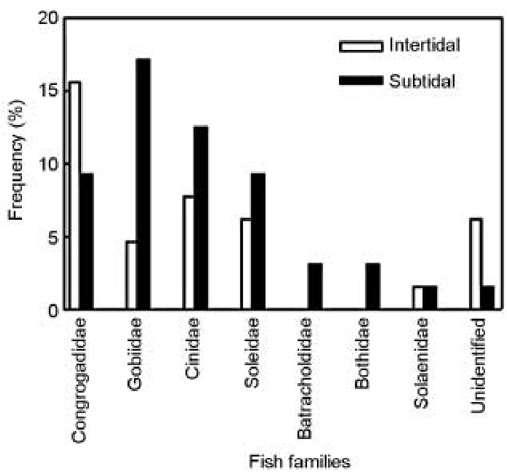

Figure 5. Teleosts families identified from otoliths and eggs found in the stomach contents of *Octopus vulgaris* collected on the south-east coast of South Africa.

significant difference in the subtidal sex ratio (1:1, $P > 0.05$).

Morphometrics

The relationship between dorsal mantle length and total length was linear (TL=5.02(ML) + 54.03, $r^2=0.87$, N=440), while the dorsal mantle length and total mass relationship was best described by a power curve ($TM=0.0038(ML)^{2.58}$, $r^2=0.89$, N=440). The mean TM, TL, DML and GM for both inter- and sub-tidal specimens are presented in Table 2. There was no significant difference ($P > 0.05$) in mean mass between the sexes within a particular area. There was however, a significant difference between the intertidal and subtidal female mean mass ($P < 0.05$) and the intertidal and subtidal male mean mass ($P < 0.05$). Generally subtidal specimens had a significantly ($P < 0.05$) larger mean mass than the intertidal octopus. Differences were also apparent in the mass of the gonads with the subtidal specimens having significantly larger ($P < 0.05$) gonads (Table 2).

A clear linear relationship between gonad mass (GM) and total mass (TM) was found for male octopuses both inter- and sub-tidally (GM=0.0102(TM) − 0.76, $r^2=0.94$, N=181). The gonad mass increased with an increase in total mass. Although intertidal (mainly immature) females gave a similar result (GM=0.003(TM) − 0.18, $r^2=0.82$, N=199), the combined inter- and sub-tidal female sample showed a weak relationship ($r^2=0.34$). The subtidal females showed a large variation in the gonad-total mass relationship, with some small females having large gonads and vice versa.

Maturity

Male maturity stages ranged from juvenile to mature both inter- and sub-tidally, with mature males found year round. Intertidally, 62.4% (N=63) of males were mature, with a mean size of 733.79 g ±86.6 (SE), while subtidally, 75.3% (N=60) of the males were mature with a mean size of 1246.98 g ±127.01 (SE). All males larger than 190 g were mature, with the smallest mature male weighing 71.89 g.

Immature and maturing females were found both inter- and sub-tidally. No mature females were found in the intertidal region. Subtidal collections yielded 14 mature females without spawned eggs, nine brooding females and one spent individual. The brooding females, of which two individuals were mature, and seven were spent, all had eggs present in the den. Six subtidal females had flaccid, degenerate bodies, indicating the possible end of the life span. Four of these were spent individuals, one was brooding but not spent, and one mature. The mean size of the mature females was 2425.92 g ±314.9 (SE), with spawning probably taking place between 1000–3000 g total mass. Of these females, 50% were mature at approximately 1600 g. The smallest mature female collected weighed 405 g.

Gonadosomatic index (GSI)

The mean GSI was below 1% for both the intertidal and subtidal males (intertidal: 0.69% ±0.032 (SE), N=101, subtidal: 0.95% ±0.053 (SE), N=81) and the mainly immature intertidal females (0.26% ±0.011 (SE), N=199). The GSI for immature subtidal females ranged 0.1–2.5% and for mature females between 1.33–10.34% (5.21 ±0.72 (SE), N=17).

Fecundity

The total number of eggs produced was estimated from seven spent females and ranged from 42,133–789,111. The mean number of eggs per egg string ranged 602–2133 and the mean number of egg strings per individual ranged 70–452. The mean length of the eggstrings was 74.48 mm ±0.76 (SE) and ranged 36–114 mm. Both the number of eggs per eggstring ($r^2=0.87$, $P < 0.05$, Figure 6) and the total number of eggs ($r^2=0.78$, $P < 0.05$,) were significantly related to the size of the female.

Table 2. *The total mass (TM), total length (TL), dorsal mantle length (DML) and gonad mass (GM) of* Octopus vulgaris *individually collected from intertidal and subtidal sites. Values are mean ±SE.*

	Intertidal		
	Female (N=199)	Male (N=101)	All (N=300)
TM (g)	627.72 ±41.44	529.54 ±61.34	594.67 ±34.43
TL (mm)	567.05 ±11.59	515.15 ±18.40	549.57 ±9.96
DML (mm)	103.03 ±2.77	90.82 ±3.13	98.92 ±2.15
GM (g)	1.69 ±0.14	4.08 ±0.47	2.49 ±0.19
	Subtidal		
	Female (N=66)	Male (N=81)	All (N=147)
TM	1302.93 ±169.27	931.05 ±102.63	1098.02 ±95.61
TL	641.64 ±27.78	608.33 ±24.71	623.29 ±18.45
DML	125.53 ±5.75	110.48 ±4.215	117.24 ±3.52
GM	37.43 ±10.19	9.35 ±1.13	21.96 ±4.74

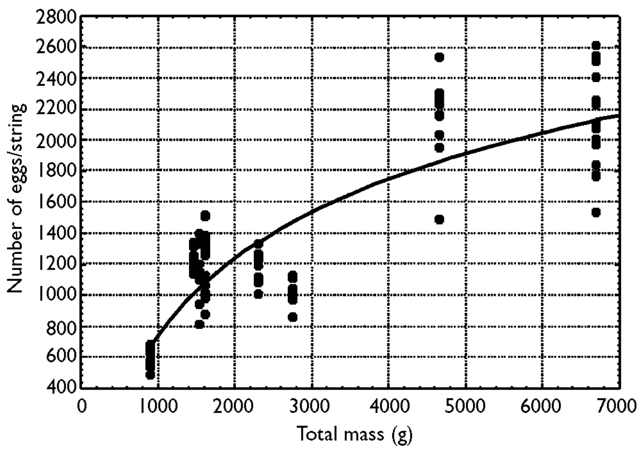

Figure 6. Number of eggs per string related to the total mass (g) of *Octopus vulgaris* females collected on the south-east coast of South Africa ($\text{Number} = -4322.72 + 1685.99 \times \log_{10}(\text{mass})$).

Seasonal trends

Intertidal mean mass and GSI showed no significant difference between seasons ($P > 0.05$). Subtidally, seasonal trends were evident in male mass, with a significantly lower mass observed in winter (479.18 g) than during spring (1251.77 g, $P < 0.05$,) and summer (1487.07 g, $P < 0.001$). The mean mass for females (861.84 g) in winter was also significantly lower than the mean mass (1999.80 g, $P < 0.05$) observed for summer. Seasonal mean mass for both inter- and sub-tidal males and females are presented in Figure 7. The mean intertidal and subtidal mass also differed significantly between summer ($P < 0.05$) and spring ($P < 0.05$).

Subtidal female GSI was significantly higher ($P < 0.05$) in summer (3.23%) when compared to winter (1.06%) (Figure 7). Further evidence of seasonality is given in the distribution of mature, brooding and spent females in Figure 8. Mature and brooding females peaked during summer and autumn and were lowest during winter. There was no seasonal variation in the sex ratios, which remained 1:1 and 2:1 (female:male) for the subtidal and intertidal octopus, respectively.

Incidences of possible mating (mature male and maturing female found in same or adjoining dens) were recorded on five occasions intertidally and five times subtidally, throughout all seasons.

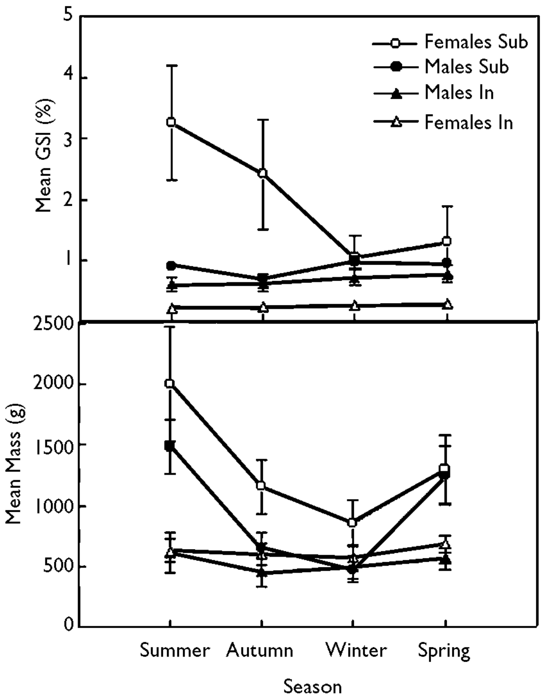

Figure 7. The mean mass (g) and mean GSI (%) for male and female *Octopus vulgaris* collected inter- and sub-tidally per season on the south-east coast of South Africa.

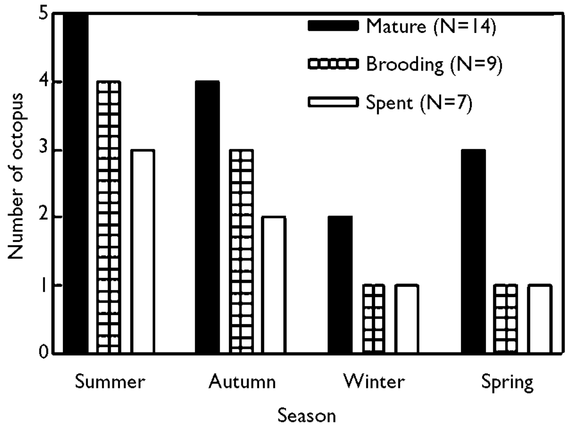

Figure 8. Seasonal distribution of mature, brooding and spent female *Octopus vulgaris* collected on the south-east coast of South Africa. (Total N=37% of all subtidal females).

DISCUSSION

Despite the possibility of a species complex in *Octopus vulgaris* the dynamics and biology in southern Africa was found to be similar to that for *O. vulgaris* on the north-west coast of Africa (Mangold & Boletzky, 1973; Hatanaka, 1979) and the Mediterranean Sea (Sánchez & Obarti, 1993). Octopuses tend to be opportunistic feeders that make use of a variety of prey items in different habitats (Mangold, 1983). This is clearly reflected in *O. vulgaris* along the South African coastline with the diet varying considerably between the different coastal regions. On the subtropical east coast, the brown mussel was the dominant prey item (Smale & Buchan, 1981), abalone and crustaceans were found to be the bulk of prey on the south-west coast (Smith, 1999), and crustaceans, teleosts and octopus dominated prey items on the south-east coast (this study). It was noteworthy that the fish taken were small and typical of reef areas. Regional variation in diet reflects differences in prey spectra available in different zoogeographic areas, and demonstrates behavioural plasticity that allows these predators to successfully exploit a wide variety of prey taxa. The prey species recorded in southern Africa falls within the range of prey observed in the Mediterranean (Nixon, 1987) and north-west Africa (Nigmatullin & Ostapenko, 1976; Hatanaka, 1979; Caverivière, 2002).

Morphometric descriptions are also very similar to studies on the subtropical east coast (Smale & Buchan, 1981), cool temperate south-west coast (Smith & Griffiths 2002) of South Africa, and the Mediterranean (Sánchez & Obarti, 1993). The dynamics of the population appear to be dominated by the migration of maturing females to deeper subtidal areas, where they mature, spawn, and brood. This migration is supported by the fact that no mature or brooding females were found intertidally. Smale & Buchan (1981) and Smith (1999) also found evidence of such migration patterns amongst female octopuses. Similar distributions of mature *O. vulgaris* females were found on the north-west coast of Africa (Hatanaka, 1979), in the Mediterranean (Sánchez & Obarti, 1993) and in South Carolina (Whitaker et al., 1991). The difference between inter- and sub-tidal female size on the South African coast suggests that younger, smaller individuals (small GM) inhabit the intertidal area whereas larger and older individuals (larger GM) occur subtidally. However, this still needs to be validated by ageing studies. The link between somatic and gonadal growth is restricted to the premature phase (Mangold, 1983), and generally the correlation between body mass and gonad mass is better in males than in females, as was evident in this study. The cause of variation in size at maturity is still unknown but many factors such as food, light, temperature, age and large variation in individual growth have been implicated (Mangold, 1983). The specific influence of temperature on cephalopod growth and size has been illustrated by several authors (Forsythe & van Heukelem, 1987; Forsythe, 1993). A female hatching in spring will grow faster than one hatched during the previous winter, due to higher water temperatures, and will therefore reach a larger size at a younger age (Forsythe, 1993). The influence of temperature is evident when comparing size at maturity for the temperate south-east coast and the subtropical east coast of South Africa. Males and females respectively matured larger (400 g) and smaller (900 g) on the east coast (Smale & Buchan, 1981) compared to observed for males (190 g) and females (1600 g) on the south-east coast (this study). Smith & Griffiths (2002) on the south-west coast of South Africa and Mangold (1983) in the Mediterranean also noted that male maturity was reached at approximately 170 g and 190 g respectively.

Male octopuses also differed in size between the intertidal and subtidal areas. This could indicate a migration of the older, larger males to the subtidal area, to mate with mature, ready to spawn females. Migration to deeper waters in the cold season, possibly for reproduction has been suggested from studies off north-west Africa (Caverivière, 2002). A current study on the South African squid (*Loligo vulgaris reynaudii*) indicates that the last male to fertilize a female, substantially increases his success rate in paternity (W.H.H. Sauer, personal communication). A similar strategy could be employed by *O. vulgaris* males. The sex ratios were maintained throughout the months sampled, which differed from findings by Smale & Buchan (1981) and Smith (1999).

Spawning peaked during autumn and winter on the subtropical east coast of South Africa (Smale & Buchan, 1981). On the cold temperate south-west coast, the GSI peaked during spring and summer, however no mature females were found (Smith, 1999). This differs from the trend found on the warm temperate south-east coast, in which brooding females were more abundant in summer. Spawning of *O. vulgaris* in the Mediterranean was observed during summer (Mangold & Boletzky, 1973), while spawning peaked during spring on the north-west African coast (Guerra, 1979). The embryonic development of *O. vulgaris* can vary between 55–89 days at temperatures of 15–17°C (Boletzky, 1987; Caverivière et al., 1999) and the planktonic larval stage is estimated at approximately 60 days at 21°C (Villanueva, 1995). The south-east coast of South Africa has prevailing bottom temperatures of 15–17°C (Oosthuizen, 1999), and with peak spawning occurring in summer, the first settlement will probably peak late autumn to spring. During this period the spawned females would have died and the decrease in mean mass between the seasons would be evident. Smith (1999) also observed this seasonal variation in size, but attributed this to lower water temperatures.

The fecundity calculated for the southern African *O. vulgaris* differs from that found in the Mediterranean. *Octopus vulgaris* in southern Africa exhibited a wider range of between 42,000–790,000 eggs, compared to in the Mediterranean where between 100,000 and 500,000 eggs are laid (Mangold, 1983). The number of egg strings per female were similar at 70–452 (this study) and 100–400 (Mediterranean) however, the length of the eggstrings differed at 74 mm (this study) and 100 mm (Mediterranean) (Mangold, 1983).

At present only the intertidal area on the South African coast is exploited. This study did not aim to estimate biomass, nonetheless a variation in biomass in the intertidal component of the *O. vulgaris* population was noted (personal observation). Intensive research collection during one year, plus increased disturbance of the rocky shore area and octopus collection by bait diggers the following year, could have resulted in lower octopus numbers in the area. However, anthropogenic effects on the biomass cannot be proven in this study and the reduction of biomass could be due to natural fluctuations within the population. Although the intertidal population could be seen as a renewable resource, (where the subtidal source feeds the intertidal source) the combined exploitation of inter- and sub-tidal areas could be detrimental to the octopus stock, as the over exploitation of one area will impact on the other. These two areas, which differ in locality and fishing activity, should thus be managed as one, to ensure sustainable use of the octopus resource. Octopus fisheries worldwide have shown that careful planning is needed for a biologically and economically sustainable fishery (Whitaker et al., 1991; Roper, 1997; Defeo & Castilla, 1998; Caddy, 1999).

We thank the numerous people that assisted during the SCUBA diving collections. Special thanks to Dr Nadine Strydom (South African Institute for Aquatic Biodiversity) for field and editorial assistance and larval fish identification, Dr Warwick Sauer (Rhodes University) for editing a draft manuscript and suggestions throughout the project. The infrastructure for the project was provided by Bayworld (Port Elizabeth Museum) and funded by the National Research Foundation.

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Submitted 8 August 2002. Accepted 11 March 2003.