

Spatio-temporal patterns in maturation of the chokka squid (*Loligo vulgaris reynaudii*) off the coast of South Africa

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Knowledge of the temporal and spatial characteristics of chokka squid (*Loligo vulgaris reynaudii*) biology in South African waters is limited, so the possibility of there being a geographically fragmented stock was examined by investigating the distribution of maturity patterns for the species, covering all known spawning areas and using both historical and recent data. Gonadosomatic indices (GSI) varied between year-round consistency and apparent seasonal peaks in both summer and winter; there was no clear spatial pattern. Monthly percentage maturity provided further evidence for two peak reproductive periods each year, although mature squid were present throughout. Sex ratios demonstrated great variability between different areas and life history stages. Male-biased sex ratios were only apparent on the inshore spawning grounds and ranged between 1.118:1 and 4.267:1. Size at sexual maturity was also seasonal, squid maturing smaller in winter/spring than in summer/autumn. Also, squid in the east matured smaller than squid in the west. Although the results from the present study do not provide conclusive evidence of distinct geographic populations, squid likely spawn over a significantly larger area of the Agulhas Bank than previously estimated, and squid on the west coast of South Africa may return to spawn on the western portion of the Agulhas Bank. It remains likely, however, that the east and west coast populations are a single stock and that migration of juveniles to the west coast and their subsequent return as sub-adults is an integral but non-essential and variable part of the life history.

Introduction

A high value export fishery focusing on chokka squid (*Loligo vulgaris reynaudii*) developed in 1985 on the southeast coast of South Africa (Augustyn, 1990), and 90% of the catch is now caught by hand-jigging, with the remainder harvested as bycatch in hake- and sole-directed trawl fisheries (Cochrane *et al.*, 1997). As an important commercial resource, research on the species has, since the early 1980s, investigated aspects pertaining to its distribution and abundance, reproductive biology, spawning behaviour, and age and growth (Augustyn *et al.*, 1994 and Augustyn and Roel, 1998). Initially, studies made use of samples collected from trawlers fishing on the western Agulhas Bank (Augustyn, 1990), but as attention focused on the jig fishery which concentrated on spawning aggregations (Sauer and Lipiński, 1991, Sauer *et al.*, 1992, Sauer and Smale, 1993, Sauer, 1995 and Lipiński *et al.*, 1998), commercial samples were collected exclusively from the inshore areas of the Agulhas Bank, primarily from the eastern regions.

The intense fishing effort on spawning aggregations raised concerns not only about the risk of stock depletion, but also the loss of spawning animals (Augustyn *et al.*, 1992 and Moltschanivskyj *et al.*, 2002). Management of the resource is by effort limitation, with limits on both the number of fishers involved in the fishery and the duration of the season, the latter enforced through a complete closure for 5 weeks. Recently, concern has been raised over the possibility of an increase in effort through substantial changes in fishing gear and strategy, with vessels now able to fish in deeper waters, offshore of the shallow spawning grounds, using large drogue anchors.

Management of chokka is therefore closely linked to understanding aspects of its biology, particularly those aspects that have a strong spatio-temporal component. Although the limits of distribution of chokka are reasonably well known, data on the temporal and spatial nature of the stock are limited. Data from Augustyn (1991)

indicate that there appears to be a single stock, with at least a proportion migrating west to feed before returning to spawn on the central Agulhas Bank or off the coast of the Eastern Cape. The current study investigates the possibility of there being a geographically fragmented stock by examining both historical and recent biological data from commercial and research sources. Seasonal and spatial variability in size at maturity, the percentage mature, the gonadosomatic index, and the sex ratio are examined.

Methods

Study area

The Agulhas Bank (Figure 1) is a triangular extension of the continental shelf extending along the southeast coast of South Africa from Cape Agulhas (20°E) to Port Alfred (27°E) and south to the 1000-m isobath, encompassing an area of ca. 29 000 square nautical miles (Japp *et al.*, 1994). For the purpose of this study, it has been divided into three regions: western (west of 20°E), central (20–23°E), and eastern Agulhas Bank (23–27°E). The cold, north-flowing Benguela Current forms the western boundary of the Agulhas Bank, and the central and eastern Bank are strongly influenced by the warm, southeast-flowing Agulhas Current.

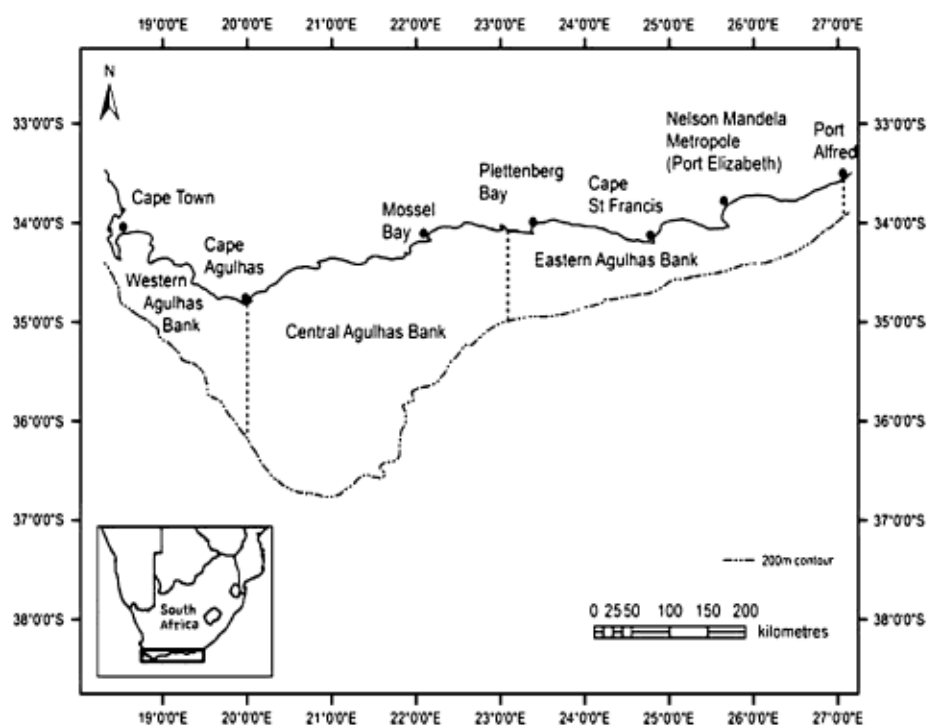


Figure 1. The southeast coast of South Africa showing the various regions of the Agulhas Bank used in this analysis (after Japp *et al.*, 1994), and the 200-m isobath.

Sampling

Biannual research cruises (commencing in the early 1980s) are conducted by the South African Department of Environmental Affairs and Tourism's Chief Directorate: Marine and Coastal Management (MCM) in spring and autumn. The surveys provide most of the abundance and biological data for a variety of demersal fish and cephalopod species. Gear employed and sampling methodology (a random stratified method) are described by Payne *et al.* (1985). Research data used in this study were obtained from surveys between 1986 and 1999. The research vessel is large, however, restricting trawling operations in shallow (up to 50 m) inshore waters where spawning squid aggregate. Over the past 12 years, just 12% of the research trawls were conducted shallower than 50 m, leading to an under-representation of such areas in the samples.

Samples from commercial jiggers and trawlers augment the database. Jiggers actively target spawning squid (Sauer, 1995) and provide data for the inshore environment on a monthly basis. In contrast, hake- or sole-directed trawlers take squid as a bycatch. Trawlers operate over a larger area and to generally greater depths than jiggers (Roel *et al.*, 2000). Therefore, a wider range of sizes are available, including small squid which are largely unavailable to jiggers. Commercial jig samples were collected during two periods. Initially, samples were collected monthly from the inshore spawning grounds (6–50 m deep) between Algoa Bay (33°46'S 26°00'E) and Oyster Bay (34°12'S 24°37'E) from March 1988 to January 1989 (Sauer, 1995). Monthly samples were also collected between June 1999 and June 2000 from the South African Bureau of Standards (SABS) Food Testing Laboratory in Port Elizabeth, and from commercial squid jiggers. Over the same period, Marine and Coastal Management observers collected additional biological samples from the hake- and sole-directed trawl fleet operating out of Mossel Bay (34°22'S 21°25'E). These vessels operate at depths up to 200 m predominantly on the central and occasionally on the western Agulhas Bank. Commercial samples were frozen at sea and thawed prior to biological analysis. Research samples were analysed immediately after each trawl, with data from commercial samples frozen for later analysis. A simplified system of maturity staging based on a modified Lipiński and Underhill (1995) scale was used (Table 1).

Table 1. Maturity scales used to assess chokka maturity and life history stages. The Lipiński and Underhill (1995) scale is based on macroscopic conditions of gonadal tissue, whereas the simplified stage was widely employed during research surveys.

Lipiński and Underhill stage	Simplified stage	Life history stage
I	1	Juvenile
II	2	Sub-adult
III	2	Sub-adult
IV	3	Adult
V	3	Adult
VI	3	Adult

Biological material

Dorsal mantle length (DML) was measured to the nearest millimetre, and gonad length (testis in males, nidamental gland in females) and mantle thickness to the nearest 0.1 mm. Body mass, gonad mass (testis or ovary), and stomach content mass were measured to the nearest 0.1 g. Gonadosomatic indices (GSI), adapted from Pierce *et al.* (1994), were calculated from

$$GSI = \frac{100GW}{(BW - (SW + GW))}$$

where GW is the gonad weight, BW the body weight, and SW is the stomach content weight. To examine both temporal and spatial trends in maturity, two hypotheses were tested. First, whether the median GSI between months was equal, and second whether the median GSI between areas was equal. A Kruskal–Wallis test was used to test for differences in median GSI between all months for both sexes. Mann–Whitney *U*-tests, with the probability adjusted for the number of cases being tested, were used in

pairwise comparisons between months (Zar, 1999). A comparison of GSIs on a spatial basis across the Agulhas Bank was made using biomass survey data. Kruskal–Wallis tests were used to test for differences in median GSI between longitudinal areas (from 20° to 27°E at 1° intervals) for males and females in spring and autumn. Mann–Whitney *U*-tests were used to test for equality in median GSI between adjacent areas in a method similar to that for monthly GSI.

Commercial trawl data were used to calculate the monthly percentage composition of the various maturity stages. Differences in the monthly percentage of various maturity stages in each sex from February 1999 to June 2000 were compared.

Data from commercially trawled and jigged samples were used to describe monthly sex ratios on both the spawning grounds and offshore non-spawning areas. To test if samples differed from unity, a binomial test for equal proportions was used (Zar, 1999). Data from biomass research surveys were used to describe sex ratios in spring and autumn within different longitudinal areas. The binomial test was also applied to these data.

Size-at-maturity data were obtained from research samples. The percentages of mature squid within selected size ranges (20-mm intervals) were calculated for the research data in autumn and spring for each sex. The smallest size range in each sample was <80 mm. The data were fitted to a two-parameter logistic ogive (Booth, 1997) of the form

$$P(L) = (1 + e^{-(ML - ML_{50})/\delta})^{-1},$$

where $P(L)$ represents the proportion of mature squid in mantle length class ML , ML_{50} the mantle length at 50% sexual maturity, and δ the width or steepness of the ogive. The model parameters were estimated by minimizing the negative binomial likelihood. Likelihood ratio tests (Zar, 1999) were employed to test for differences in both ML_{50} and δ between seasons. To investigate longitudinal trends, data from 20° to 22°E were grouped as the western region, data from 22° to 24°E as the central region, and data from 24° to 27°E as the eastern region. Longitude-specific parameter estimates were compared using a likelihood ratio test.

The size at which no squid were mature was considered as the upper limit of the juvenile size range, whereas the size at which 100% of squid were mature was considered as the lower limit of the adult size range. The sub-adult size range was intermediate, and was defined as squid that lay between these two limits. Such a classification excludes so-called “sneaker males”, which can erroneously be grouped as either juveniles or sub-adults.

Results

Monthly and spatial comparison of GSI

Monthly median GSI values of mature animals for the 1988–1989 and 1999–2000 jig data and the 1999–2000 commercial trawl data are presented for males in Figure 2, and for females in Figure 3. Except for a decrease in GSI between April and June 1988 (austral winter), little variation was noted in the 1988–1989 male data (Figure 2a). However, between February (austral summer) and May, GSI decreased in both 1999–2000 male data sets, though this was followed by fairly constant values between autumn (May 1999) and winter (July) in the jig data (Figure 2b). In late

winter (August 1999), the GSI peaked in the jig data, then decreased in September before rising again in November and decreasing again in January. Between April and May 2000 there was an increase followed by a decrease in June 2000. The male trawl data followed a similar trend with peaks in June and September 1999 and February 2000 (Figure 2c).

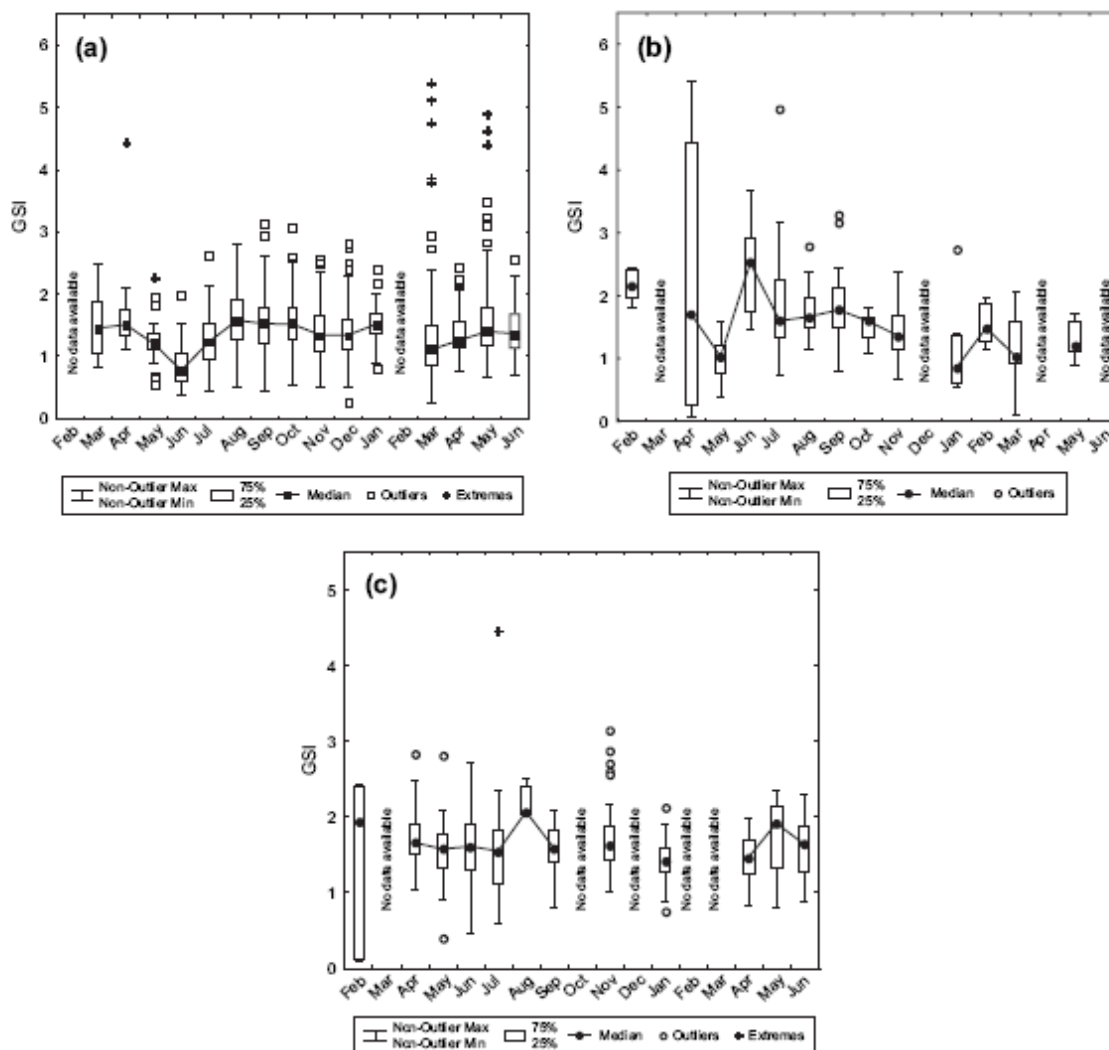


Figure 2. Monthly gonadosomatic indices (GSI) for mature male chokka from (a) 1988–1989 jig, (b) 1999–2000 jig, and (c) 1999–2000 trawl data.

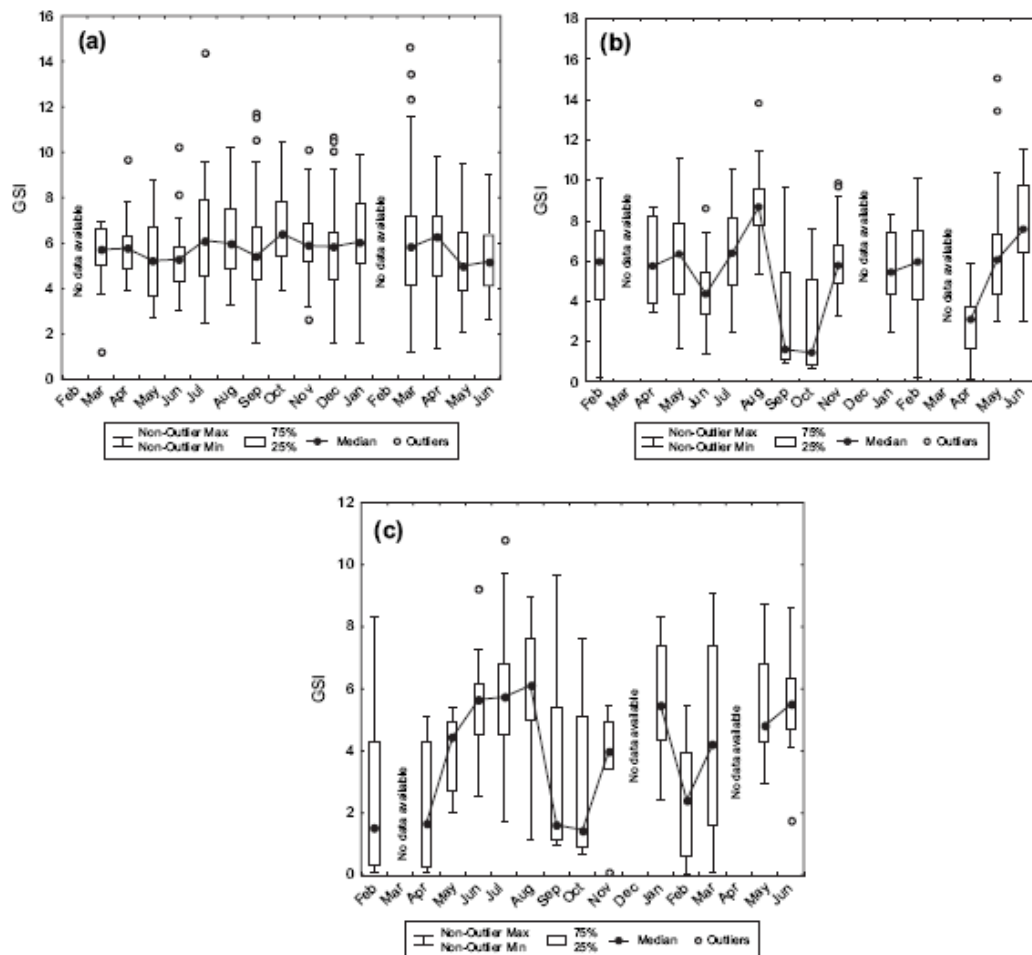


Figure 3. Monthly gonadosomatic indices (GSI) for mature female chokka from (a) 1988–1989 jig, (b) 1999–2000 jig, and (c) 1999–2000 trawl data.

Limited variability was noted in the 1988–1989 female GSI data (Figure 3a). The female jig and trawl data for 1999–2000 both described an initial decrease in GSI between February and April 1999. GSI increased from a low in autumn (April 1999) to a peak in winter (August 1999) for both data sets (Figure 3b, c). An exception to this general pattern was in June 1999 when there was a decrease in the jig GSI that temporarily disrupted the trend of increasing winter GSI (Figure 3b). The overall increase was followed by a decline to lower values in spring (September and October 1999). An increase in November provided a second GSI peak in summer (January 2000) in the trawl data (Figure 3c). A decrease between January and February 2000 was evident, followed by an increase in March 2000 and a similar peak in winter GSI (June 2000). The female jig data followed the same trend, although there was no corresponding dip in February.

The results of the Kruskal–Wallis tests for differences in median GSI between months are presented in Table 2. Although highly significant differences ($p < 0.001$) were recorded between months in all data sets, the small size of the samples in some months means that these data should be interpreted with caution. No clear longitudinal patterns were noticeable in GSI values. Although there were significant differences in some seasons, these were not consistent to both sexes, and were a result of a single area having either significantly higher or lower GSI value compared with adjacent areas.

Table 2. Results of the Kruskal–Wallis test for differences in GSI between months for three commercial data sets, where n refers to the number of squid sampled, H is the Kruskal–Wallis test statistic, and d.f. is the number of degrees of freedom.

Data	Sex	n	H	d.f.	p
Jig 1988	Male	1462	127.36	16	<0.001
	Female	783	50.73	16	<0.001
Jig 1999	Male	368	44.39	16	<0.001
	Female	320	135.60	16	<0.001
Trawl 1999	Male	172	70.67	16	<0.001
	Female	154	50.63	16	<0.001

Maturity and sex ratio

Mature squid were present every month in commercial trawl samples (Figure 4). Abundance of both sexes peaked in February 1999 and again in August 1999. Similar peaks in adult abundance were evident in May of 1999 and 2000 for females (Figure 4a), and in June 2000 for males (Figure 4b). Abundance of sub-adults of both sexes peaked in June 1999 and March 2000, and September and November 1999 for females and October 1999 for males.

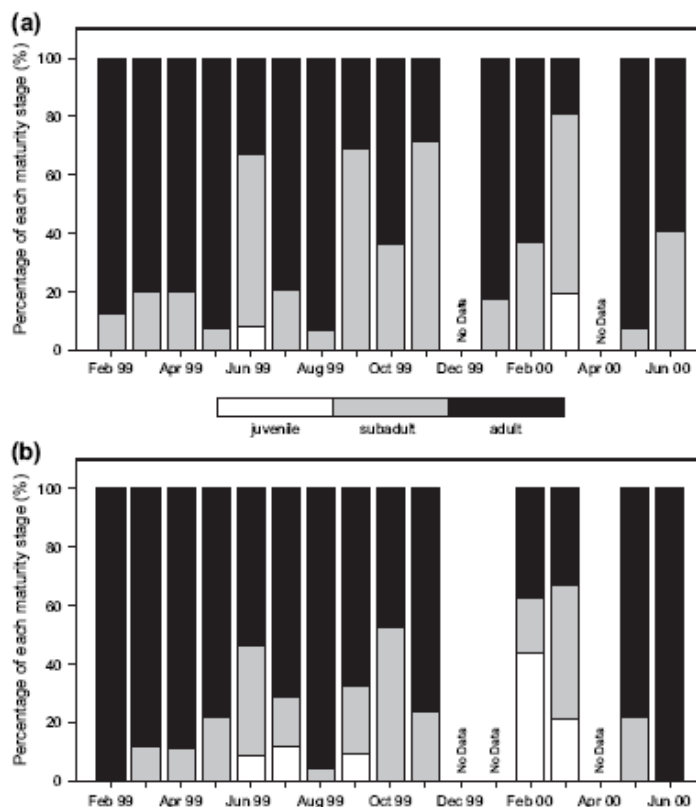


Figure 4. Monthly percentages of each life history stage for (a) female and (b) male chokka, based on commercial trawl samples collected between February 1999 and June 2000.

Monthly sex ratios of mature squid are presented in Table 3. In the 1988 jig data, males outnumbered females in 11 of the 15 months investigated. Between March and July 1988, the sex ratio of males:females fluctuated between 0.72 (in June 1988) and 1.35 (in May 1988). The highest disparity between males and females was in September 1988, when males outnumbered females by a factor of 3.36. The second highest ratio was in December 1988 (3:1) followed by a third disparity in May 1989 (2.36:1). The 1999 jig and trawl data showed similar trends, the trawl data peaking

approximately a month before the jig data. Both data sets describe an increase from February 1999 (1.14:1 and 0.39:1 for trawl and jig, respectively) to a peak in May 1999 (4:1) for the trawl data and in June 1999 (4.27:1) for the jig data. Ratios dropped in June 1999 to 0.34:1 for the trawl data, and in August 1999 to 0.14:1 for the jig data. Gradually increasing ratios through winter and early spring (July–September) were recorded in the trawl data, resulting in a second peak of 2.6:1 (males:females) in November 1999. The ratio then fell to 0.53:1 in February 2000, increased though March 2000, then peaked in May 2000 (1.166:1). Jig samples showed similar fluctuating ratios, but data were not available for the same months as the trawl data. Additional peak male:female ratios were recorded in July 1999 (3.4:1) and June 2000 (2.14:1). The results of the binomial test for equal proportions showed significant departures from unity in most months for the two jig data sets, but only in two months (May and June 1999) for the trawl data. In some months, significance was probably due to the higher proportions of females than males. These are denoted by negative values of z .

Table 3. Monthly sex ratios for three commercial data sets. Italicized values indicate significant departures from a 1:1 ratio based on the binomial test for equal proportions.

Data	Month	Frequencies		Sex ratio (M:F)	z	p
		Male	Female			
Jig 1988/ 1989	March	11	12	0.917:1	-0.209	0.834
	April	26	35	0.743:1	-1.152	0.249
	May	35	26	1.346:1	1.152	0.249
	June	28	39	0.718:1	-1.344	0.179
	July	58	62	0.935:1	-0.365	0.715
	August	92	47	1.960:1	3.817	<0.001
	September	235	70	3.360:1	9.448	<0.001
	October	118	63	1.873:1	4.088	<0.001
	November	198	105	1.886:1	5.344	<0.001
	December	195	65	3.000:1	8.062	<0.001
	January	61	45	1.355:1	1.554	0.120
	March	90	62	1.451:1	2.271	0.023
	April	61	43	1.419:1	1.765	0.078
May	170	72	2.361:1	6.300	<0.001	
June	94	54	1.741:1	3.288	0.001	
Jig 1999/ 2000	February	7	18	0.388:1	-2.200	0.028
	April	29	11	2.636:1	2.846	0.004
	May	41	22	1.864:1	2.394	0.017
	June	64	15	4.267:1	5.513	<0.001
	July	58	17	3.411:1	4.734	<0.001
	August	5	35	0.143:1	-4.743	<0.001
	September	24	34	1.118:1	-1.131	0.189
	November	38	24	1.583:1	1.778	0.075
	April	19	52	0.177:1	-3.916	<0.001
	May	11	62	0.177:1	-5.969	<0.001
June	32	15	2.133:1	2.480	0.013	
Trawl 1999/ 2000	February	16	14	1.143:1	0.365	0.715
	April	15	8	1.875:1	1.460	0.144
	May	20	5	4.000:1	3.000	0.003
	June	7	21	0.333:1	-2.646	0.008
	July	29	21	1.381:1	1.131	0.258
	August	24	14	1.714:1	1.622	0.105
	September	23	13	1.769:1	1.666	0.096
	October	8	8	1:1	0	
	November	13	5	2.600:1	1.886	0.059
	February	10	19	0.526:1	-1.671	0.095
	March	11	12	0.916:1	0.209	0.835
	May	7	6	1.166:1	0.277	0.782
	June	7	9	0.778:1	-0.500	0.617

Sex ratios obtained from autumn research cruises were significantly different from unity. For adults, the ratio was biased towards females in the eastern region (0.70:1), but in the central (1.34:1) and western regions (1.30:1), males dominated. Sub-adult ratios showed a bias towards males in the east (1.29:1) and west (1.54:1), but not in the central region (0.79:1). Juveniles showed ratios biased in favour of females in all

areas. Spring sex ratios were also significantly different from unity. For adults, the sex ratio was female-biased in the eastern region (0.94:1), but in the central (3.25:1) and western regions (2.79:1) males dominated catches. Sub-adult sex ratios were male-biased in the central (1.52:1) and western (1.73:1) regions, but not in the east (0.85:1). Juveniles showed a male-biased sex ratio in the central area (1.19:1).

Mean length

Temporal trends in the median adult squid length, caught commercially, are presented for males and females in Figure 5 and Figure 6, respectively. The 1988 male jig data (Figure 5a) show an increase in mean length between April and June, followed by a decrease in August, then a steady increase through spring and summer to peak in December.

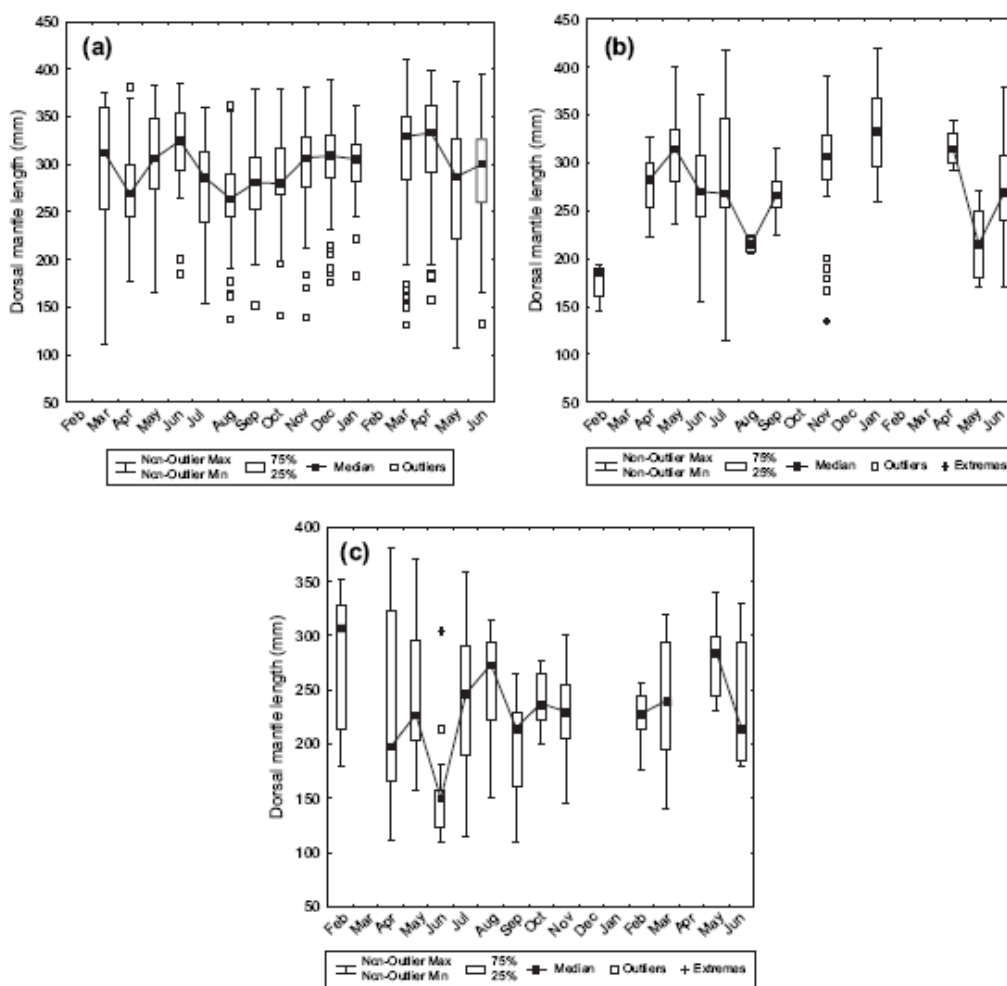


Figure 5. Median monthly lengths of mature male chokka from (a) 1988–1989 jig, (b) 1999–2000 jig, and (c) 1999–2000 trawl data.

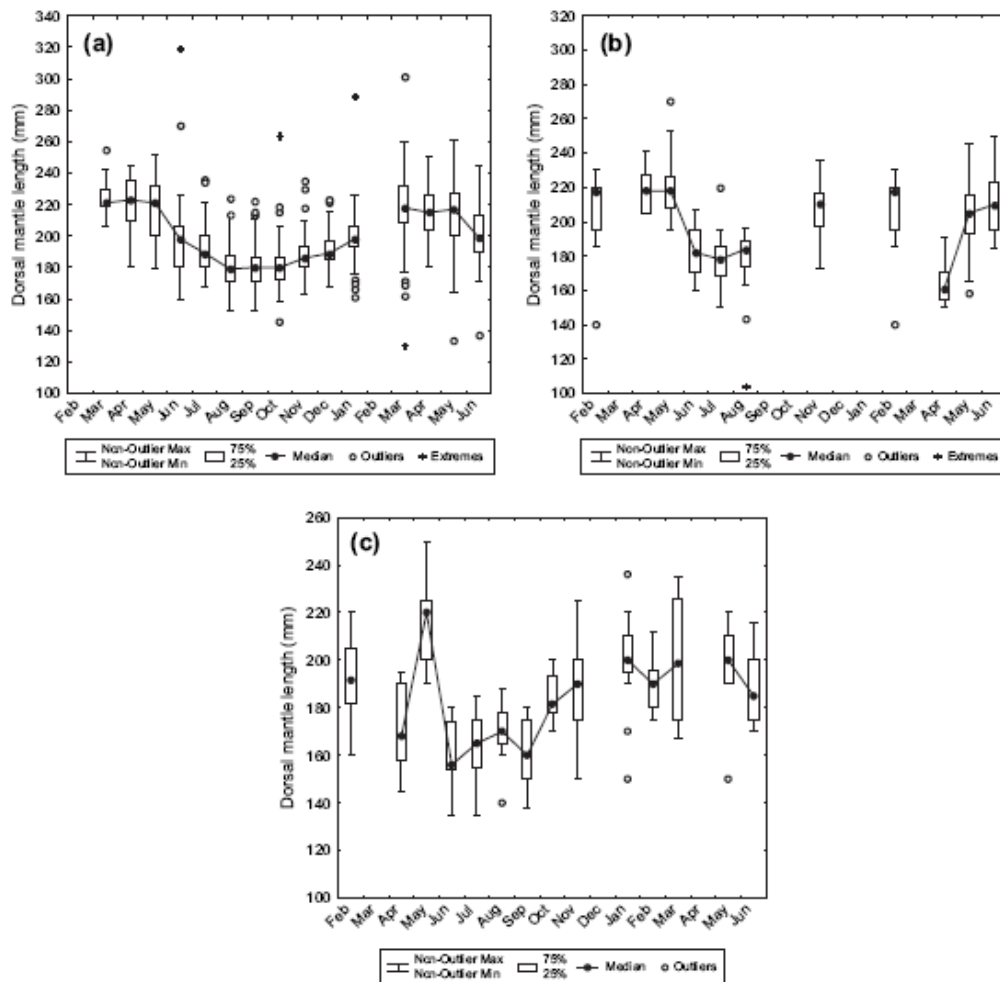


Figure 6. Median monthly lengths of mature female chokka from (a) 1988–1989 jig, (b) 1999–2000 jig, and (c) 1999–2000 trawl data.

A high average mantle length was evident in April 1989, but this was followed by a drop in May and a subsequent rise in June. The 1999 male jig data (Figure 5b) show a similar pattern of high median length in autumn, decreasing through winter, but then increasing through spring to peak in summer. The 1999–2000 commercial trawl data follow a similar trend, but reached the lowest median length two months before the jig data (June 1999) and the highest value in August 1999 (Figure 5c). In the 1988 female jig data (Figure 6a), the pattern of lower median mantle length through winter and early spring was even more apparent than in the male data. Both the 1999 jig (Figure 6b) and trawl data (Figure 6c) for females showed trends similar to the 1988 data.

The results of the Kruskal–Wallis tests for differences in median monthly lengths are presented in Table 4. Median monthly lengths and standard deviations together with the results of the Mann–Whitney *U*-tests for between-month differences for each data set are presented in the Appendix. In all data sets, male standard deviations were larger than those for females, and between-month differences were significant.

Table 4. Results of the Kruskal–Wallis test for differences in median lengths between months for three commercial data sets, where n refers to the number of squid sampled, H is the Kruskal–Wallis test statistic, and d.f. is the degrees of freedom.

Data		n	H	d.f.	p
Jig 1988	Male	1 462	147.5	14	<0.001
	Female	789	340.5	14	<0.001
Jig 1999	Male	379	94.3	11	<0.001
	Female	283	167.3	10	<0.001
Trawl 1999	Male	198	43.9	12	<0.001
	Female	158	87.8	13	<0.001

Seasonal and spatial comparisons of size at maturity

In females, ML_{50} was 173.4 mm in spring and 181.3 mm in autumn (Figure 7a). Male maturity was attained at 188.3 mm in spring and at 202.7 mm in autumn (Figure 7b). A small peak in the proportion of mature squid of ML_{50} 100–120 mm in spring and 140–160 mm in autumn was also apparent (Figure 7b). The results of the likelihood ratio tests revealed significant differences in both ML_{50} ($\lambda = 32.11$, d.f. = 1, $p < 0.001$) and δ ($\lambda = 6.04$, d.f. = 1, $p = 0.014$) between seasons for males. For females, ML_{50} was significantly different between seasons ($\lambda = 28.62$, d.f. = 1, $p < 0.001$), but not the steepness of the ogive, δ ($\lambda = 1.86$, d.f. = 1, $p = 0.173$).

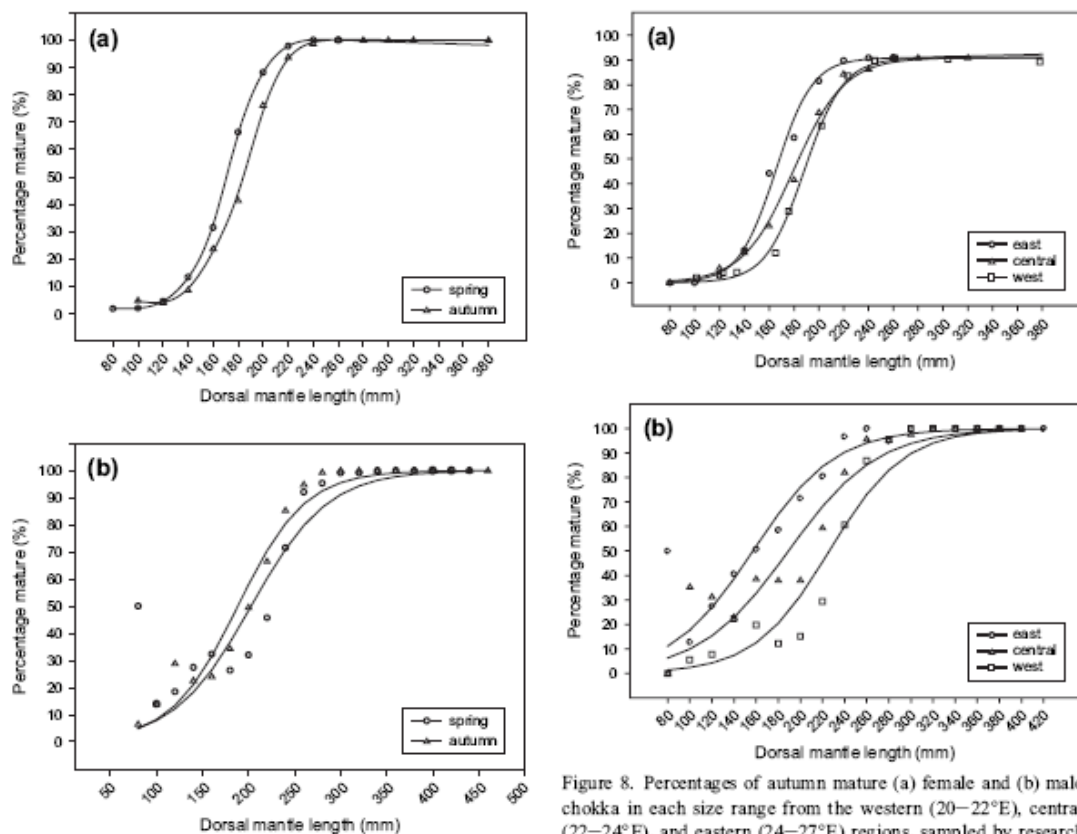


Figure 7. Percentages of mature (a) female and (b) male chokka in each size range collected in autumn and spring research surveys on the Agulhas Bank between 1986 and 1999.

Figure 8. Percentages of autumn mature (a) female and (b) male chokka in each size range from the western (20–22°E), central (22–24°E), and eastern (24–27°E) regions, sampled by research trawl.

A spatial comparison of size at maturity was conducted by separating research trawls into western, central, and eastern components. Maturity ogives for males and females in autumn are presented in Figure 8. Females in the east matured at 165.4 mm ML_{50} , those in the central region at 180.2 mm, and those in the west at 188.3 mm (Figure 8a). Likelihood ratio tests noted that the ML_{50} of autumn-caught females was

significantly different between all areas ($\lambda = 108.96$, d.f. = 1, $p < 0.001$). Significant differences in δ were also noted between eastern and central regions ($\lambda = 5.54$, d.f. = 1, $p = 0.019$), and between western and central regions ($\lambda = 6.28$, d.f. = 1, $p = 0.012$), but not between western and eastern regions ($\lambda = 0.060$, d.f. = 1, $p = 0.806$). Males in the east matured at 157.1 mm, those in the central region at 189.2 mm, and those in the west at 226.1 mm. Smaller increases in male percentage maturity occurred between 80 and 100 mm and between 160 and 180 mm in the central region, and between ML₅₀ 120 and 140 mm in the west (Figure 8b). The ML₅₀s of males caught in autumn were significantly different between all areas ($\lambda = 244.10$, d.f. = 1, $p < 0.001$), but δ was not different ($\lambda = 2.681$, d.f. = 1, $p = 0.262$). Spring-caught female chokka matured at 145.4 mm in the east, at 168.7 mm in the central region, and at 181.1 mm in the west (Figure 9a). For spring-caught females, ML₅₀ was significantly different in all areas ($\lambda = 237.49$, d.f. = 1, $p < 0.001$), but again the steepness of the ogive, δ , was not ($\lambda = 2.61$, d.f. = 1, $p = 0.271$). Spring-caught males matured at 132.6 mm in the east, at 182.3 mm in the central region, and at 217.5 mm in the west. Smaller increases in the percentages of mature male squid were noted at ML₅₀ of 80–100 mm in the east, at 100–120 mm in the central region, and at 130–140 mm in the west (Figure 9b). Likelihood ratio tests on spring-caught males showed highly significant differences in both ML₅₀ ($\lambda = 201.43$, d.f. = 1, $p < 0.001$) and δ ($\lambda = 37.43$, d.f. = 1, $p < 0.001$).

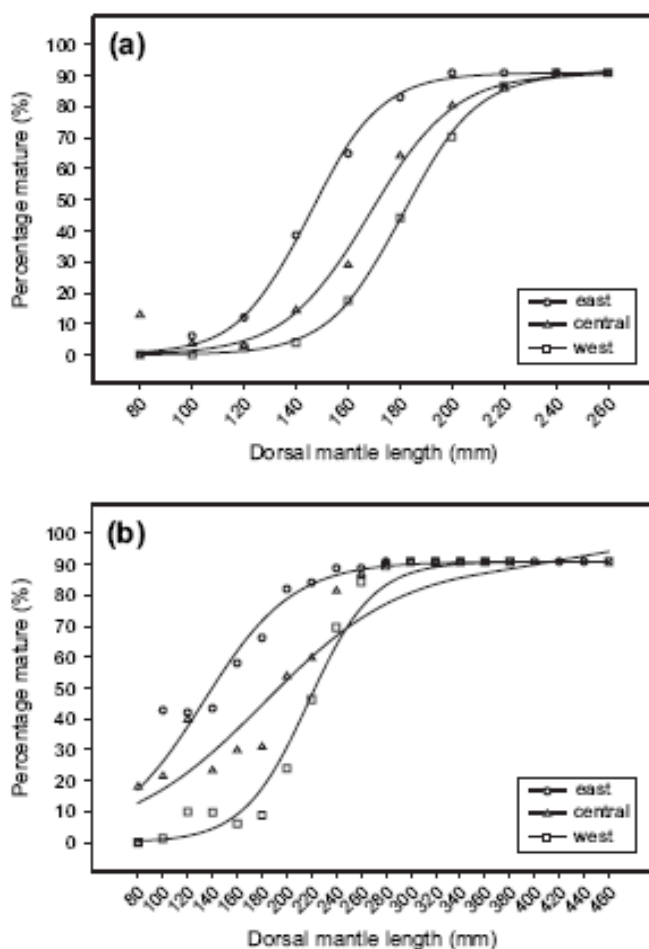


Figure 9. Percentages of mature (a) female and (b) male chokka in each size range in spring from the western (20–22°E), central (22–24°E), and eastern (24–27°E) regions sampled by research trawl.

Table 5 and Table 6 list the seasonal length ranges of all maturity stages by sex in each longitudinal region across the Agulhas Bank.

Table 5. Size ranges of various life history stages of autumn-caught chokka in three longitudinal regions of the Agulhas Bank, west (20–22°E), central (22–24°E), and east (24–27°E).

Life history stage	Male (mm)			Female (mm)		
	West	Central	East	West	Central	East
Juvenile	<65	<115	<80	<65	<125	<125
Sub-adult	65–230	115–185	80–160	65–190	125–180	125–165
Adult	>230	>185	>160	>190	>180	>165

Table 6. Size ranges of various life history stages of spring-caught chokka in three longitudinal regions of the Agulhas Bank, west (20–22°E), central (22–24°E), and east (24–27°E).

Life history stage	Male (mm)			Female (mm)		
	West	Central	East	West	Central	East
Juvenile	<130	<100	<100	<130	<130	<125
Sub-adult	130–220	100–180	100–135	130–180	130–170	125–145
Adult	>220	>180	>135	>190	>180	>165

Discussion

Fisheries in developing countries, and South Africa is no exception, are under strong and increasing pressure (FAO, 2000). There has been increasing focus from the South African government on making South Africa's marine resources available to more participants, and the squid resource is one seen as able to accommodate more small- or medium-sized companies. Short-lived resources fluctuate naturally in recruitment from year to year, and overdeployment of effort during a period of poor recruitment can have disastrous consequences. Added to this is the variability in both the structure of spawning populations and the biological characteristics of the squid present throughout the spawning season and throughout their geographical range; therefore, prediction of recruitment levels is challenging. Clear evidence of geographically separate populations of squid would require a rethink of the current management strategy and perhaps a separation of the fisheries into distinct geographical zones. Examination of a number of biological characteristics may provide some indication of whether such zones exist.

GSI

Traditionally, GSI has proved to be an unreliable indicator of maturity in other studies on squid, because it is influenced by a wide range of variables that can produce confounding results. Consequently, interpretation of squid dynamics on the basis of GSI should only be attempted with caution (Lipiński and Underhill, 1995). Although annual catches fluctuate, mature squid are caught by jigs throughout the year, with the largest catches in spring and early summer. As an indicator of seasonality in maturity, GSI values largely confirmed this interannual variability. In the 1988/1989 fishing season, results indicate that there was some spawning throughout the year. High commercial jig catches in 1988 and 1989 (Augustyn and Roel, 1998) suggest higher levels of spawning based on the nature of the fishery (i.e. targeting spawning aggregations). By contrast, in the 1999/2000 season, a more typical pattern of peak GSI was seen, especially in summer. The lack of spatial variability in GSI was surprising, because earlier studies (Augustyn *et al.*, 1994) indicated that the GSI

increased from west to east, to peak on the preferred spawning grounds on the eastern Agulhas Bank. The lack of spatial variability in this study suggests that squid from across the Agulhas Bank have at least equal reproductive potential, and that some spawning may take place anywhere across the bank, at least in some years.

Maturity and sex ratio

Year-round spawning is also suggested by the number of mature squid found across the whole distributional range. In calculating monthly percentage maturity, the use of trawl data, which are less biased than jig data, allows for a more representative sample to be obtained. Mature squid were present throughout the year both inshore and offshore, providing further evidence that some spawning takes place year round, likely too both inshore and in deeper waters. Clear peaks in adult abundance in winter and summer add support to the theory of at least two major spawning peaks per year.

Law (2000) reviewed the effects of fishing on phenotypic evolution, and concluded that although the phenomenon is widely known in general terms, it is seldom an integral part of fisheries management. Impacts include changes in size at age and age at maturity, which can both lead to declines in fisheries production and long-term sustainability issues. Concern about the impact of fishing on spawning aggregations of chokka and other loliginid squid have been raised (Sauer, 1995 and Moltchanivskyj et al., 2002), particularly with reference to the often complicated mating rituals involved (Sauer et al., 1992 and Sauer and Smale, 1993). This study has shown that the ratio of males to females varies between maturity stages and is also dependent on when sampling is undertaken. Earlier studies recorded that on the spawning grounds, the ratio of males to females was 2.5:1 (Augustyn, 1989, Sauer and Smale, 1993, Augustyn et al., 1994 and Lipiński, 1994). Those studies were often timed to coincide with peak spawning periods and made use of commercial jigging gear, which is believed to be a sampling technique that is biased in favour of males (Sauer et al., 1992 and Lipiński, 1994). With the examination of monthly data in this study, a pattern of significantly male-biased ratios is only apparent during the peak spawning periods. In fact, the results from the research trawl data indicate female bias in the samples more frequently than male bias, even when the samples are restricted to inshore.

The jig fishery certainly may selectively remove large males in the immediate vicinity of the egg beds during spawning, which can have far-reaching consequences on the operational sex ratio and ultimately the fitness of the population to sustain itself, particularly if only a proportion of the biomass spawns almost exclusively inshore along the coast of the Eastern Cape. Disruption to the complex mating systems, which involve multiple sources of sperm (consort male, sneaker male, or stored sperm), through selective removal of a certain segment of the population (Lipiński, 1994 and Shaw and Sauer, 2004) can be expected to have some impact on the genetic diversity of the population. Quantifying the exact impact is complicated in loliginids by the extended spawning season, multiple spawning, variable growth rates, and movement to and from the spawning area (Pecl *et al.*, 2004). It is likely that for chokka, most inshore spawning sites have been located and targeted by jig fishers. The extent of offshore spawning (>50 m), at present not heavily targeted by the fishery, is unknown. What is clear is that management strategies that incorporate either closed seasons or closed areas are highly desirable to protect the natural spawning activity of loliginids, and continued fishing of spawning aggregations needs to be carefully monitored. The single closed period annually of 5 weeks should be re-assessed, particularly in the light of there being at least two spawning peaks per year and the possibility of there being more than one spawning cohort.

Size at maturity

Although total age estimates for chokka squid have been estimated (Lipiński and Durholtz, 1994), size-at-age data are not yet available. Variability in size at maturity has been observed previously (Augustyn, 1990) and also in this study. A seasonal cycle of changes in mantle length of mature squid was evident on the spawning grounds as well as offshore, squid caught in winter and spring having a smaller average mantle length than those caught in summer/autumn. It could be attractive to suggest that the same squid are spawning twice within the same year, but an equally plausible explanation is that the smaller winter spawning group are merely younger squid that are able to spawn within one year, while the larger summer spawners represent an alternative life history characterized by delayed reproduction. Both these hypotheses require population level age determination and analysis.

Longitudinal differences in size at maturity were also apparent, with adult squid caught in the east maturing smaller than squid caught farther west. Similar spatial and temporal variability has been noted for *L. pealeii* (Hatfield and Cadrin, 2002). Spatial differences in size at maturity provide further support for the suggestion by Augustyn *et al.* (1994) that a proportion of the biomass does not undertake a westward migration, but rather remains in the east offshore of the spawning grounds. Why exactly these squid should mature at a smaller size remains unclear. It is unlikely that warmer water temperatures would result in accelerated reproductive development, but have no impact on somatic growth. Accurate age data and genetic data are needed to further test this hypothesis, but it does suggest that different management strategies may need to be considered for the various areas of the Agulhas Bank. For the first time, area-specific size ranges of various life history stages have been presented and these may be useful for future population distribution studies, particularly with reference to estimating biomass and recruitment.

Conclusion

Management of chokka squid is complicated by the relatively large spatial component to their life cycle, set against a relatively short temporal component. Within one year it is possible that a squid may remain within a relatively small area or travel more than 2000 km. The results from the present study do not provide conclusive evidence of distinct geographical populations, but they do highlight the possibility that squid spawn over a significantly larger area of the Agulhas Bank than previously estimated, and that squid on the west coast of South Africa may predominantly return to spawn on the western portion of the Agulhas Bank. It remains likely, however, that the populations on each of South Africa's coasts are a single stock and that migration of juveniles to the west coast and their subsequent return migration as sub-adults is an integral but non-essential and variable part of the chokka life history (Augustyn *et al.*, 1992 and Augustyn *et al.*, 1994). The results also highlight the importance of elucidating the age structure of the population on an annual basis, to ensure that data cover the entire life cycle throughout the distribution of the species, and that all possible stock implications are examined. In order to further examine this topic we need to undertake population genetic studies combined with monthly age determination covering both sectors of the fishery.

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Appendix.

Statistical results of Mann–Whitney *U*-tests for between-month differences in mean length of mature squid caught in commercial catches.

Table A.1. Monthly mean and median lengths and standard deviations of mature squid caught by hand-jigging between February 1988 and June 1989. The *z* statistic, degrees of freedom, and probability are reported for the results of the between-month Mann–Whitney *U*-tests.

Month	<i>n</i>	Mean length (mm)	Median length (mm)	s.d.	<i>z</i>	d.f.	<i>p</i>
<i>Mature males</i>							
February							
March	10	288.2	312	80.94			
April	26	276.4	269	45.34	0.936	10, 26	0.349
May	34	307.7	306.5	52.21	−2.633	26, 34	0.008
June	27	315.6	325	49.44	−0.653	34, 27	0.513
July	57	273.7	286	51.99	3.597	27, 57	<0.001
August	91	265.2	264	42.64	1.099	57, 91	0.272
September	234	279.2	281	38.27	−2.562	91, 234	0.010
October	117	287.6	280	44.92	−1.659	234, 117	0.097
November	197	300.0	307	39.94	−2.825	117, 197	0.005
December	194	304.7	309	37.42	−1.071	197, 194	0.284
January	60	300.4	305.5	32.50	1.023	194, 60	0.307
February							
March	90	308.4	329.5	61.55			
April	61	315.5	333	63.17	−1.157	90, 61	0.247
May	170	274.3	287	67.07	4.352	61, 170	<0.001
June	94	290.4	300	50.61	−1.616	170, 94	0.106
<i>Mature females</i>							
February							
March	11	225.5	221	13.43			
April	34	221.4	223	16.80	0.238	11, 34	0.812
May	25	216.3	221	22.21	0.829	34, 25	0.407
June	38	198.9	198	28.90	3.295	25, 38	<0.001
July	61	190.9	189	14.50	1.544	38, 61	0.123
August	46	181.0	179	14.60	3.598	61, 46	<0.001
September	69	180.9	180	14.50	0.010	46, 69	0.920
October	62	181.2	180	17.06	−0.044	69, 62	0.965
November	104	188.1	186	12.15	−3.891	62, 104	<0.001
December	64	191.4	189	12.19	−1.884	104, 64	0.060
January	44	199.1	198	19.84	−2.962	64, 44	0.003
February							
March	62	217.9	218	24.54			
April	43	214.0	215	16.46	1.408	62, 43	0.159
May	72	214.6	217	22.50	−2.544	43, 72	0.799
June	54	200.7	199	18.23	3.743	72, 54	<0.001

Table A2. Monthly mean and median lengths and standard deviations of mature squid caught by hand-jigging between February 1999 and June 2000. The z statistic, degrees of freedom, and probability are reported for the results of the between-month Mann–Whitney U -tests.

Month	n	Mean length (mm)	Median length (mm)	s.d.	z	d.f.	p
<i>Mature males</i>							
February	7	174.7	185	19.25			
March							
April	29	277.8	283	29.11			
May	41	309.8	315	38.90	-3.674	29, 41	<0.001
June	64	272.6	270	49.07	3.869	41, 64	<0.001
July	57	287.9	268	62.12	-1.192	64, 57	0.233
August	5	214.8	215	8.79	3.297	57, 5	0.001
September	24	267.8	266	23.02	-3.439	5, 24	<0.001
October							
November	38	293.5	307	59.82			
December							
January	36	333.6	332.5	41.54			
February							
March							
April	35	248.6	295	76.10			
May	11	214.4	215	33.02	4.518	35, 11	<0.001
June	32	277.1	268.5	51.01	-3.425	11, 32	<0.001
<i>Mature females</i>							
February	18	207.3	217.5	22.14			
March							
April	11	217.8	218	12.26			
May	22	220.8	218	19.56	-0.230	11, 22	0.818
June	15	183.7	182	14.46	4.756	22, 15	<0.001
July	17	178.4	178	19.93	1.002	15, 17	0.316
August	35	179.3	184	16.87	-0.850	17, 35	0.395
September							
October							
November	24	206.0	210.5	16.69			
December							
January							
February							
March							
April	46	162.2	160	12.67			
May	62	204.3	205	17.31	2.511		0.012
June	15	213.5	210	20.42	-1.327	62, 15	0.185

Table A3. Monthly mean and median lengths and standard deviations of mature squid caught by demersal trawl between February 1999 and June 2000. The z statistic, degrees of freedom, and probability are reported for the results of the between-month Mann–Whitney U -tests.

Month	n	Mean length (mm)	Median length (mm)	s.d.	z	d.f.	p
<i>Mature males</i>							
February	16	280.4	307.5	63.40			
March							
April	16	230.9	197.5	89.97			
May	20	247.5	227.5	60.94	-3.431	16, 20	0.002
June	13	157.7	150	53.39	4.336	20, 13	0.001
July	30	236.8	246.5	66.47	-3.885	13, 30	0.001
August	24	257.4	273.5	49.11	-1.422	30, 24	0.161
September	23	195.0	215	44.87	5.092	24, 23	0.000
October	8	240.8	237.5	26.97	-2.701	23, 8	0.011
November	13	228.2	230	47.72	0.679	8, 13	0.510
December							
January							
February	10	225.5	228	22.77			
March	11	239.5	240	53.42	-0.764	10, 11	0.454
April							
May	7	280.0	285	37.75			
June	7	241.1	215	58.25	1.481	7, 7	0.164
<i>Mature females</i>							
February	14	193.6	191.5	16.45			
March							
April	8	171.5	168	18.31			
May	5	217.0	220	23.35	-2.653	8, 5	0.008
June	23	159.7	156	13.32	3.453	5, 23	<0.001
July	9	164.6	165	13.46	-0.630	23, 9	0.528
August	14	170.5	170	12.11	-1.300	9, 14	0.194
September	13	158.8	160	15.02	1.997	14, 13	0.046
October	8	184.4	181.5	10.89	-3.098	13, 8	0.002
November	5	188.0	190	27.97	-0.369	8, 5	0.712
December							
January	19	200.8	200	18.44			
February	12	190.5	190	11.91	2.217	19, 12	0.027
March	6	200.0	198.5	27.1	-0.516	12, 6	0.606
April							
May	12	197.3	200	18.11			
June	9	187.9	185	16.24	1.542	12, 9	0.123

