

**A DESCRIPTION OF SPATIAL AND TEMPORAL
ASPECTS OF THE LIFECYCLE OF CHOKKA SQUID
LOLIGO VULGARIS REYNAUDII ON THE INSHORE
SPAWNING GROUNDS AND AGULHAS BANK OFF THE
SOUTH COAST OF SOUTH AFRICA**

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ABSTRACT

The chokka squid, *Loligo vulgaris reynaudii*, is a commercially important species supporting a large, high-value export fishery for South Africa. This study reviewed its population dynamics and reproductive biology. Biological information collected on biannual research cruises from September 1986 to April 1999 on the Agulhas Bank as well as information from commercial vessels operating in the inshore environment collected between April 1988 and July 1989 and again between June 1999 and May 2000 were analysed.

Size ranges of juveniles, subadults and adults were calculated and used to determine seasonal distribution and abundance patterns. Based on Gonadosomatic Indices (GSI) and percentages of mature squid in each month, two peak reproductive seasons in summer and winter were identified although mature squid were present all year round. Seasonal peaks in sex ratio were also apparent with males outnumbering females by up to 4:1 in the peak-breeding season. The size at which squid matured, demonstrated both spatial and temporal patterns. Squid caught in spring matured at a smaller size than squid caught in autumn and at successively smaller sizes from west to east across the Agulhas Bank. Size at maturity was highly variable especially in males where “sneaker males” were evident in both seasons. Length-to-weight linear regression revealed significant differences between maturity stages and between sexes. Females demonstrated steeper length-to-weight regression slopes than males in the peak-breeding seasons.

Aspects of squid biology pertinent to fishery management were highlighted as well as potential areas where research should be directed in order to develop future stock assessment models.

To my family and friends
who helped me to get here.

TABLE OF CONTENTS

	Page
Abstract	ii
Acknowledgements	vi
Chapter 1 – Introduction	1
Chapter 2 – General Methods	14
Chapter 3 – Population Structure	20
3.1 Length Frequency	
3.2 Length to weight relationships	
Chapter 4 – Reproductive Biology	64
4.1 Seasonality	
4.2 Sex Ratio	
4.3 Growth and Maturation	
4.4 Distribution and Abundance	
Chapter 5 – The Chokka Squid Life Cycle	114
References	126
Appendices	
Appendix I: Statistical descriptions of length-weight regression of research data	133
Appendix II: Statistical descriptions of length-weight regression of commercial data	138
Appendix III: Statistical results of the Mann-Whitney U-tests for between month differences in mean length of mature squid caught in commercial catches	140

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CHAPTER 1

Introduction

A high value export industry focusing on chokka squid (*Loligo vulgaris reynaudii* d'Orbigny 1845) has developed since 1985 on the southeast coast of South Africa (Augustyn 1990). Ninety percent of the catch is caught by hand jig-fishing (Boonstra 1997) with the remainder harvested as bycatch in hake and sole-directed trawl fisheries.

The chokka industry is characterised by variable annual catches. Between 1985 and 1997 catches fluctuated between approximately 2700 and 11000 tonnes. Currently catches are approximately 6000t (Augustyn and Roel 1998). Earnings peaked at R108 million in 1989 (Augustyn *et al.* 1992) and are currently worth at least R104 million (Cochrane *et al.* 1997) with most of the catch being exported frozen to European and Asian markets. Jig fishing is mostly conducted from deckboats, which range in length between 12 and 21m and hold a compliment of 12 to 28 crew (Schön 2000). Fishermen are paid based on their individual catches, with wages often being erratic.

While an extensive understanding of the biology of chokka cannot necessarily result in job security, it can go some extent towards providing better management advice and possible forecasting (O' Dor 1998). Fortunately, research on chokka biology and the fishery began in the early 1980's (Augustyn 1989) and has been well supported by the South African Squid Management Industrial Association (SASMIA) which was formed in 1991. SASMIA aims "...to represent the squid fishery as an industrial body or interest group; to furnish information, to advocate and protect the interests of the squid fishery, and make representations to government, the minister of Environmental Affairs, the chief directorate of

Sea Fisheries¹ about any matter which concerns the squid industry; and to constitute a forum for discussion of all matters pertaining to the entire spectrum of the squid industry” (Stuttaford 1997). The organisation consists of factory and boat owners, fishermen and scientists (Augustyn *et al.* 1992). Both biologists and the fishermen have expressed mutual concern for the sustainability of the stock and, as a result, management strategies tend to be well received. Additionally, SASMIA is playing a vital role in advising the government on restructuring of the industry as well as funding scientific and economic research projects of interest to the squid industry.

The fishery was initially chaotic but restricted to mainly white skippers with access to boats and adequate financing. Management measures were initially *ad hoc* but pragmatic given the lack of knowledge of stock size and the need to sustainably manage the resource. Chokka permits were issued based on performance over the first two years of the fishery and as a result, the number of boats was reduced from more than 500 to 235. A recreational limit was set at 20 squid.person⁻¹.day⁻¹ and the unit of effort for the commercial fishery were fishers with the number of crew for each vessel fixed (Augustyn and Roel 1998). The chokka squid fishing industry is now required to comply with the regulations of the Marine Living Resources Act (Act 18, 1998). This involves meeting the Act’s tenants of stability, sustainability and equity (South African Government 1998).

Past research has addressed aspects of resource management (Augustyn *et al.* 1992, Augustyn *et al.* 1994, Roel and Payne 1998, Roel *et al.* 1998), focusing on the role of sound biological data within a goal-orientated research programme such that informed decisions can be made. Additionally, Roel and Payne (1998) noted that the sustainable exploitation of the resource depends entirely on the acceptance by the industry of scientific advice.

¹ Now Chief Directorate: Marine and Coastal Management

Some of the areas of concern that have been identified by Augustyn *et al.* (1992) include:

- i) Many aspects of the squid life cycle are poorly understood, particularly with regard to ageing,
- ii) Recruitment is probably sensitive to environmental influences and
- iii) The short life cycle (12-18 months) implies that there is little time to implement management measures once changes in biomass trends are noticed.

An application of these factors to the management of the fishery implies that fishery collapse can occur within a season. As a result, the Precautionary Principle (FAO 1999), which is firmly entrenched in the Marine Living Resources Act, should be adopted. The Principle has to a large extent been in operation through the effort control measures currently in practise. Since 1987 there has been a limit on the number of boats and crewmen per boat (Augustyn *et al.* 1992). The only other form of effort control is an annual closed season of four weeks over the peak breeding period between October and December, which was first implemented in 1988.

The Tsitsikamma National Park, a no harvest area, while although not specifically established for squid, also provides a refuge for spawners in some years (Sauer 1995a, Roel *et al.* 1998). Despite the control measures and the no harvest area, steady increases in effort are apparent but have not been quantified. These increases have taken the form of extra fishermen disguised as “packers”; the increased use of powerful lights at night to maintain a high catch per unit of effort (CPUE) (Roel *et al.* 1998); improved navigation to spawning aggregations through the use of Global Positioning Systems; improved communication through the use of cellular phones resulting in co-operative fishing (Schön 2000) and the use

of parachutes as drogues which allow boats to fish in deeper water (>60m) by slowly drifting over squid aggregations (*pers. obs.*).

The problems of erratic catches, together with the need to incorporate previously disadvantaged new entrants (in compliance with the new Act) into what is already a fully subscribed fishery, applies pressure on resource managers to reject the Precautionary Principle in favour of a more liberal management strategy. The optimal policy in terms of the industry and the Act, would allow existing enterprises to maintain their full crew complement and at the same time, allow new entrants into the fishery.

An alternative management strategy to effort control would be in the form of some sort of dynamic quota control. This in terms of the South African situation is, however, largely unfeasible due to difficulty with within season estimates of biomass and a lack of ageing and stock-recruitment data (Augustyn *et al.* 1992). Both of these management strategies have their merits and disadvantages (Caddy 1983) and often a combination of strategies achieves the best possible solution.

The need for the development of a Fishery Information System (FIS) to collect and analyse chokka squid data was identified in 1997 and preliminary work on estimation of the distribution as well as cohort structure of chokka squid biomass on the Agulhas Bank was attempted using a Geographical Information System (GIS) and a General Additive Model (GAM) (Booth *et al.* 1997). This thesis represents a continuation of that work and attempts to reanalyse biological data pertinent to management using spatial and temporal trends best visualised with GIS techniques.

GIS in marine fishery management

The use of Geographical Information Systems (GIS) technology in marine fisheries has lagged behind its terrestrial equivalents (Meaden 1994, Meaden 1996, Simpson 1992). This situation is surprising given that fishing is one of the most spatially diverse of human activities. Effective management of the activity then seems impossible and illogical without consideration being given to the spatial dimension. Depending on the worker, spatial effects are either ignored or overlooked; yet many forms of fishery analysis could be enhanced through integration of spatial effects (Booth 1998).

Computers in fishery science are not a new concept and many stock assessment models make extensive use of computing power to provide suitable resource management information. Vessels make use of sophisticated electronic equipment such as sonar, remote sensing and Global Positioning Systems (GPS), which provide excellent sources of suitable data. The question then remains why; with such an apparently good background and available data sources has GIS not claimed its rightful position as a management tool in global fisheries?

The answers vary depending on the type of fishery as well as the economic status of the nationality concerned (Meaden 1996). Developing nations that are barely able to regulate their fisheries are seldom willing to invest funds in extensive and often expensive data gathering activities that may or may not provide suitable answers. Where data are available, as is often the case in developed countries, a fragmented and privately operated fishery is unlikely to reach the level of co-operation required for a GIS to be effective. Public sector funded fisheries would seem to have all the necessary resources, such as infrastructure, funding and databases, yet the level of interdepartmental cooperation and communication required is often deemed too difficult for a GIS approach to be adopted.

Despite these negative responses, fishery scientists involved with GIS remain confident that the technology will receive wider acceptance and utilisation (Caddy and Garcia 1986, Li and Saxena 1993). Areas where GIS have already been applied include coastal zone management (Bartlett 1994, Welch *et al.* 1992, Riddell 1992 in Meaden 1996), marine water quality management (Collins and Hurlbut 1993 in Meaden 1996) as well as looking at the spatial distribution of zooplankton in relation to oceanographic features (Sánchez-Velasco and Shirisago 1999) and in fishery research to examine the spatial allocation of fishing intensity (Caddy and Carocci 1999).

The South African chokka industry, which is self-regulated by a cohesive management body (SASMIA), is in a position to provide funds for the establishment of a GIS, to benefit co-operating members. The introduction of Vessel Monitoring Systems planned for 2002 will be an excellent source of real time spatial data for the GIS. The existence of a broad research database also negates the need for expensive data collection. Transformation of the data into a useable format is therefore of paramount importance.

At the most basic level a GIS is: “ a system for capturing, storing, checking, manipulating, analysing and displaying data which are spatially referenced to the Earth” (Maguire *et al.* 1991, Haines-Young *et al.* 1993, Chou 1996). The system in its entirety involves the following components: “...an organized collection of computer hardware, software, geographic data and personnel...” (ESRI 1999).

GIS compliment traditional cartographic techniques with the added benefit that maps generated electronically, can be updated instantaneously. They can also be customized to display specific aspects or themes such as depth, size of catch or length frequency

distributions of animals (Caddy and Garcia 1986). Locations of sensitive or particularly relevant environmental areas can also be represented on the same map. Thematic mapping, although extremely useful, does not allow the full power of the technology to be appreciated. As a result, most fishery scientists become disillusioned with GIS techniques and the systems are used for little more than producing colourful maps (Booth 2001).

Over and above the spatial representation, GIS provide extensive opportunities for predictive scenario modelling. A typical example may include investigating the distribution of exploited organisms based on their temperature preference (Waluda and Pierce 1998). Similarly the selection of areas of a particular combination of features such as depth, dissolved oxygen content, substrate and bottom temperature can be made and easily visualised (Bailey *et al.* 1998, Helle and Pennington 1999).

GIS and cephalopod research

GIS can assimilate and analyse the different data sets associated with chokka squid biology and is a recent concept in South African research. GIS has been applied to studies on other cephalopod species such as *Octopus vulgaris* in Senegal (Foucher *et al.* 1998) and in European waters on *L. forbesi*, *L. vulgaris* (Pierce *et al.* 1998, Waluda and Pierce 1998) and in Japanese waters on *Todarodes pacificus* (Sakurai *et al.* 2000). Most of these projects, with the exception of Foucher *et al.* (1998) have been concerned with mapping basic data such as sea surface and substratum temperature and investigating distribution patterns of catch and CPUE based on these variables.

The dynamic data exchange capability, adaptability and easy visualisation provided by the GIS are useful tools to contribute towards a dynamic management programme. An important

word of caution is that the advantages of Geographical Information Systems to environmental or natural resource management projects are only as valuable as the data that are used and results produced. Acquiring data of a suitable standard of accuracy and quality is one of the key features of any GIS. With advances being made in software and hardware affordability, data acquisition is now becoming the most expensive and time consuming component.

Past research on chokka squid

Augustyn *et al.* (1994) and Augustyn and Roel (1998) provide reviews of the state of knowledge about the life history and ecology of *L. v. reynaudii*, management considerations together with a bibliography on chokka research from 1974 to 1993. An up-to-date bibliography can be found in Schön (2000). The relevance of life cycle studies to the management of the species was also made with particular reference to delimiting the recruitment-stock relationship. Further considerations about the role of life cycle studies in management were made by Lipiński (1998). These authors noted that spatial considerations have particular importance to the chokka life cycle.

Defining recruitment-stock relationships is considered an essential (although often elusive) component of the management policy for other nations that exploit their squid stocks including the Falkland Islands (Beddington *et al.* 1990, Basson *et al.* 1996). Caddy (1983) has, however, expressed caution about the role of climatic fluctuations in influencing the relationship. It is expected that data such as survivorship of pre-recruits to adulthood will greatly enhance the management strategy for the South African squid fishery. Alternatively, in the absence of information on early life stage mortality and distribution, an investigation into the relationship between distribution and abundance of immature and adult squid based

on commercial catches can provide useful management data. Recent investigations in *L. forbesi* catches in Scottish waters have attempted to establish a relationship between survey and fishery abundance (Pierce *et al.* 1998).

Advances made in acoustic methodology (Sauer *et al.* 1992, Starr and Thorne 1998, Roberts *et al.* in press) have improved estimates of squid aggregation density. These data, coupled with good recruitment indices may allow managers to predict stock sizes in advance of the fishing season and assist the implementation of an adjustable quota system. A significant factor in pre-recruit abundance studies relates to female fecundity and recent investigations into oocyte development (Melo and Sauer 1998) have yielded interesting results confirming the hypothesis that chokka are serial spawners.

Aspects of sexual maturation processes and the relevant macroscopic stages are provided by Sauer and Lipiński (1990) and Lipiński and Underhill (1995). These data combined with ageing data would provide insight into the apparent cohort patterns observed in the south coast squid population.

Results from statolith analysis for chokka have shown some promise (Augustyn *et al.* 1994, Lipiński *et al.* 1998) but require considerable work before they can be of value to population level studies. The use of both statoliths and gladii as records of cephalopod life histories as well as the potential application of the data is clearly outlined in Arkhipkin and Perez (1998).

Chokka are iteroparous and probably only live for a year. Previous estimates (Augustyn *et al.* 1994) have suggested that they generally live for up to 18 months, while males may live for up to three years (Augustyn 1989).

Usually three major cohorts are present on the south-eastern Cape coast at any time, separated by approximately six months between each cohort (Augustyn *et al.* 1994).

This is in contrast to the west coast, where the population appears to belong to a single cohort of immature to sub-adult squid (Augustyn 1991) with a mantle length ranging between 110 and 180 mm. This supports the notion that the east and west coast populations are a single stock and that migration of juveniles to the west coast and subsequent return migration of sub-adults are an integral but non-essential and variable part of the chokka life history (Augustyn *et al.* 1992, 1994).

Additional data concerning the life history of chokka squid have been collected. Detailed observations on spawning behaviour are provided by Sauer and Smale (1993) and Sauer *et al.* (1997). Feeding biology (Augustyn 1990, 1991, Sauer and Lipiński 1991) and predation on squid on the spawning grounds (Smale *et al.* 1995) has also been investigated. Migration between spawning sites has been postulated (Lipiński *et al.* 1998) and a tagging study to monitor migration between inshore spawning locations was also undertaken (Sauer *et al.* 2000).

Although it is implicitly recognised that environmental influences are as important to the chokka life cycle as they are for other *Loligo* species, the exact mechanisms are only now beginning to be investigated (Roberts and Sauer 1994, Roberts *et al.* 1998).

The role of the environment in influencing spawning site selection (Sauer *et al.* 1991, 1992), paralarvae distribution and survival (Augustyn *et al.* 1992, 1994), have been documented. Most observations have attempted to correlate high catches of squid with prevailing weather

conditions of temperature and wind direction. Recent opinion (Roberts and Sauer 1994, Roberts 1998, Schön 2000) however, is that a simple correlation cannot be used to explain the choice of spawning location for chokka due to the complexity of spawning behaviour, and that a far greater number of physico-chemical signals potentially impact on the selection process. These variables operate at different temporal and spatial scales ranging from global phenomena such as El Niño events (Roberts 1999) to localised upwelling episodes.

The effects of current systems on the distribution of chokka paralarvae and their prey (Roberts and Van Den Berg in press), the relationship between environmental factors and squid catches (Schön 2000) and the effect of benthic turbidity events on spawning (Roberts in prep) are being investigated.

GIS techniques may provide a useful tool for visualising these interactions between biological parameters and physical influences, and could provide predictive modelling when combined with the outputs of Regional Circulation Models or similar oceanographic analysis.

Aims and objectives of the thesis

This study aims to incorporate and analyse existing biological data in a GIS as well as establishing a protocol for collecting new data. Several biological factors were investigated with spatial patterns visualised to provide additional insight into possible relationships that have been previously obscured using traditional analysis techniques.

Key Questions

Several limitations to chokka squid management were identified by Roel and Payne (1998) which included: the lack of a reliable relationship between the scientific survey estimates and true biomass; the lack of biological knowledge about the life cycle of squid in South African waters and a precise determination of suitable spawning areas and knowledge of spawning activity on a monthly basis. This project asked the following questions:

- 1) Is there a pattern to the distribution and abundance of squid of various maturity stages and can the pattern be visualised on daily, monthly or yearly scales?
- 2) Do biological parameters such as size at maturity, gonadosomatic index and length-to-weight relationships have temporal or spatial patterns?
- 3) Is it possible, using the available data, to model the pattern of distribution for the entire Agulhas Bank?
- 4) Are the available data sources of equal value and if not, which data sources are of the most benefit?
- 5) What accounts for the observed patterns of distribution and abundance?
- 6) Using the available information from research cruises, is it possible to forecast distribution and abundance ahead of the fishing season?
- 7) Can data from commercial demersal trawls be used as an additional source of biological data?

Thesis outline

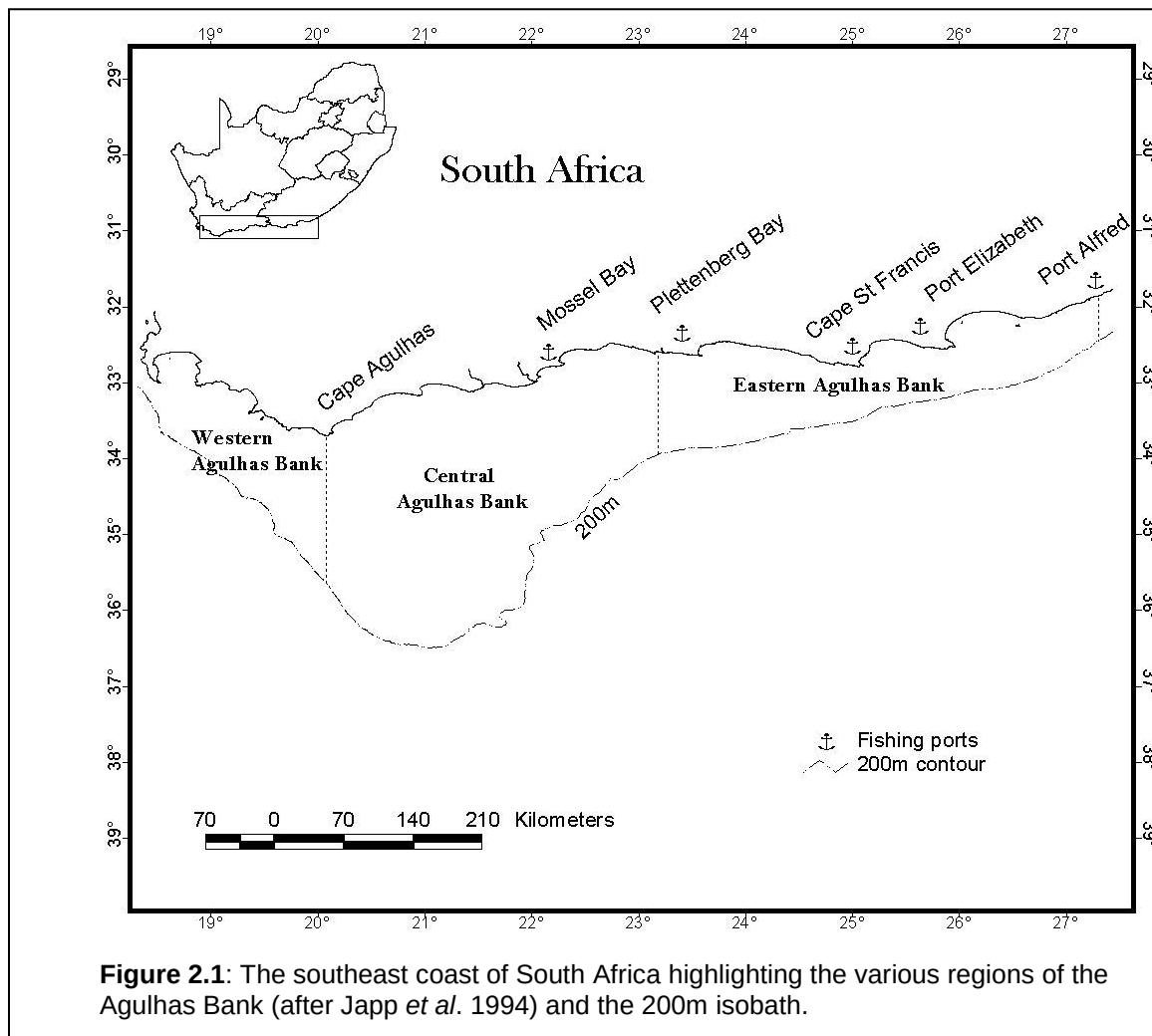
The thesis has been divided into five chapters: Chapter 2 describes the study area, available data and analysis methods. Chapter 3 examines both spatial and temporal aspects of the population using length frequency histograms and length-to-weight regression analysis. Issues of maturity, seasonality and sex ratios, again including both temporal and spatial influences, are addressed in Chapter 4. Distribution and abundance patterns of various life history stages are also considered. Chapter 5 examines how the current findings can be merged with existing data to provide an updated view of the chokka life cycle that takes both spatial and temporal factors into account. This chapter also reviews the different data sources and ways of addressing shortcomings in the datasets are addressed. The applications of biological studies and the GIS to management are also discussed.

CHAPTER 2

General Methods

Study Area

The Agulhas Bank (Figure 2.1) extends along the southeast coast of South Africa from Cape Agulhas (20°E) to Port Alfred (27°E) to the 1000m isobath with an area of *ca.* 29000 nm² (Japp *et al.* 1994). The Agulhas Bank, for the purpose of this thesis, has been divided into three regions; the Western Agulhas Bank (west of 20° E), the Central Agulhas Bank (20° E to 23° E) and the Eastern Agulhas Bank (23° E to 27° E). The cold northerly Benguela Current forms the western boundary of the Agulhas Bank and influences the ecology of the small western area. Oceanographic processes on the central and eastern Bank are strongly influenced by the warm, southeast-flowing Agulhas Current.



Localised currents along the south coast are predominantly wind-forced in the direction of the prevailing westerly winds (Schumann *et al.* 1982, Goschen and Schumann 1988). Reversals with the currents flowing westwards do, however, occur (Ross 1988).

Easterly winds in summer and autumn result in localised upwelling events particularly off rocky capes or headlands (Schumann *et al.* 1982, 1988). Three distinct areas of current movement were described by Largier *et al.* (1992); a wind forced inner shelf, an oceanically forced outer shelf and a mid shelf region of strong stratification with little water movement.

Biological data

Research data

Biannual research cruises on the Agulhas Bank (20-27°E) conducted by the Chief Directorate: Marine and Coastal Management (MCM) in spring and autumn have been the major source of abundance and biological data. A disadvantage of the biannual surveys is that they can only provide brief temporal “snapshots” of biological processes. In a short lived species such as chokka; monthly data are of particular relevance.

The major advantage of research surveys is that a large spatial area is covered, however, the depth stratified random sampling strategy of the survey only samples a small proportion of suitable squid habitat due to the fish-directed nature of the surveys. Research vessels are large, restricting operation in the shallow (50m) inshore waters where spawning squid aggregate, with only 12% of the trawls in the last 12 years, being in depths 50m or less. Similarly rocky grounds are avoided, as the use of bobbins ahead of trawl gear are not employed as they would result in large-scale environmental damage.

Research data were obtained from MCM using the research vessel *RV Africana* between 1986 and 1999. Gear employed and sampling methodology used was defined by Augustyn (1991) and summarised as follows.

Table 2.1: Maturity scales used to assess chokka maturity and life history stages. The Lipiński (1979) scale is based on macroscopic conditions of gonadal tissue, while the simplified stage was widely employed in research surveys.

Lipiński (1979)	Simplified Stage	Life history stage
I	1	Juveniles
II III	2	Subadults
IV V VI	3	Adults

Research samples were analysed immediately after each trawl. A simplified system of maturity staging based on a modified Lipiński (1979) scale was used (Table 2.1). This was necessary because of inconsistency in sampling over years. The following measurements were made: Dorsal mantle length (DML) measurements (to the nearest millimetre), gonad length (the testis in males and the nidamental gland in females) and mantle thickness to the nearest 0.1 mm (measured with vernier callipers). For the nidamental glands, either the left or the right gland was measured. All lengths were measured *in situ*. Wet body (including fins and head), gonad (testis or ovary) and stomach content masses to the nearest 0.1 grammes were obtained using a digital Mettler pan top scale. The female ventral buccal membrane was examined for the presence of attached spermatophores.

Gonadosomatic indices (GSI), adapted from Pierce *et al.* (1994) were calculated as:

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

where GW is gonad weight, BW is body weight and SW is stomach content weight.

Gonad mass and length were not available for all surveys and it was not possible to calculate the GSI for every research sample.

Commercial data

Commercial samples from jig and trawl fishing vessels augmented the database. Jig vessels actively target spawning squid aggregations (Sauer 1995a) and provide good data for the inshore environment on a monthly basis. In contrast, hake or sole-directed trawl vessels catch squid as bycatch. These vessels generally operate over a larger area and to greater depths than the jig fishing deckboats and provide a broader range of samples. A wider range of sizes is collected using trawl gear, including the smallest size class that is largely unavailable to jig gear. By combining these varied sources of data, a more representative pattern of the chokka life cycle was produced.

Commercial samples were collected during two time periods. Initially samples were collected monthly from the inshore environment (0-60m isobath) between Algoa Bay (33° 46'S, 26° 00'E) and Oyster Bay (34° 12'S, 24° 37'E) from March 1988 to January 1989. These samples were collected at depths between 6 and 50m and were caught by handline jigging (Sauer 1995a). Samples were also collected between June 1999 and June 2000. These jig caught samples were obtained from the South African Bureau of Standards (SABS) Food Testing Laboratory in Port Elizabeth. These samples submitted for health testing prior to export, were available as size sorted blocks (10-12kg frozen mass) containing, depending on the size of the animals, twenty to thirty squid. These sizes are graded for market purposes; small (15-

20cm), medium (20-25cm), large (25-30cm) and extra large (>30cm). For a representative sample, a full range of sizes was required each month. This proved impossible to achieve since the tendency of fishing companies was to submit the most abundant size class - usually medium. To compound the problem, different size classes were obtained from different vessels caught on different dates and at different locations. Pooling specimens from assorted blocks to form a single sample was not satisfactory since any geographical variation in biological parameters would be obscured. Lack of location data for each sample also meant that the spatial component of the study, using these samples, was largely unfeasible. A solution was found by approaching a co-operative skipper and fishing company that were prepared to collect a sample of mixed sizes on a monthly basis, recording both the position and date. Jig caught samples were collected between Algoa Bay and Plettenberg Bay (33° 59'S 23° 32'E) between June 1999 and June 2000. Depths ranged between 9 and 60m. Over the same time 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 200m predominantly on the central (20-23°E) and occasionally the western Agulhas Bank (19-20°E). Commercial samples were frozen at sea and thawed prior to measurements being made.

Spatial analysis and database design

A relational, spatial database and Fishery Information System (FIS) was designed using ESRI ArcView[®] and MicroImages TNT-MIPS[®].

Tables were constructed for each research cruise. Trawl summary information contained station and trawl number, research grid, depth, date, time and duration as well as latitude and

longitude at the start of each trawl; catch totals, number of measures, number of biologicals, and oceanographic data such as dissolved oxygen (DO) and temperature.

Area and date specific maturity and length frequency data were tabulated. The tables were imported in DBASE IV format (*.dbf).

Microsoft Access[®] software was used to design the primary database and prepare the tables for import into the GIS. Relationships between the tables based on the common field of Station number were established.

CHAPTER 3

Population Structure

Introduction

This chapter describes the population structure of chokka squid on the Agulhas Bank by examining length frequency histograms and length-to-weight relationships.

In the absence of size-at-age data, an examination of length frequency histograms allows discrete cohorts to be identified. Concern has been expressed that traditional fishery analysis programs such as ELEFAN do not adequately model cephalopod growth and most assessments of growth rate and/or maximum age are inaccurate (Jackson *et al.* 1997, 2000). Nevertheless, the study of length frequencies provides insight into the population dynamics and provides useful information to fishery managers. Three major cohorts have been previously identified in chokka squid (Augustyn 1990, Augustyn *et al.* 1994). The present study attempted to verify the existence of these cohorts and determine their origin as well as any spatial variation in population dynamics.

The relationship between the length of the animal and its weight provides insight into its feeding biology and reproductive status. By comparing differences between sexes, it was possible to infer the relative energy investment in gonads of each sex. Temporal comparisons provide evidence of seasonal patterns of growth or reproduction while comparisons between animals from different geographic locations within the same season identifies spatial trends, making it possible to predict specific feeding or breeding areas based on the presence of relatively heavier animals.

In order to examine the variability in length-weight relationships, the following hypotheses were tested: firstly, that there was no significant difference in the length-weight relationships of different maturity stages in each sex within each longitudinal area; secondly that there was no significant difference in the length-weight relationships of each maturity stage for each sex between different longitudinal areas and finally that there was no significant difference between male and female length-weight relationships in each maturity stage within each longitudinal area. Differences in length-weight relationships between seasons for each maturity stage in either sex within each longitudinal area were also tested. Monthly length-weight regression slopes were also compared for the three commercial datasets.

Materials and Methods

3.1 Length frequency

Research trawls were grouped by season (spring or autumn) and sex disaggregated length frequency histograms constructed. Trawls within each season were grouped by longitude (one degree intervals from 20° to 27°E). The length frequency data were subjected to cohort separation using the Bhattacharya technique (Bhattacharya 1967) to estimate initial mean length and standard deviation values for each cohort in the sample. The NORMSEP procedure was then applied to confirm the results of the Bhattacharya analysis. Both routines are available in the FISAT II suite of fishery stock assessment tools developed by FAO and ICLARM. Commercial samples were subjected to similar analysis. All data were assumed to be normally distributed prompting the use of standard parametric statistical tests.

3.2 Length-weight relationships

Data from all biannual biomass surveys were combined and disaggregated by season, sex and longitudinal area. Simple least squares linear regressions were performed on the natural log transformed DML (dorsal mantle length) and BW (wet body weight) data.

Whole body weight data combining both somatic and reproductive tissue was used due to the low number of gonad weight measurements available for research samples.

Slopes of the regression for males and females in each longitudinal area for each season were compared using a student's t-test as described by Zar (1999). Differences in the regression slopes between different longitudinal areas within a season and different maturity stages within a longitudinal area were compared for each sex using an analysis of covariance (ANCOVA) (Zar 1999). A Tukey test was used to identify which particular areas were significantly different from the others.

Samples from commercial sources were tested using similar statistics to determine monthly trends in length-weight relationships. Jig samples tend to concentrate on catches of mature animals (Sauer 1995b) and for the purpose of this analysis only mature animals were used. The small sample sizes, particularly in the commercial trawl data suggest that the results should be interpreted with some caution.

Results

3.1 Length frequency

Length frequency histograms of sex disaggregated squid caught in research trawls are presented by season and longitudinal area in Figures 3.1.1 to 3.1.4. The approximate positions of the means of each cohort as calculated by the NORMSEP procedures are indicated by vertical arrows.

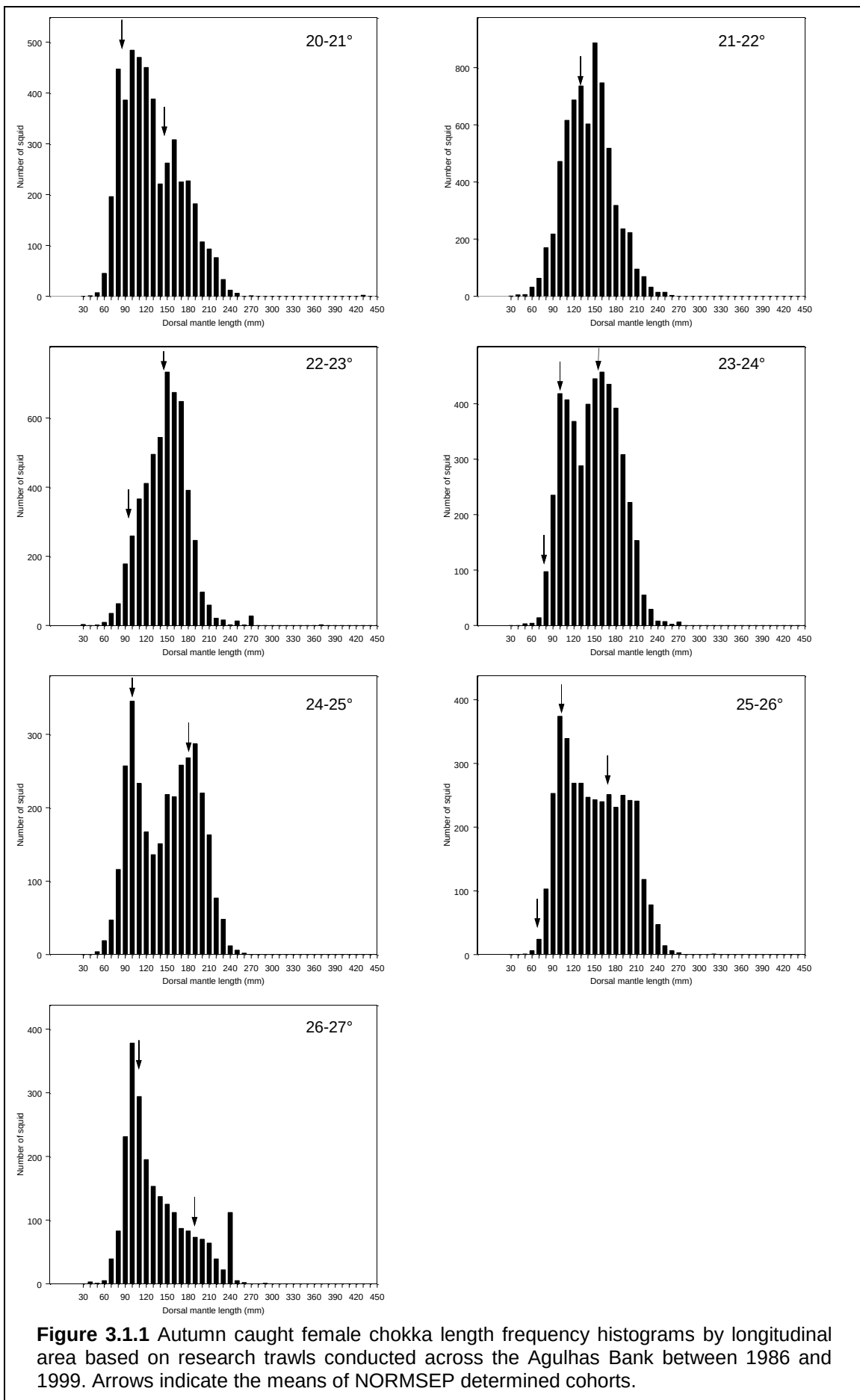


Figure 3.1.1 Autumn caught female chokka length frequency histograms by longitudinal area based on research trawls conducted across the Agulhas Bank between 1986 and 1999. Arrows indicate the means of NORMSEP determined cohorts.

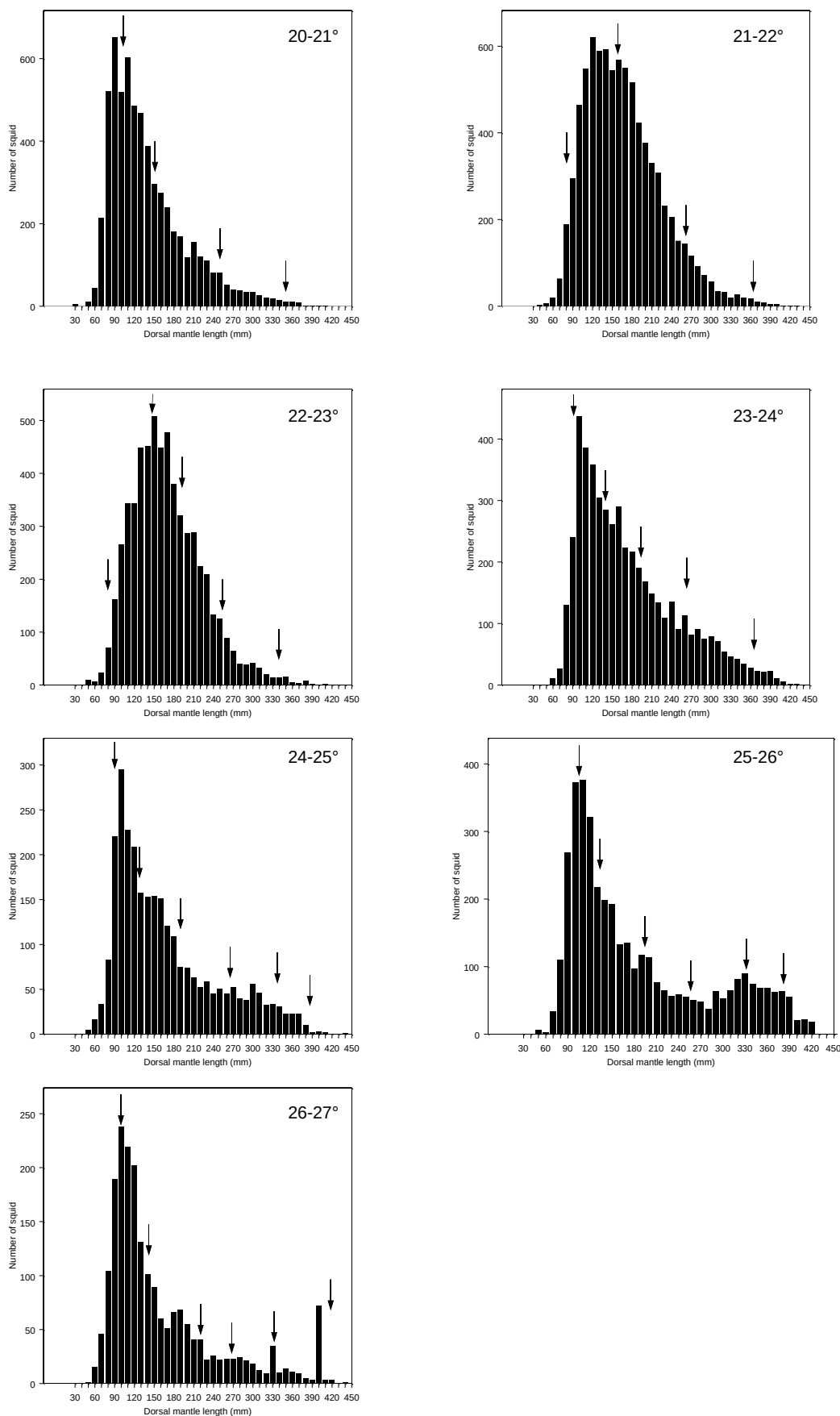


Figure 3.1.2 Autumn caught male chokka length frequency histograms by longitudinal area based on research trawls conducted across the Agulhas Bank between 1986 and 1999. Arrows indicate the means of NORMSEP determined cohorts.

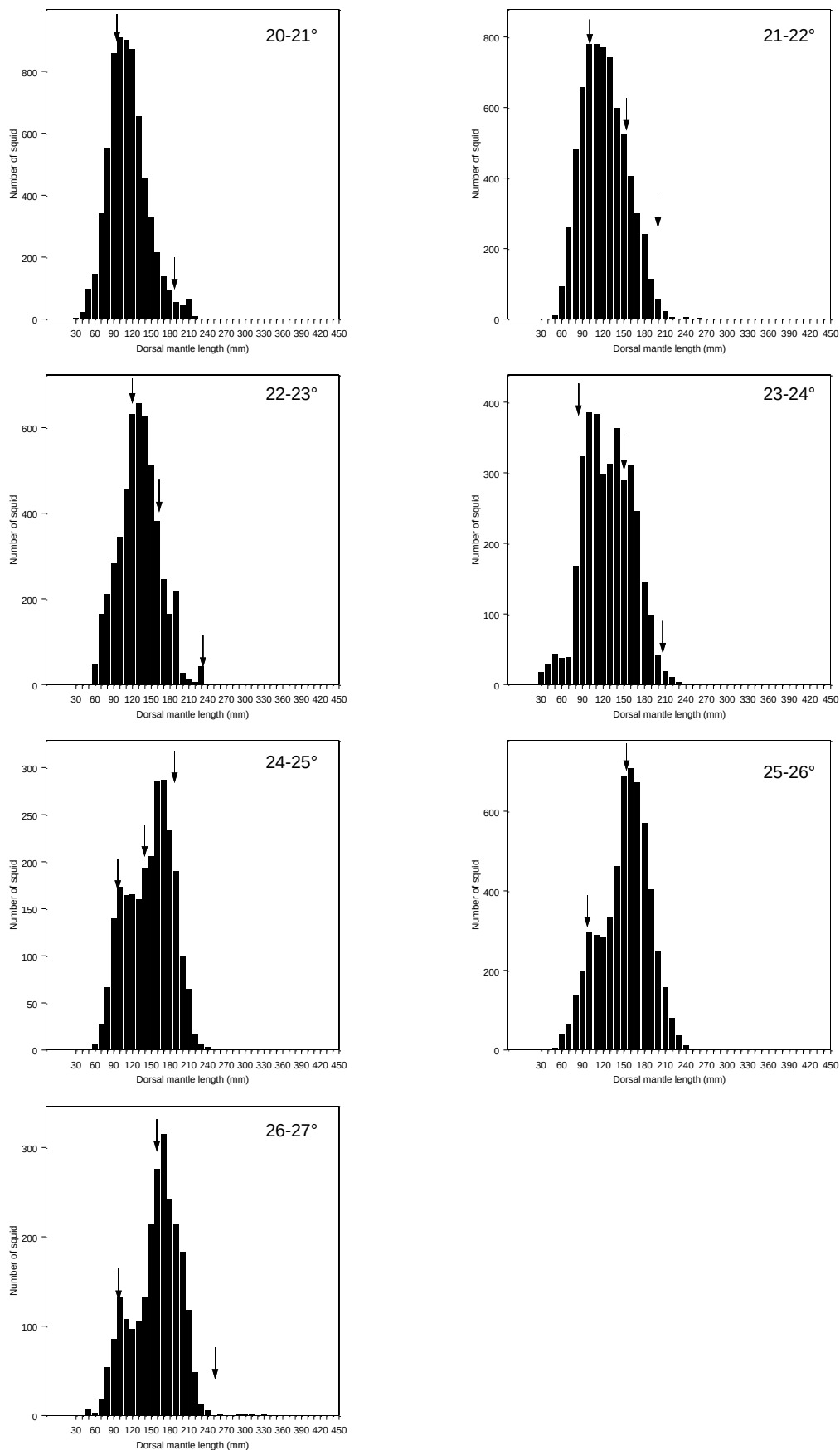


Figure 3.1.3 Spring caught female chokka length frequency histograms by longitudinal area based on research trawls conducted across the Agulhas Bank between 1986 and 1999. Arrows indicate the means of NORMSEP determined cohorts.

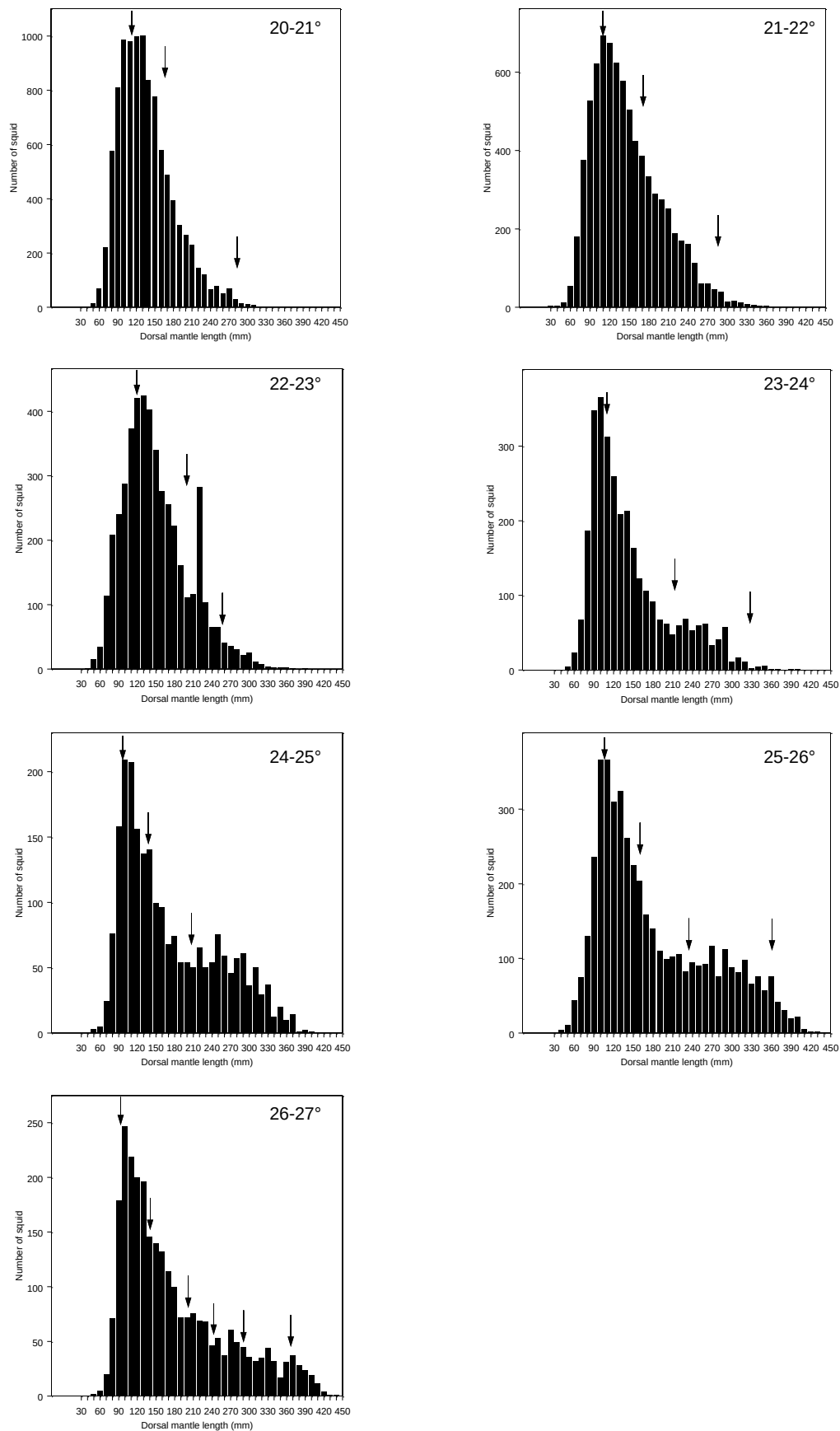


Figure 3.1.4 Spring caught male chokka length frequency histograms by longitudinal area based on research trawls conducted across the Agulhas Bank between 1986 and 1999. Arrows indicate the means of NORMSEP determined cohorts.

Although some of the cohorts can be determined on visual inspection, particularly cohort I, other cohorts identified by NORMSEP were not as distinct. This is because fairly large overlaps were evident in the data.

The mean dorsal mantle length (mm) and standard deviations of size cohorts calculated by NORMSEP are presented in Tables 3.1.1 to 3.1.4. The numbers of squid sampled in each season in each area are presented in Tables 3.1.5 and 3.1.6.

Table 3.1.1 Mean dorsal mantle length (mm), standard deviation (SD) and proportion of the sample in each cohort (%) of autumn caught male size cohorts of chokka by longitudinal area based on research trawls across the Agulhas Bank.

<i>Longitude</i>	<i>Cohort I</i>			<i>Cohort II</i>			<i>Cohort III</i>		
	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>
20°-21°E	105.88	24.85	50.57	154.86	32.32	33.26			
21°-22°E	108.03	24.39	33.74	160.23	35.26	39.01			
22°-23°E	105.68	23.33	29.29	139.05	17.62	37.77	187.65	19.22	24.40
23°-24°E	104.54	17.33	39.19	140.01	20.62	29.14	193.74	19.80	15.66
24°-25°E	104.74	20.50	46.24	135.00	19.03	23.55	189.13	22.19	14.36
25°-26°E	100.09	18.32	43.31	134.37	15.77	19.08	183.12	21.80	13.73
26°-27°E	104.58	19.72	56.81	145.59	27.29	22.55	207.65	16.20	7.01
	<i>Cohort IV</i>			<i>Cohort V</i>			<i>Cohort VI</i>		
	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>
20°-21°E	236.34	30.48	12.51	321.40	25.66	3.66			
21°-22°E	256.70	40.34	19.57	340.10	27.93	7.68			
22°-23°E	242.05	20.99	7.17	319.83	31.08	1.37			
23°-24°E	256.69	23.83	11.26	333.83	36.09	4.76			
24°-25°E	256.98	23.53	9.50	315.54	13.94	4.15	359.06	19.89	2.20
25°-26°E	261.71	35.21	12.37	334.39	14.47	6.89	380.79	21.04	4.62
26°-27°E	258.96	18.99	5.57	323.86	26.96	4.27	396.74	15.89	3.79

At least three and as many as six cohorts were statistically identified for each area across the Agulhas Bank for autumn caught male chokka (Table 3.1.1). The smallest cohort (*ca.* 105mm DML) was evident in all areas while the biggest (350-380mm DML) was only identified in the eastern areas. Cohorts I and II predominated in all areas.

Table 3.1.2 Mean dorsal mantle length (mm), standard deviation (SD) and proportion of the sample in each cohort (%) of autumn caught female size cohorts of chokka by longitudinal area based on research trawls across the Agulhas Bank.

<i>Longitude</i>	<i>Cohort I</i>			<i>Cohort II</i>			<i>Cohort III</i>		
	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>
20°-21°E				105.33	22.69	76.10			
21°-22°E							141.20	33.82	100.0
22°-23°E	90.57	19.40	5.63	106.58	19.05	26.00	158.11	26.04	74.00
23°-24°E	83.51	13.76	7.45	105.49	13.40	31.17			
24°-25°E				102.51	17.95	43.67			
25°-26°E	80.71	14.75	20.01	106.91	18.70	35.41			
26°-27°E	91.37	19.92	15.77	109.41	15.42	44.04			
	<i>Cohort IV</i>			<i>Cohort V</i>			<i>Cohort VI</i>		
	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>
20°-21°E	176.29	27.51	23.90						
21°-22°E									
22°-23°E									
23°-24°E	166.21	26.84	61.38						
24°-25°E	178.90	26.11	56.33						
25°-26°E	178.79	31.25	44.58						
26°-27°E	180.46	35.10	40.19						

Female autumn caught chokka (Table 3.1.2) were comprised of three cohorts in each area with the exception of the areas between 20° and 21°E and between 24° and 25°E where only two cohorts were identified ($105.33 \pm 22.69\text{mm}$ and $176.29 \pm 27.51\text{mm}$ DML) and ($102.51 \pm 17.95\text{mm}$ and $178.90 \pm 26.11\text{mm}$ DML) respectively and the area between 21° and 22°E where only a single mean was identified ($141.20 \pm 33.82\text{mm}$). The greatest proportions of female squid in all areas were in either Cohorts II or IV.

Spring caught male chokka (Table 3.1.3) consisted of a similar cohort structure to the autumn caught males with most areas having three cohorts and only one having six (between 26° and 27°E). Cohorts I and II were dominant in all areas while Cohorts IV and V were in greater abundance in the east than further west.

Table 3.1.3 Mean dorsal mantle length (mm), standard deviation (SD) and proportion of the sample in each cohort (%) of spring caught male size cohorts of chokka by longitudinal area based on research trawls across the Agulhas Bank.

<i>Longitude</i>	<i>Cohort I</i>			<i>Cohort II</i>			<i>Cohort III</i>		
	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>
20°-21°E	106.66	27.28	72.66	154.98	22.64	23.43			
21°-22°E	108.63	26.24	65.16	163.86	33.32	31.27			
22°-23°E				129.78	38.22	83.90	216.91	41.64	12.51
23°-24°E	113.13	27.16	78.21				194.54	47.38	18.04
24°-25°E	100.99	15.21	30.28	141.69	32.11	44.08			
25°-26°E	99.70	23.50	41.35	139.30	20.81	25.84	207.02	28.34	16.29
26°-27°E	102.36	17.55	41.57	140.24	18.84	25.19	191.70	17.17	11.84
	<i>Cohort IV</i>			<i>Cohort V</i>			<i>Cohort VI</i>		
	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>
20°-21°E	228.79	30.14	3.91						
21°-22°E	249.36	29.26	3.57						
22°-23°E				290.03	19.47	3.59			
23°-24°E				276.04	21.78	3.75			
24°-25°E				262.15	51.64	25.64			
25°-26°E				308.46	47.86	16.53			
26°-27°E	241.91	15.35		288.00	20.18	8.01	359.85	34.69	6.24

Table 3.1.4 Mean dorsal mantle length (mm), standard deviation (SD) and proportion of the sample in each cohort (%) of spring caught female size cohorts of chokka by longitudinal area based on research trawls across the Agulhas Bank.

<i>Longitude</i>	<i>Cohort I</i>			<i>Cohort II</i>			<i>Cohort III</i>		
	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>
20°-21°E	108.66	26.42	86.05				179.44	23.53	13.95
21°-22°E	104.07	25.18	86.53	146.99	14.00	10.64	185.17	14.60	2.83
22°-23°E	123.23	29.00	55.85	157.86	22.34	34.95			
23°-24°E	103.86	25.42	49.16	152.79	25.83	46.29	202.19	14.61	4.55
24°-25°E	104.97	21.20	35.57	137.61	22.75	42.81	182.01	15.72	21.62
25°-26°E	107.26	24.62	32.61				168.68	23.07	67.39
26°-27°E	107.44	21.45	22.07				174.69	24.37	58.43
	<i>Cohort IV</i>			<i>Cohort V</i>			<i>Cohort VI</i>		
	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>	<i>Mean</i>	<i>SD</i>	<i>%</i>
20°-21°E									
21°-22°E									
22°-23°E	218.22	25.45	9.20						
23°-24°E									
24°-25°E									
25°-26°E									
26°-27°E	222.24	0.38	19.50						

Spring caught females (Table 3.1.4) consisted of three cohorts in most areas but only two cohorts between 20° and 21°E (108.66 ± 26.42mm and 179.44 ± 23.53mm DML) and between 25° and 26°E (107.26 ± 24.62mm and 168.68 ± 23.07mm DML). The smallest spring cohort (103-108mm) except for between 22° and 23°E (123.23 ± 29.0mm) corresponded in size to the second smallest cohort (Cohort II) of autumn females.

Cohort I was most prevalent in the west, decreasing in proportion eastwards. Cohort II was most prevalent on the central Agulhas Bank and Cohort III and IV were more abundant in the east.

Table 3.1.5 Numbers in each cohort of autumn caught chokka by longitudinal area based on research trawls across the Agulhas Bank.

<i>Longitude</i>	<i>Female</i>				<i>Male</i>					
	I	II	III	IV	I	II	III	IV	V	VI
20°-21°E		3521		1106	3059	2012	756	222		
21°-22°E			6766		2217	3761	1854	306	91	
22°-23°E	298	1034	1770	2191	1737	2240	1447	425	81	
23°-24°E	354	1481		2917	1945	1446	777	559	236	
24°-25°E		1419		1830	1304	664	405	268	117	62
25°-26°E	770	1363		1716	1716	756	544	490	273	183
26°-27°E	365	1019		930	1184	470	146	116	89	79

Table 3.1.6 Numbers in each cohort of spring caught chokka by longitudinal area based on research trawls across the Agulhas Bank.

<i>Longitude</i>	<i>Female</i>				<i>Male</i>					
	I	II	III	IV	I	II	III	IV	V	VI
20°-21°E	5822		944		7356	2372		396		
21°-22°E	6110	751	200		5021	2410		275		
22°-23°E	2811	1759		463		4092	610		175	
23°-24°E	1835	1728	170		2458		567		118	
24°-25°E	885	1065	538		693	1009			587	
25°-26°E	1854		3832		1899	1187	748		759	
26°-27°E	653		1729	577	1152	698	328	198	222	173

Spatial visualisation of the distribution of the various cohorts is presented in Figures 3.1.5 and 3.1.6. Pie charts showing the proportion of each cohort in each one-degree longitudinal area between 20 and 27°E are used to display the data described above.

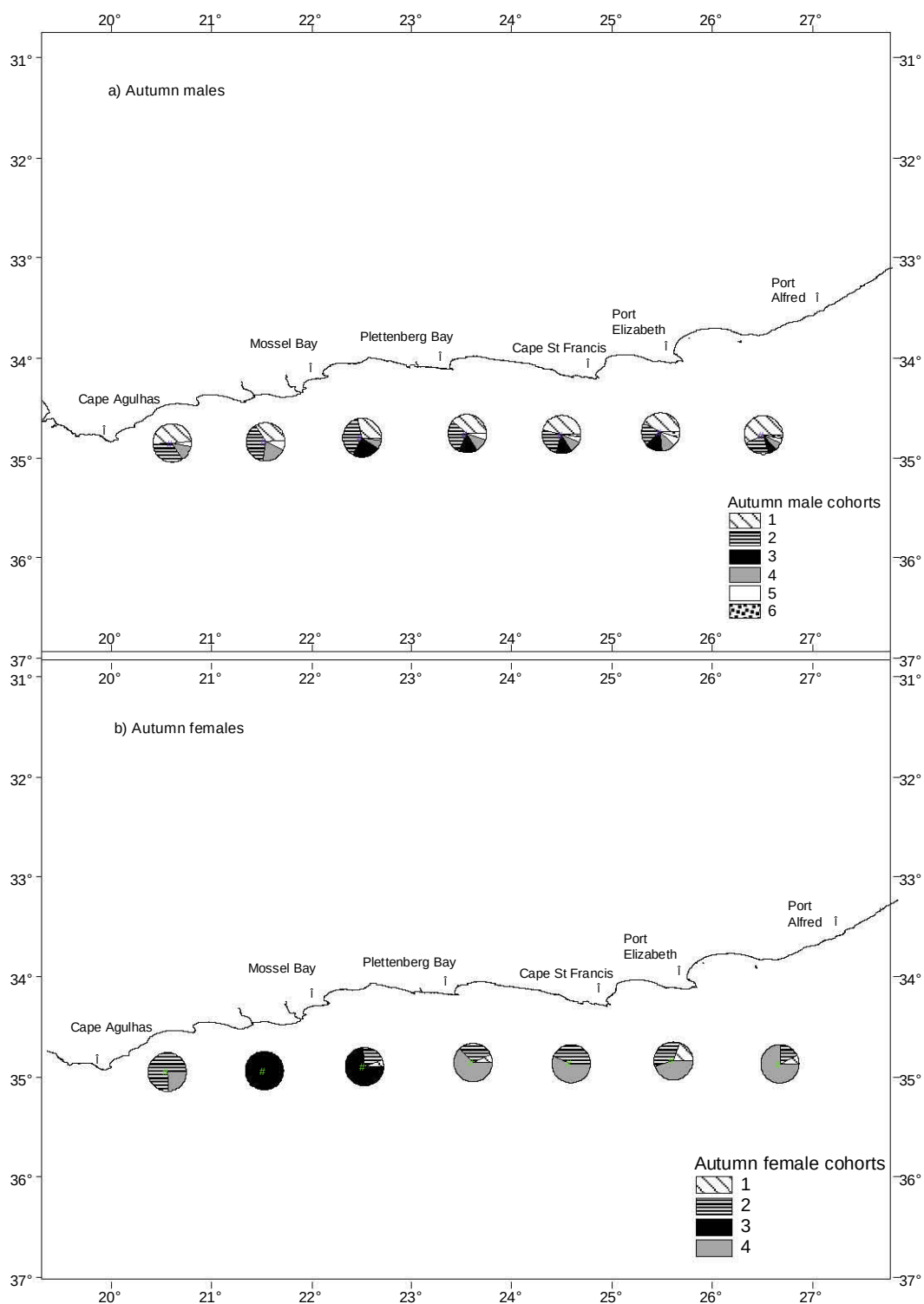


Figure 3.1.5 Spatial visualisation of the longitudinally grouped (one degree between 20 and 27°E) cohort structures of autumn caught a) male and b) female chokka based on research surveys conducted across the Agulhas Bank between 1986 and 1999.

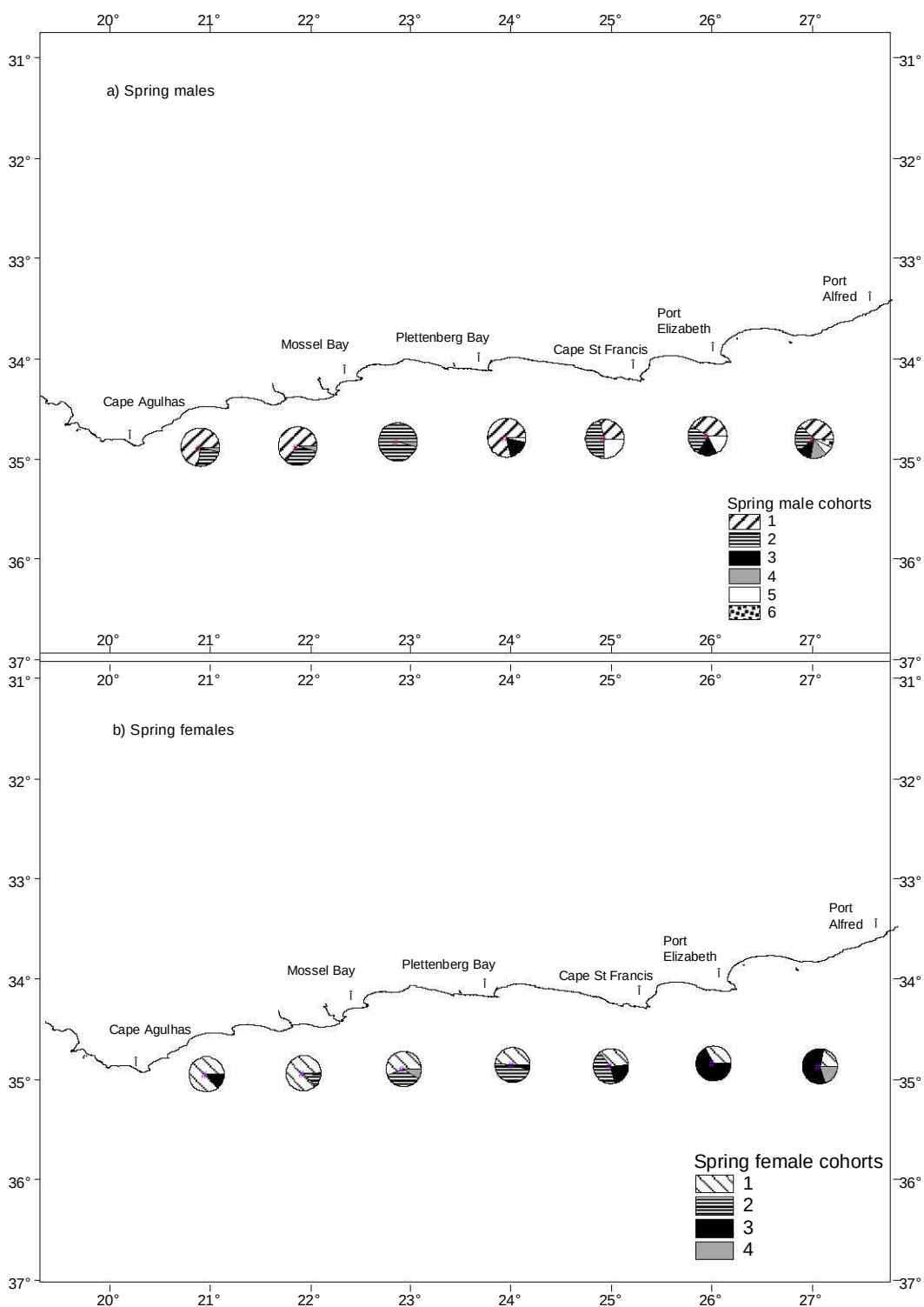


Figure 3.1.6 Spatial visualisation of the longitudinally grouped (one degree between 20 and 27°E) cohort structures of spring caught a) male and b) female chokka based on research surveys conducted across the Agulhas Bank between 1986 and 1999.

3.2 Length-weight relationships

Maturity stage comparisons

The statistical descriptions of the seasonal natural log-transformed length-to-weight regression slopes for each maturity stage are presented for both sexes by longitudinal area in Appendix I.

For the autumn cruises (Table 3.2.1), all three male life-history stages were found to have highly significant differences ($p < 0.001$) in their length-to-weight regression slopes between 20° and 21°E. Tukey tests between each life-history stage were highly significant ($p < 0.001$). In males, the slope order was stage I > stage III > stage II. Similarly female life-history stage slopes were also highly significantly different ($p < 0.001$) from each other. Slopes in order of decreasing steepness were stage III > stage I > stage II.

Table 3.2.1 Length-to-weight regression slopes for autumn caught chokka in each of three maturity stages in one-degree longitudinal areas across the Agulhas Bank. ANCOVA F-values were all significant ($p < 0.001$).

<i>Longitude</i>	<i>Males</i>					<i>Females</i>				
	I	II	III	F	df	I	II	III	F	df
20°-21°E	2.432	2.296	2.324	201.403	775	2.386	2.319	2.562	315.993	722
21°-22°E	2.409	2.405	2.434	158.73	912	2.230	2.237	2.596	226.811	946
22°-23°E	2.558	2.396	2.416	11.419	526	2.518	2.581	2.604	155.383	529
23°-24°E	2.264	2.452	2.220	96.719	456	2.449	2.459	2.559	248.841	363
24°-25°E	2.488	2.332	2.165	108.609	313	2.523	2.525	2.237	238.990	313
25°-26°E	2.439	2.368	2.295	15.010	201	2.561	2.547	2.417	45.138	210
26°-27°E	2.315	2.435	2.245	44.782	195	2.371	2.453	2.412	92.524	194

Between 21° and 22°E, the stages were again highly significantly different ($p < 0.001$). In the males, stage III > stage I > stage II. For females, stage III > stage II > stage I. The results of the Tukey test showed that there was no significant difference between stages I and II for males ($q = 0.406$, $p = 0.667$) and females ($q = 1.044$, $p = 0.352$). Significant ($p \leq 0.05$) to highly significant ($p < 0.001$) differences existed between all other stages.

Between 22° and 23°E, highly significant ($p < 0.001$) differences existed for both sexes with Tukey tests showing significant ($p \leq 0.05$) to highly significant ($p < 0.001$) differences between all stages. The order of male slopes was stage I > stage III > stage II and in females, stage III > stage II > stage I.

Both sexes showed highly significant ($p < 0.001$) between stage differences in the length-to-weight regression slopes between 23° and 24°E area with Tukey tests revealing no significant difference between female I and female II ($q = 1.363$, $p = 0.196$) and significant ($p \leq 0.05$) to highly significant ($p < 0.001$) differences for all other stages. The regression slope steepness order for males was stage II > stage I > stage III and for females, stage III > stage II > stage I. Highly significant differences between stages were demonstrated for males and females collected between 24° and 25°E. Tukey tests again revealed that female I and II stages were not significantly different from each other ($q = 0.222$, $p = 0.801$) but that all other stages had highly significant ($p < 0.001$) differences between them. Male regression slopes in decreasing order of steepness were stage I > stage II > stage III. Female regression slopes in descending order were stage II > stage I > stage III.

In the area between 25° and 26°E, both sexes demonstrated highly significant differences in the length-weight regression slopes between the three maturity stages. Tukey tests confirmed that significant ($p \leq 0.05$) to highly significant ($p < 0.001$) differences existed between the different stages. The male slope steepness order was stage I > stage II > stage III. Females followed a similar trend with stage I > stage II > stage III.

Both males and females displayed highly significant differences between maturity stages between 26° and 27°E. Tukey test results were significant ($p \leq 0.05$) to highly significant ($p <$

0.001). Male regression slope order was stage II > stage I > stage III. For females, stage II > stage III > stage I.

Table 3.2.2 Length-to-weight regression slopes for spring caught chokka in each of three maturity stages in one-degree longitudinal areas across the Agulhas Bank. ANCOVA F-values were all significant ($p < 0.001$).

<i>Longitude</i>	<i>Males</i>					<i>Females</i>				
	I	II	III	F	df	I	II	III	F	df
20°-21°E	2.353	2.345	2.370	215.056	508	2.369	2.385	2.520	186.114	540
21°-22°E	2.446	2.394	2.332	152.808	636	2.538	2.446	2.414	183.492	682
22°-23°E	2.220	2.510	2.382	72.217	358	2.471	2.447	2.372	145.007	367
23°-24°E	2.396	2.492	2.311	27.782	248	2.347	2.499	2.539	82.559	273
24°-25°E	2.614	2.625	2.281	99.456	139	2.530	2.560	2.536	20.478	148
25°-26°E	2.363	2.136	2.326	13.999	174	2.463	2.171	2.443	102.493	174
26°-27°E	2.330	2.087	2.282	24.787	228	1.892	2.383	2.445	82.676	227

An examination of the spring cruise data (Table 3.2.2) reveals that highly significant ($p < 0.001$) differences existed between the length-to-weight regression slopes of the three maturity stages in both sexes collected between 20° and 21°E. Tukey tests revealed significant ($p \leq 0.05$) to highly significant ($p < 0.001$) differences between the maturity stages except between stage I and stage II ($q = 1.490$, $p = 0.226$) and stage I and stage III ($q = 2.863$, $p = 0.058$, which showed no significant differences. The order of decreasing steepness of male regression slopes was stage III > stage I > stage II and for females, stage III > stage II > female I.

In the area between 21° and 22°E, both males and females showed highly significant ($p < 0.001$) differences between stages with Tukey test results being highly significant ($p < 0.001$) for all stages. Male slope order was stage I > stage II > stage III. Female slopes followed a similar trend with stage I > stage II > stage III.

Highly significant ($p < 0.001$) differences were also apparent between maturity stages for samples collected between 22° and 23°E for both males and females. Tukey tests showed

significant ($p \leq 0.05$) to highly significant ($p < 0.001$) differences between all stages. Male regression slopes in order of decreasing steepness were stage II > stage III > stage I. Female slopes had stage I > stage II > stage III.

In the area between 23° and 24°E, both sexes showed highly significant ($p < 0.001$) ANCOVA results. Tukey results were highly significant ($p < 0.001$) for all stages. Male squid regression slopes followed stage II > stage I > stage III in decreasing steepness order and for females, stage III > female II > female I.

Male and female maturity stages showed highly significant ($p < 0.001$) differences in their length-weight regression slopes between 24° and 25°. Tukey test results demonstrated no significant differences between male I and male II and between all female stages. Male squid regression slopes in decreasing steepness were stage II > stage I > stage III. For females, stage II > stage III > stage I.

In samples collected between 25° and 26°E, highly significant differences ($p < 0.001$) between regression slopes existed for both sexes. Tukey test results revealed highly significant ($p < 0.001$) differences between all slopes except for stage I and III of both sexes, which showed no significant differences for males ($q = 1.954$, $p = 0.1447$) and females ($q = 2.184$, $p = 0.116$). The steepness regression slope order for males was stage I > stage III > stage II. For females, stage I > stage III > stage II.

Between 26° and 27°E, both sexes showed highly significant ($p < 0.001$) ANCOVA results. Tukey test results showed that no significant differences existed between male I and male III ($q = 2.514$, $p = 0.042$) but for all other stages in both sexes, results were significant ($p \leq 0.05$)

to highly significant ($p < 0.001$). The male regression slope order was stage I > stage III > stage II. For females, stage III > stage I > stage II.

Longitudinal comparisons

Results of the ANCOVA of longitudinally grouped length-to-weight regression slopes are reported in Table 3.2.3.

Table 3.2.3 ANCOVA results for longitudinally grouped autumn and spring caught chokka.

Stage	Autumn			Spring		
	F	df	p	F	df	p
Male I	4.303	353	< 0.001	2.289	396	0.035
Male II	28.168	1330	< 0.001	5.284	752	< 0.001
Male III	10.397	1695	< 0.001	7.878	1263	< 0.001
Female I	2.683	460	0.014	4.751	565	< 0.001
Female II	16.045	1297	< 0.001	3.729	742	0.001
Female III	6.817	1521	< 0.001	3.919	984	< 0.001

Ranked length-weight regression slopes of autumn males for all three maturity stages in decreasing order of steepness are presented in Table 3.2.4.

Highly significant ($p < 0.001$) differences in the length-weight regression slopes were found between longitudinal areas for autumn male I squid. Tukey tests revealed highly significant ($p < 0.001$) differences between all areas except between 20° to 21°E and 25° to 26°E ($q = 0.499$, $p = 0.808$).

Table 3.2.4 Length-to-weight regression slopes by longitude for autumn caught male chokka ranked in descending slope steepness in each of three reproductive stages. Superscript letters indicate regression slopes not significantly different from each other within each maturity stage.

Male I			Male II			Male III		
Rank	Longitude	Slope	Rank	Longitude	Slope	Rank	Longitude	Slope
1	22°-23°E	2.558	1	23°-24°E	2.452 ^a	1	21°-22°E	2.434
2	24°-25°E	2.488	2	26°-27°E	2.435 ^a	2	22°-23°E	2.416
3	25°-26°E	2.439 ^a	3	21°-22°E	2.405	3	20°-21°E	2.324
4	20°-21°E	2.432 ^a	4	22°-23°E	2.396	4	25°-26°E	2.295
5	21°-22°E	2.409	5	25°-26°E	2.368	5	26°-27°E	2.245
6	26°-27°E	2.315	6	24°-25°E	2.332	6	23°-24°E	2.220
7	23°-24°E	2.264	7	20°-21°E	2.296	7	24°-25°E	2.165

Highly significant ($p < 0.001$) differences were also apparent for autumn male II squid. Tukey tests revealed significant ($p \leq 0.05$) to highly significant ($p < 0.001$) differences for all areas except between 23° to 24°E and 26° to 27°E ($q = 1.924$, $p = 0.074$). Autumn male III squid also demonstrated highly significant ($p < 0.001$) differences in the length-weight regression slopes between different longitudinal areas. Tukey tests revealed highly significant ($p < 0.001$) differences between all areas.

Ranked length-weight regression slopes of autumn females for all three maturity stages in decreasing order of steepness are presented in Table 3.2.5.

The autumn female I group showed significant ($p = 0.014$) differences between areas with Tukey tests showing no significant difference between area 22° to 23°E and area 24° to 25°E ($q = 0.493$, $p = 0.813$) but significant ($p \leq 0.05$) to highly significant ($p < 0.001$) differences for all other areas. The length-weight regressions of autumn female II squid were characterised by highly significant ($p < 0.001$) differences between areas, although the Tukey test found no significant differences between area 23° to 24°E and area 26° to 27°E ($q = 0.940$, $p = 0.465$). Autumn female III squid also demonstrated highly significant ($p < 0.001$) differences between areas with no significant difference between area 25° to 26°E and area 26° to 27°E ($q = 0.957$, $p = 0.453$).

Table 3.2.5 Length-to-weight regression slopes by longitude for autumn caught female chokka ranked in descending slope steepness in each of three reproductive stages. Superscript letters indicate regression slopes not significantly different from each other within each maturity stage.

<i>Female I</i>			<i>Female II</i>			<i>Female III</i>		
<i>Rank</i>	<i>Longitude</i>	<i>Slope</i>	<i>Rank</i>	<i>Longitude</i>	<i>Slope</i>	<i>Rank</i>	<i>Longitude</i>	<i>Slope</i>
1	$25^\circ\text{-}26^\circ\text{E}$	2.561	1	$22^\circ\text{-}23^\circ\text{E}$	2.581	1	$22^\circ\text{-}23^\circ\text{E}$	2.604
2	$24^\circ\text{-}25^\circ\text{E}$	2.523 ^a	2	$25^\circ\text{-}26^\circ\text{E}$	2.547	2	$21^\circ\text{-}22^\circ\text{E}$	2.596
3	$22^\circ\text{-}23^\circ\text{E}$	2.518 ^a	3	$24^\circ\text{-}25^\circ\text{E}$	2.525	3	$20^\circ\text{-}21^\circ\text{E}$	2.562
4	$23^\circ\text{-}24^\circ\text{E}$	2.449	4	$23^\circ\text{-}24^\circ\text{E}$	2.459 ^a	4	$23^\circ\text{-}24^\circ\text{E}$	2.559
5	$20^\circ\text{-}21^\circ\text{E}$	2.386	5	$26^\circ\text{-}27^\circ\text{E}$	2.453 ^a	5	$25^\circ\text{-}26^\circ\text{E}$	2.417 ^a
6	$26^\circ\text{-}27^\circ\text{E}$	2.371	6	$20^\circ\text{-}21^\circ\text{E}$	2.319	6	$26^\circ\text{-}27^\circ\text{E}$	2.412 ^a
7	$21^\circ\text{-}22^\circ\text{E}$	2.230	7	$21^\circ\text{-}22^\circ\text{E}$	2.237	7	$24^\circ\text{-}25^\circ\text{E}$	2.237

Ranked length-weight regression slopes of spring males for all three maturity stages in decreasing order of steepness are presented in Table 3.2.6.

Table 3.2.6 Length-to-weight regression slopes by longitude for spring caught male chokka ranked in descending slope steepness in each of three reproductive stages. Superscript letters indicate regression slopes not significantly different from each other within each maturity stage.

<i>Male I</i>			<i>Male II</i>			<i>Male III</i>		
<i>Rank</i>	<i>Longitude</i>	<i>Slope</i>	<i>Rank</i>	<i>Longitude</i>	<i>Slope</i>	<i>Rank</i>	<i>Longitude</i>	<i>Slope</i>
1	24°-25°E	2.614	1	24°-25°E	2.625	1	22°-23°E	2.471
2	21°-22°E	2.446	2	22°-23°E	2.510 ^a	2	20°-21°E	2.370
3	23°-24°E	2.396 ^{ab}	3	23°-24°E	2.492 ^a	3	21°-22°E	2.332 ^a
4	25°-26°E	2.363 ^b	4	21°-22°E	2.394	4	25°-26°E	2.326 ^a
5	20°-21°E	2.353 ^a	5	20°-21°E	2.345	5	23°-24°E	2.311
6	26°-27°E	2.330 ^a	6	25°-26°E	2.136	6	26°-27°E	2.282 ^b
7	22°-23°E	2.220	7	26°-27°E	2.087	7	24°-25°E	2.281 ^b

Spring research data showed similar trends to autumn samples. Spring male stage I squid were significantly ($p = 0.035$) different in their length-weight regressions between different longitudinal areas, although no significant differences were found between area 20° to 21°E and area 25° to 26°E ($q = 0.689$, $p = 0.658$); area 20° to 21°E and area 26° to 27°E ($q = 1.611$, $p = 0.143$); between area 23° to 24°E and area 25° to 26°E ($q = 1.531$, $p = 0.166$) and between area 25° to 26°E and area 26° to 27°E ($q = 1.555$, $p = 0.159$) as revealed by Tukey tests.

Spring male II squid similarly displayed highly significant ($p < 0.001$) differences between areas. All areas had highly significant ($p < 0.001$) differences except for between area 22° to 23°E and area 23° to 24°E ($q = 1.895$, $p = 0.079$).

Spring male III ANCOVA results were highly significant ($p < 0.001$) although no significant differences existed between area 21° to 22°E and area 25° to 26°E ($q = 1.091$, $p = 0.365$) and between area 24° to 25°E and area 26° to 27°E ($q = 0.078$, $p = 0.998$).

Ranked length-weight regression slopes of spring females for all three maturity stages in decreasing order of steepness are presented in Table 3.2.7.

Table 3.2.7 Length-to-weight regression slopes by longitude for spring caught female chokka ranked in descending slope steepness in each of three reproductive stages. Superscript letters indicate regression slopes not significantly different from each other within each maturity stage.

<i>Female I</i>			<i>Female II</i>			<i>Female III</i>		
<i>Rank</i>	<i>Longitude</i>	<i>Slope</i>	<i>Rank</i>	<i>Longitude</i>	<i>Slope</i>	<i>Rank</i>	<i>Longitude</i>	<i>Slope</i>
1	21°-22°E	2.538	1	24°-25°E	2.560	1	23°-24°E	2.539 ^a
2	24°-25°E	2.530	2	23°-24°E	2.499	2	24°-25°E	2.536 ^a
3	22°-23°E	2.471 ^a	3	22°-23°E	2.447 ^a	3	20°-21°E	2.520
4	25°-26°E	2.463 ^a	4	21°-22°E	2.446 ^a	4	26°-27°E	2.445 ^b
5	26°-27°E	2.417	5	20°-21°E	2.385 ^b	5	25°-26°E	2.443 ^b
6	20°-21°E	2.386	6	26°-27°E	2.383 ^b	6	21°-22°E	2.412
7	23°-24°E	2.347	7	25°-26°E	2.171	7	22°-23°E	2.372

Female spring ANCOVA results also showed that significant differences were present in the length-weight regression slopes of the various maturity stages between different longitudinal areas. Spring female I revealed highly significant ($p < 0.001$) differences between all areas except for between area 22° to 23°E and area 25° to 26°E ($q = 0.742$, $p = 0.616$). Similarly spring female II squid showed highly significant ($p = 0.001$) ANCOVA results. Differences were present between all areas except for between area 20° to 21°E and area 26° to 27°E ($q = 0.168$, $p = 0.985$) and between area 21° to 22°E and area 22° to 23°E ($q = 0.138$, $p = 0.991$). Spring female III ANCOVA results were also highly significant ($p < 0.001$) except for between area 23° to 24°E and area 24° to 25°E ($q = 0.580$, $p = 0.747$) and between area 25° to 26°E and area 26° to 27°E ($q = 0.455$, $p = 0.842$).

Spatial patterns in length-to-weight regression

The spatial visualisation of the length-to-weight regression slopes for each sex in each season is presented in Figures 3.2.1 to 3.2.4.

For male I squid (Figure 3.2.1a), the three steepest regression slopes occurred between 22° and 26°E. Less steep slopes were generally found to the east and west of this except for the

least steep slope which occurred between 23° and 24°E. Male II squid (Figure 3.2.1b) showed a grouping of regression slopes of similar steepness between 21° and 24°E. The area between 26° and 27°E was not significantly different to the area between 23° and 24°E. Male III (Figure 3.2.1) showed grouping of the three steepest regression slopes between 20° and 23°E.

The distribution pattern of autumn female length-weight regression slopes (Figure 3.2.2) was similar to that of the males with the exception that the pattern of female II slopes (Figure 3.2.2b) was almost identical to female I (Figure 3.2.2a).

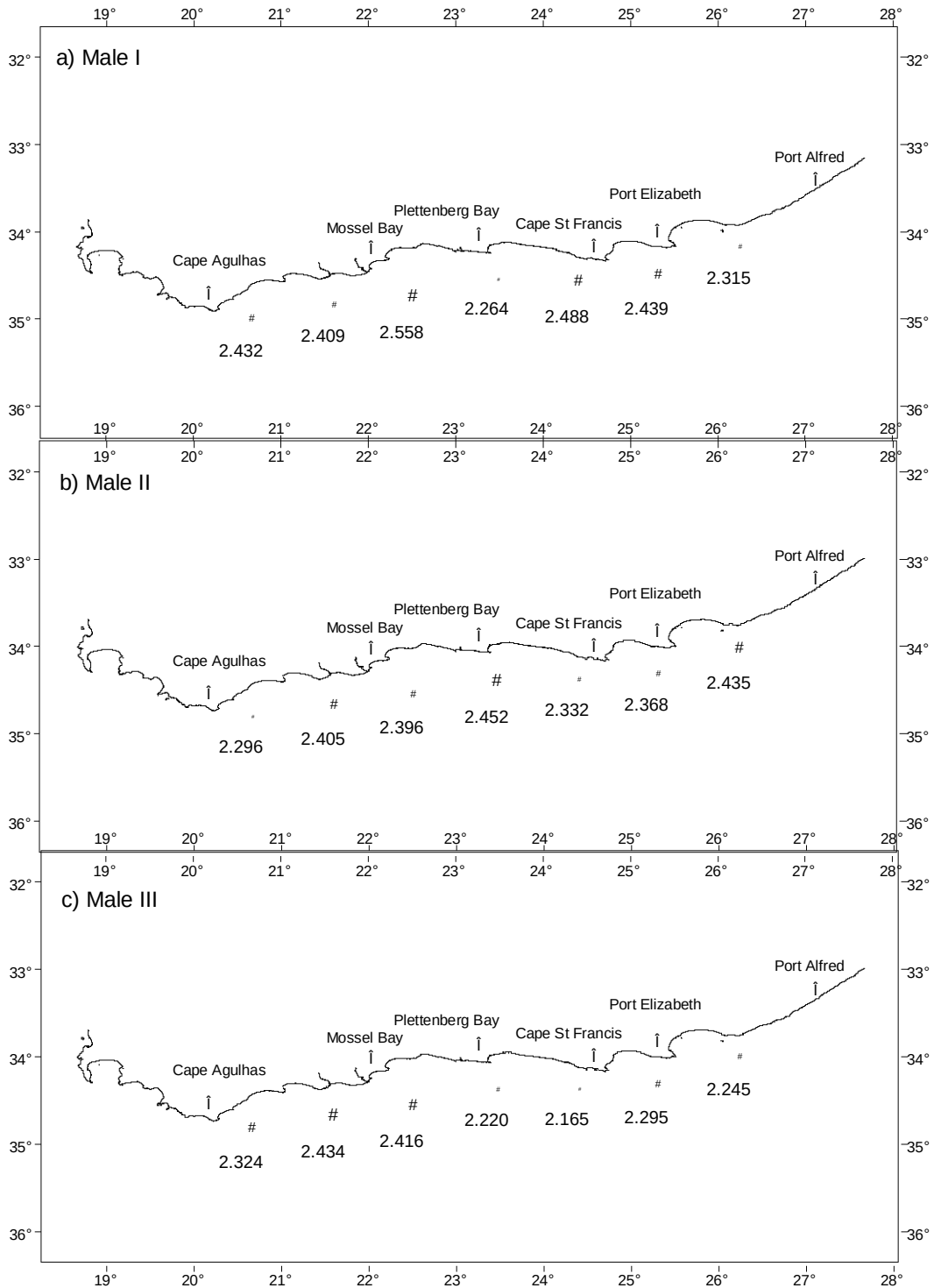


Figure 3.2.1 Spatial distribution of longitudinally grouped (one degree between 20° and 27°E) length-weight regression slopes of autumn caught male squid. The size of the dots represents the steepness.

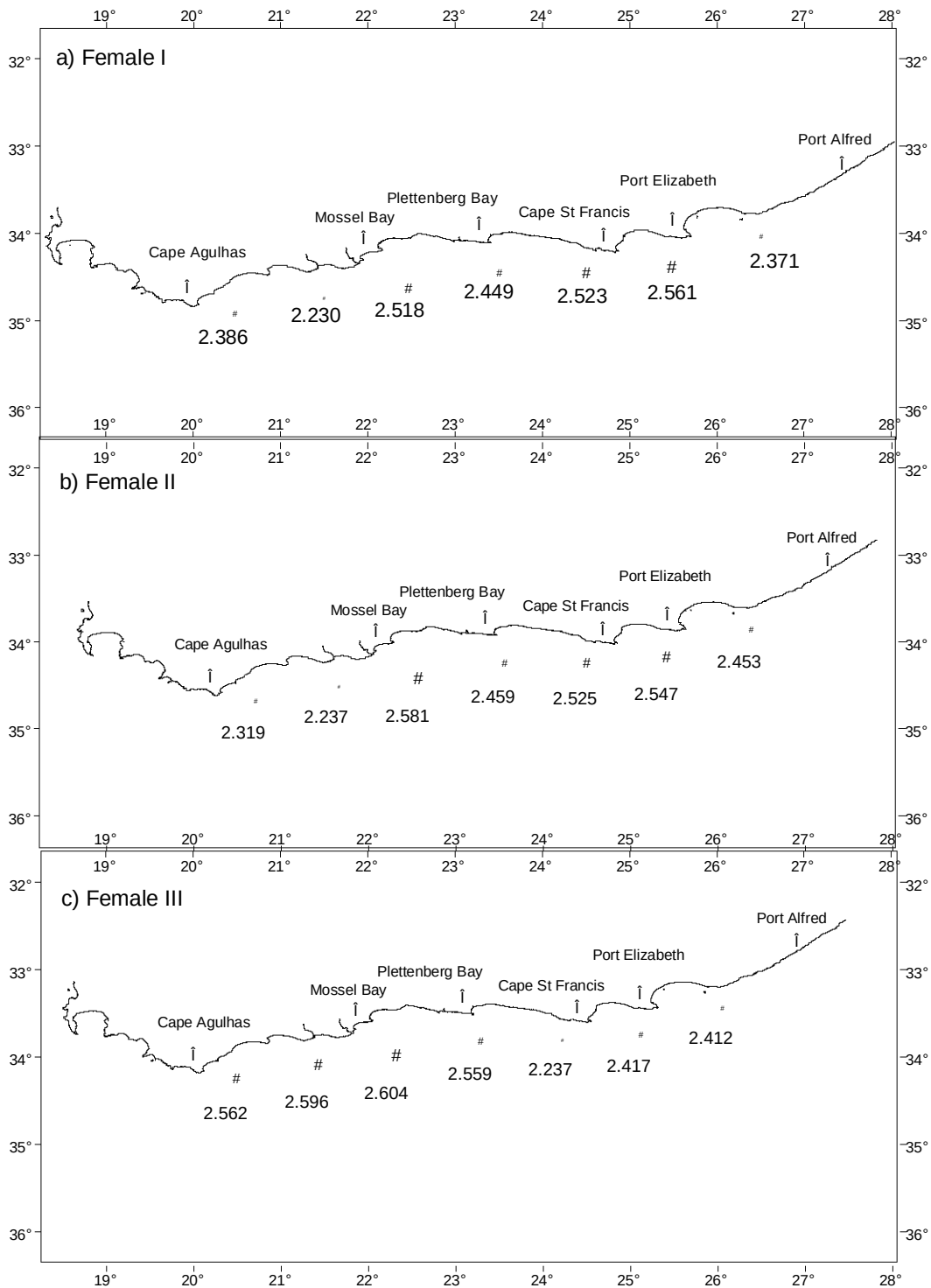


Figure 3.2.2 Spatial distribution of longitudinally grouped (one degree between 20° and 27°E) length-weight regression slopes of autumn caught female squid. The size of the dots represents the steepness.

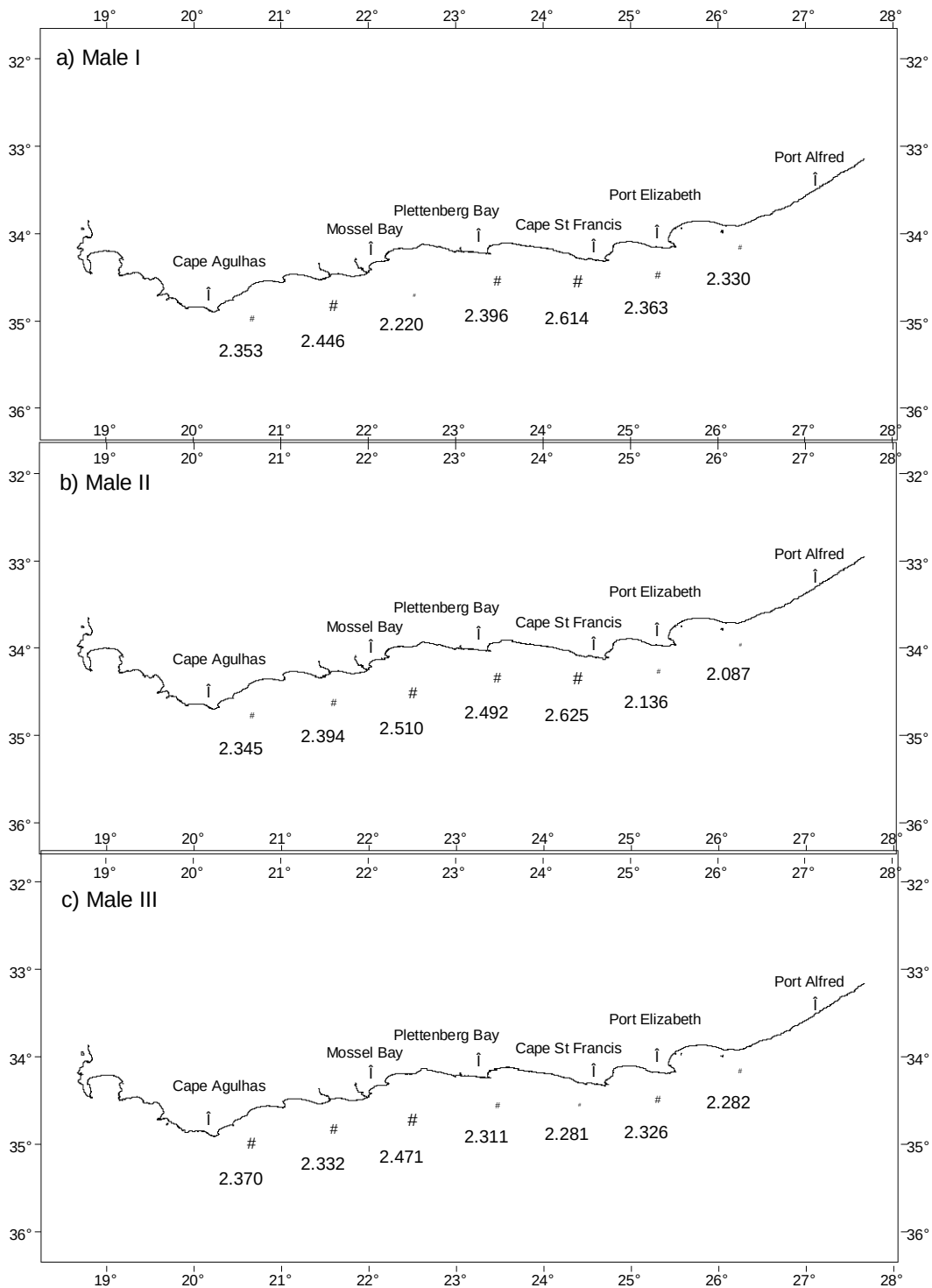


Figure 3.2.3 Spatial distribution of longitudinally grouped (one degree between 20° and 27°E) length-weight regression slopes of spring caught male squid. The size of the dots represents the steepness.

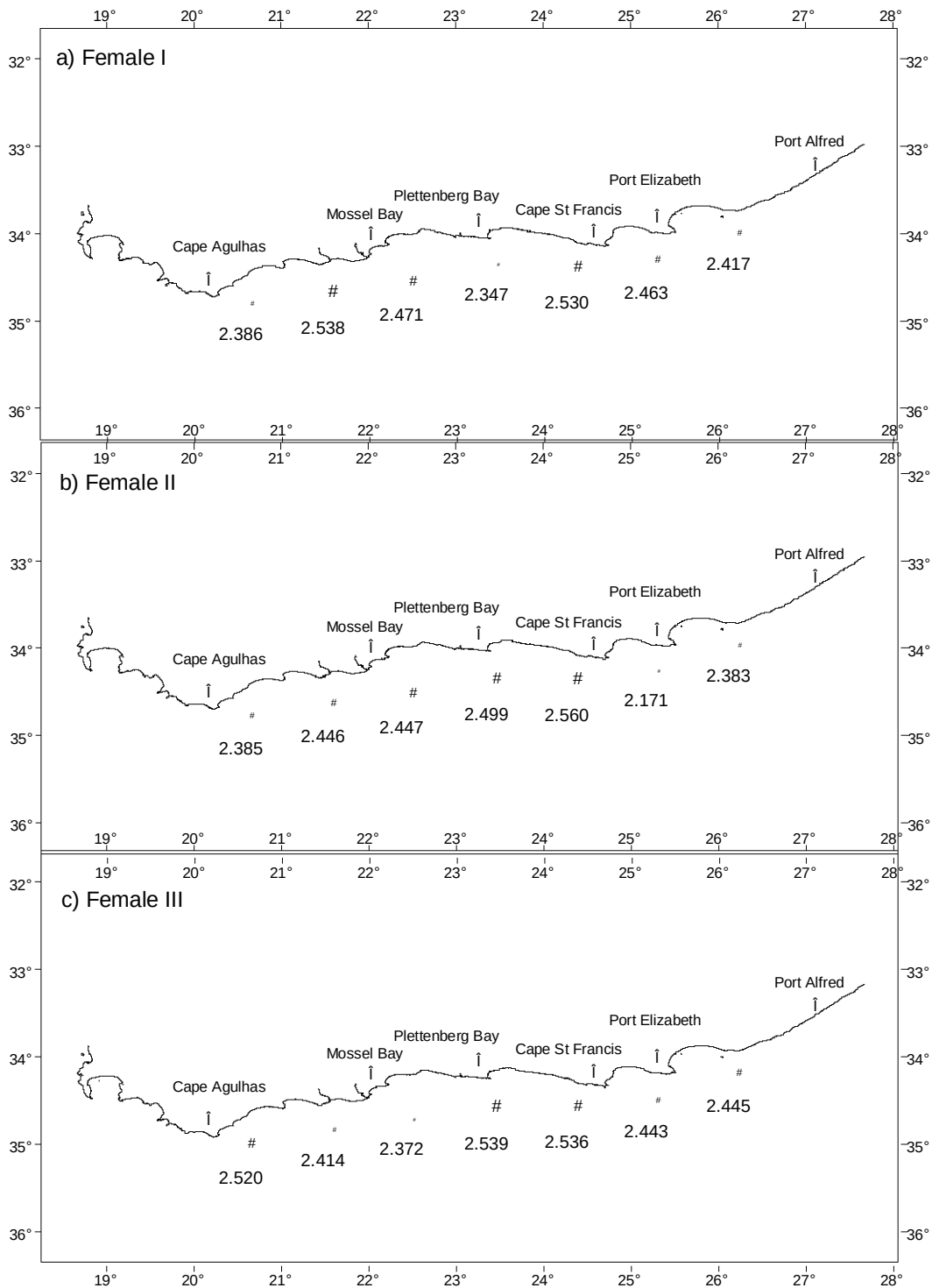


Figure 3.2.4 Spatial distribution of longitudinally grouped (one degree between 20° and 27°E) length-weight regression slopes of spring caught female squid. The size of the dots represents the steepness.

Spring male I regression slopes (Figure 3.2.3a) showed a grouping of steep regression slopes between 23° and 26°E although steep slopes were also apparent 20° and 22°E. Male II slopes (Figure 3.2.3b) showed a grouping of steep slopes between 22° and 25°E with less steep slopes to the east and west. Male III squid (Figure 3.2.3c) showed a grouping of the three steepest regression slopes in the west between 20° and 23°E with less steep slopes to the east.

Female I and II slopes showed similar patterns of distribution to the males of the same stages although the steepest regression slope for female I (Figure 3.2.4a) was between 20° and 23°E. Female III slopes (Figure 3.2.4c) showed a distinctly different pattern to the males having the two steepest slopes between 23° and 25°E and the next steepest slope between 20° and 21°E.

Between sex comparisons

Comparisons of male and female length-to-weight regression slopes are presented in Tables 3.2.8 to 3.2.13. Each maturity stage in each grouped longitudinal area was compared for both autumn and spring cruises.

In autumn stage I squid, significant differences between male and female regression slopes were found in all longitudinal areas (Table 3.2.8). In the areas between 20° and 23°E, males tend to be heavier than females of a similar size whereas females appear to be heavier than males between 23° and 27°E.

Table 3.2.8. Between sex comparisons of length-to-weight regression slopes of stage I male and female autumn caught chokka by longitudinal areas.

<i>Longitude</i>	<i>Male</i>	<i>Female</i>	<i>t</i>	<i>p</i>
20°-21°E	2.432	2.386	4.986	< 0.001
21°-22°E	2.409	2.230	19.701	< 0.001
22°-23°E	2.558	2.518	2.603	0.011
23°-24°E	2.264	2.449	12.152	< 0.001
24°-25°E	2.488	2.523	2.192	0.031
25°-26°E	2.439	2.561	5.320	< 0.001
26°-27°E	2.315	2.371	2.631	0.011

In autumn stage II squid, significant differences between male and female regression slopes were found in all longitudinal areas except for between 23° and 24°E and between 26° and 27°E (Table 3.2.9). In the areas between 21° and 23°E, the regression results suggest that males are heavier than females of a similar size. Between 23° and 27°E, females appear to be as heavy or heavier than males.

Table 3.2.9. Between sex comparisons of length-to-weight regression slopes of stage II male and female autumn caught chokka by longitudinal areas.

<i>Longitude</i>	<i>Male</i>	<i>Female</i>	<i>t</i>	<i>p</i>
20°-21°E	2.296	2.319	4.245	< 0.001
21°-22°E	2.405	2.237	45.355	< 0.001
22°-23°E	2.396	2.581	32.321	< 0.001
23°-24°E	2.452	2.459	0.828	0.408
24°-25°E	2.332	2.525	17.531	< 0.001
25°-26°E	2.368	2.547	9.278	< 0.001
26°-27°E	2.435	2.453	1.352	0.180

In autumn stage III squid, highly significant differences between male and female regression slopes were found in all longitudinal areas (Table 3.2.10). Females also had steeper regression slopes than males in all areas.

Table 3.2.10. Between sex comparisons of length-to-weight regression slopes of stage III male and female autumn caught chokka by longitudinal areas.

<i>Longitude</i>	<i>Male</i>	<i>Female</i>	<i>t</i>	<i>p</i>
20°-21°E	2.324	2.562	42.443	< 0.001
21°-22°E	2.434	2.596	37.543	< 0.001
22°-23°E	2.416	2.604	32.027	< 0.001
23°-24°E	2.220	2.559	52.598	< 0.001
24°-25°E	2.165	2.237	11.182	< 0.001
25°-26°E	2.295	2.417	12.359	< 0.001
26°-27°E	2.245	2.412	15.804	< 0.001

Spring stage I squid showed significant differences between male and female regression slopes in all longitudinal areas except for between 20° and 21°E (Table 3.2.11). Females had steeper regression slopes than males in all other areas except for areas between 23° and 25°E where males had steeper regression slopes.

Table 3.2.11. Between sex comparisons of length-to-weight regression slopes of stage I male and female spring caught chokka by longitudinal areas.

<i>Longitude</i>	<i>Male</i>	<i>Female</i>	<i>t</i>	<i>p</i>
20°-21°E	2.353	2.369	1.758	0.080
21°-22°E	2.446	2.538	8.181	< 0.001
22°-23°E	2.220	2.471	19.562	< 0.001
23°-24°E	2.396	2.347	2.459	0.016
24°-25°E	2.614	2.530	2.185	0.036
25°-26°E	2.363	2.463	3.872	< 0.001
26°-27°E	2.330	2.417	4.765	< 0.001

In spring stage II squid, significant differences between male and female regression slopes occurred in all longitudinal areas except for between 23° and 24°E (Table 3.2.12). Females had steeper regression slopes than males in all other areas except for between 22° and 23°E and between 24° and 25°E where males had steeper regression slopes.

Table 3.2.12. Between sex comparisons of length-to-weight regression slopes of stage II male and female spring caught chokka by longitudinal areas.

<i>Longitude</i>	<i>Male</i>	<i>Female</i>	<i>t</i>	<i>p</i>
20°-21°E	2.345	2.385	7.527	< 0.001
21°-22°E	2.394	2.446	9.218	< 0.001
22°-23°E	2.510	2.447	7.528	< 0.001
23°-24°E	2.492	2.499	0.450	0.654
24°-25°E	2.625	2.560	3.092	0.004
25°-26°E	2.136	2.171	2.168	0.035
26°-27°E	2.087	2.383	11.037	< 0.001

For spring stage III squid, highly significant differences between male and female regression slopes occurred in all longitudinal areas except for between 22° and 23°E where there was no significant difference (Table 3.2.13). Females had steeper regression slopes than males in all other areas.

Table 3.2.13. Between sex comparisons of length-to-weight regression slopes of stage III male and female spring caught chokka by longitudinal areas.

<i>Longitude</i>	<i>Male</i>	<i>Female</i>	<i>t</i>	<i>p</i>
20°-21°E	2.370	2.520	22.089	< 0.001
21°-22°E	2.332	2.414	15.836	< 0.001
22°-23°E	2.382	2.372	1.174	0.241
23°-24°E	2.311	2.539	24.613	< 0.001
24°-25°E	2.281	2.536	22.963	< 0.001
25°-26°E	2.326	2.443	11.075	< 0.001
26°-27°E	2.282	2.445	20.162	< 0.001

Seasonal comparisons

Seasonal comparisons for each sex in all longitudinal areas are presented in Tables 3.2.14 to 3.2.16.

No clear trend in seasonal differences was evident in stage I squid (Table 3.2.14). Autumn length-to-weight regression slopes were steeper than spring in three of seven longitudinal areas (between 20° and 21°E; between 22° and 23°E and between 23° and 24°E) for males and in four of seven areas for females (between 20° and 21°E; between 22° and 23°E; between 23° and 24°E and between 25° and 26°E). No significant differences in slopes were found between 26° and 27°E for males and between 24° and 25°E for females.

Table 3.2.14 Between season comparisons of length-to-weight regression slopes in male and female stage I autumn and spring caught chokka by longitudinal areas.

<i>Longitude</i>	<i>Male</i>				<i>Longitude</i>	<i>Female</i>			
	<i>autumn</i>	<i>spring</i>	<i>t</i>	<i>p</i>		<i>autumn</i>	<i>spring</i>	<i>t</i>	<i>p</i>
20°-21°E	2.432	2.353	7.305	< 0.001	20°-21°E	2.386	2.369	2.083	0.038
21°-22°E	2.409	2.446	2.820	0.005	21°-22°E	2.230	2.538	34.426	< 0.001
22°-23°E	2.558	2.220	20.388	< 0.001	22°-23°E	2.518	2.471	3.817	< 0.001
23°-24°E	2.264	2.396	5.673	< 0.001	23°-24°E	2.449	2.347	7.567	< 0.001
24°-25°E	2.488	2.614	4.028	0.002	24°-25°E	2.523	2.530	0.326	0.745
25°-26°E	2.439	2.363	2.413	0.021	25°-26°E	2.561	2.463	5.028	< 0.001
26°-27°E	2.315	2.330	0.645	0.523	26°-27°E	2.371	2.417	2.375	0.021

No clear trend in seasonal differences was evident in stage II squid (Table 3.2.15) with autumn length-to-weight regression slopes being steeper than spring in three of seven longitudinal areas (between 21° and 22°E; between 25° and 26°E and between 26° and 27°E) for males and in three of seven areas for females (between 22° and 23°E; between 25° and 26°E and between 26° and 27°E).

Table 3.2.15 Between season comparisons of length-to-weight regression slopes in male and female stage II autumn and spring caught chokka by longitudinal areas.

<i>Longitude</i>	<i>Male</i>				<i>Longitude</i>	<i>Female</i>			
	<i>autumn</i>	<i>spring</i>	<i>t</i>	<i>p</i>		<i>autumn</i>	<i>Spring</i>	<i>t</i>	<i>p</i>
20°-21°E	2.296	2.345	8.744	< 0.001	20°-21°E	2.319	2.385	12.593	< 0.001
21°-22°E	2.405	2.394	2.210	0.027	21°-22°E	2.237	2.446	49.203	< 0.001
22°-23°E	2.396	2.510	13.982	< 0.001	22°-23°E	2.581	2.447	22.977	< 0.001
23°-24°E	2.452	2.492	3.166	0.002	23°-24°E	2.459	2.499	4.432	< 0.001
24°-25°E	2.332	2.625	14.635	< 0.001	24°-25°E	2.525	2.560	2.563	0.012
25°-26°E	2.368	2.136	14.166	< 0.001	25°-26°E	2.547	2.171	17.789	< 0.001
26°-27°E	2.435	2.087	16.497	< 0.001	26°-27°E	2.453	2.383	3.834	< 0.001

No clear trend in seasonal differences was evident in stage III squid (Table 3.2.16) with autumn length-to-weight regression slopes being steeper than spring in two of seven longitudinal areas (between 21° and 22°E and between 22° and 23°E) for males and in four of seven areas for females (between 20° and 21°E; between 21° and 22°E; between 22° and 23°E and between 23° and 24°E).

Table 3.2.16. Between season comparisons of length-to-weight regression slopes in male and female stage III autumn and spring caught chokka by longitudinal areas.

<i>Longitude</i>	<i>Male</i>				<i>Longitude</i>	<i>Female</i>			
	<i>autumn</i>	<i>spring</i>	<i>t</i>	<i>p</i>		<i>autumn</i>	<i>spring</i>	<i>t</i>	<i>p</i>
20°-21°E	2.324	2.370	6.594	< 0.001	20°-21°E	2.562	2.520	7.207	< 0.001
21°-22°E	2.434	2.332	19.029	< 0.001	21°-22°E	2.596	2.414	49.778	< 0.001
22°-23°E	2.416	2.382	4.399	< 0.001	22°-23°E	2.604	2.372	46.828	< 0.001
23°-24°E	2.220	2.311	11.172	< 0.001	23°-24°E	2.559	2.539	3.670	< 0.001
24°-25°E	2.165	2.281	12.336	< 0.001	24°-25°E	2.237	2.536	50.914	< 0.001
25°-26°E	2.295	2.326	2.699	0.007	25°-26°E	2.417	2.443	3.426	< 0.001
26°-27°E	2.245	2.282	3.330	< 0.001	26°-27°E	2.412	2.445	4.717	< 0.001

Commercial Data

Statistical descriptions of the monthly commercial length-weight regressions are presented in Appendix II.

Monthly between sex comparisons

The results of the student's t-tests comparing male and female slopes in each month are presented for the 1988-89 jig data in Table 3.2.17. Highly significant ($p < 0.001$) differences

between males and females existed in all months. Female slopes were steeper than males in March 1988, August 1988, November 1988, December 1988, March 1989 and April 1989.

Table 3.2.17 Statistical comparison of monthly length-to-weight regression slopes for mature male and female chokka caught on the inshore spawning grounds (approximately 25°-27°E) between March 1988 and June 1989.

<i>Month</i>	<i>Male</i>	<i>Female</i>	<i>t</i>	<i>df</i>	<i>p</i>
Mar '88	2.556	2.992	13.103	17	< 0.001
Apr '88	2.042	1.944	9.492	47	< 0.001
May '88	1.903	1.944	2.742	55	0.008
June '88	1.779	1.054	88.602	61	< 0.001
July '88	1.848	1.602	34.187	114	< 0.001
Aug '88	2.056	2.143	32.812	133	< 0.001
Sept '88	2.321	2.052	36.007	301	< 0.001
Oct '88	2.354	2.284	10.478	175	< 0.001
Nov '88	2.199	2.407	48.286	297	< 0.001
Dec '88	2.242	3.210	162.79	254	< 0.001
Jan '89	2.497	2.067	63.755	99	< 0.001
Mar '89	2.256	2.444	22.583	148	< 0.001
Apr '89	2.268	2.387	9.411	100	< 0.001
May '89	2.314	2.260	6.126	238	< 0.001
Jun '89	2.325	1.988	45.222	144	< 0.001

The results of the student's t-tests comparing male and female slopes in each month are presented for the 1999-2000 jig data in Table 3.2.18. Highly significant ($p < 0.001$) differences between males and females were evident in all months except for June 1999 ($p = 0.060$) and August 1999 ($p = 0.118$).

Female slopes were steeper than males in February 1999, July 1999, November 1999, February 2000 and June 2000.

The results of the student's t-tests comparing male and female slopes in each month are presented for the 1999-2000 trawl data in Table 3.2.19. There were highly significant ($p < 0.001$) differences between males and females in all months except for November 1999 ($p = 0.477$). Female slopes were steeper than males in February 1999, April 1999, June 1999, October 1999, November 1999, January 1999 and May 2000.

Table 3.2.18 Statistical comparison of monthly length-to-weight regression slopes for mature male and female chokka caught on the inshore spawning grounds (approximately 25°-27°E) between May 1999 and June 2000.

<i>Month</i>	<i>Male</i>	<i>Female</i>	<i>t</i>	<i>df</i>	<i>p</i>
Feb '99	1.810	2.481	35.375	20	< 0.001
Apr '99	1.708	1.565	15.147	36	< 0.001
May '99	2.336	2.100	26.478	59	< 0.001
June '99	2.257	2.227	1.912	74	0.060
July '99	2.285	2.939	39.417	70	< 0.001
Aug '99	0.276	0.296	1.602	36	0.118
Nov '99	2.426	2.779	28.502	68	< 0.001
Feb '00	1.810	2.517	31.450	21	< 0.001
April '00	1.708	1.565	15.147	36	< 0.001
May '00	2.205	1.867	34.484	69	< 0.001
June '00	1.748	2.429	52.958	43	< 0.001

Table 3.2.19 Statistical comparison of monthly length-to-weight regression slopes for mature male and female chokka caught in demersal trawl gear on the central and eastern Agulhas Bank (approximately 22°-24°E) between April 1999 and May 2000.

<i>Month</i>	<i>Male</i>	<i>Female</i>	<i>t</i>	<i>df</i>	<i>p</i>
Feb '99	2.169	2.863	38.647	26	< 0.001
Apr '99	2.336	2.651	8.063	19	< 0.001
May '99	2.428	1.156	40.813	21	< 0.001
June '99	1.616	2.074	19.554	31	< 0.001
July '99	2.600	2.519	4.295	56	< 0.001
Aug '99	2.370	0.188	142.89	33	< 0.001
Sept '99	2.526	2.387	5.968	32	< 0.001
Oct '99	2.251	3.942	84.813	12	< 0.001
Nov '99	2.611	2.638	0.729	14	0.477
Jan '00	2.114	2.509	22.703	22	< 0.001
Feb '00	3.205	2.406	49.537	18	< 0.001
Mar '00	2.579	2.430	5.406	12	< 0.001
May '00	2.430	2.734	17.097	15	< 0.001

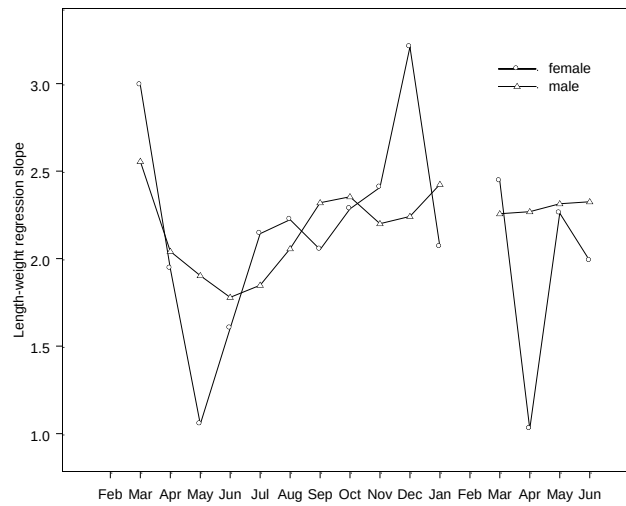
Between month comparisons

Figure 3.2.5 describes the monthly changes in length-weight regression slopes for a) the 1988-1989 jig data, b) the 1999-2000 jig data and c) the 1999-2000 commercial trawl data. The 1988-1989 jig data (Figure 3.2.5a) describe a decrease in regression slope steepness between March and May 1988 for females (from 2.99 to 1.05) and March and June 1988 for males (from 2.56 to 1.78) followed by a recovery through spring to peak in summer before female slopes decreased in autumn and males remained constant.

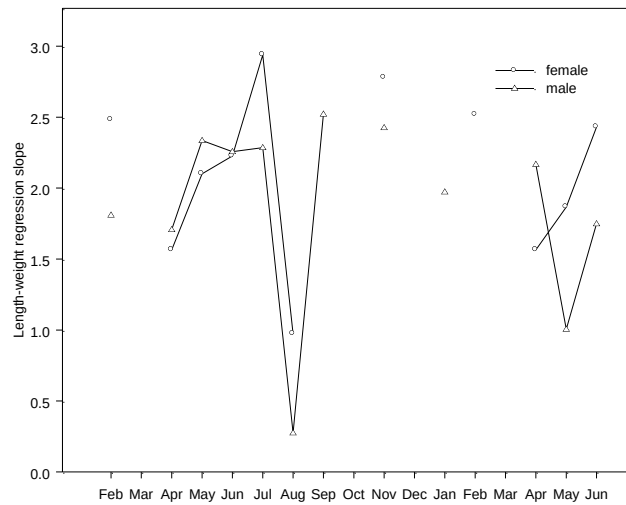
In the 1999-2000 jig data (Figure 3.2.5b), an increase between April and June 1999 was followed by a sharp decrease in both males (from 2.29 in July to 0.28 in August 1999) and females (from 2.94 in July to 0.97 in August 1999). This was followed by higher values in spring and summer and a subsequent decrease the following autumn.

The trawl data for the same time period (Figure 3.2.5c) describe a slight decrease in male regression slopes (from 2.43 in May to 1.62 in June 1999) relative to females (from 2.52 in July to 0.19 in August 1999). Higher slopes were evident in both sexes through spring and summer.

a)



b)



c)

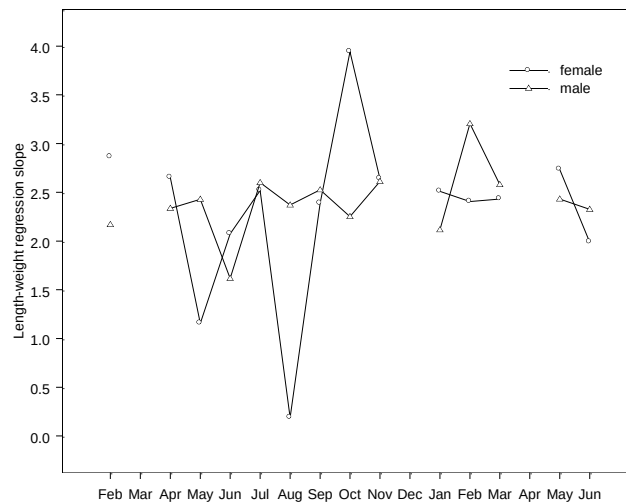


Figure 3.2.5. Monthly length-to-weight regression slopes for mature male and female chokka caught by a) hand jigging on the inshore spawning grounds (approximately 25°-27°E) between March 1988 and June 1989, b) hand jigging on the inshore spawning grounds between February 1999 and June 2000 and c) commercial demersal trawl gear on the central and eastern Agulhas Bank (approximately 22°-24°E) between February 1999 and May 2000.

Discussion

Length frequency analysis

Up to six length cohorts were identified for males although the largest cohort was confined to the east and more prevalent in autumn. In most cases, four or five cohorts were identified. A major seasonal difference was in the distribution of the smallest cohort, which was widespread in autumn but more abundant in the west in spring. In the females there were usually only three cohorts in each area and the smallest cohort was smaller in autumn than spring. Cohort I females were also more prevalent in the west. This finding is in agreement with Augustyn *et al.* (1994) who ascribe the smallest autumn cohort to the summer spawning period.

While it is likely that the smallest cohort can be traced to the most recent spawning, there is no direct link between the size-cohorts presented here and actual age-cohorts. What appear as discrete cohorts may be a mixture of two or more age cohorts, that because of variable growth rates are the same size but in fact are of different ages. An alternative hypothesis is that cohorts I and II and III and IV are sub-sets of a single spawning episode that experience variable growth rates. This would account for the “pseudo-cohorts” apparent in the length frequency histograms.

Similar mixed cohort problems have been investigated in *L. forbesi* where Collins *et al.* (1999) were able to trace two cohorts with different growth characteristics back to a single winter spawning event and suggested that squid born early in the season hatch quicker and experience faster growth as a result of warmer water temperatures while those born later in the season may have delaying hatching and slower growth.

In chokka, which have a peak summer spawning event, it is unlikely that water temperatures would negatively impact on growth and further investigation into water temperature fluctuation over the spawning season needs to be made.

In *L. gahi* in Falkland Island waters, Hatfield (1996) and Agnew *et al.* (1998) identified up to three different cohorts of squid recruiting to the fishery at different times of the year. Knowing the timing of recruitment and growth of each cohort has led to a revision of fishery management with coherent stock assessment based on individual cohorts establishing biological reference points such as minimum escapement biomass.

Until adequate ageing data are available for chokka, resolution of these cohorts cannot be achieved from an age perspective. Identification of discrete size cohorts does, however, create a framework on which to base further ageing studies. Further identification of pulses of recruitment could also have fishery management implications and each cohort could be managed as a discrete fishery unit.

Length-weight relationships

Research data

Inter-stage comparisons

Length-to-weight relationship equations are frequently used in stock assessment to estimate biomass based on length measurements of animals. Currently a single length-to-weight equation is used when estimating chokka biomass from research surveys and this equation is applied to all life history stages. Significant differences in the steepness of the regression slopes were found between all maturity stages for each sex suggesting that it may be more

appropriate using life history stage specific length-to-weight equations in biomass calculations rather than applying a single equation to the entire squid life cycle.

No clear maturity stage trends were noticed. The order of steepness in regression slopes was inconsistent with immature squid having the steepest regression slopes in some areas and maturing or mature squid having the steepest slopes in other areas.

Spatial comparisons

Significant differences were apparent in the length-weight regression slopes of all life history stages between different longitudinal areas. It was assumed, that if steep regression slopes in juvenile squid were related to increased feeding (unlikely to be related to gonad development), discrete areas of similarly steep regression slopes would identify areas of rapid growth that may indicate feeding grounds.

In the autumn data, a potential feeding area for juveniles was identified between 22° and 26° E and the area between 21° and 22° E was indicated as a potential spring feeding area. The area between 20° and 21° E also warrants attention as it was shown have no difference in regression slope steepness to area 25° to 26° E in autumn males and to the area between 23° and 24° E in spring males.

This distribution pattern seems to match the area of high zooplankton productivity described by Augustyn *et al.* (1992; Figure 9). While paralarvae probably feed on copepods (chiefly *Calanus agulhensis*), juvenile to adult chokka are opportunist predators capable of feeding at all trophic levels throughout the water column (Sauer and Lipiński 1991, Augustyn *et al.* 1994).

Seasonal as well as diurnal changes in prey type have been identified in the offshore (Augustyn 1990, 1991), and inshore environments (Sauer and Lipiński 1991, Augustyn *et al.* 1994). A shift from crustacean to teleost prey also seems to be apparent with growth, squid larger than 100mm feeding more on pelagic (anchovies) and demersal fish species (Sauer and Lipiński 1991, Augustyn *et al.* 1994).

If the area of high plankton productivity is also an area of high abundance of other chokka prey items, this is a plausible explanation for the observed pattern in the regression slopes. Similarly, the offshore Agulhas Bank together with the west coast has traditionally been considered as the chokka feeding grounds (Augustyn 1990, Augustyn *et al.* 1994, Lipiński 1998), and steep regression slopes in this area would support their hypothesis.

In mature squid, various condition indices have been used including digestive gland weight as a percentage of total body weight (Pierce *et al.* 1994) and mantle thickness (Augustyn 1990). Length-to-weight regressions have also been used as a proxy for condition factor. Usually the regression of mantle mass against mantle length is used and with the partitioning of energy to gonad production, a decreasing steepness of regression slope is noted with the onset of sexual maturity.

In this thesis, whole body weight which included the gonad mass was used to produce samples of sufficient statistical size. It was assumed that steeper regression slopes would indicate a combination of increased food intake as well as the development of gonadal tissue preceding the peak spawning season.

For both mature male and female squid, a clustering of steep regression slopes occurred between 20° and 23° E in autumn and for mature males in spring. Spring males also showed similarly steep slopes between 25° and 26° E. Spring mature females had steepest regression slopes between 23° and 25° E although the third steepest slope was between 20° and 21° E. The steeper regression slopes in the west are potentially a consequence of the timing of the research surveys (autumn and spring) ahead of and immediately after the peak breeding seasons (winter and summer) and could represent a combination of gonadal development and greater feeding in preparation for the inshore spawning migration. Steep spring regression slopes in the east may indicate an earlier migration pulse of mature animals, while less steep slopes indicate animals that have already spawned and are losing condition. Further evidence of loss of condition on the inshore spawning grounds is found in the thinner mantles of spawning squid compared to those from offshore habitats (Augustyn 1990). Based on existing data that suggest that greater feeding does in fact occur offshore on the feeding grounds than on the inshore spawning grounds (evidenced by steeper regression slopes in mature animals from the offshore habitat) (Augustyn 1990, 1991), this theory is feasible and remains to be tested.

Between sex comparisons

Significant differences in regression slope steepness between sexes revealed some of the most interesting results. Firstly, the most obvious pattern is one of mature females having steeper regression slopes than males in all areas in both seasons. Sauer and Lipiński (1991) found that there were no significant differences between sexes in stomach content mass as a percentage of body mass on the spawning grounds. They also found that the level of feeding on the spawning grounds was low with only 6.7 percent of day caught squid and 28.5 percent of night caught squid having food in their stomachs.

Augustyn (1990) also found that only 3.4 percent of squid sampled on the spawning grounds had been feeding compared to 18.2 percent in offshore samples and 30.3 percent on the west coast.

The consequences (assuming both sexes have equal levels of feeding) are that females invest more energy into gonad production than males. Such findings agree with length-to-weight equations for other loliginid squid where differences between males and females were noted but not tested i.e. *L. v. vulgaris* (Coelho *et al.* 1994, Guerra and Rocha 1994) and *L. forbesi* (Guerra and Rocha 1994, Pierce *et al.* 1994). Coelho *et al.* (1994) argued that the differences between sexes are not as great in *L. v. vulgaris* as for other species and vary depending on sampling season. Using samples collected at the same time, Moreno *et al.* (1994) tested for and found significant differences between sexes in *L. forbesi* but not *L. v. vulgaris*.

Comparison of male and female slopes in juveniles and subadults revealed an apparent spatial pattern in autumn sampled squid. Squid from the western longitudinal areas (between 20° and 23° E) showed males to be relatively heavier than females. Spring data revealed a somewhat different pattern where heavier males are present between 23° and 25° E.

Seasonal comparisons

Seasonal differences in regression slopes also failed to produce clear patterns. Although in most cases, there were significant seasonal differences, they were highly variable with autumn slopes being steeper than spring slopes in some areas and spring being steeper than autumn in other areas. Common trends between sexes also failed to emerge.

If steeper regression slopes are a consequence of greater growth preceding capture than it stands to reason that prevailing environmental conditions and food availability during that growth period will influence the steepness of the regression slope. Squid growth is highly sensitive to temperature, particularly during the early life history stages, with higher temperatures resulting in greater growth and faster maturation (Forsythe and Hanlon 1988, Jackson 1995, Jackson *et al.* 1997, Hatfield 2000). Expanding on this idea, autumn caught squid often exhibit steeper slopes than spring caught as a consequence of growing in warmer, summer water. This pattern is evident in many loliginid species e.g. *L. forbesi* (Collins *et al.* 1995), *L. gahi* (Hatfield 2000), *L. opalescens* (Jackson 1998), *L. pealei* (Brodziak 1998), *L. chinensis* (Jackson 1995), *L. vulgaris* (Raya *et al.* 1998), *Lolliguncula brevis* (Jackson *et al.* 1997) and also in the ommastrephids; *Illex coindetii* (Arkhipkin *et al.* 2000) and *Dosidicus gigas* (Masuda *et al.* 1998).

In contrast to Northern Hemisphere habitats (Whitaker 1980, Waluda and Pierce 1998), the Agulhas Bank does not experience marked seasonal differences in either sea surface or bottom temperature (Roberts and Sauer 1994; Table I) with mean bottom temperatures along the coast at 18°C in summer and at 17°C in winter. Along the shelf edge, average summer (9°C) temperatures are actually cooler than winter (11°C). Temperature then seems unlikely as an influence in determining seasonal growth rates in chokka.

Differences in seasonal feeding may also be a possible source of variable growth rates with squid feeding primarily on fish in summer and crustaceans in winter on the west coast and offshore Agulhas Bank (Augustyn *et al.* 1994). Compared to crustacean prey, fish have a higher energy value and greater digestibility and it is plausible that feeding on fish would

result in better growth rates. Faced with the overwhelming evidence as a factor in seasonal growth in other loliginids, temperature should not, however, be dismissed.

Commercial data

By comparing trawl data to jig data it was hoped that it would be possible to visualise squid moving from the offshore feeding grounds in the west to the inshore spawning grounds in the east. This would have been evidenced by a lag between the time of peak regression slope steepness with the western samples (trawl) peaking a month or two before the eastern (jig) samples. This was not achieved for two reasons; firstly, the trawl samples were not taken from a tightly defined spatial area and overlapped with the jig samples did occur, and secondly because of the limited number of samples both inshore and offshore trawl samples were used. Given a greater number of samples each month it would be possible to select samples that were both offshore ($> 60\text{m}$ deep) and in the western area (between 20° and 22° E).

All three datasets revealed an annual cycle of changing steepness of regression slopes in both sexes. Peak regression slopes coincided with peak spawning periods in spring to summer (October to February) and autumn to winter (May to August). Steep regression slopes were often persistent for several months followed by rapid decreases in steepness after the breeding season. The only difference between the 1988-1989 jig data and the 1999-2000 data is the month of peak regression slopes which would be expected to fluctuate depending on interannual seasonal variation. Of particular interest are the differences between male and female slopes with females only having steeper slopes than males during the peak breeding seasons. This supports the research data in suggesting that females are only investing energy in gonadal development at these specific times.

This chapter demonstrated that the population structure of chokka on the Agulhas Bank is both spatially and temporally variable. Complex patterns of multiple recruitment, variable growth rates and maturation mean that it is difficult to use the data to develop population dynamics models. The results do, however, provide testable hypotheses for future studies.

CHAPTER 4

Reproductive Biology

Introduction

In a short-lived species such as chokka, knowledge of seasonal and spatial patterns of reproduction is of vital importance to fishery management. By setting appropriately timed closed seasons and effectively positioned closed areas, sustainable utilisation of the stock can be promoted. This is of special relevance to the South African jig fishery, which targets spawning aggregations (Sauer 1995b, Augustyn *et al.* 1992, Augustyn and Roel 1998).

Historically, peak spawning periods in chokka squid have been inferred from an increase in commercial jig catches. Such inference is justified since jig vessels target spawning aggregations (Sauer 1995b). It follows that, seasonal weather conditions notwithstanding, the highest catches will occur when the greatest numbers of spawning squid are present. Spawning intensity in this case is reflected by the abundance of squid present rather than by any biological measure. Peak catches traditionally occur in spring and summer following the closed season (October to November) and may last for several months until February (Augustyn *et al.* 1994). A smaller peak catch occurs in the austral winter months although this is not consistent in all years (Augustyn 1990, Augustyn *et al.* 1994). Mature squid are present all year round and it is likely that sporadic low intensity spawning occurs throughout the year.

Spatially, the traditional spawning grounds for chokka are the shallow, inshore bays between 23 and 26°E (Augustyn 1990, Sauer *et al.* 1992, 2000). Limited spawning occurs as far west as Danger Point and as far east as Great Fish Point (Augustyn *et al.* 1994).

Evidence for deep (>60m) spawning (Roberts and Sauer 1994, Roberts *et al.* in press) and possible reasons for this behaviour (Roberts in prep) are currently being investigated.

Knowledge of operational sex ratios can also prove vital to effective management particularly when it is shown that the fishing activity is sex biased as is the case in the chokka jig fishery which has a catch skewed towards large males (Lipiński 1994, Sauer 1995, Hanlon 1998). In order to set minimum size limits, size-at-maturity data is required and in order to examine recruitment trends, size ranges of various life history stages need definition.

This chapter examines aspects of chokka squid biology pertinent to reproduction. It considers two measures of reproductive seasonality: Gonadosomatic index (GSI) and the percentage of mature animals in each month. Sex ratio and size at maturity are also described and the size ranges of various maturity stages examined.

Materials and Methods

4.1 Seasonality

To examine both temporal and spatial trends in maturity, two hypotheses were tested. Firstly, median GSI between months was equal and secondly that median GSI between areas was equal. Percentage maturity was also investigated for spatial and temporal patterns. The monthly data were non-parametric and 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 pair-wise comparisons between months (Zar 1999).

The commercial trawl data were used to calculate the monthly percentage composition of the various maturity stages. Both the five and three-stage classification systems were used (Chapter 2) with the three-stage improving visualisation of trends. Differences in the monthly percentage of various maturity stages in each sex from February 1999 to June 2000 were described.

A comparison of GSI on a spatial basis across the Agulhas Bank was made using biomass survey data. Kruskal-Wallis tests were used to test for differences in mean 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 the monthly GSIs.

4.2 Sex ratio

Data from commercial trawl and jig-caught samples were used to describe monthly sex ratios on the spawning grounds and offshore. 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. Sex ratios for subadults and adults were calculated but were not possible to determine for juveniles since they are not sexed before measuring. The binomial test was also applied to these data.

4.3 Growth and maturation

Monthly mean length of mature squid

Mean lengths of mature squid were calculated monthly for the 1999-2000 jig and trawl data and the 1988-1989 jig data. Most datasets were non-parametric and a Kruskal-Wallis test was used to test for differences between months. The mean lengths of mature squid were compared to values from spring and autumn research samples.

Size-at-maturity

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

$$P(L) = \frac{1}{1 + e^{-(L-L_{50})/\delta}}$$

where $P(L)$ represents the proportion of mature squid in size class L , L_{50} the length at 50% sexual maturity and δ the width or steepness of the ogive. The model parameters were estimated by minimising the negative binomial likelihood. Likelihood ratio tests (Zar 1999) were employed to test for differences in both L_{50} and δ between seasons.

To investigate longitudinal trends, data from 20°-22°E were grouped as the western region, data from 22°-24°E were grouped to form the central region and samples from 24°-27°E formed the eastern region. These data were analysed with a likelihood ratio test.

Maturity stage size ranges

Using research data, percentage frequency occurrence of each of three maturity stages: juvenile, subadult and adult in 20mm size classes, were calculated for each area and plotted for both sexes in each season.

4.4 Distribution and abundance

The size ranges for each maturity stage were applied to length frequencies of research samples and seasonal distribution and relative abundance patterns for each maturity stage were mapped.

Results

4.1 Seasonality

Monthly 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 (Figures 4.1.1) and females (Figure 4.1.2).

Except for a slight decrease in GSI in June 1988, very little variation was noted in the 1988-1989 male data (Figure 4.1.1a). Between February and May, GSI decreased in both 1999-2000 male datasets. This was followed by fairly constant values between autumn (May 1999) and winter (July 1999) for the jig data (Figure 4.1.1b). In late winter (August 1999), the GSI peaked in the jig data. GSI subsequently decreased in September before rising again in November and then decreasing in January. Between April 2000 and May 2000 there was an increase, which subsequently decreased in June 2000. The male trawl data followed a similar trend with peaks in June and September 1999 and February 2000 (Figure 4.1.1c).

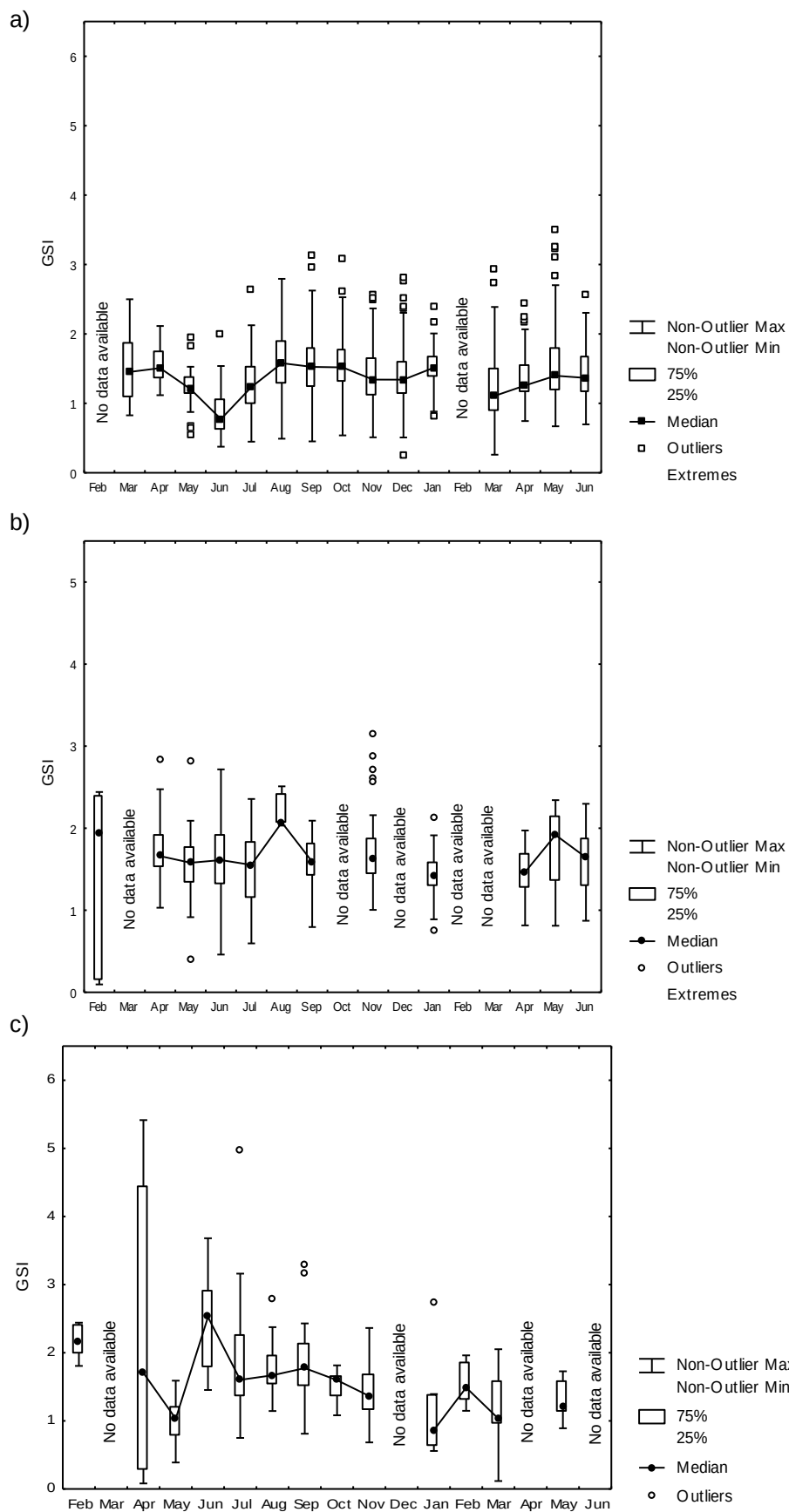


Figure 4.1.1 Monthly Gonadosomatic indices (GSI) for mature male chokka from a) 1988-1989 jig, b) 1999-2000 jig and c) 1999-2000 trawl data.

Reduced variability was noted in the 1988-1989 female GSI data (Figure 4.1.2a). 1999-2000 female jig and trawl data both described an initial decrease in GSI between February and April 1999, with the trawl data showing marked changes. GSI increased from a low in autumn (April 1999) to a winter (August 1999) peak for both data sets (Figure 4.1.2). An exception to this general pattern occurred in June 1999 when there was a decrease in the jig GSI that temporarily disrupted the trend of an increasing winter GSI (Figure 4.1.2b). This increase was followed by a decline to lower values in spring (September to October 1999). An increase in November provided a second GSI peak in summer (January 2000) for the trawl data (Figure 4.1.2c). A decrease between January 2000 and February 2000 was evident with an increase in March 2000 and a similar peak winter GSI (June 2000). The female jig data followed the same trend but there was no corresponding dip in February.

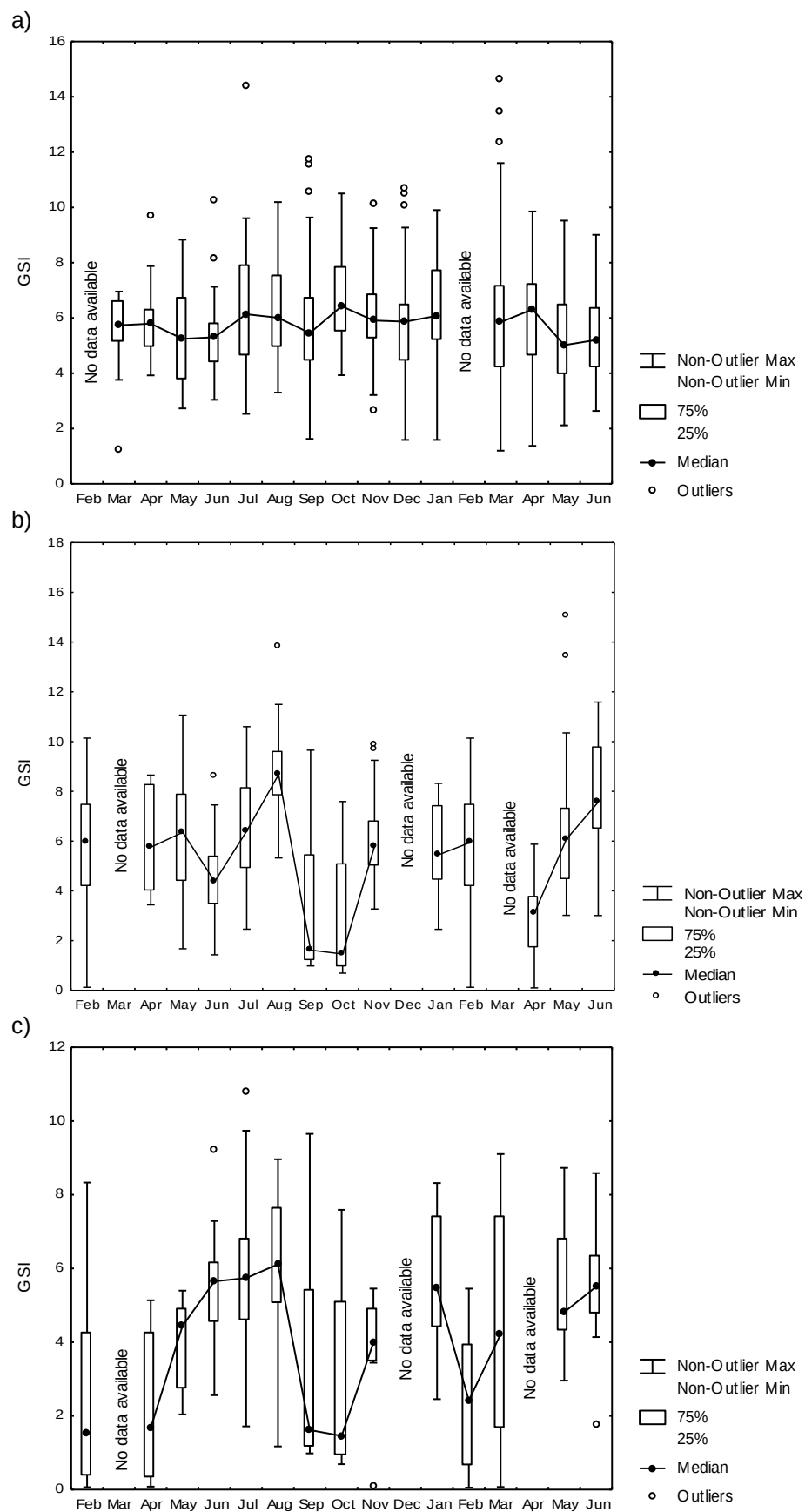


Figure 4.1.2 Monthly Gonadosomatic indices (GSI) for mature female chokka from a) 1988-1989 jig, b) 1999-2000 jig and c) 1999-2000 trawl data.

The results of the Kruskal-Wallis tests for differences in GSI between months are presented in Table 4.1.1. Although highly significant differences ($p < 0.001$) were recorded between months in all datasets, the small sample sizes in some months suggest that these data should be interpreted with caution.

Table 4.1.1. Results of the Kruskal-Wallis test for differences in GSI between months for three commercial datasets where n refers to the number of squid sampled, H is the Kruskal-Wallis test statistic and df is degrees of freedom.

	<i>Data</i>	<i>n</i>	<i>H</i>	<i>df</i>	<i>p</i>
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	135.6	16	< 0.001
Trawl 1999	Male	172	70.67	16	< 0.001
	Female	154	50.53	16	< 0.001

Spatial comparison of GSI

No autumn female longitudinal GSI values (Figure 4.1.3a), were significantly different. ($H = 9.005$, $df = 6$, $p = 0.173$).

In the male data (Figure 4.1.3b), highly significant differences were noted ($H = 30.145$, $df = 6$, $p < 0.001$). The results of the Mann-Whitney U-tests were highly significant ($z = -4.609$, $p < 0.001$) between adjacent areas 22° to 23°E and 23° to 24°E and between adjacent areas 23° to 24°E and 24° to 25°E ($z = 4.343$, $p < 0.001$). A highly significant ($z = -4.242$, $p < 0.001$) difference was also observed between the lowest (1.98 between 20° and 21°E) and highest (3.57 between 23° and 24°E) values.

In the spring female data (Figure 4.1.4a), the Kruskal-Wallis test produced a significant ($H = 15.008$, $df = 6$, $p = 0.020$) result. Significantly different median GSI's were noted between adjacent areas 21° to 22°E and 22° to 23°E ($z = 2.574$, $p = 0.010$) and a significant difference between adjacent areas 22° to 23°E and 23° to 24°E ($z = -2.484$, $p = 0.013$).

A highly significant ($z = -3.042$, $p = 0.002$) difference was also observed between the lowest (5.04 between 22° and 23°E) and highest (6.16 between 26° and 27°E) areas.

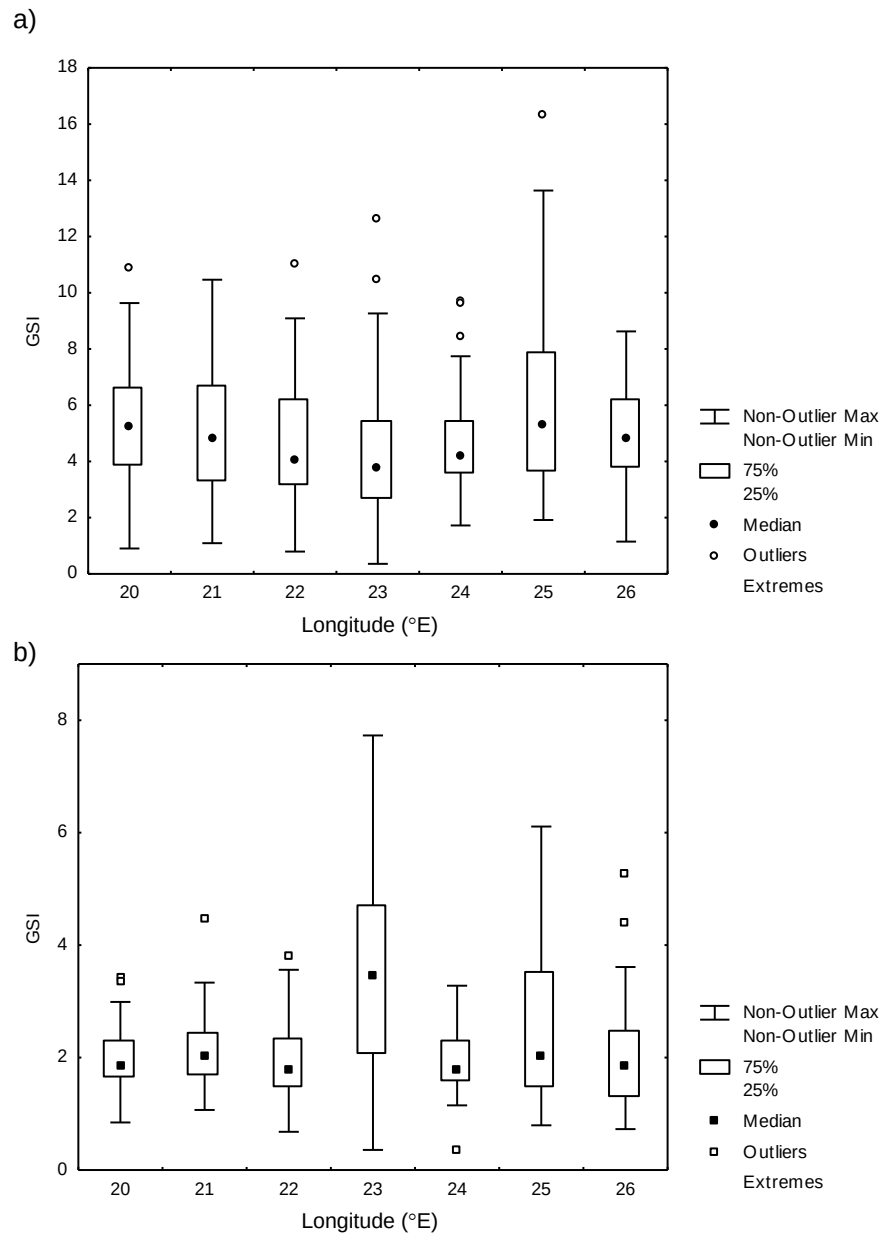


Figure 4.1.3 Autumn Gonadosomatic indices (GSI) for a) female and b) male chokka squid for each one-degree longitudinal area caught in research trawls across the Agulhas Bank.

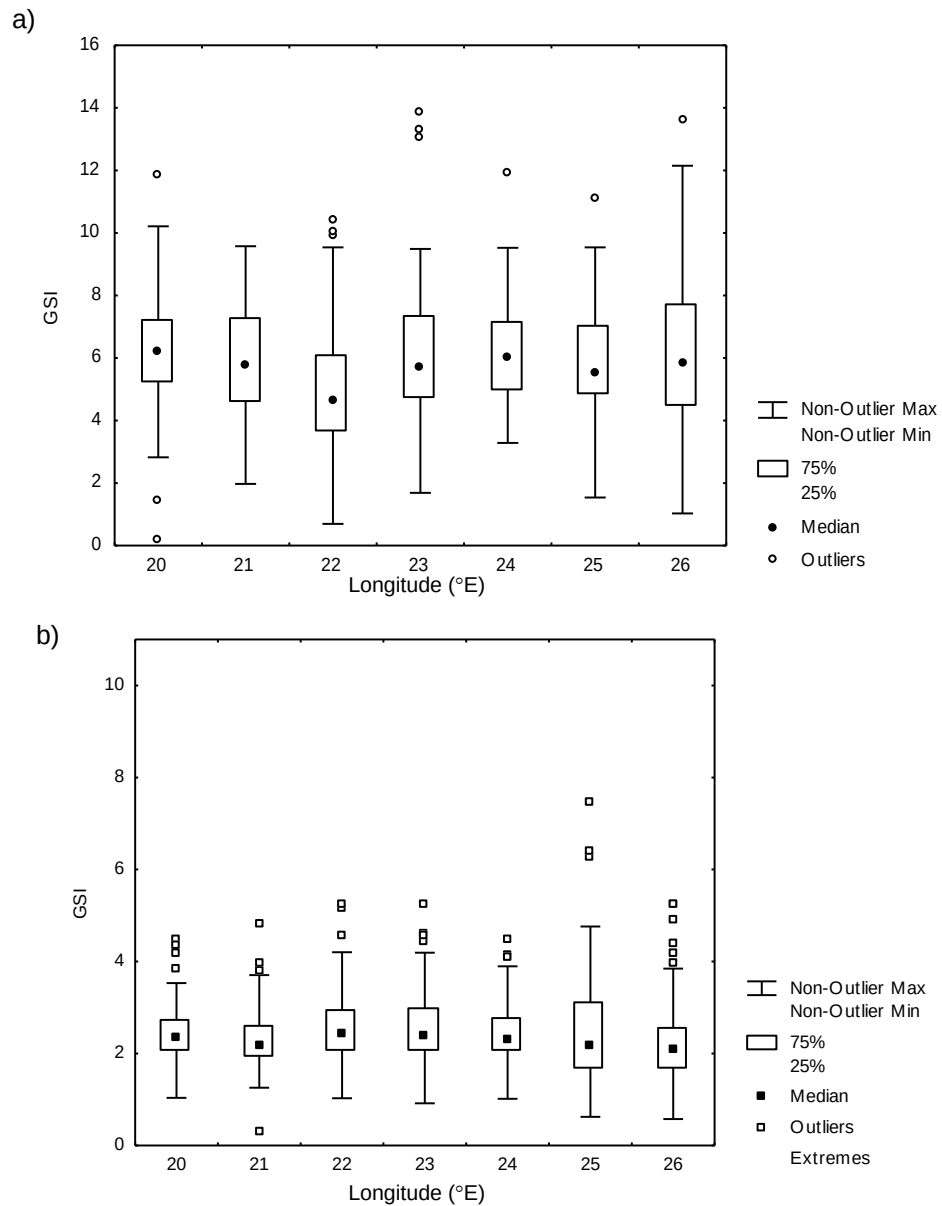
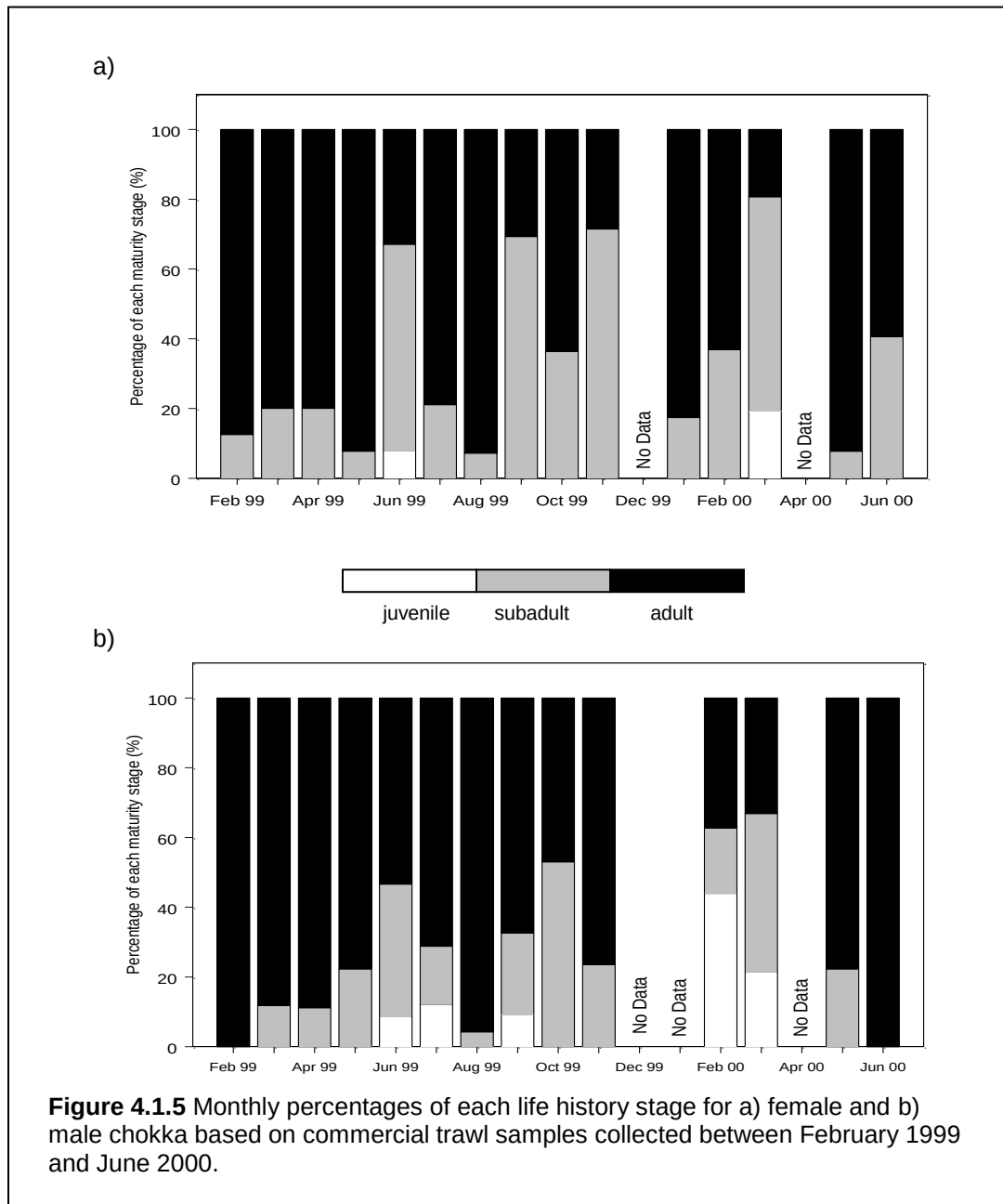


Figure 4.1.4 Spring Gonadosomatic indices (GSI) for a) female and b) male chokka squid for each one-degree longitudinal area caught in research trawls across the Agulhas Bank.

The results of the Kruskal-Wallis test for male spring data (Figure 4.1.4b) were highly significant ($H = 20.937$, $df = 6$, $p = 0.002$). Mann-Whitney U-tests noted significant differences between adjacent areas 21° to 22° E and 22° to 23° E ($z = -2.450$, $p = 0.013$).

Percentage maturity

Mature squid were present in every month (Figure 4.1.5), peaking in abundance in February 1999 and again in August 1999 for both sexes. Similar peaks in adult abundance were evident in May 1999 and 2000 for females and in June 2000 for males. Peak abundances of subadults occurred in June 1999 and March 2000 for both sexes, September 1999 and November 1999 for females and in October 1999 for males.



4.2 Sex ratio

Monthly ratios of mature males to females are presented in Figure 4.2.1. In the 1988 jig data (Figure 4.2.1a), males outnumbered females in 11 of the 15 months investigated. Between March and July 1988, the sex ratio fluctuated between 0.72 (June 1988) and 1.35 (May 1988) males per female. The highest disparity between males and females occurred in September 1988 when males outnumbered females by a factor of 3.36. The second highest ratio occurred in December 1988 (3:1) with a third peak in May 1989 (2.36:1).

The 1999 jig (Figure 4.2.1b) and trawl (Figure 4.2.1c) data show similar trends, with the trawl data peaking a month before the jig data. Both datasets describe an increase from February 1999 (1.14:1 and 1.39:1 for trawl and jig respectively) to peak in May 1999 (4:1) for the trawl data and in June 1999 (4.27:1) for the jig data. Sex Ratios dropped to a low in June 1999 (0.34:1) for the trawl data and in September 1999 (0.83:1) for the jig data.

An increase to 1.38:1 in July with high male abundance through winter to early spring (July-September) was recorded in the trawl data with a decrease to unity in October 1999. A second peak ratio of 2.6:1 males to females was evident in November 1999. This ratio then fell to 0.83:1 in February 2000, increased in March 2000 (1.83:1) and then dropped to 0.58:1 in May 2000.

Between September and November, the jig ratio fluctuated between 0.80:1 and 1.12:1. A high ratio of 2.13:1 was recorded in January with a subsequent drop in February (0.4:1). April, May and June 2000 seemed to follow a similar trend to the trawl data.

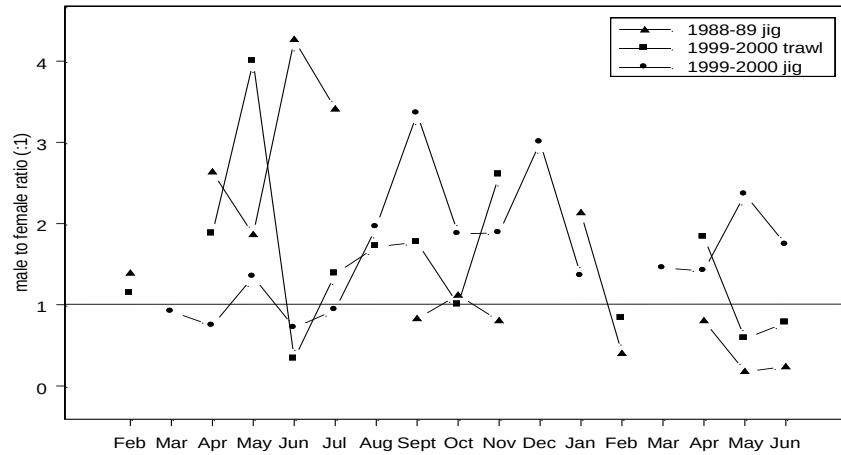


Figure 4.2.1 Monthly male to female ratios. The horizontal line represents a 1:1 sex ratio.

The results of the binomial test for equal proportions (Table 4.2.1) showed significant departures from unity in most months for the two jig datasets but in only two (May and June 1999) for the trawl data.

In some months, significant results were due to higher proportions of females than males. These are denoted by negative values.

A research trawl conducted on 22nd April 1999 (34.43° S 23.63° E) and a commercial trawl conducted on 19th April 1999 (34.39° S 23.58° E) were compared. Both trawls were at 100m depths. To account for the difference in mesh size used between the two gear types, squid of 100mm mantle length and greater were considered. The sex ratio for all stages combined in the commercial trawl was 1.70:1, and for mature squid 1.88:1 males to females. Unstaged squid in the research trawl produced a ratio of 0.92:1 males to females.

Table 4.2.1 Monthly sex ratios for three commercial datasets. Italicised figures indicate significant departures from a 1:1 ratio based on the binomial test for equal proportions.

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

Monthly subadult sex ratios (Table 4.2.2) were calculated for the commercial trawl data. Equal sex ratios were recorded in April and August 1999. In six of the eleven months sampled, sex ratios were female biased ranging between 0.5 and 0.94 males to females. The ratio was not significantly different from unity in all months although in most months, sample sizes were very low.

Table 4.2.2 Comparison of subadult male to female ratios obtained from commercial trawl samples in 1999.

<i>Month</i>	<i>Frequencies</i>		<i>Sex ratio</i>	<i>Z</i>	<i>p</i>
	<i>Male</i>	<i>Female</i>	<i>Male: Female</i>		
Feb	0	2		-1.414	0.157
Mar	0	3		-1.732	0.083
Apr	2	2	1:1	0	
May	8	7	1.143:1	0.258	0.796
Jun	5	10	0.5:1	-1.291	0.197
Jul	5	8	0.625	-0.832	0.405
Aug	1	1	1:1	0	
Sep	9	18	0.5:1	-1.732	0.083
Oct	10	4	2.5:1	1.604	0.101
Nov	6	10	0.6:1	-1.000	0.317
Feb	5	7	0.714:1	-0.577	0.563
Mar	16	17	0.941:1	-0.174	0.862
May	2	1	2:1	0.577	0.564
Jun	3	0		1.732	0.083

Sex ratios obtained from autumn research cruises by longitudinal area are presented in Table 4.2.3. The size ranges of the maturity stages were calculated from biological samples taken on research cruises. All ratios were highly 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 the catch. Subadult ratios showed a bias towards males in the eastern (1.29:1) and western (1.54:1) regions but not in the central region (0.79:1). Juveniles showed ratios biased in favour of females in all areas.

Table 4.2.3 Comparison of autumn male to female ratios obtained from research trawl samples, samples from all depth ranges are included.

Area	Maturity stage	Frequencies		Sex ratio	Z	p
		Male	Female	Male: Female		
East	Adult	2403	3486	0.697:1	-13.729	< 0.001
	Subadult	2886	2246	1.285:1	8.933	< 0.001
	Juvenile	1784	3779	0.472:1	-26.748	< 0.001
Central	Adult	2307	1726	1.337:1	9.149	< 0.001
	Subadult	5279	6653	0.793:1	-12.578	< 0.001
	Juvenile	1961	3165	0.620:1	-16.820	< 0.001
West	Adult	1055	812	1.299:1	5.624	< 0.001
	Subadult	9490	6162	1.540:1	26.601	< 0.001
	Juvenile	2564	3529	0.727:1	-12.363	< 0.001

Autumn research sex ratios in the same areas for depths less than 60m are presented in Table 4.2.4. In all samples, ratios were significantly to highly significantly different from unity. For adults, the ratio was biased towards females in all regions. Subadult ratios showed a bias towards males in the eastern (1.29:1) and western (1.19:1) regions but not in the central region (0.53:1). Juveniles showed ratios biased in favour of females in all areas.

Table 4.2.4 Comparison of autumn male to female ratios obtained from research trawl samples less than 60m deep.

Area	Maturity stage	Frequencies		Sex ratio	Z	p
		Male	Female	Male: Female		
East	Adult	1337	1574	0.849:1	-4.393	< 0.001
	Subadult	1387	1072	1.294:1	6.352	< 0.001
	Juvenile	962	1772	0.543:1	-15.491	< 0.001
Central	Adult	146	302	0.483:1	-7.370	< 0.001
	Subadult	372	701	0.531:1	-10.044	< 0.001
	Juvenile	344	570	0.604:1	-7.475	< 0.001
West	Adult	76	103	0.738:1	-2.018	0.044
	Subadult	637	537	1.186:1	2.919	0.004
	Juvenile	360	773	0.466:1	27.803	< 0.001

Sex ratios obtained from spring research cruises by longitudinal area are presented in Table 4.2.5. All ratios were highly 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 the catch.

Subadult sex ratios were male biased in the central (1.52:1) and western (1.73:1) regions but not in the eastern region (0.85:1). Juveniles showed a male biased sex ratio in the central area (1.19:1).

Table 4.2.5 Comparison of spring male to female ratios obtained from research trawl samples, samples from all depth ranges are included.

Area	Maturity stage	Frequencies		Sex ratio	Z	p
		Male	Female	Male: Female		
East	Adult	5001	5329	0.938:1	-3.227	0.001
	Subadult	2115	2496	0.847:1	-5.611	< 0.001
	Juvenile	1862	2560	0.727:1	-10.500	< 0.001
Central	Adult	2011	618	3.254:1	27.168	< 0.001
	Subadult	3879	2547	1.523:1	16.616	< 0.001
	Juvenile	1875	1571	1.194:1	5.179	< 0.001
West	Adult	920	330	2.788:1	16.688	< 0.001
	Subadult	5722	3306	1.731:1	25.427	< 0.001
	Juvenile	7616	9921	0.768:1	-17.406	< 0.001

Spring research sex ratios in the same areas for depths less than 60m are presented in Table 4.2.6. For adults, the ratio was female biased (0.96:1) in the eastern region but was not significantly different from a unity ratio ($Z = -1.190$, $p = 0.058$). In the central region a significantly male biased sex ratio was apparent (1.49:1) ($Z = 4.708$, $p < 0.001$) and in the western region males were slightly more abundant than females (1.09:1) but the ratio was not significantly different from unity ($Z = 0.823$, $p = 0.411$).

Table 4.2.6 Comparison of spring male to female ratios obtained from research trawl samples less than 60m deep.

Area	Maturity stage	Frequencies		Sex ratio	Z	p
		Male	Female	Male: Female		
East	Adult	3395	3553	0.956:1	-1.190	0.058
	Subadult	1585	1795	0.883:1	-3.612	0.0003
	Juvenile	1398	1697	0.824:1	-5.375	< 0.001
Central	Adult	339	227	1.493:1	4.708	< 0.001
	Subadult	444	288	1.542:1	5.770	< 0.001
	Juvenile	622	174	3.575:1	15.879	< 0.001
West	Adult	197	181	1.088:1	0.823	0.411
	Subadult	708	508	1.394:1	5.735	< 0.001
	Juvenile	1424	1440	0.989:1	-0.299	0.765

Subadult sex ratios showed highly significant male bias in the central (1.54:1) and western (1.39:1) regions but not in the eastern region where the bias was highly significant towards females (0.88:1) ($Z = -3.612$, $p < 0.001$). Juveniles showed a male biased sex ratio in the central area (3.58:1), which was highly significant ($Z = 15.879$, $p < 0.001$). In the eastern region, a ratio biased in favour of females (0.82:1) was highly significantly different ($Z = -5.375$, $p < 0.001$). No significant difference was recorded for juveniles in the western region ($Z = -0.299$, $p = 0.765$).

4.3 Growth and maturation

Monthly mean lengths

Temporal trends in the mean size of adult squid caught from commercial vessels are presented for males and females in Figures 4.3.1 and 4.3.2 respectively.

The 1988 male jig data (Figure 4.3.1a) illustrates an increase in mean length between April and June followed by a decrease in August. A steady increase occurred through spring and summer to peak in December. A high average mantle length was evident in April 1989 and was followed by a drop in May with a subsequent rise in June.

The 1999 male jig (Figure 4.3.1b) shows a similar pattern of high median length in autumn, decreasing through winter and then increasing through spring to peak in summer. The 1999-2000 commercial trawl data also follows a similar trend but reached its lowest median length two months before the jig data (June 1999) and its highest value in August 1999 (Figure 4.3.1c).

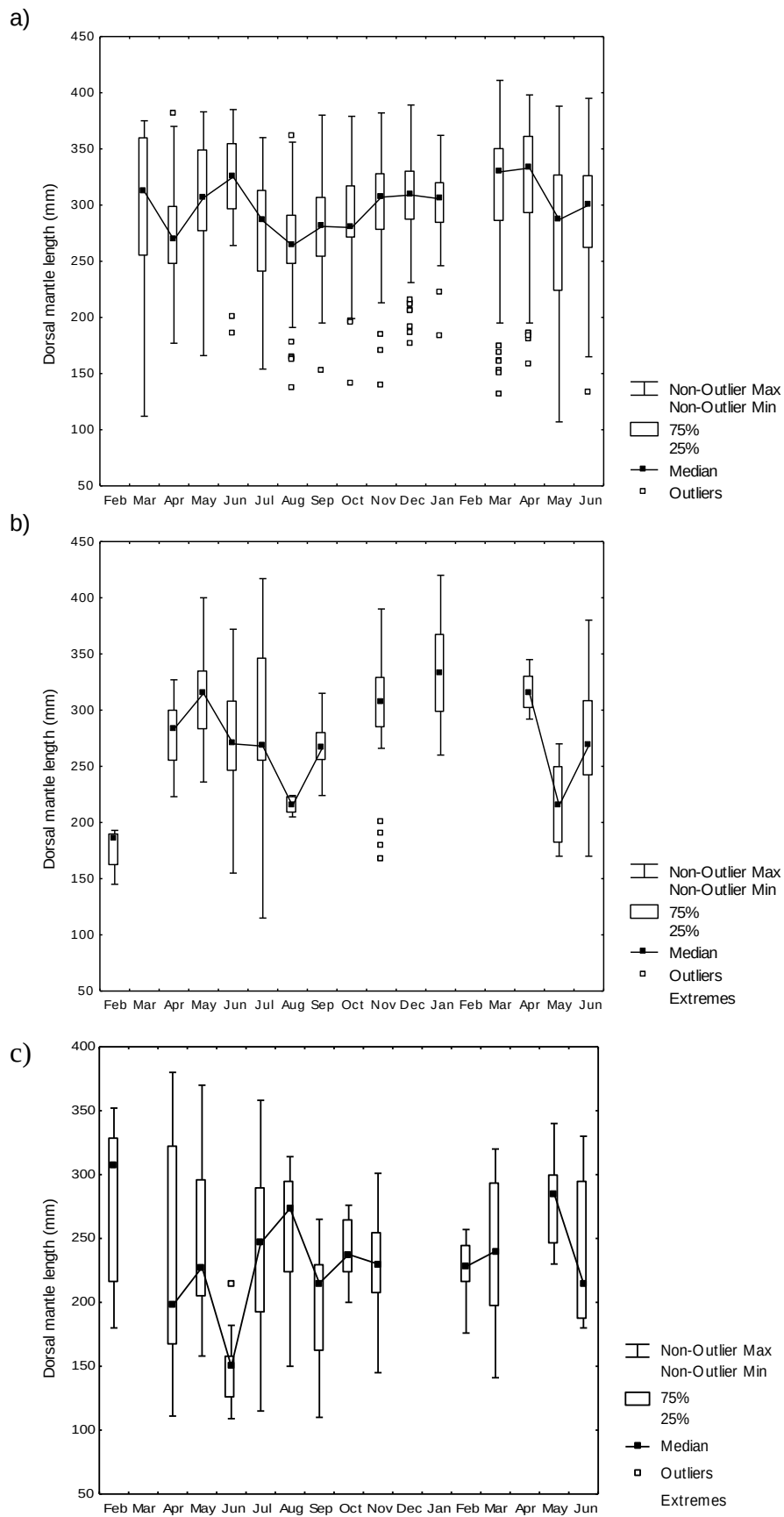


Figure 4.3.1 Median monthly lengths for mature male chokka from a) 1988-1989 jig b) 1999-2000 jig and c) 1999-2000 trawl data.

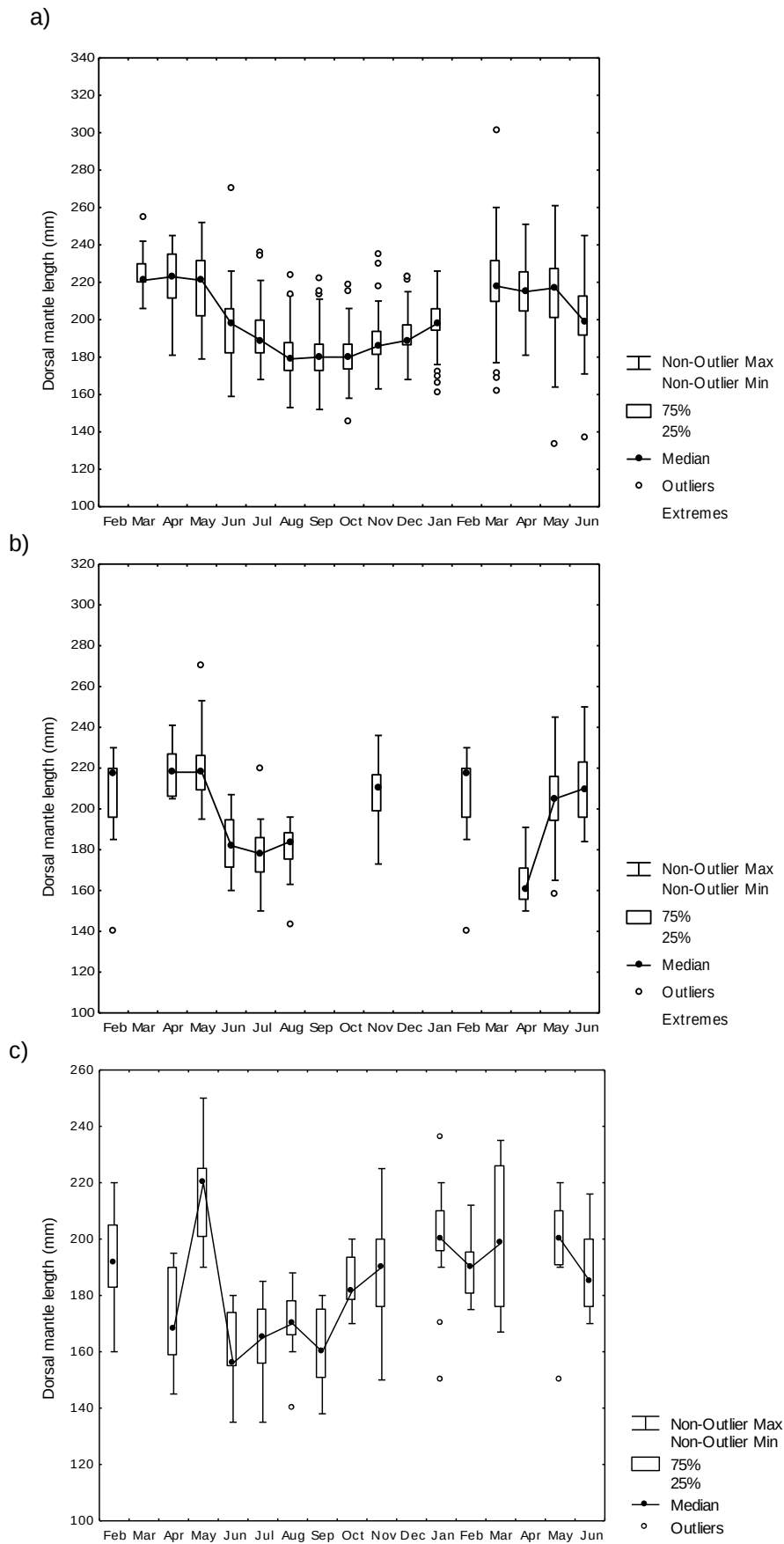


Figure 4.3.2 Median monthly lengths for mature female chokka from a) 1988-1989 jig b) 1999-2000 jig and c) 1999-2000 trawl data.

In the 1988 female jig data (Figure 4.3.2a), the pattern of lower median mantle lengths through winter and early spring was even more apparent than in the male data.

Both the 1999 female jig (Figure 4.3.1b) and trawl data (Figure 4.3.2c) showed trends similar to the 1988 female data.

The results of the Kruskal-Wallis tests for differences in median monthly lengths are presented in Table 4.3.1. Mean monthly lengths and standard deviations together with the results of the Mann-Whitney U-tests for between month differences for each dataset are presented in Appendix III. In all datasets, male standard deviations were larger than those of the female. Significant between month differences were noted in all datasets.

Table 4.3.1. Results of the Kruskal-Wallis test for differences in median lengths between months for three commercial datasets where n refers to the number of squid sampled, H is the Kruskal-Wallis test statistic and df the degrees of freedom.

<i>Data</i>		<i>n</i>	<i>H</i>	<i>df</i>	<i>p</i>
Jig 1988	Male	1462	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 comparison of size- at- maturity

In females, ML50% was 173.4mm in spring and 181.3mm in autumn (Figure 4.3.3a). Males reached 50% maturity at 188.3mm in spring and 202.7mm in autumn (Figure 4.3.3b). A small peak in the proportion of mature squid at between 100 and 120mm in spring and 140 and 160mm in autumn was also apparent (Figure 4.3.3b). The results of the likelihood ratio tests revealed significant differences in both ML50 ($\lambda = 32.11$, $df = 1$, $p < 0.001$) and δ ($\lambda = 6.04$, $df = 1$, $p = 0.014$) between seasons for males. For females, ML50 was significantly different ($\lambda = 28.62$, $df = 1$, $p < 0.001$) but δ was not ($\lambda = 1.86$, $df = 1$, $p = 0.173$).

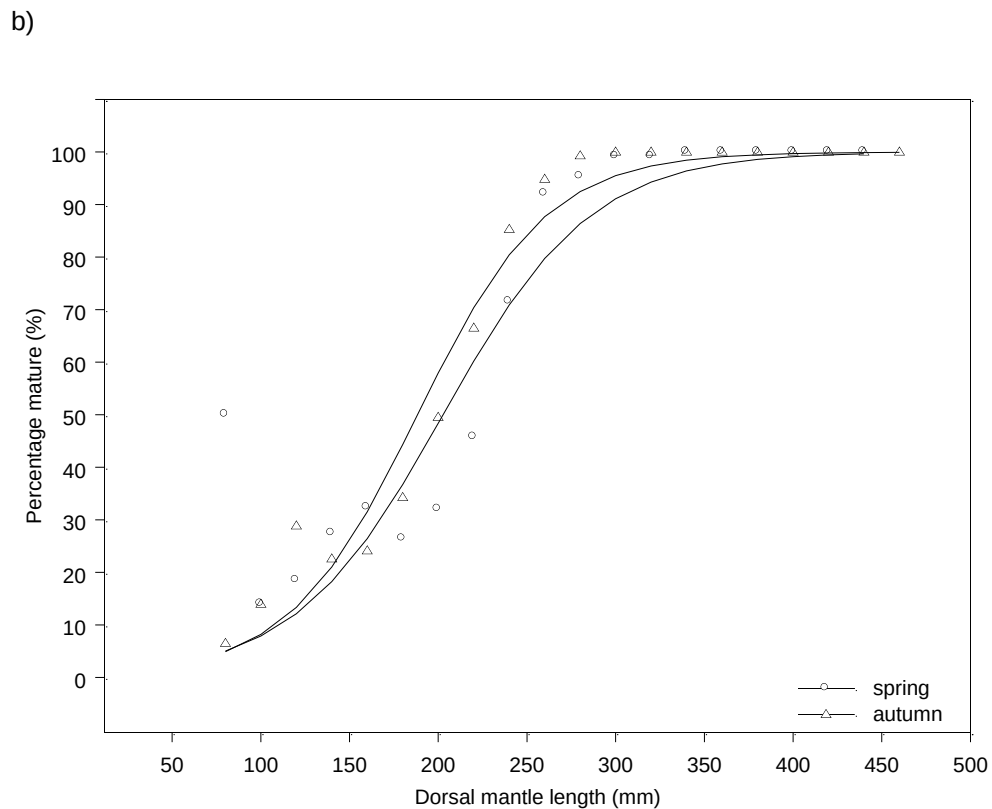
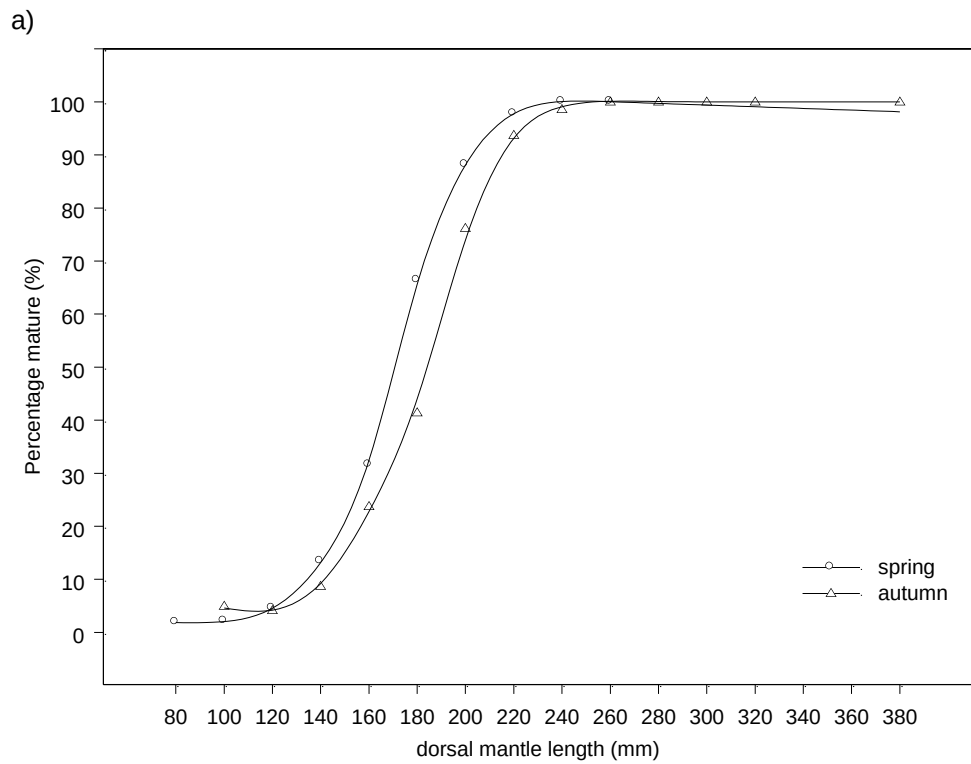


Figure 4.3.3 Percentages of mature a) female and b) male chokka in each size range collected in autumn and spring research surveys on the Agulhas Bank between 1986 and 1999.

Spatial comparison of size-at-maturity

A spatial comparison of size-at-maturity was conducted by separating research trawls into western (20°-22°E), central (22°-24°E) and eastern (24°-27°E) regions. Logistic maturity ogives for males and females in autumn are presented in Figure 4.3.4. Females from the eastern region reached 50% maturity at 165.4mm, those in the central region at 180.2mm and those in the western at 188.3mm DML (Figure 4.3.4a).

Likelihood ratio tests noted that ML50 of autumn caught females was significantly different between all areas ($\lambda = 108.96$, $df = 1$, $p < 0.001$). Significant differences in δ were also noted between the eastern and central areas ($\lambda = 5.54$, $df = 1$, $p = 0.019$), western and central areas ($\lambda = 6.28$, $df = 1$, $p = 0.012$) but not between the western and eastern areas ($\lambda = 0.060$, $df = 1$, $p = 0.806$).

Males from the eastern region reached 50% maturity at 157.1mm, those in the central region at 189.2mm and in the western region at 226.1mm. Smaller increases in percentage maturity occurred between 80 and 100mm and between 160 and 180mm in the central region and between 120 and 140mm in the western region (Figure 4.3.4b).

Male caught autumn ML50 were highly significantly different in all areas ($\lambda = 244.10$, $df = 1$, $p < 0.001$) but not the steepness of the ogive (δ) ($\lambda = 2.681$, $df = 1$, $p = 0.262$).

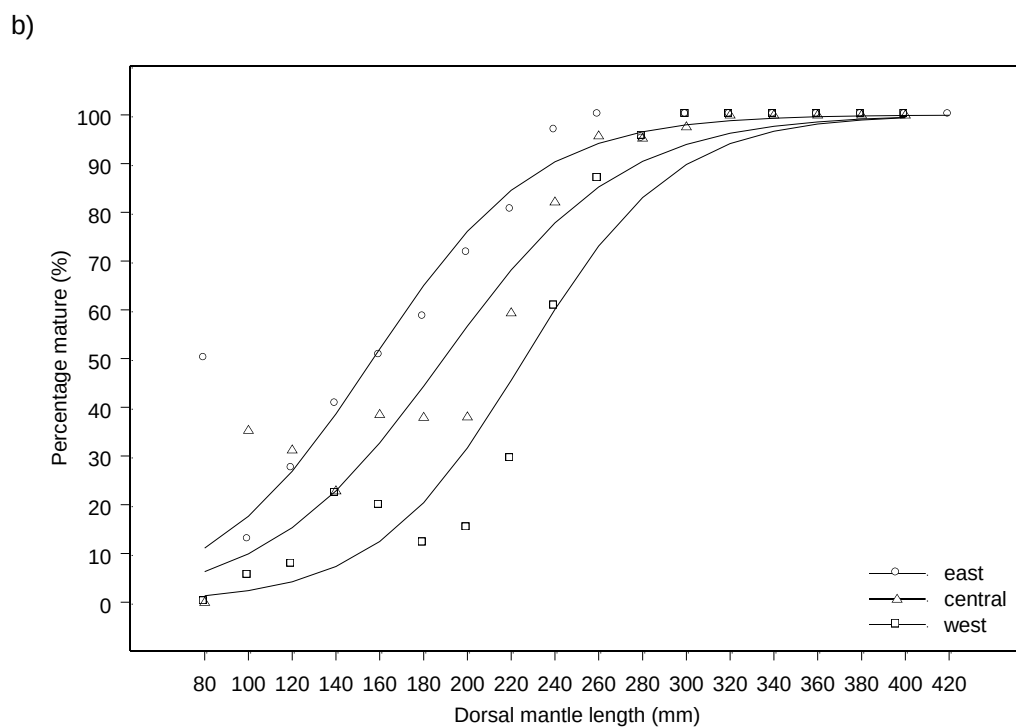
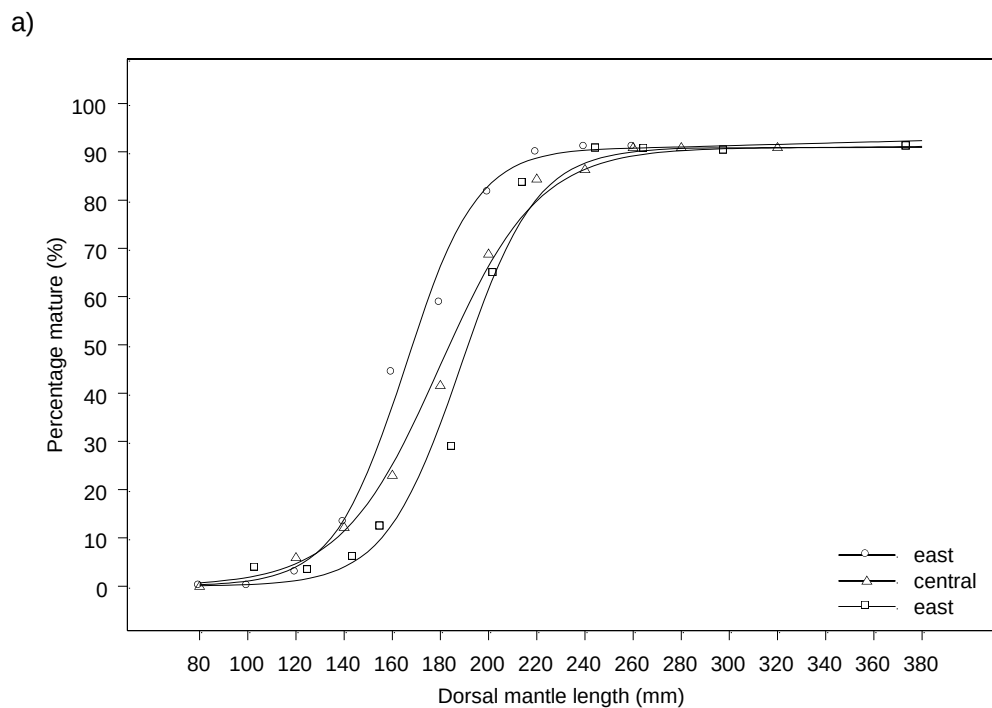
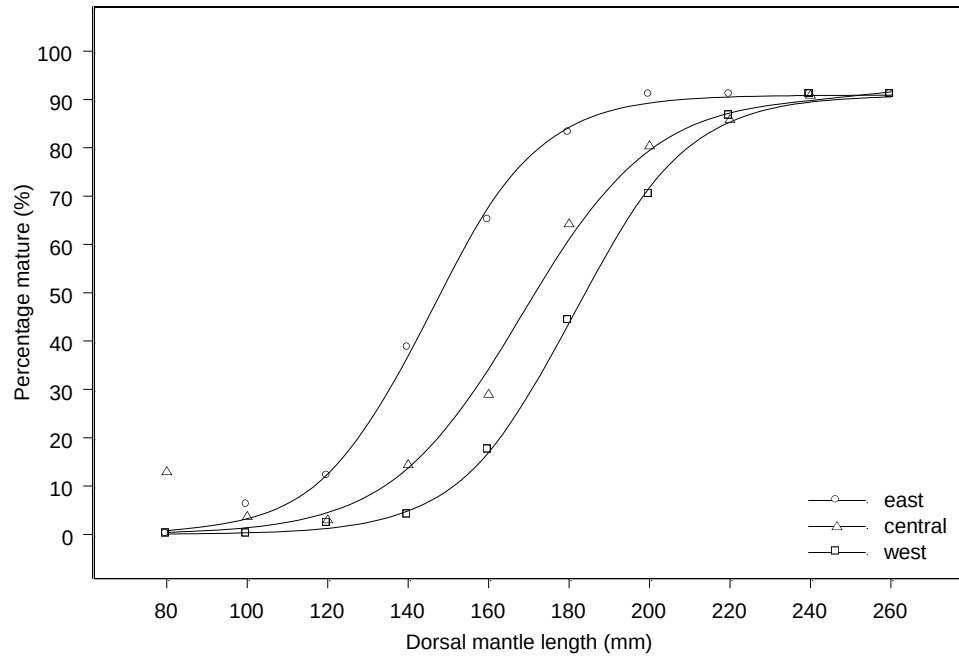


Figure 4.3.4 Percentages of autumn mature a) female and b) male chokka in each size range from the western (20-22°E), central (22-24°E) and eastern (24-27°E) areas sampled by research trawls.

a)



b)

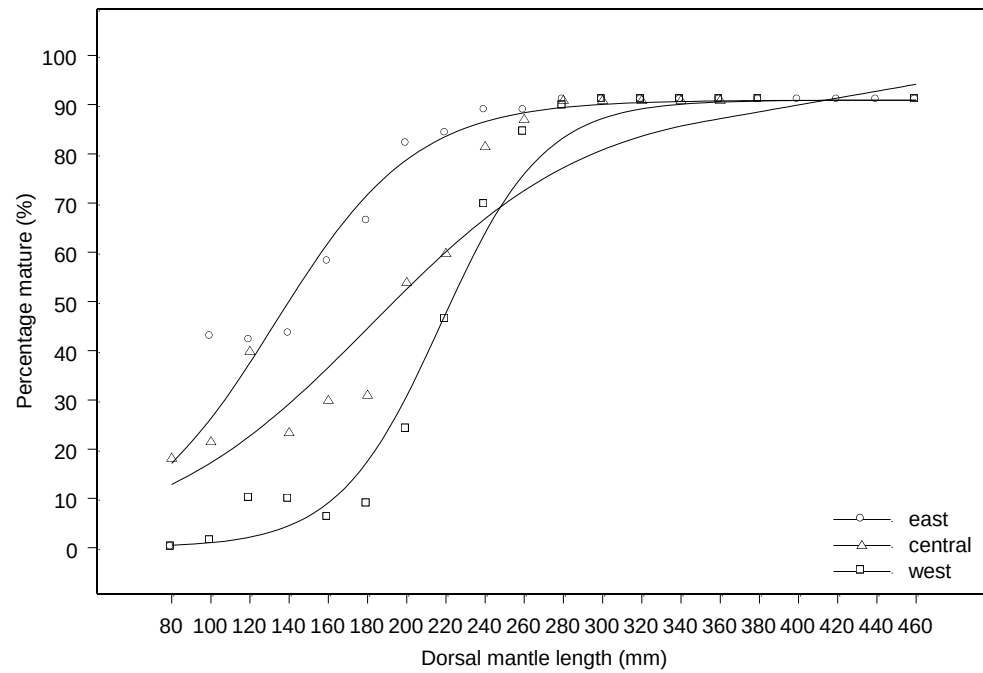


Figure 4.3.5 Percentages of spring mature a) female and b) male chokka in each size range from the western (20-22°E), central (22-24°E) and eastern (24-27°E) areas sampled by research trawls.

Spring caught female chokka reached 50% maturity at 145.4mm in the eastern region, at 168.7mm in the central region and at 181.1mm in the western region (Figure 4.3.5a).

For spring caught females, ML50 was significantly different in all areas ($\lambda = 237.49$, $df = 1$, $p < 0.001$) but not the steepness of the ogive ($\lambda = 2.61$, $df = 1$, $p = 0.271$).

Spring caught males reached 50% maturity at 132.6mm in the eastern region, at 182.3mm in the central region and at 217.5mm in the western region. Smaller increases in percentages of mature squid occurred at between 80 and 100mm in the eastern region, at between 100 and 120mm in the central region and at between 130 and 140mm in the western region (Figure 4.3.5b).

Likelihood ratio tests on spring caught males recorded highly significant differences in both ML50 ($\lambda = 201.43$, $df = 1$, $p < 0.001$) and δ ($\lambda = 37.43$, $df = 1$, $p < 0.001$).

Maturity stage size ranges

The size at which no squid were mature was considered as the upper limit of the juvenile size range, while the size at which 100% of the squid were mature was considered as the lower limit of the adult size range. The subadult size range was intermediate and defined as those squid that lay between these two limits. Such a classification excludes “sneaker males” which will be erroneously grouped as either juveniles or subadults. Tables 4.3.2 and 4.3.3 define the seasonal length ranges of juveniles, subadults and adults for both sexes in each longitudinal region across the Agulhas Bank.

Table 4.3.2 Size ranges of autumn caught chokka in three longitudinal areas across the Agulhas Bank, West (20-22°E), Central (22-24°E) and East (24-27°E)

<i>Life history stage</i>	<i>Male</i>			<i>Female</i>		
	<i>West</i>	<i>Central</i>	<i>East</i>	<i>West</i>	<i>Central</i>	<i>East</i>
Juvenile	<65mm	<115mm	<80mm	<65mm	<125mm	<125mm
Subadult	65-230mm	115-185mm	80-160mm	65-190mm	125-180mm	125-165mm
Adult	>230mm	>185mm	>160mm	>190mm	>180mm	>165mm

Table 4.3.3 Size ranges of spring caught chokka in three longitudinal areas across the Agulhas Bank, West (20-22°E), Central (22-24°E) and East (24-27°E)

<i>Life history stage</i>	<i>Male</i>			<i>Female</i>		
	<i>West</i>	<i>Central</i>	<i>East</i>	<i>West</i>	<i>Central</i>	<i>East</i>
Juvenile	<130mm	<100mm	<100mm	<130mm	<130mm	<125mm
Subadult	130-220mm	100-180mm	100-135mm	130-180mm	130-170mm	125-145mm
Adult	>220mm	>180mm	>135mm	>190mm	>180mm	>165mm

Percentage frequencies of occurrence of spring caught male squid by maturity stages in 20mm interval size classes are presented for the western, central and eastern regions in Figure 4.3.6.

Spring caught juvenile males (Figure 4.3.6a) dominated (80-100%) the smaller size classes up to 120mm but decreased in frequency to 2% in the 220-240mm size class. Immature males in the western region increased from 18.6% in the 80-100mm class to 68.1% in the 140-160mm class, followed by a steady decrease in occurrence to a low of 1.4% in the 260-280mm interval. Western region adult males ranged from 1.4% in the 80-100mm class and increased to 50% in the 200-220mm class. All squid greater than 300mm were mature. The same pattern of a clearly defined juvenile range, a small subadult range and a wide adult size range was noted in both the central (Figure 4.3.6b) and eastern regions (Figure 4.3.6c).

Frequency occurrence of juvenile spring females in the western region (Figure 4.3.7a) decreased steadily from 100% in the <80mm size class to 1.9% in the 160-180mm range. Immature females increased from 14% in the 80-100mm range to 65.0% in the 140-160mm range. Thereafter, the percentage decreased to 4.8% in the 200-220mm size class.

Mature females increased in abundance from 2.4% in the 100-120mm class to 100% at 220mm. The same pattern was repeated in the central (Figure 4.3.7b) and eastern (Figure 4.3.7c) regions.

Autumn caught juvenile males comprise 25% in the <80mm size class in the western region (Figure 4.3.8a) although only 4 squid were sampled in this size class. In the 80-100mm size class, juveniles accounted for 51.4% and subsequently decreased in successive size classes to 2.4% in the 200-220mm size class. Subadult males increased in frequency of occurrence from 43.2% in the 80-100mm size class to 79.7% in the 160-180mm size range. Thereafter, the percentage decreased to 4.5% in the 260-280mm size class.

In the 80-100mm size class, 5.4% of the squid were mature. This figure increased successively up to 22.2% in the 120-140mm size class and thereafter decreased to 12.1% in the 160-180mm size class before steadily increasing until, all squid greater than 280mm were mature. A similar pattern was noted in the central (Figure 4.3.8b) and eastern (Figure 4.3.8c) regions.

Autumn caught female juvenile chokka comprise 20% of the <80mm size class in the western region (Figure 4.3.9a) despite only 5 squid being sampled in this size class. In the 80-100mm size class, juveniles accounted for 48.7% and in the 100-120mm size class, 51.4%. This figure subsequently decreased in successive size classes to 0.9% in the 180-200mm size class. Subadult females increased in frequency from 40% (2 of 5 squid sampled) in the <80mm size class to 48.7% in the 80-100mm size class. This trend was followed by a decrease to 45% in the 100-120mm size class.

The frequency of occurrence then steadily increased to 72.5% in the 140-160mm size range, decreasing to 1.3% in the 220-240mm size class. Adult females accounted for 2 of the 5 squid measured <80mm. In the 80-100mm size class, 2.6% of the squid were mature. This figure increased through successive size ranges until all squid greater than 240mm were mature.

Both the central (Figure 4.3.9b) and eastern (Figure 4.3.9c) regions demonstrated a pattern of size ranges closer to the expected than the western area with juvenile females decreasing from 100% in the <80mm size class through successive size ranges to 1.7% in the 180-200mm size range. Subadult females increased from 15% in the 80-100mm size range to 65.8% in the 140-160mm size class. The percentage occurrence then decreased in successive size ranges to 5.6% in the 240-260mm size class. The percentage of mature females steadily increased from 6.6% in the 100-120mm size range until all squid larger than 240mm were mature.

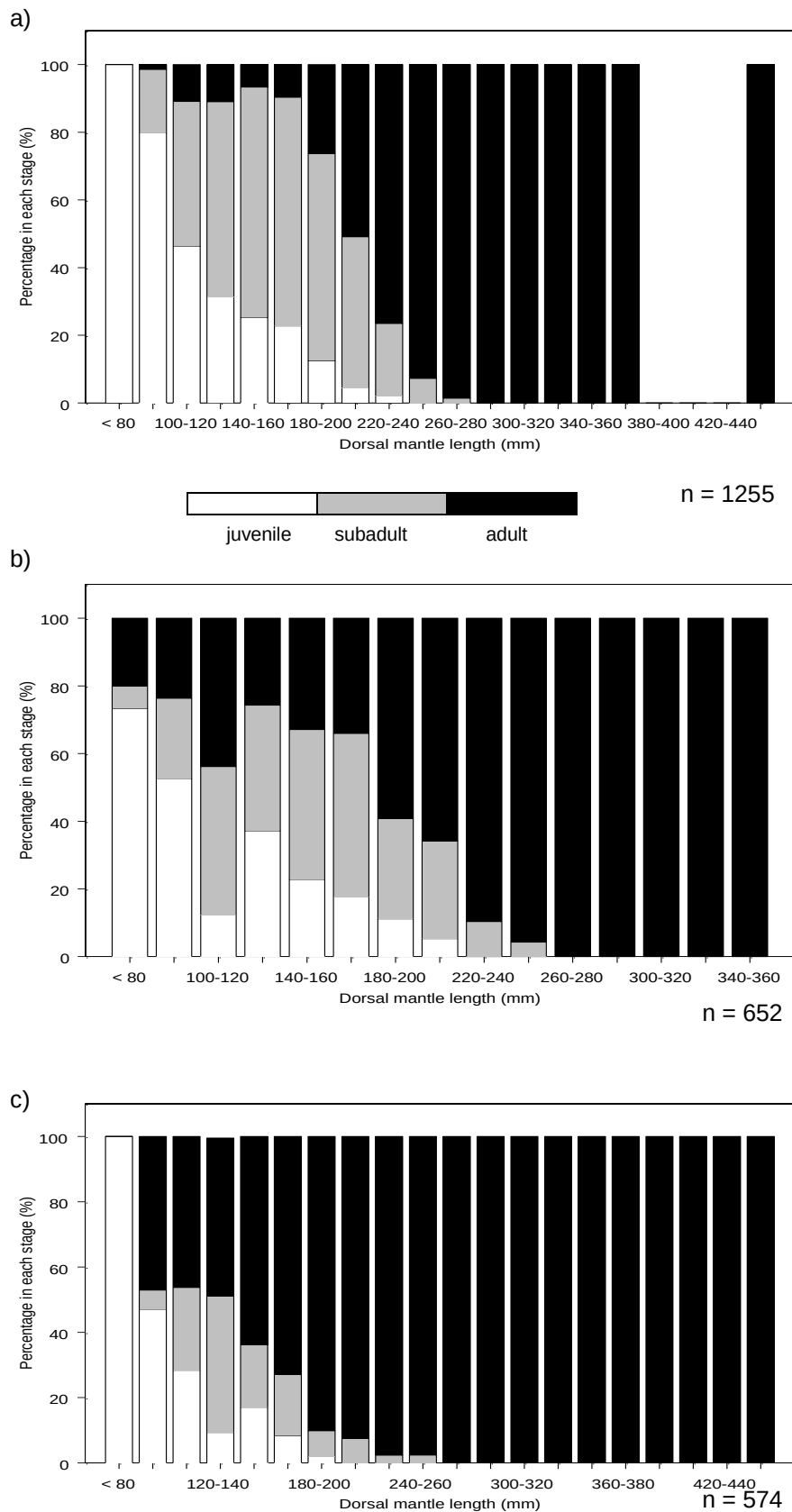


Figure 4.3.6 Frequency of occurrence of each maturity stage in 20mm interval size classes for spring sampled male chokka in the a) western, b) central and c) eastern regions of the Agulhas Bank.

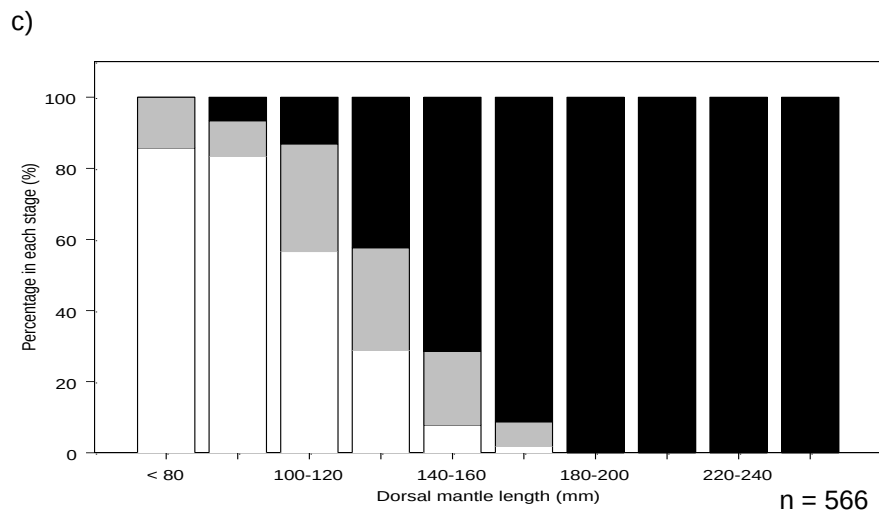
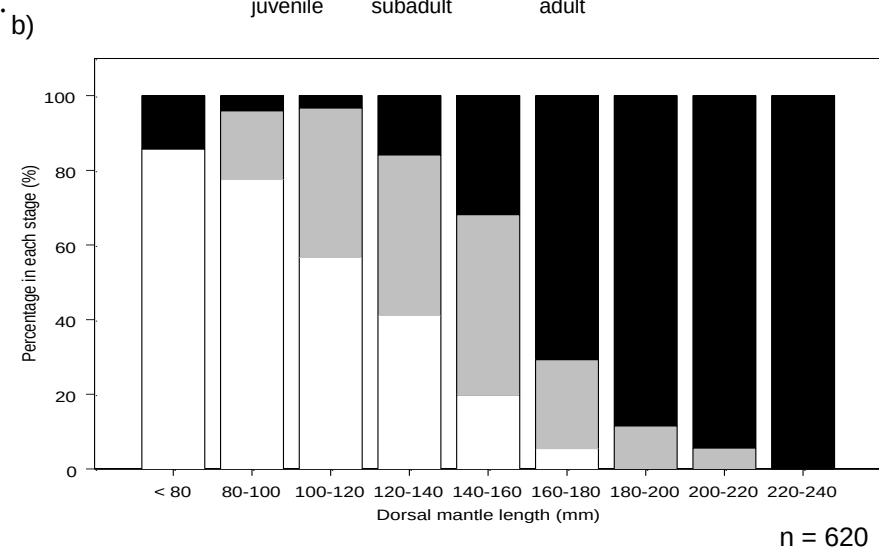
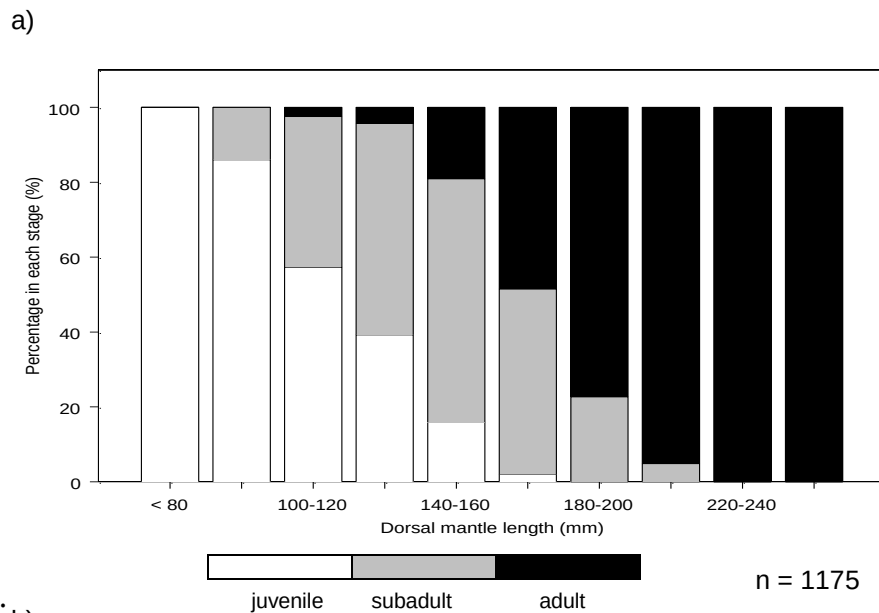


Figure 4.3.7 Frequency of occurrence of each maturity stage in 20mm interval size classes for spring sampled female chokka in the a) western, b) central and c) eastern regions of the Agulhas Bank.

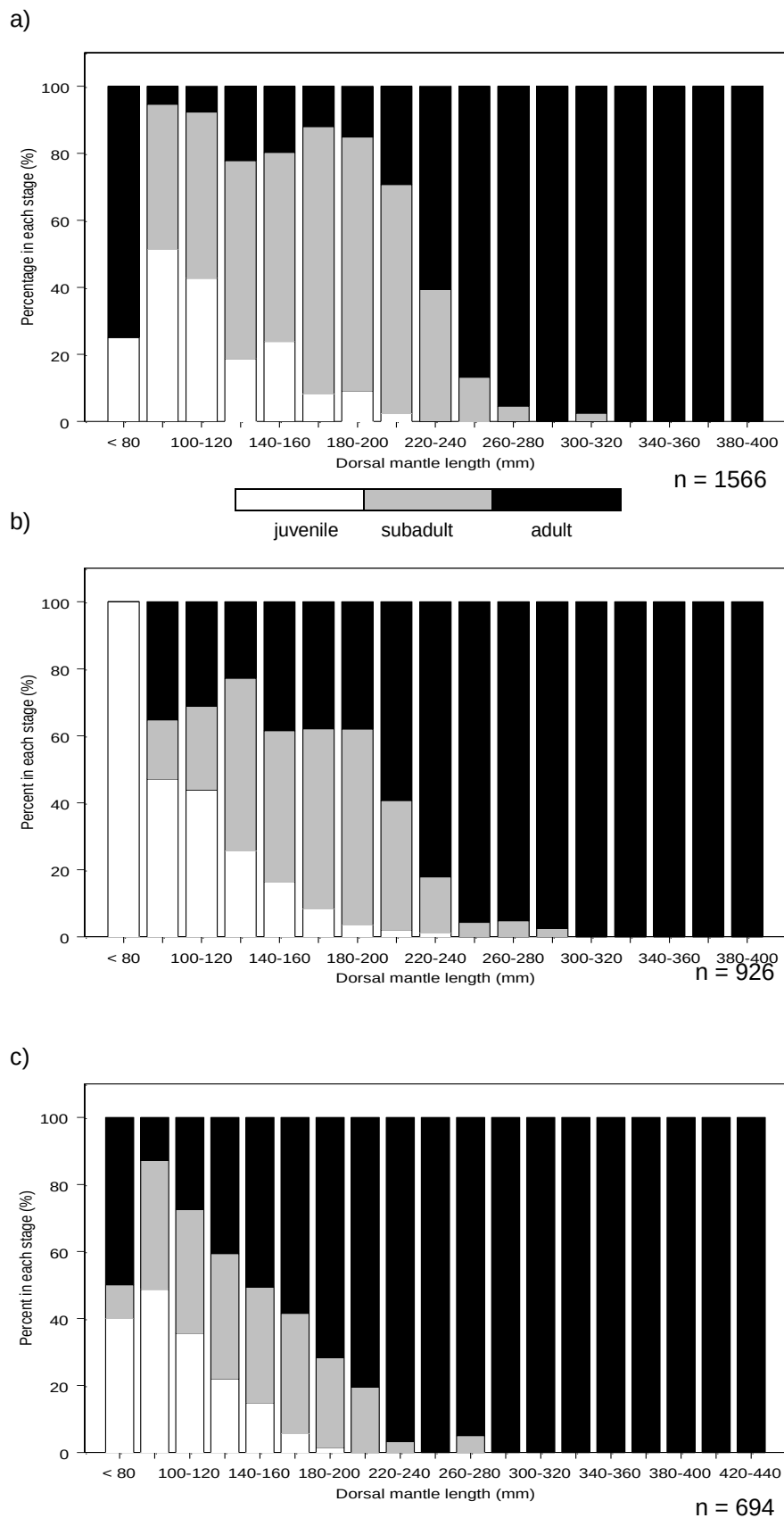


Figure 4.3.8 Frequency of occurrence of each maturity stage in 20mm interval size classes for autumn sampled male chokka in the a) western, b) central and c) eastern regions of the Agulhas Bank.

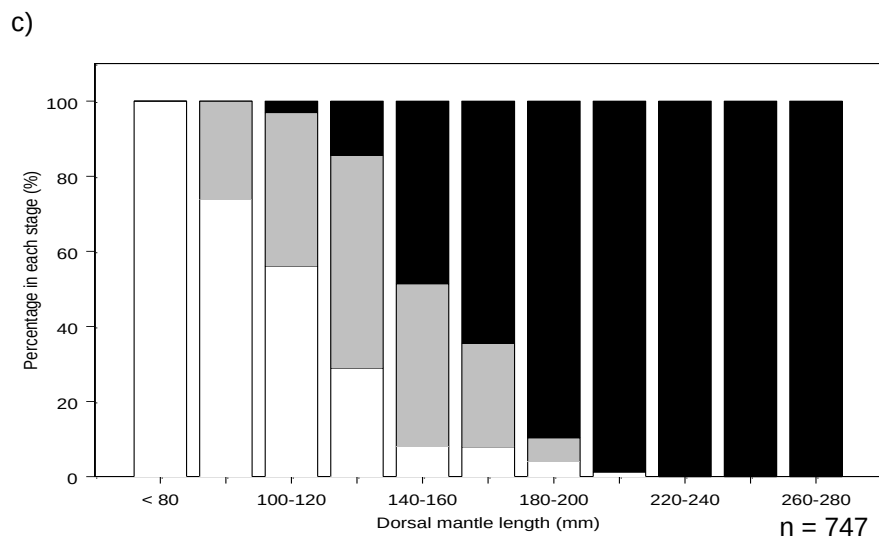
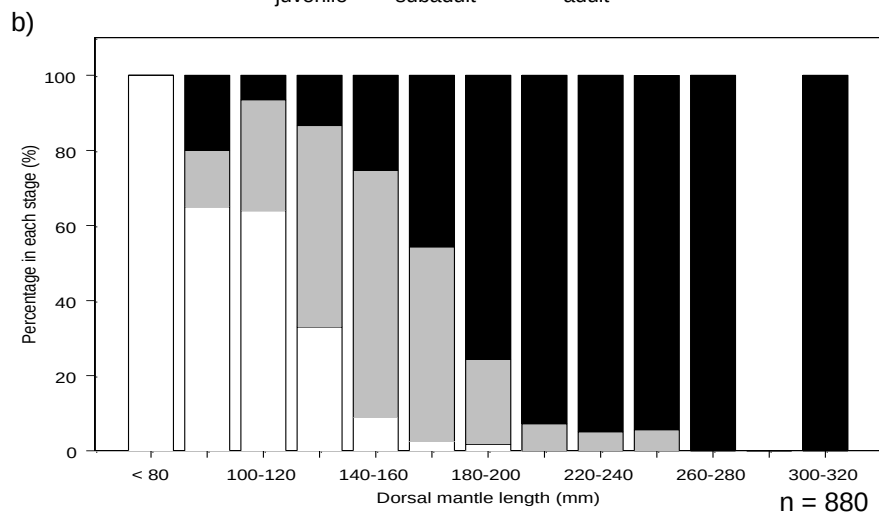
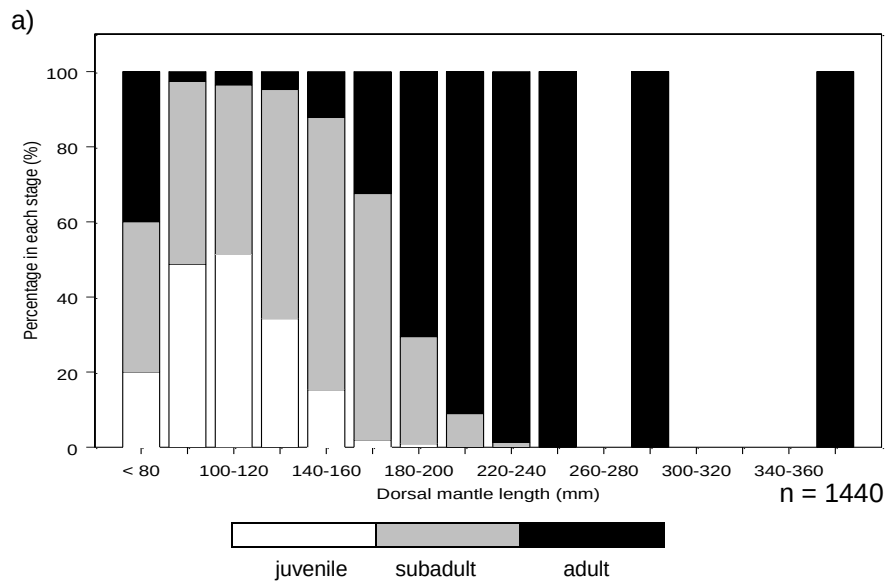


Figure 4.3.9 Frequency of occurrence of each maturity stage in 20mm interval size classes for autumn sampled female chokka in the a) western, b) central and c) eastern regions of the Agulhas Bank.

4.4 Distribution and abundance

Using the calculated size ranges, distribution and abundance patterns for each life history stage based on research length frequencies were mapped.

In autumn caught male squid, juveniles showed highest abundance between the coast and the 60m isobath (Figure 4.4.1a). Concentrations of juveniles were apparent in protected bays in the east off Port Elizabeth, Cape St Francis and Plettenberg Bay. Fairly high abundances were also recorded in the west to depths of 200m. Juveniles were notably absent along the 200m isobath between 23° and 26°E.

Subadult autumn caught males (Figure 4.4.1b) were widely dispersed across the Agulhas Bank. High abundances were evident between the 60m and 100m isobaths and also in the eastern bays. Fairly high concentrations were also apparent between 21° and 23°E at depths between 100m and 200m.

Autumn caught adult males (Figure 4.4.1c) showed the highest abundances in the east between the coast and the 60m isobath. High catches were also made between the 100m and 200m isobath, particularly in the area between 23° and 24°E. Adult males were either absent or present in low numbers in the western region.

Autumn caught female chokka (Figure 4.4.2) demonstrated a similar pattern to the males.

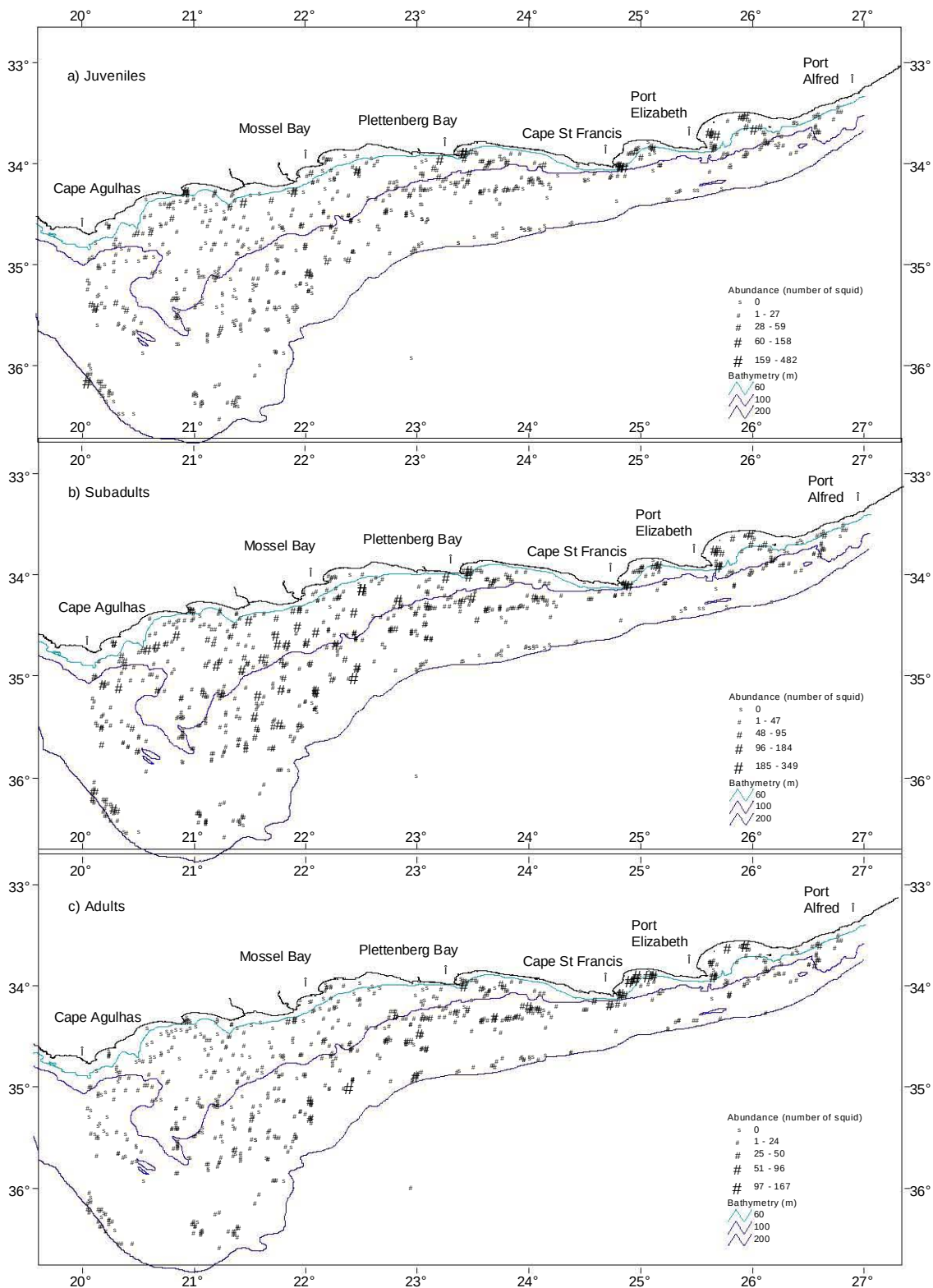


Figure 4.4.1 Distribution of male chokka in three life history stages caught in autumn research cruises on the Agulhas Bank

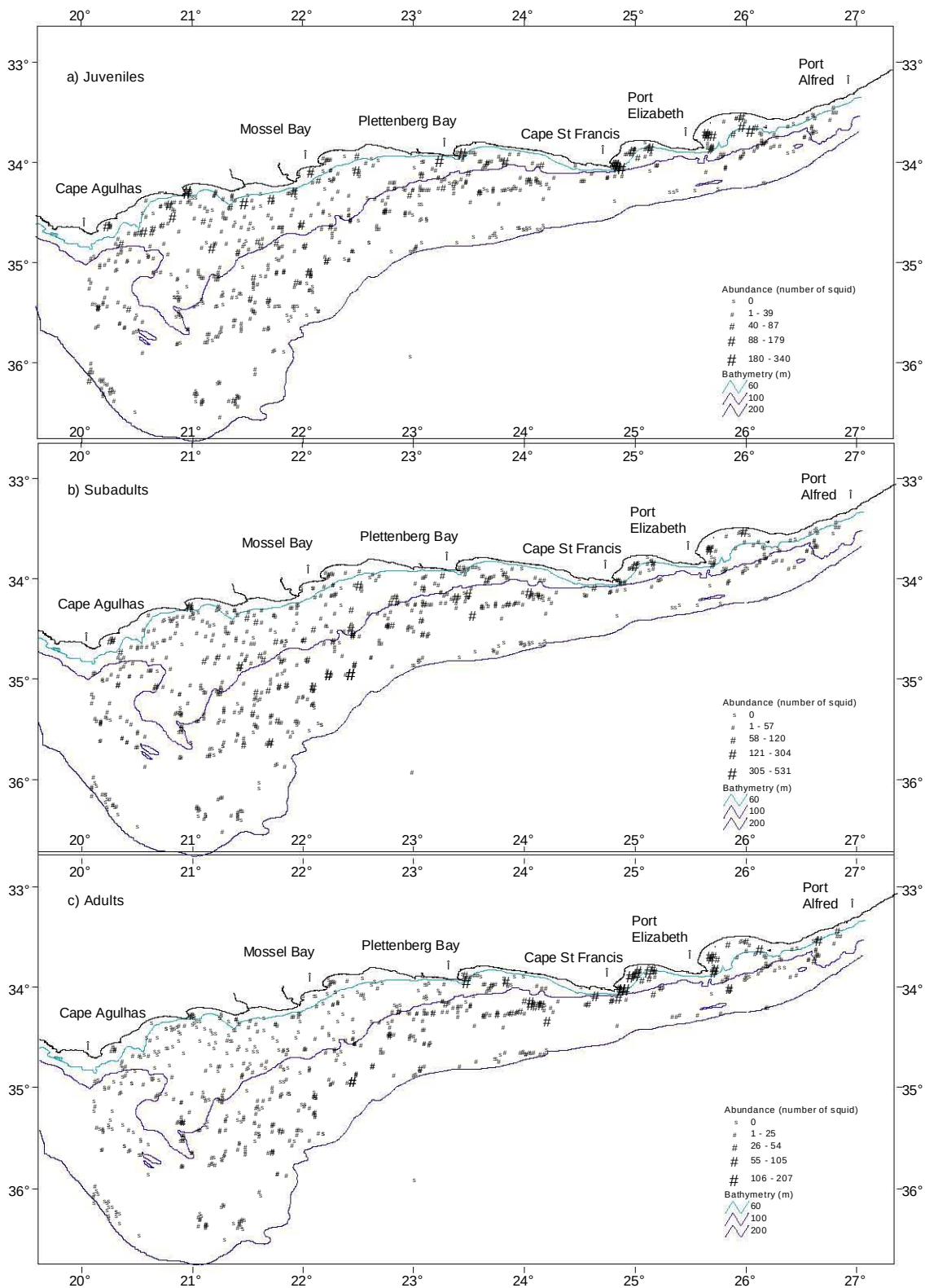


Figure 4.4.2 Distribution of female chokka in three life history stages caught in autumn research cruises on the Agulhas Bank

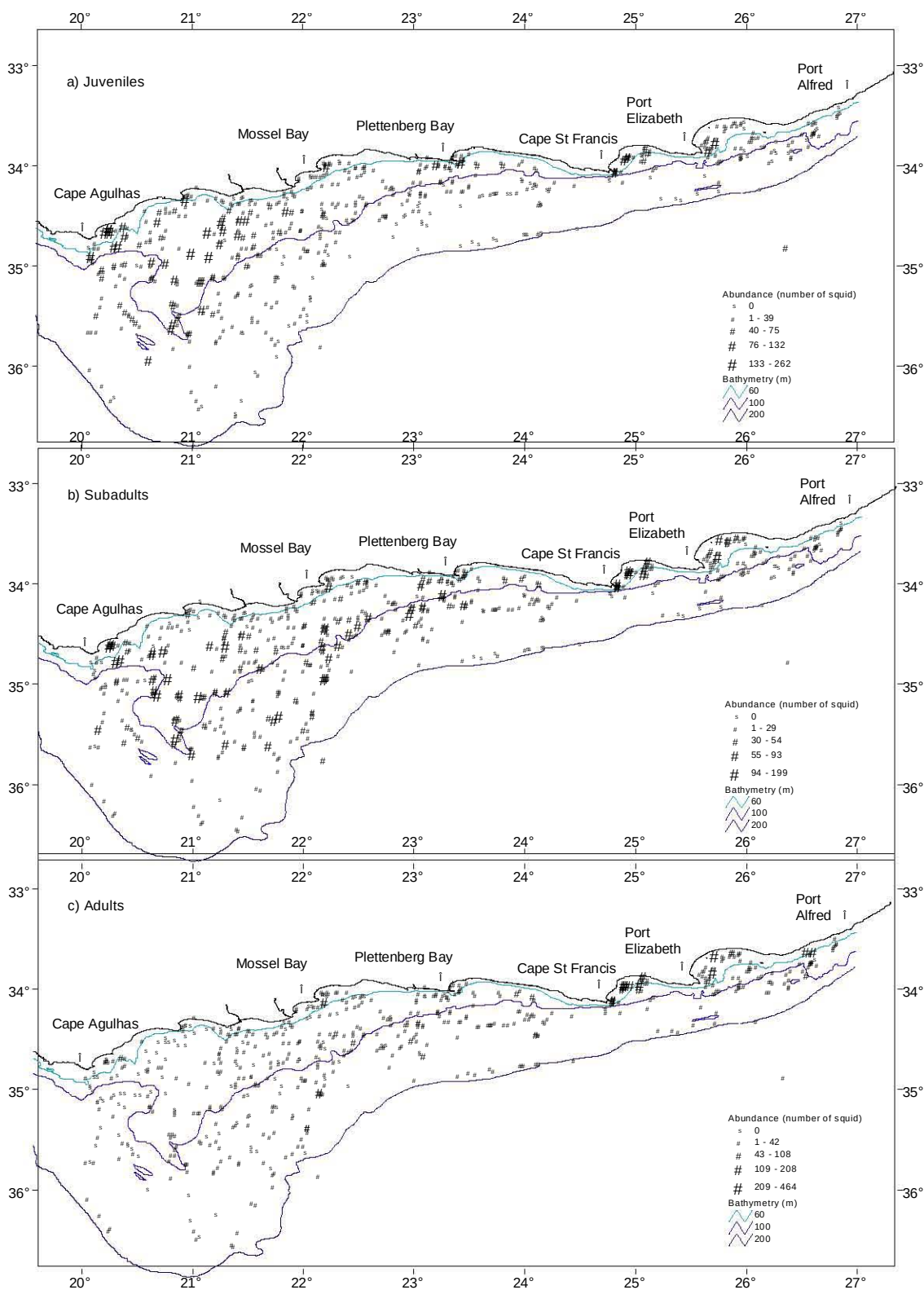


Figure 4.4.3 Distribution of male chokka in three life history stages caught in spring research cruises on the Agulhas Bank

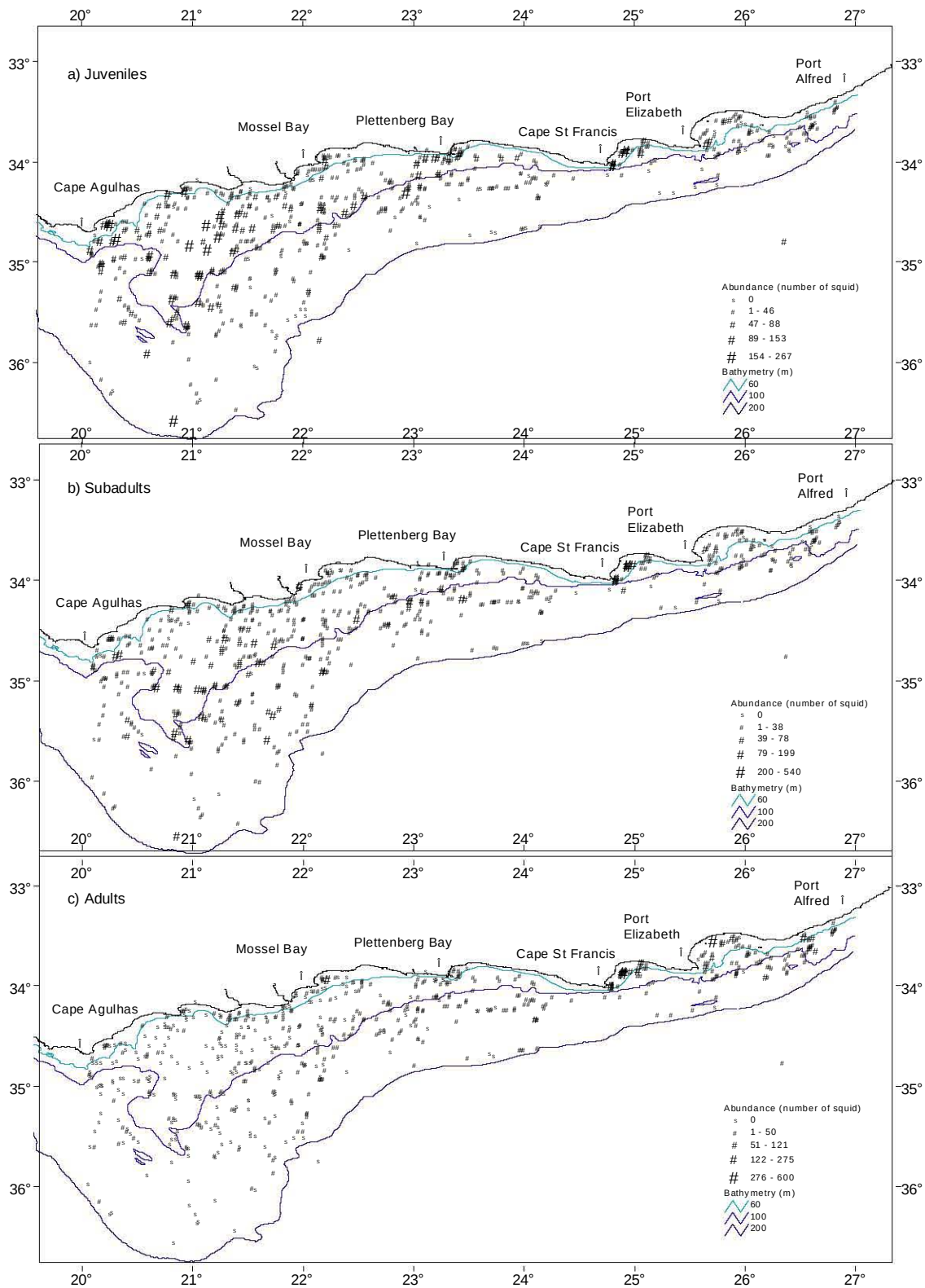


Figure 4.4.4 Distribution of female chokka in three life history stages caught in spring research cruises on the Agulhas Bank

Spring caught juvenile males (Figure 4.4.3a) were more concentrated in the western region between the 60m and 100m isobaths than in autumn. Concentrations in the eastern bays are also apparent. Abundance between the 100m and 200m isobaths is low, particularly between 22° and 26°E.

Spring caught subadult males (Figure 4.4.3b) show a similar pattern to the juveniles of high concentrations on the Central Agulhas Bank and inshore in the east but also have higher abundances between 100m and 200m.

Adult males caught in spring (Figure 4.4.3c) are almost exclusively concentrated in the eastern bays between the coast and the 60m isobath particularly in Jeffrey's Bay and Algoa Bay.

Spring caught females (Figure 4.4.4) seem to match the distribution pattern of the males, particularly in the adults (Figure 4.4.4c), which were virtually absent from the western region.

Discussion

Seasonality

Seasonal spawning has been described for many loliginid squid i.e. *Loligo vulgaris vulgaris* (Moreno *et al.* 1994), *Loligo pealei* (Lange and Sissenwine 1980), *Loligo opalescens* (Hixon 1983), *Loligo forbesi* (Moreno *et al.* 1994), *Loligo gahi* (Hatfield and Des Clers 1998, Hatfield 2000) and in chokka (Augustyn *et al.* 1994). For most species, a single peak spawning episode occurs each year although two spawning peaks are suggested for *L. gahi* in Falkland Island waters (Hatfield 2000), *L. pealei* in the NW Atlantic (Brodziak 1998) and in

chokka (Augustyn *et al.* 1994). Multiple spawning episodes within these time periods, coupled with differential temperature regimes and nutrient supplies would therefore give rise to multiple cohorts and explain some of the variability seen in length frequency histograms.

GSI

Seasonal comparison of GSI

The original assumption in this thesis was that the trawl data would compliment the jig data by following the same trend in GSI but lagging a month to two behind. The rationale was, that as successive pulses of mature squid moved from west to east and offshore to inshore, GSI would decrease in the western areas and increase in the eastern areas i.e. tracking the movement of sexually active animals. The peaking of trawl GSI values a month before jig values in both sexes supports this hypothesis although the pattern was not consistent in every month.

Two peaks in GSI; in the 1999-2000 austral winter (June to August) and summer (December to February) were evident for females, although the summer peak is weakly supported due to missing data. These data suggest, therefore, that two peak reproductive periods occurred within the 1999-2000 season. The male data support the winter peak but differs from the females by showing a secondary, smaller GSI peak in spring.

By contrast, female GSI in the 1988 data remained consistently high throughout the year. Other than a steady increase between autumn and spring, there is no clear peak to indicate a discrete breeding season. It may be possible to equate this consistently high state of gonadal development to favourable environmental conditions, which in turn might explain the apparent success of the 1989 season when high catches of squid were made.

Spatial comparison of GSI

The hypothesised spatial pattern of GSI was that an increase from west to east would be apparent for both sexes as a consequence of migration to the traditional inshore spawning grounds. It was assumed that as the squid migrated, their reproductive activity would be tracked by the GSI and consequently, mature squid sampled in the eastern region would have significantly higher GSI values than squid sampled further west.

This hypothesis was not clearly supported by the data. Although higher GSI values did occur within the traditional spawning area, there was no significant difference in GSI between areas across the Agulhas Bank. The consequences of this are that squid are at the same stage of reproductive development regardless of their longitudinal location. Following this argument, it is possible that should environmental conditions prove favourable, squid in the western extent of their distribution have an equal likelihood of spawning in that area as their conspecifics further east. The original spawning grounds were thought to lie in False Bay (Augustyn 1989) and anecdotal evidence (W.H.H. Sauer *pers. comm.*) suggests that squid may in fact spawn in the western area. Inshore spawning areas in the west were also identified by Lipiński (1998; Figure 2). There is therefore a need to address the abundance of spawners spatially. Even though squid in the west are capable of spawning, they do not necessarily contribute to the reproductive effort but rather act as back-up spawners as described by Lipiński (1998).

Percentage maturity

The relative percentages of adults in each month substantiate the patterns of seasonality evident in monthly GSI values. High adult abundance in summer and winter infers that

higher levels of reproductive activity are possible. It is also evident that mature squid are present on the Agulhas Bank all year round.

With limited knowledge of juvenile life history and survival, peaks in abundance of subadult animals provide within-season estimates of the timing of recruitment. Back calculated hatching dates for these squid would provide growth estimates and statoliths have been submitted for analysis. With growth data, it may be possible to predict when these pulses of subadults would become available to the jig fishery should they migrate eastwards as hypothesised. This link between recruitment and catch may be a useful predictor on which fishery advice can be based. Quantifying these pulses and being able to predict their arrival would provide some stability to the industry and allow skippers to maximise their fishing time to coincide with recruitment episodes. Identifying and tracking these recruiting cohorts could also lead to coherent stock assessment models that may be considered in the setting of quotas as an alternative to effort control.

Sex ratio

Temporal trends

The three commercial datasets were used to describe monthly trends in sex ratio. The most complete dataset was the 1988-1989 jig data, which illustrated that males outnumber females in almost every month. Significantly different sex ratios occurred in the peak breeding seasons- spring to summer and autumn to winter when males outnumbered females by up to 3.36:1.

These data were supported by the 1999-2000 jig data with males being significantly more numerous in four of the eleven months investigated. In the same dataset, females

significantly outnumbered males in five months. Sample sizes were, however, low and it is likely that the 1988-1989 data is representative. The trawl data, however, revealed a significant departure from unity in only two months: May 1999 when males dominated the catch and June 1999 when the ratio was skewed towards females although the small sample sizes need to be taken into consideration.

Monthly ratios of subadult males to females were also calculated using the commercial trawl data and showed that throughout the year, the sex ratio was not significantly different from 1:1.

Spatial trends

Sex ratios from research trawl data demonstrated differences between the western, central and eastern areas as well as differences between maturity stages. The pattern of female biased ratios for mature squid in the inshore area evident in autumn was contrasted by a pattern of male biased ratios in spring (although only significant in the central region). The timing of the research cruises may not have coincided exactly with the peak spawning seasons but it was expected that all inshore ratios should be male biased if skewed sex ratios are related to spawning.

Augustyn (1990) and Augustyn *et al.* (1994) have previously reported a ratio biased in favour of males for chokka on the spawning grounds. This has been reported for other *Loligo* species i.e. *L. forbesi* in the Azores (Porteiro and Martins 1994) and *L. v. vulgaris* from the Algarve region in southern Portugal (Coelho *et al.* 1994) but these estimates were based on jig caught samples. The potential bias of this fishing technique has been previously suggested (Lipiński 1994) and skewed ratios could reflect more attacks on the jigs by males than

females rather than greater male abundance. When the same Northern Hemisphere species (*L. forbesi* and *L. v. vulgaris*) were sampled using trawl gear, equal sex ratios were apparent throughout the year except in the peak-spawning period when females were more numerous than males in *L. v. vulgaris* in Spanish waters (Guerra and Rocha 1994) and in *L. forbesi* in Scottish waters (Pierce *et al.* 1994).

Lipiński (1994) has shown that using different fishing gear can result in different ratios being obtained but concluded that on the spawning grounds, the overall ratio for chokka was 2.5:1, males to females. To account for the male bias in jig data, Augustyn (1990) has suggested that either males are more susceptible to capture by jigging than females or males demonstrate greater longevity than females, which may also explain some of the multiple cohorts evident in male length frequencies.

The current study had an opportunity to study monthly sex ratios as well as compare the results of two sampling methods: hand-jigging and demersal trawling. Although male-biased ratios were evident in most months, the greatest departures from a 1:1 ratio were in the peak spawning months. Interpretation of sex ratio results was complicated because chokka form sex segregated schools (Sauer *et al.* 1992) and that mixing only occurs during spawning activity. Even when fishing on an apparently spawning aggregation, catches dominated by either males or females are not uncommon (*pers. ob.*).

Despite these misgivings, based on the trawl data, which is arguably less biased than jigging, significant departures from a 1:1 ratio apparently only occur during spawning. It was also evident that in some samples, females outnumbered males. Support for the notion of a 1:1 ratio at non-spawning times or away from the inshore spawning grounds was found by

Augustyn (1991) who recorded sex ratios of 1:1 on the Western and Central Agulhas Bank. Using the research data that has substantially larger sample sizes but is temporally restricted raises further questions relating to spawning sex ratios with adult females being significantly more numerous than males in the eastern region. Even when the analysis was restricted to the inshore area, a ratio in favour of females was still apparent.

Growth and maturation

Loliginid squid have extremely variable growth rates even within a single population (Collins *et al.* 1995, 1999, Hatfield 2000). Generally, the largest squid are the adults with males growing to a larger size than females. Exceptions do exist and smaller males in the typical subadult size class are often fully mature. These have been recorded in other *Loligo* species i.e. *L. forbesi* (Pierce *et al.* 1994, Moreno *et al.* 1994, Guerra and Rocha 1994, Collins *et al.* 1995) and *L. v. vulgaris* (Coelho *et al.* 1994, Guerra and Rocha 1994) and have been observed to act as “sneaker males” in chokka (Sauer *et al.* 1997, Hanlon 1998).

Monthly mean length-at- maturity

The mean length of adult squid does not remain constant throughout the year. In the three commercial datasets used, mature females caught in winter and early spring were considerably smaller than squid caught in summer. Patterns in the male data were less clearly discernable, mainly due to the large standard deviations in the samples, but seemed to follow the same trend. The large standard deviations in the male data were attributed to the presence of “sneaker males” in the samples.

Seasonal comparisons of size-at- maturity

Seasonal (spring and autumn) differences in the size at which 50% of the squid sampled are mature were found in females. Spring caught squid matured at a smaller size than those caught in autumn. Similar differences were evident in males together with initial smaller increases in percentage maturity in both spring and autumn that represent the occurrence of “sneaker males”. These data compliment the observed pattern of seasonal differences in mantle length-at-maturity and the maturing of squid at a smaller size in spring may be a direct consequence of the mean length of mature squid available.

Two explanations for the observed differences in size at maturity between seasons are proposed. Firstly, the seasonal cohorts theory outlined in Chapter 3 whereby cohorts with different growth parameters arise from either summer or winter spawning or alternatively; that autumn caught squid represent a cohort from the previous year’s summer spawning at an older, larger stage. Without adequate ageing and environmental data, both theories are at best speculative and must be considered hypotheses suitable for testing in future research.

Spatial comparison of size-at- maturity

Spatial differences in size-at-maturity provide conflicting evidence for the hypothesised pattern of chokka squid migration and maturation.

In both sexes, squid matured at smaller sizes in the eastern region and at successively larger sizes in the central and western areas. If the squid caught in the central and western areas represent the return migration of animals that have been feeding on the central and western Agulhas Bank or on the west coast they would possibly be older than the spawners in the east

that have not undergone such a migration (Augustyn 1994). Their larger size then would be a consequence of their age.

Conversely, using the hypothesis that all squid make a return migration to the eastern region to spawn, mature squid in the eastern area should be larger as a result of having travelled further and grown for longer than squid further west. Again, resolution of these arguments will only be possible once sufficient ageing data is available.

Sneaker males

No “sneaker males” were evident in squid caught from the eastern region in autumn but a large number were evident in spring. Two minor increases in percentage maturity were noted in autumn caught males from the central region and while the first could be explained as “sneaker males” it is difficult to account for the second. The role of sneaker males in the population remains to be investigated. Three sources of sperm are available to females; stored spermatophores from previous matings, sperm from mating a large male before egg capsule deposition or sperm from sneaker interception (Hanlon 1998). Paternity studies to determine the source of sperm used to fertilise particular batches of eggs are currently underway (W.H.H. Sauer *pers. comm.*).

Quantifying the size of the sneaker population as well as their physiology may prove vital to the management of the fishery since it has been shown that jigs selectively target large male chokka (Lipiński 1994). Size selectivity of jigs has also been demonstrated for *Sepioteuthis lessoniana* in Japanese waters (Tokai and Ueta 1999).

The possible disruption to the ratio of males to females as well as sneakers to large males needs to be considered (Rodhouse *et al.* 1998).

Maturity stage size ranges

Defining the size range of various maturity stages is essential for determining abundance and distribution patterns. Due to highly variable individual growth rates, the overlap of size ranges is great, particularly in males, which can be mature at 80mm and immature at 200mm. Previously published size ranges of various maturity stages have been vague and conflicting although spatial and temporal influences have been recognized (Augustyn *et al.* 1994). Differences in the size range between eastern, central and western regions as a consequence of differences in size at maturity were taken into consideration when defining the size ranges of juveniles, subadults and adults in this study.

Distribution and abundance

The patterns of distribution and relative abundance support the hypothesized patterns of chokka migration. In both seasons, adults were most abundant on the inshore spawning grounds in the east. In autumn, occurrences of adult squid in deeper water were also apparent. Subadult distribution patterns varied between seasons with squid in this maturity stage being more evenly distributed across the Agulhas Bank in autumn. In both seasons, subadult abundance was highest between 60m and 100m. Variability in juvenile distribution between seasons was also noted with a clear concentration of juveniles on the Central Agulhas Bank between 20° and 22°E.

It is hoped that the size ranges presented here will be further refined and combined with the outputs of statolith ageing provide accurate information that can be used to model distribution and abundance patterns using spatial statistics methods such as semi-variograms and kriging (Journel and Huijbregts 1978) as well as General Additive Models (GAM) (Booth 1997).

Overall, the patterns in reproductive biology as well as distribution support previous studies on chokka and are also in agreement with the characteristics of the family Loliginidae.

CHAPTER 5

The Chokka Squid Life Cycle

Introduction

Loligo vulgaris reynaudii is arguably one of the best studied of the commercially exploited loliginid squids. Research began in the early 1980's when it was recognized that it was a potential new fisheries resource (Augustyn and Roel 1998). A multidisciplinary research programme has been established and is in place to provide management advice to both government and industry stakeholders.

Despite the wealth of biological and environmental data collected, some key features remain unresolved. These were outlined in Chapter 1 and this thesis has attempted to address some of the issues. In this chapter, an overview of the lifecycle, combining published data and the results of this study, is presented and additional areas of further research identified. Data collection issues are also addressed.

Population structure

Attempts to identify cohorts in chokka squid has demonstrated that the population structure is highly variable depending both on the location and time of sampling (Augustyn 1990, Augustyn *et al.* 1994). The present study found three cohorts in females, but in males, usually four and sometimes six cohorts were present.

The techniques used to define cohorts in squid are essentially the same used for teleosts (Augustyn 1990, Hatfield 1996, Collins *et al.* 1999) and rely on various mixture distribution algorithms such as the EM algorithm (Everitt and Hand 1981) or similar (Macdonald and Green 1988) that utilise maximum likelihood routines.

The simplest technique, which has a long history of use in fishery analysis, is that of Bhattacharya (1967). The subjectivity of the technique has been criticised (Pauly 1985) but nevertheless it has been applied to loliginids albeit with acknowledgement of its lack of objectivity (Pierce *et al.* 1994). Using the technique to generate initial estimates of means and standard deviations does, however, have merit and when combined with the results of ageing studies, true age cohorts in chokka will be identified.

Accounting for three cohorts in the population of an animal that has only two apparent peak breeding seasons was attempted for *L. gahi* in Falkland Island waters (Hatfield 1996, Hatfield and Des Clers 1998). Despite the evidence of three cohorts, only two peak hatching events have been identified and Hatfield and Des Clers (1998) suggest that the smaller magnitude and unpredictable occurrence of the third brood may make it difficult to identify. Once sufficient population level ageing data are available for chokka, it will be possible to determine the hatching dates and identify distinct broods.

Reproductive Biology

Previous studies on chokka have identified the summer peak spawning season as the major source of biomass in the chokka stock with the winter spawning season having a lesser contribution (Augustyn 1990, Augustyn *et al.* 1994). These deductions were based on peaks in commercial jig catches at these times, which show the summer peak catch to be higher, on average, than the winter catch. Nevertheless in some years, winter catches are as high or even higher than summer catches (Augustyn and Roel 1998; Figure 3). This thesis (Chapter 4) found that there was no evidence of a winter peak in the 1988-1989 data and that levels of reproductive activity were almost constant throughout the year.

The 1999-2000 data by contrast showed that two distinct peaks in reproductive activity occurred in autumn/winter and spring/summer.

Although no mass mortalities have been observed in chokka, it is assumed that because of the wide range of spawning sites used, senescence is dispersed through time and space with predators and scavengers on the spawning grounds consuming dead or dying squid (Augustyn 1990, Sauer and Smale 1993). Accounting for two spawning episodes in an animal that is widely considered to be an annual terminal spawner requires creative scientific reasoning. Evidence of serial spawning in chokka based on the work of Melo and Sauer (1998) was mentioned in Chapter 1. If individual female chokka are able to reach peaks in maturity both in winter and summer of the same year, then squid born in winter would first spawn in summer and then again the following winter. This is, however, unlikely, due to the loss of condition and starvation that occurs on the spawning grounds (Augustyn 1990).

A hypothesized life cycle of two overlapping reproductive cycles with the first hatching in spring and spawning the following summer at an age of 14 months and the second hatching in autumn and spawning in their second spring (presumably at an age of 24 months) was proposed for *L. pealei* by Mesnil (1977) to explain variable size at maturity as well as an extended (six month) spawning season. The theory was expanded on by Lange and Sissenwine (1980). A serious flaw in the hypothesis was addressed by Brodziak and Macy (1996) who found, using statolith ageing, that the proposed lifespan of two years required to complete the cross-over was unlikely.

The critical ingredient in these hypotheses is ageing data or rather in chokka squid, the lack thereof; without knowing the age at first maturity, it is not possible to determine how long

after birth squid would be capable of spawning. Until such data are available, determining the origin of the three or more cohorts evident in the population is purely speculative.

Growth and maturation

Due to the factors of short lifespans, multiple broods and highly variable growth rates, teleost fishery techniques such as ELEFAN are not readily applicable to cephalopod growth studies (Jackson *et al.* 2000). What is required is direct ageing of statoliths as well as validation of growth rings, which would compliment length frequency analysis.

Variability in size-at-maturity has been observed (Augustyn 1990) and in the present study, a seasonal cycle of changes in mantle length was evident on the spawning grounds as well as offshore with squid caught in winter/spring having a smaller average mantle length than those caught in summer/autumn. Reasons for this apparent variability were suggested in Chapter 4 but without adequate ageing data, could not be substantiated. Further evidence for changes in the average size of squid could be obtained by examining the monthly commercial catch data, which may reveal changes in the relative proportions of the commercial size classes viz. small, medium, large and extra large caught each month.

Longitudinal differences in size-at-maturity were also discussed in Chapter 4 with adult squid caught in the east, maturing at a smaller size than squid caught further west. It has been suggested (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. Given the influence of temperature on the growth of other loliginids discussed in Chapter 3 and if it can be proven that they experience warmer water temperatures, these squid would experience faster growth and hence, mature at a smaller size than squid further west.

Proving that they were also the same age as squid further west would make for a convincing argument. Further investigation into seasonal temperature variation would have to be included and the possibility of other growth influences such as food supply would also need to be considered.

Migration

An annual pattern of squid hatching in the east, migrating westwards to offshore feeding grounds on the Central and Western Agulhas Bank and the west coast and subsequent return migration to the eastern inshore areas to spawn is now accepted for chokka (Augustyn *et al.* 1994, Augustyn and Roel 1998). The distribution patterns presented in this study add support to this hypothesis; adults were predominantly inshore and in the east with juveniles inshore in the east and offshore in the west and immature squid showing an intermediate distribution pattern. Catches of adult animals in deeper water, particularly in autumn in the central study area were not uncommon and may represent deeper spawning squid. These deep-water samples also seemed to consist entirely of adult squid.

Sex ratio

This study showed that the ratio of males to females varies between maturity stages and is also dependent on the time of sampling. Past studies considered that on the spawning grounds, the ratio of males to females was in the region of 2.5:1. (Augustyn 1989, Sauer and Smale 1993, Augustyn *et al.* 1994, Lipiński 1994). These studies were often timed to coincide with peak spawning periods. With the examination of monthly data in this study, a pattern of significantly male biased ratios is only apparent during the peak spawning periods.

The results from the research trawl data are also interesting and indicate female bias in the samples more frequently than male bias, even when the samples are restricted to the inshore region. Between stage differences were also noted with juvenile sex ratios for the three study areas being more female biased and subadult sex ratios being more male biased. How and why sex ratios should change between maturity stages are challenging questions for future research.

Critical research areas

Of prime importance to any further biological studies is the need for direct ageing data using statoliths. Many of the hypotheses outlined in this thesis rely on assumptions made about the age of chokka. These assumptions might prove to be incorrect but can only be tested once sufficient population level ageing data are available. Another area of potential research relates to chokka growth rates and the possible influences of temperature and feeding. Such a study would be multi-disciplinary and require laboratory testing as well as an examination of oceanographic data. The role of sneaker males in the population also needs to be quantified. Linked to this, a thorough investigation into sex ratios both inshore and offshore needs to be made and any impacts as a consequence of selective fishing techniques quantified. Finally, further tagging studies need to be attempted on a large scale to determine both long and short-term migration patterns.

Data, management and the role of GIS

Three sets of data were used in this study, commercial jig data, commercial demersal trawl data and research demersal trawl data. The characteristics of the different datasets are outlined in Table 5.

Table 5 Comparison of biological datasets used in chokka squid research.

<i>Data</i>	<i>Time Series</i>	<i>Advantages</i>	<i>Disadvantages</i>	<i>Use</i>
Research	1986-1999 (biannually)	Good spatial coverage, research focussed, trained personnel.	Restricted to two seasons, does not cover all squid habitat.	Establish basic biology patterns across Agulhas Bank, good for distribution and abundance.
Commercial Trawl	1999-2000 (monthly)	Trawl gear is unbiased, not squid directed, monthly resolution, fair spatial coverage.	Sample sizes are small, observers/collectors are not scientists, need for more samples each month.	Good source of monthly biological data, potential for recruitment prediction.
Commercial Jig	1988-1989 (monthly) 1999-2000 (monthly)	Inshore on spawning grounds, monthly resolution.	Jigging is size and sex selective, need for full size range in samples, collectors are not scientists, need to record catch position and depth.	Good source of monthly reproduction data, potential for spatial comparisons and tagging studies.

The various datasets compliment each other in terms of their outputs and focus and it would be difficult to single out a perfect or optimal dataset to use. By drawing on a combination of data sources, being aware of their shortcomings and limitations, a more complete overview of chokka biology can be obtained.

In this study it was apparent that shortcomings in the data collection methods do exist: in some months either the commercial trawl or jig or sometimes both were unavailable; the sample size in some months was also too small for statistically significant results to be recorded. Given the necessity of data on a monthly resolution to facilitate real time management it is vital that a structured research programme to examine monthly biological data be established. Improvements to collection techniques, particularly of the commercial trawl data would include larger samples from several of vessels each month. This would allow more of the chokka habitat to be sampled at the same time leading to a more comprehensive dataset.

Given that observers are already present on these vessels, this should be an achievable goal. The trawl data also most closely resembles the research data in terms of gear selectivity and would probably deliver better biological data than the more selective jig gear.

Jig samples need to be collected aboard the vessel at the time of weighing each catch and consist of statistically valid numbers of the full size range caught. Accurate location and date information needs to be provided with each sample. Several skippers and boat owners have indicated their interest and it would be a good opportunity to get personal involvement of the industry in research. Some basic training in collection techniques would need to be provided and a single senior crew member given the responsibility of collecting the sample and ensuring its safe delivery to the researchers. If this system proved successful it would be possible to obtain a range of samples from different locations within each month and would provide comprehensive monthly data of reproductive biology over a large geographical area.

The role of GIS

In chokka research, there has been a need to better visualise the spatial aspects of the life cycle. The incorporation of the results of oceanographic studies with biological data is also desirable to produce predictive models of the interaction between chokka and its environment. This thesis attempted to demonstrate how GIS could aid in these visualisations and the maps produced in the preceding chapters are examples of typical GIS outputs.

Many marine scientists are critical of GIS and see them as little more than tools for generating attractive maps. This is no fault of the GIS technology but rather of its use by researchers who fail to understand the concept or grasp the technological capabilities of the system. Visualising and understanding spatial relationships are the skills of the geographer

while stock assessment, understanding biological interactions and modelling resource utilization are the tasks of a fishery scientist. For a fishery GIS to be effective, there needs to be an understanding of both spatial analysis and fishery science.

Booth (in press) has suggested that existing commercial GIS packages were developed for the terrestrial environment and cannot suitably handle the range of data generated by marine systems. The chief issue is one of dimensions, in that fisheries tend to be multi-dimensional and terrestrial resources only 2D. Although this is a valid criticism of most GIS packages, the advanced GIS used by mining and engineering concerns are intrinsically 3D and well developed to handle multi-dimensional data.

Development of fishery-orientated GIS software may be one answer but customisation of existing commercial packages to suit fishery needs is probably a better alternative. In-house or discipline specific packages often have limited capacity to export data in a format suitable for use in other packages. GIS software such as ArcView[®] have been developed over a number of years and include links to statistical packages such as S-Plus[®] and database and spreadsheet software such as Access[®] and Excel[®]. Additionally they have powerful interfaces for publishing data on the Internet. Regrettably these packages are expensive but as a percentage of the industry's value, they are usually only a minor expense. The role of GIS specialists or personnel trained in spatial analysis is also unavoidable if the full value of the system is to be realised.

These factors are of concern to the chokka research programme in particular and the development of a fishery information system for all species on the Agulhas Bank in general.

MCM's database is currently being upgraded from the existing in-house system to an Access[®] system at considerable cost in time and effort. As a result, a large source of geo-referenced data will be available for relatively easy incorporation in a GIS. Similarly, oceanographic data is currently collected using Excel[®] spreadsheets and should be suitable for inclusion in a GIS. Spatial analysis in oceanographic studies is done using the Surfer[®] surface analysis package. The outputs of this system are also suitable for GIS use. The further development of a chokka fishery information system that utilises GIS then seems feasible provided a suitable system designer could be found.

Although the full capabilities of the GIS were not demonstrated in this study, the basic system is in place. Both research and commercial biological data have been transformed into Excel[®] spreadsheets and incorporated into Access[®] databases. Bathymetry, coastline and some sediment data are available. MCM's oceanographic data from research cruises are also geo-referenced and can be included in the GIS.

Management

The development of the GIS as a decision-making support tool is one particular objective. It need not be exclusive of a research-directed GIS but its focus will differ. Management GIS are concerned with predicting stock abundance and modelling recruitment to provide decision makers with solutions while research needs would rely more on the capture, storage and integration of multivariate data in order to test hypotheses. The need for real time data is more acute in a management focussed GIS, particularly, as with chokka, where the fishery is effort and not catch controlled. With the introduction of vessel monitoring systems planned for the industry in 2002, an opportunity to collect a virtually continuous stream of geo-referenced data exists.

If an agreement to transmit daily catch data could also be reached, within season estimates of abundance could become available. Such a dynamic system of stock assessment may be beyond the resources of MCM but is technologically possible.

A further point relating to management involves the delivery of research findings to the stakeholders. The establishment of the South African Squid and Climate Change program webpage (www.environment.gov.za/mcm/offshore/squid/index.htm) by MCM oceanographers represents an ideal opportunity to deliver reports, spreadsheets and graphs to a wider audience. GIS lend themselves to this kind of publication and software exists to enable interactive maps to be accessed and queried. Once the stakeholders see the benefits of the system, greater support and co-operation is likely to result.

Conclusion

The chokka squid life cycle has a relatively large spatial component compared to a short temporal one. Within one year, its life cycle is complete but it may have travelled over 2000km (Figure 5.1). To make the best-informed decisions, data must cover the entire life cycle throughout its distribution. Studies on migratory animals are notoriously difficult but for the chokka, the opportunity exists to integrate multi-source data collected at a variety of spatial and temporal scales. GIS represents a practical tool to handle and analyse the data and may provide the framework to develop the forecasting capacity needed in the fishery.

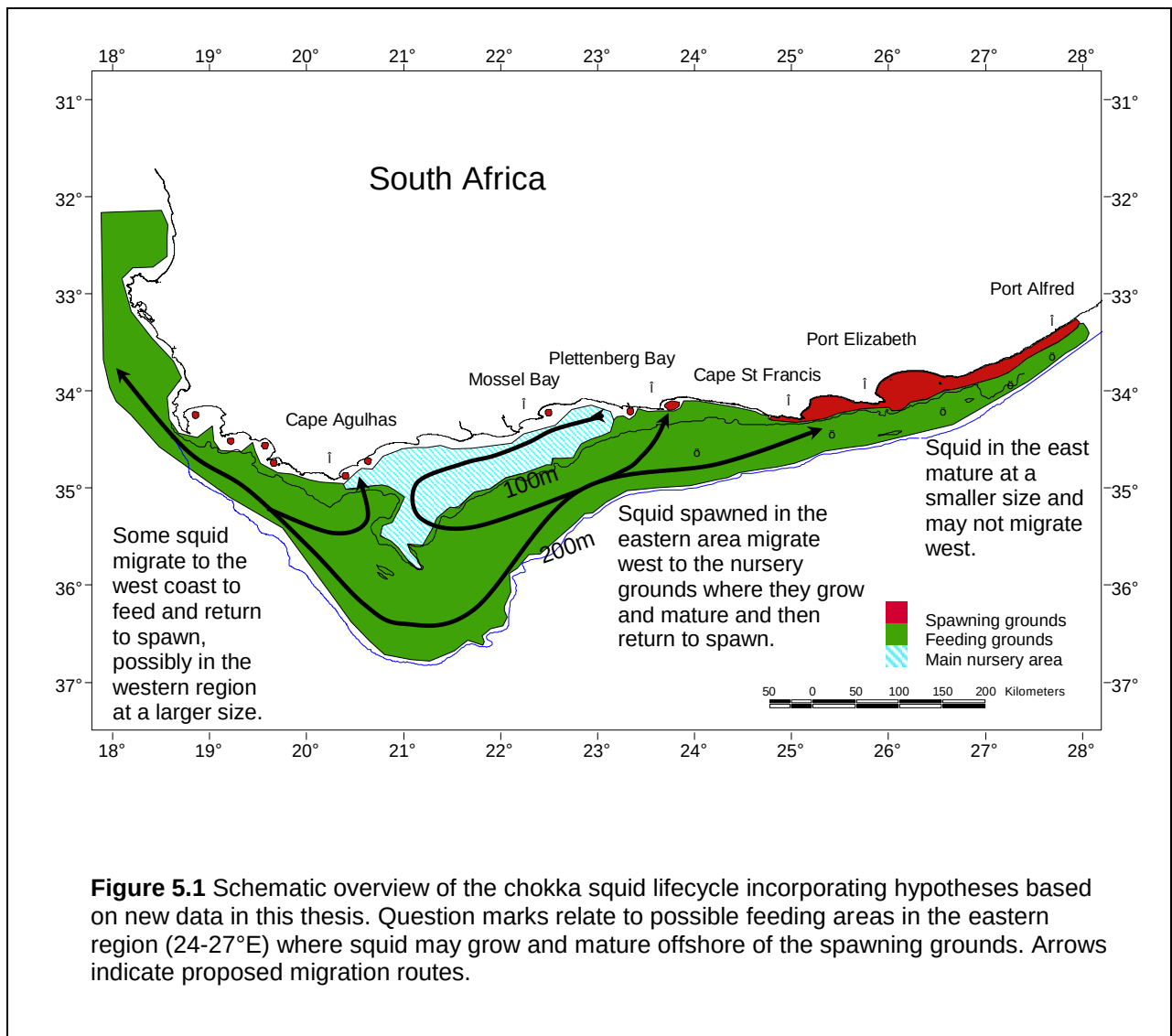


Figure 5.1 Schematic overview of the chokka squid lifecycle incorporating hypotheses based on new data in this thesis. Question marks relate to possible feeding areas in the eastern region (24-27°E) where squid may grow and mature offshore of the spawning grounds. Arrows indicate proposed migration routes.

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Appendix I (Statistical descriptions of length-weight regression of research data)

Table 1. Length-to-weight relationship for autumn caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 20° and 21°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	<u>Slope</u>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RMS</i>
M I	104	2.432	-7.638	0.97	0.295	0.061	0.020
M II	380	2.296	-6.888	0.96	0.179	0.035	0.030
M III	297	2.324	-7.079	0.96	0.204	0.037	0.035
F I	127	2.386	-7.379	0.95	0.330	0.069	0.016
F II	336	2.319	-6.960	0.92	0.272	0.055	0.037
F III	265	2.562	-8.230	0.93	0.322	0.061	0.021

Table 2. Length-to-weight relationship for autumn caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 21° and 22°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	<u>Slope</u>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RMS</i>
M I	91	2.409	-7.553	0.99	0.192	0.039	0.007
M II	487	2.405	-7.464	0.96	0.167	0.032	0.019
M III	340	2.434	-7.678	0.97	0.177	0.032	0.022
F I	114	2.230	-6.634	0.91	0.472	0.097	0.027
F II	446	2.237	-6.545	0.91	0.240	0.048	0.025
F III	392	2.596	-8.367	0.94	0.246	0.047	0.014

Table 3. Length-to-weight relationship for autumn caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 22° and 23°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	<u>Slope</u>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RMS</i>
M I	58	2.558	-8.275	0.96	0.466	0.096	0.031
M II	196	2.396	-7.428	0.95	0.306	0.059	0.030
M III	278	2.416	-7.590	0.98	0.150	0.028	0.018
F I	55	2.518	-8.048	0.97	0.383	0.079	0.011
F II	235	2.581	-8.306	0.95	0.279	0.055	0.014
F III	245	2.604	-8.432	0.93	0.333	0.064	0.018

Table 4. Length-to-weight relationship for autumn caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 23° and 24°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	Slope	Intercept	<i>r</i>	Intercept SE	Slope SE	RMS
M I	28	2.264	-6.804	0.96	0.634	0.130	0.020
M II	128	2.452	-7.756	0.98	0.227	0.045	0.016
M III	306	2.220	-6.558	0.96	0.203	0.037	0.046
F I	57	2.449	-7.691	0.97	0.382	0.080	0.012
F II	110	2.459	-7.716	0.97	0.278	0.056	0.008
F III	202	2.559	-8.195	0.95	0.320	0.061	0.012

Table 5. Length-to-weight relationship for autumn caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 24° and 25°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	Slope	Intercept	<i>r</i>	Intercept SE	Slope SE	RMS
M I	41	2.488	-7.937	0.98	0.412	0.087	0.011
M II	66	2.332	-7.170	0.94	0.514	0.102	0.036
M III	212	2.165	-6.280	0.97	0.120	0.037	0.029
F I	58	2.523	-8.064	0.98	0.297	0.062	0.011
F II	84	2.525	-8.080	0.97	0.340	0.069	0.011
F III	177	2.237	-6.520	0.91	0.417	0.079	0.022

Table 6. Length-to-weight relationship for autumn caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 25° and 26°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	Slope	Intercept	<i>r</i>	Intercept SE	Slope SE	RMS
M I	20	2.439	-7.759	0.98	0.505	0.106	0.012
M II	30	2.368	-7.330	0.98	0.422	0.086	0.009
M III	157	2.295	-7.124	0.99	0.162	0.029	0.021
F I	28	2.561	-8.249	0.98	0.401	0.084	0.007
F II	55	2.547	-8.184	0.99	0.217	0.044	0.008
F III	133	2.417	-7.538	0.97	0.291	0.055	0.017
F VI	5	2.099	-6.009	0.94	2.487	0.463	0.006

Table 7. Length-to-weight relationship for autumn caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 26° and 27°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	<u>Slope</u>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RMS</i>
M I	25	2.315	-7.053	0.97	0.550	0.116	0.018
M II	57	2.435	-7.667	0.98	0.289	0.059	0.010
M III	119	2.245	-6.813	0.98	0.231	0.043	0.032
F I	34	2.371	-7.255	0.93	0.773	0.164	0.040
F II	45	2.453	-7.690	0.98	0.391	0.080	0.008
F III	121	2.412	-7.493	0.92	0.497	0.095	0.036

Table 8. Length-to-weight relationship for spring caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 20° and 21°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	<u>Slope</u>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RMS</i>
M I	117	2.353	-7.279	0.99	0.162	0.033	0.008
M II	276	2.345	-7.215	0.99	0.118	0.023	0.007
M III	153	2.370	-7.366	0.98	0.203	0.037	0.009
F I	153	2.369	-7.310	0.96	0.249	0.053	0.017
F II	255	2.385	-7.348	0.94	0.274	0.055	0.020
F III	106	2.520	-7.999	0.97	0.291	0.056	0.008

Table 9. Length-to-weight relationship for spring caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 21° and 22°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	<u>Slope</u>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RMS</i>
M I	134	2.446	-7.743	0.99	0.161	0.033	0.015
M II	244	2.394	-7.481	0.98	0.156	0.031	0.011
M III	310	2.332	-7.170	0.98	0.131	0.024	0.012
F I	184	2.538	-8.118	0.98	0.194	0.042	0.015
F II	245	2.446	-7.687	0.96	0.235	0.047	0.015
F III	213	2.414	-7.456	0.94	0.291	0.056	0.010

Table 10. Length-to-weight relationship for spring caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 22° and 23°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	<u>Slope</u>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RMS</i>
M I	79	2.220	-6.620	0.95	0.423	0.087	0.054
M II	122	2.510	-8.047	0.99	0.178	0.035	0.008
M III	172	2.382	-7.440	0.98	0.175	0.033	0.016
F I	111	2.471	-7.816	0.99	0.186	0.039	0.008
F II	130	2.447	-7.681	0.97	0.259	0.052	0.010
F III	123	2.372	-7.245	0.92	0.478	0.093	0.010

Table 11. Length-to-weight relationship for spring caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 23° and 24°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	<u>Slope</u>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RMS</i>
M I	30	2.396	-7.539	0.99	0.316	0.065	0.012
M II	61	2.492	-7.910	0.99	0.256	0.051	0.011
M III	188	2.311	-7.059	0.98	0.195	0.037	0.033
F I	45	2.347	-7.240	0.97	0.458	0.097	0.015
F II	63	2.499	-7.938	0.97	0.385	0.078	0.013
F III	146	2.539	-8.113	0.95	0.361	0.070	0.021

Table 12. Length-to-weight relationship for spring caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 24° and 25°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	<u>Slope</u>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RMS</i>
M I	13	2.614	-8.543	0.99	0.518	0.111	0.021
M II	18	2.625	-8.681	0.99	0.534	0.105	0.008
M III	123	2.281	-6.986	0.97	0.263	0.049	0.039
F I	27	2.530	-8.130	0.99	0.222	0.048	0.003
F II	26	2.560	-8.237	0.98	0.569	0.116	0.010
F III	92	2.536	-8.121	0.96	0.386	0.074	0.011

Table 13. Length-to-weight relationship for spring caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 25° and 26°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	<u>Slope</u>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RMS</i>
M I	21	2.363	-7.356	0.99	0.204	0.044	0.004
M II	28	2.136	-6.187	0.98	0.466	0.095	0.010
M III	131	2.326	-7.313	0.96	0.311	0.057	0.056
F I	35	2.463	-7.777	0.98	0.360	0.077	0.009
F II	23	2.171	-6.348	0.89	1.210	0.249	0.033
F III	122	2.443	-7.660	0.94	0.427	0.082	0.026

Table 14. Length-to-weight relationship for spring caught *Loligo vulgaris reynaudii* in each of three reproductive stages collected between 26° and 27°E. M and F refer to male and female; stages I, II and III, the modified maturity stages described in Chapter 2 and stage VI refers to spent or post spawning animals. *n* refers to the number of squid sampled, *r*, the correlation coefficient of the regression, *RMS*, the residual mean sum of squares and *SE*, the standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

Stage	<i>n</i>	<u>Slope</u>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RMS</i>
M I	13	2.330	-7.141	0.95	1.004	0.208	0.016
M II	17	2.087	-5.983	0.81	1.913	0.392	0.086
M III	200	2.282	-7.012	0.99	0.129	0.024	0.016
F I	24	2.417	-7.541	0.96	0.622	0.140	0.011
F II	14	2.383	-7.398	0.99	0.526	0.110	0.006
F III	196	2.445	-7.656	0.92	0.396	0.076	0.034

Appendix II (Statistical descriptions of length-weight regression of commercial data)

Table 1. Statistical description of length-to-weight relationships for mature *Loligo vulgaris reynaudii* caught by hand jigging on the inshore spawning grounds (approximately 25°-27°E) between May 1999 and June 2000. M and F refer to male and female, *n* to the sample size, *r*, the regression coefficient, SE, standard error and RSE, residual standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

<i>Data</i>	<i>n</i>	Slope	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RSE</i>
May'99 M	41	2.336	-7.365	0.89	0.726	0.127	0.103
May'99 F	22	2.100	-5.835	0.66	1.806	0.335	0.131
Jun '99 M	64	2.257	-6.999	0.86	0.651	0.116	0.173
Jun '99 F	14	2.227	-6.743	0.70	2.211	0.424	0.125
Jul '99 M	57	2.285	-7.195	0.93	0.513	0.910	0.157
Jul '99 F	17	2.939	-10.427	0.83	1.778	0.343	0.129
Aug'99 M	5	0.276	3.631	0.09	2.672	0.498	0.040
Aug'99 F	35	0.296	3.513	0.06	0.991	0.191	0.125
Sept'99 M	24	2.521	-8.515	0.74	1.777	0.318	0.131
Nov'99 M	38	2.426	-7.903	0.97	0.409	0.072	0.108
Nov'99 F	34	2.779	-9.499	0.90	0.866	0.162	0.077
Jan '00 M	18	2.236	-6.797	0.87	1.261	0.214	0.063
Feb '00 M	7	1.840	-4.742	0.82	1.965	0.381	0.106
Feb '00 F	19	2.517	-8.055	0.91	1.050	0.198	0.128
Apr '00 M	29	1.708	-3.869	0.65	1.347	0.240	0.136
Apr '00 F	11	1.565	-3.030	0.43	3.209	0.596	0.105
May'00 M	11	2.205	-6.598	0.80	1.964	0.367	0.177
May'00 F	62	1.867	-4.556	0.66	0.921	0.173	0.117
Jun '00 M	32	1.748	-4.074	0.72	1.106	0.197	0.203
Jun '00 F	15	2.429	-7.464	0.86	1.434	0.267	0.094

Table 2. Statistical description of length-to-weight relationships for mature *Loligo vulgaris reynaudii* caught by hand jigging on the inshore spawning grounds (approximately 25°-27°E) between March 1988 and January 1989. M and F refer to male and female, *n* to the sample size, *r*, the regression coefficient, SE, standard error and RSE, residual standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

<i>Data</i>	<i>n</i>	Slope	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RSE</i>
Mar '88 M	10	2.556	-8.545	0.99	0.498	0.089	0.096
Mar '88 F	11	2.992	-10.572	0.77	2.923	0.540	0.099
Apr '88 M	26	2.042	-5.624	0.82	1.101	0.196	0.161
May '88 M	34	1.903	-4.825	0.52	1.864	0.326	0.350
May '88 F	25	1.944	-4.871	0.72	1.367	0.254	0.131
June '88 M	27	1.779	-4.286	0.77	1.105	0.192	0.173
June '88 F	38	1.054	-0.353	0.47	0.982	0.186	0.148
July '88 M	57	1.848	-4.619	0.78	0.749	0.134	0.205
July '88 F	61	1.602	-3.202	0.43	1.263	0.241	0.137
Aug '88 M	91	2.056	-5.758	0.88	0.441	0.079	0.132
Aug '88 F	46	2.143	-6.010	0.71	1.082	0.208	0.110
Sept '88 M	234	2.321	-7.192	0.83	0.385	0.068	0.149
Sept '88 F	69	2.052	-5.532	0.61	1.045	0.201	0.130
Oct '88 M	117	2.354	-7.438	0.91	0.395	0.070	0.124
Oct '88 F	62	2.284	-6.823	0.74	0.915	0.176	0.122
Nov '88 M	197	2.199	-6.630	0.86	0.364	0.064	0.130
Nov '88 F	104	2.407	-7.472	0.69	0.839	0.160	0.103
Dec '88 M	194	2.242	-6.842	0.77	0.505	0.088	0.163
Dec '88 F	64	3.210	-11.747	0.68	1.463	0.279	0.139
Jan '89 M	59	2.425	-7.819	0.80	0.922	0.162	0.121
Jan '89 F	44	2.067	-5.708	0.78	0.909	0.172	0.106

Table 3. Statistical description of length-to-weight relationships for mature *Loligo vulgaris reynaudii* caught in demersal trawl gear on the central and eastern Agulhas Bank (approximately 22°-24°E) between April 1999 and May 2000. M and F refer to male and female, *n* to the sample size, *r*, the regression coefficient, SE, standard error and RSE, residual standard error. Slopes given are those of the natural log transformed total wet body weight against the natural log transformed dorsal mantle length.

<i>Data</i>	<i>n</i>	<i>Slope</i>	<i>Intercept</i>	<i>r</i>	<i>Intercept SE</i>	<i>Slope SE</i>	<i>RSE</i>
Apr '99 M	15	2.336	-7.301	0.99	0.437	0.081	0.114
Apr '99 F	8	2.651	-8.715	0.86	2.287	0.445	0.126
May '99 M	20	2.428	-7.737	0.98	0.411	0.078	0.078
May '99 F	5	1.156	-0.892	0.32	5.248	0.976	0.209
June '99 M	13	1.616	-3.681	0.51	2.407	0.479	0.479
June '99 F	22	2.074	-5.814	0.70	1.541	0.304	0.117
July '99 M	30	2.600	-8.792	0.97	0.435	0.080	0.133
July '99 F	30	2.519	-8.051	0.83	1.112	0.218	0.097
Aug '99 M	23	2.370	-7.448	0.96	0.575	0.104	0.091
Aug '99 F	14	0.188	3.981	0.01	2.754	0.536	0.143
Sept '99 M	23	2.526	-8.135	0.98	0.405	0.077	0.091
Sept '99 F	13	2.387	-7.360	0.93	0.999	0.197	0.064
Oct '99 M	8	2.251	-6.722	0.76	2.850	0.520	0.155
Oct '99 F	8	3.942	-15.528	0.87	3.215	0.616	0.095
Nov '99 M	13	2.611	-8.693	0.98	0.592	0.109	0.083
Nov '99 F	5	2.638	-8.674	0.93	2.168	0.415	0.126
Jan '00 M	7	2.114	-6.091	0.93	1.458	0.267	0.155
Jan '00 F	19	2.509	-8.038	0.94	0.807	0.152	0.063
Feb '00 M	10	3.205	-11.848	0.92	1.699	0.314	0.010
Feb '00 F	12	2.406	-7.410	0.76	2.274	0.433	0.089
Mar '00 M	10	2.579	-8.586	0.97	0.940	0.171	0.091
Mar '00 F	6	2.430	-7.550	0.94	1.696	0.320	0.098
May '00 M	7	2.431	-7.797	0.97	1.018	0.181	0.060
May '00 F	12	2.734	-9.242	0.92	1.384	0.262	0.086

Appendix III (Statistical results of the Mann-Whitney U-tests for between month differences in mean length of mature squid caught in commercial catches)

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

Mature Males							
Month	n	Mean Length	Median Length	Std Deviation	z	df	p
Feb							
Mar	10	288.2	312	80.94			
Apr	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
Jun	27	315.6	325	49.44	-0.653	34, 27	0.513
Jul	57	273.7	286	51.99	3.597	27, 57	<0.001
Aug	91	265.2	264	42.64	1.099	57, 91	0.272
Sep	234	279.2	281	38.27	-2.562	91, 234	0.010
Oct	117	287.6	280	44.92	-1.659	234, 117	0.097
Nov	197	300.0	307	39.94	-2.825	117, 197	0.005
Dec	194	304.7	309	37.42	-1.071	197, 194	0.284
Jan	60	300.4	305.5	32.50	1.023	194, 60	0.307
Feb							
Mar	90	308.4	329.5	61.55			
Apr	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
Jun	94	290.4	300	50.61	-1.616	170, 94	0.106
Mature Females							
Month	n	Mean Length	Median Length	Std Deviation	z	df	p
Feb							
Mar	11	225.5	221	13.43			
Apr	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
Jun	38	198.9	198	28.90	3.295	25, 38	<0.001
Jul	61	190.9	189	14.50	1.544	38, 61	0.123
Aug	46	181.0	179	14.60	3.598	61, 46	<0.001
Sep	69	180.9	180	14.50	0.010	46, 69	0.920
Oct	62	181.2	180	17.06	-0.044	69, 62	0.965
Nov	104	188.1	186	12.15	-3.891	62, 104	<0.001
Dec	64	191.4	189	12.19	-1.884	104, 64	0.060
Jan	44	199.1	198	19.84	-2.962	64, 44	0.003
Feb							
Mar	62	217.9	218	24.54			
Apr	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
Jun	54	200.7	199	18.23	3.743	72, 54	<0.001

Table 2 Monthly mean and median lengths (mm) and standard deviations of mature squid caught by hand-jigging between February 1999 and June 2000. The z statistic, degrees of freedom (df) and probability (p) are reported for the results of the between-month Mann-Whitney U-tests.

Mature Males							
Month	n	Mean Length	Median Length	Std Deviation	z	df	p
Feb	7	174.7	185	19.25			
Mar							
Apr	29	277.8	283	29.11			
May	41	309.8	315	38.90	-3.674	29, 41	<0.001
Jun	64	272.6	270	49.07	3.869	41, 64	<0.001
Jul	57	287.9	268	62.12	-1.192	64, 57	0.233
Aug	5	214.8	215	8.79	3.297	57, 5	0.001
Sep	24	267.8	266	23.02	-3.439	5, 24	<0.001
Oct							
Nov	38	293.5	307	59.82			
Dec							
Jan	36	333.6	332.5	41.54			
Feb							
Mar							
Apr	35	248.6	295	76.10			
May	11	214.4	215	33.02	4.518	35, 11	<0.001
Jun	32	277.1	268.5	51.01	-3.425	11, 32	<0.001
Mature Females							
Month	n	Mean Length	Median Length	Std Deviation	z	df	p
Feb	18	207.3	217.5	22.14			
Mar							
Apr	11	217.8	218	12.26			
May	22	220.8	218	19.56	-0.230	11, 22	0.818
Jun	15	183.7	182	14.46	4.756	22, 15	<0.001
Jul	17	178.4	178	19.93	1.002	15, 17	0.316
Aug	35	179.3	184	16.87	-0.850	17, 35	0.395
Sep							
Oct							
Nov	24	206.0	210.5	16.69			
Dec							
Jan							
Feb							
Mar							
Apr	46	162.2	160	12.67			
May	62	204.3	205	17.31	2.511		0.012
Jun	15	213.5	210	20.42	-1.327	62, 15	0.185

Table 3 Monthly mean and median lengths (mm) and standard deviations of mature squid caught by demersal trawl between February 1999 and June 2000. The z statistic, degrees of freedom (df) and probability (p) are reported for the results of the between-month Mann-Whitney U-tests.

Mature Males							
Month	n	Mean Length	Median Length	Std Deviation	z	df	p
Feb	16	280.4	307.5	63.40			
Mar							
Apr	16	230.9	197.5	89.97			
May	20	247.5	227.5	60.94	-3.431	16, 20	0.002
Jun	13	157.7	150	53.39	4.336	20, 13	0.001
Jul	30	236.8	246.5	66.47	-3.885	13, 30	0.001
Aug	24	257.4	273.5	49.11	-1.422	30, 24	0.161
Sep	23	195.0	215	44.87	5.092	24, 23	0.000
Oct	8	240.8	237.5	26.97	-2.701	23, 8	0.011
Nov	13	228.2	230	47.72	0.679	8, 13	0.510
Dec							
Jan							
Feb	10	225.5	228	22.77			
Mar	11	239.5	240	53.42	-0.764	10, 11	0.454
Apr							
May	7	280.0	285	37.75			
Jun	7	241.1	215	58.25	1.481	7, 7	0.164
Mature Females							
Month	n	Mean Length	Median Length	Std Deviation	z	df	p
Feb	14	193.6	191.5	16.45			
Mar							
Apr	8	171.5	168	18.31			
May	5	217.0	220	23.35	-2.653	8, 5	0.008
Jun	23	159.7	156	13.32	3.453	5, 23	<0.001
Jul	9	164.6	165	13.46	-0.630	23, 9	0.528
Aug	14	170.5	170	12.11	-1.300	9, 14	0.194
Sep	13	158.8	160	15.02	1.997	14, 13	0.046
Oct	8	184.4	181.5	10.89	-3.098	13, 8	0.002
Nov	5	188.0	190	27.97	-0.369	8, 5	0.712
Dec							
Jan	19	200.8	200	18.44			
Feb	12	190.5	190	11.91	2.217	19, 12	0.027
Mar	6	200.0	198.5	27.1	-0.516	12, 6	0.606
Apr							
May	12	197.3	200	18.11			
Jun	9	187.9	185	16.24	1.542	12, 9	0.123