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Spatial patterns in the biology of the chokka squid, *Loligo reynaudii* on the Agulhas Bank, South Africa

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Abstract Although migration patterns for various life history stages of the chokka squid (*Loligo reynaudii*) have been previously presented, there has been limited comparison of spatial variation in biological parameters. Based on data from research surveys; size ranges of juveniles, subadults and adults on the Agulhas Bank were estimated and presented spatially. The bulk of the results appear to largely support the current acceptance of the life cycle with 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. The number of adult animals in deeper water, particularly in autumn in the central study area probably represents squid spawning in deeper waters and over a greater area than is currently targeted by the fishery. The distribution of life history stages and different feeding areas does not rule out the possibility that discrete populations of *L. reynaudii* with different biological characteristics inhabit the western and eastern regions of the Agulhas Bank. In this hypothesis, some mixing of the populations does occur but generally squid from the western Agulhas Bank may occur in smaller numbers, grow more slowly and mature at a larger size. Spawning occurs on the western portion of the Agulhas Bank, and juveniles grow and mature on the west coast and the central Agulhas Bank. Future research requirements include the elucidation of the age structure of chokka squid both spatially and temporally, and a comparison of the statolith chemistry and genetic characterisation between adults from different spawning areas across the Agulhas Bank.

Keywords Chokka · *Loligo reynaudii* · Agulhas Bank · Biology · Spatial patterns

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Introduction

The Marine Living Resources Act of South Africa promulgated in 1998 provided new goals on fisheries management, transformation, and equal access to rectify historical imbalances in the fishing sector. This Act and the ideals it presented raised great expectations of access and social gain from South African marine resources.

However, the expansion of the South African fishing sector is limited by the natural productive capacity of the resources, most of which are either heavily utilized or overexploited (Cochrane et al. 1997; Britz et al. 2001).

The squid fishery for *Loligo reynaudii* is seen as one sector able to accommodate a large number of fishers and fisheries managers are under pressure to increase access. Management of a short lived species is notoriously difficult, however, and understanding of the impacts of fishing on the squid stocks is further complicated by their biology.

Squid are found along a substantial portion of the South African coast. It has been postulated that squid spawn and hatch in inshore waters along the southeast coast of South Africa, migrate offshore and westwards to feed and mature, and then return to the spawning grounds to complete their lifecycle (Augustyn 1989; Sauer et al. 1992; Augustyn et al. 1994). The dominance of adult squid in the commercial jig fishery has been considered as evidence of inshore spawning aggregations, supported by observations from SCUBA surveys in the same areas (Augustyn 1990; Sauer and Smale 1993; Sauer 1995). The distribution patterns of various life history stages based on biannual research cruises has provided further evidence for the migration patterns postulated for this species (Augustyn et al. 1994). The current management strategy assumes that fishers target the major portion of adult spawners, which are located in the inshore areas of the Eastern Cape Province. This postulated life cycle may not be as simple, however, as adult squid are caught in significant numbers towards the western boundary of their distribution, where egg masses are regularly caught in demersal trawls. In fact originally False Bay on the west coast of South Africa was thought to represent the spawning area (Augustyn 1989) and inshore spawning areas in the west have been identified by Lipiński (1998). It is therefore possible that a geographically fragmented stock is present on the western portion of the Agulhas Bank, which would necessitate a rethinking of the current management strategy.

Management of the chokka squid is therefore closely linked to understanding key aspects of its biology, particularly those aspects that have a strong spatio-temporal component. One method to investigate the possibility of separate stocks is to examine the spatial distribution of different life history stages using both commercial and research data. For many squid species, however, there is considerable spatial and temporal variability in maturation e.g. *Loligo pealeii* (Hatfield and Cadrin 2002) and *Loligo forbesi* (Pierce et al. 2005) which needs to be taken into account. Distribution patterns of various life history stages of *Loligo forbesi* have been analysed in an attempt to provide abundance and distribution estimates as well as define a stock-recruitment relationship in the North Sea fishery (Pierce et al. 1998).

Size at age data is not yet available for *Loligo reynaudii* (Lipiński and Durholtz 1994) but Olyott et al. (2006) provided evidence for spatial and seasonal variability in size at maturity. This paper extends this research by providing information on the distribution of the different life history stages using research data. The study is focused on the Agulhas Bank where the major proportion of the stock is concentrated. This oceanographic feature (Fig. 1) is a triangular extension of the continental shelf extending along the southeast coast of South Africa from Cape Agulhas (20°E) to Port Alfred (27°E) and south to the 1,000 m isobath, encompassing an area of ca. 29,000 nm^2 (Japp et al. 1994). For the purpose of this study, it has been divided into three regions: the Western Agulhas Bank (west of 20°E), the Central Agulhas Bank (20–23°E) and the Eastern Agulhas Bank (23–27°E). The cold, northerly Benguela Current forms the western boundary of the Agulhas Bank with the central and eastern Bank strongly influenced by the warm, southeast-flowing Agulhas Current.

Methods

Sampling

Biannual research cruises (commencing in the early 1980s) are conducted by the Marine and Coastal Management (MCM) Branch of the South African Department of Environmental Affairs and Tourism in spring and autumn. These

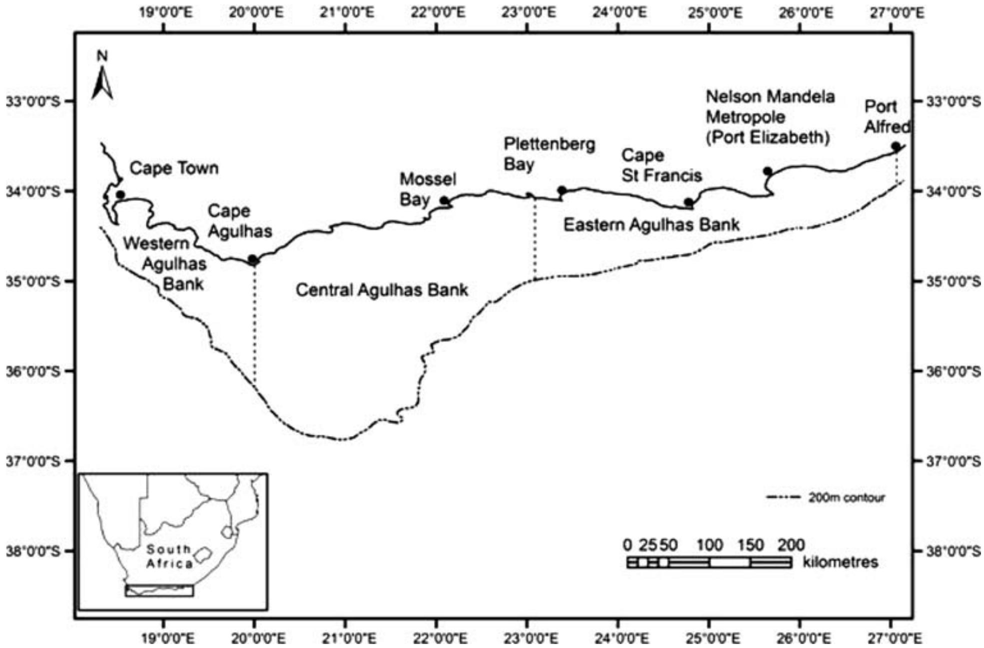


Fig. 1 The southeast coast of South Africa highlighting the various regions of the Agulhas Bank (after Japp et al. 1994) and the 200 m isobath

surveys provide the majority of abundance and biological data for a variety of fish and cephalopod species. Gear employed and sampling methodology is described by Payne et al. (1985). Research data used in this study were obtained from surveys between 1986 and 1999. It must be noted, however, that research vessels are large, restricting trawling operations in shallow (50 m) inshore waters where spawning squid aggregate and this limitation results in an under representation of these areas in the data. Biological samples were analysed immediately after each trawl. Maturity staging was according to Lipiński (1979) and mantle length (ML) was measured to the nearest millimetre.

Distribution and abundance

A simplified life history stage based on a modified Lipiński and Underhill (1995) scale was used by Olyott et al. (2006) and is reproduced here (Table 1). Based on an analysis of maturity stage and ML, seasonal size ranges for each life history stage were calculated by those authors (Table 2). These size ranges were applied to length frequencies of research samples and seasonal distribution and relative abundance patterns for each life history stage were mapped.

Table 1 Maturity scales used to assess maturity and life history stages in *Loligo reynaudii*

Lipiński and Underhill stage	Simplified stage	Olyott et al. Life history stage
I	1	Juveniles
II	2	Subadults
III		
IV	3	Adults
V		
VI		

The Lipiński and Underhill (1995) scale is based on macroscopic conditions of gonadal tissue, while the simplified stage was widely employed in research surveys [adapted from Olyott et al. (2006)]

Results

Maturity stage size ranges

Based on the spatially and seasonally stratified maturity data, frequencies of occurrence of

Table 2 Size ranges of various life history stages of *Loligo reynaudii* in three longitudinal areas across the Agulhas Bank

Life history stage	Male			Female		
	West	Central	East	West	Central	East
	Autumn					
Juvenile	<65 mm	<115 mm	<80 mm	<65 mm	<125 mm	<125 mm
Subadult	65–230 mm	115–185 mm	80–160 mm	65–190 mm	125–180 mm	125–165 mm
Adult	>230 mm	>185 mm	>160 mm	>190 mm	>180 mm	>165 mm
	Spring					
Juvenile	<130 mm	<100 mm	<100 mm	<130 mm	<130 mm	<125 mm
Subadult	130–220 mm	100–180 mm	100–135 mm	130–180 mm	130–170 mm	125–145 mm
Adult	>220 mm	>180 mm	>135 mm	>190 mm	>180 mm	>165 mm

Size ranges are based on calculated estimates of size at maturity in Olyott et al. (2006)

juveniles, subadults and adults, were calculated for each region and season. Spring caught males in the western region (Fig. 2a) comprised all three life history stages. A similar mixed composition was evident in the central region (Fig. 2b) while the eastern region (Fig. 2c) consisted of a population dominated by mature squid in most length classes. Female spring caught squid showed a similar pattern to the males, although there were still significant numbers of juvenile squid present in the eastern region (Fig. 2f). Autumn caught juvenile males comprised 25% in the <80 mm size class in the western region (Fig. 3a) although only four squid were sampled in this size class. In the other size classes, juveniles and subadults accounted for up to 50% of all squid measured although above 280 mm, most squid were mature. The predominance of adult squid in most size classes also increased towards the east. Autumn caught female juvenile squid comprised 20% of the <80 mm size class in the western region (Fig. 3d) although only five squid were sampled in this size class. Between 80 and 120 mm, juveniles accounted for up to 51.4%. Subadult females were present in most size ranges with highest relative abundance in the western region. All squid greater than 240 mm were mature. Both the central (Fig. 3e) and eastern (Fig. 3f) regions exhibited more discrete size ranges than the western area.

Distribution and abundance

The distribution and abundance patterns for each life history stage, based on research length frequencies, were mapped. In autumn, male juveniles were most abundant between the coast and the 60 m isobath (Fig. 4a). Concentrations of juveniles were apparent in protected bays in the east off Port Elizabeth, Cape St. Francis and Plettenberg Bay and similar high abundances were recorded in the west to depths of 200 m. Juveniles were notably absent along the 200 m isobath between 23° and 26°E. Subadult autumn caught males (Fig. 4b) were widely dispersed across the Agulhas Bank with high abundances noted between the 60 and 100 m isobaths and in the eastern bays. High concentrations were noticeable between 21° and 23°E at depths ranging between 100 and 200 m. Autumn caught adult males (Fig. 4c) were most abundant in the east between the coast and the 60 m isobath, high catches were also made between the 100 and 200 m 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 females (Fig. 5) showed a distribution pattern similar to males. Spring caught juvenile males (Fig. 6a) were more concentrated in the western region between the 60 and 100 m isobaths than in autumn and concentrations in the eastern bays were also apparent while abundance between the 100 and 200 m isobaths was low, particularly between 22° and 26°E. Spring caught subadult males (Fig. 6b) showed a similar pattern to the high concentrations of juveniles encountered on the Central Agulhas Bank and inshore in the east but also had higher abundances between 100 and 200 m. Adult males caught in spring (Fig. 6c) were almost exclusively concentrated in

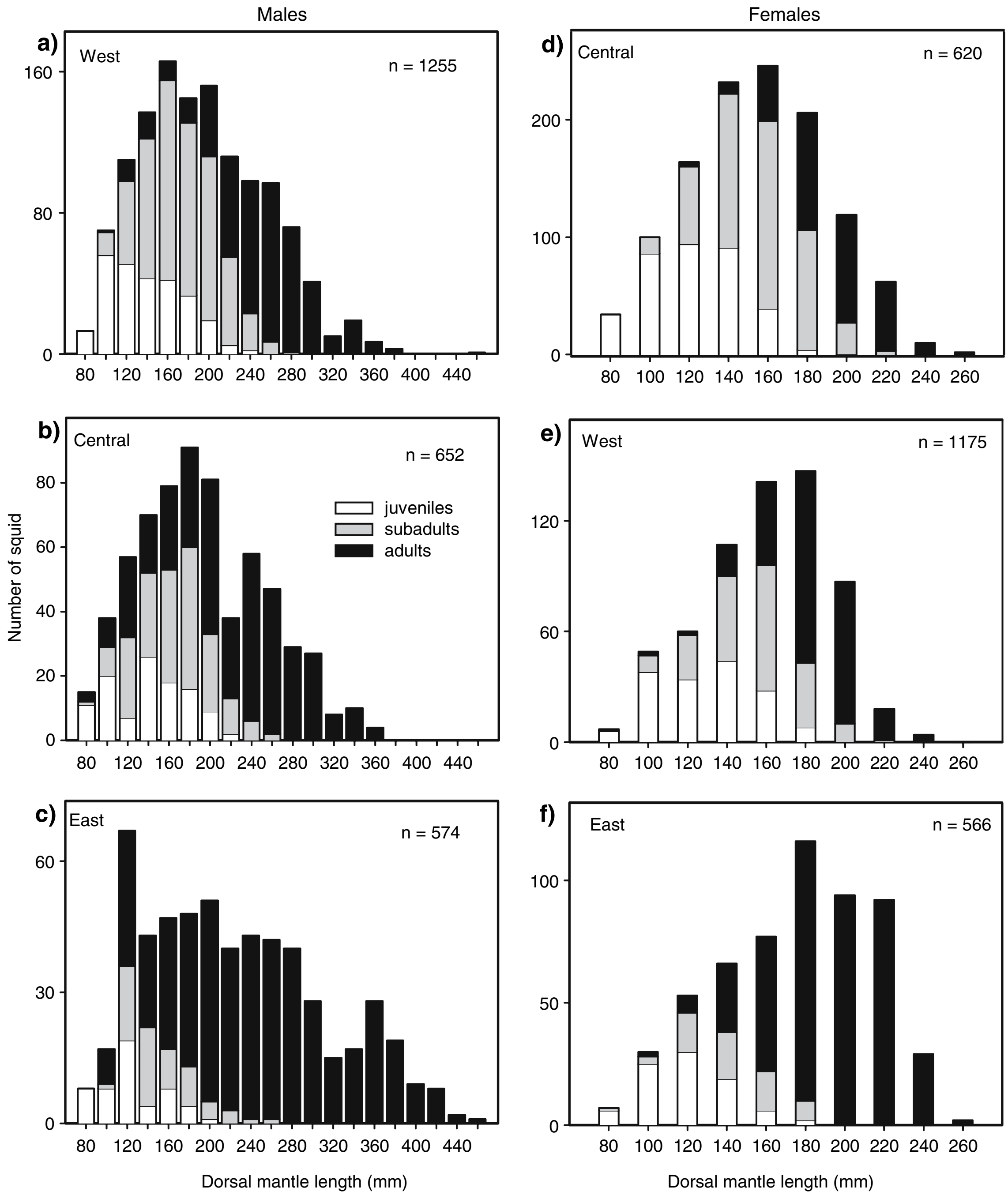


Fig. 2 Number of squid sampled in each maturity stage in 20 mm interval size classes in spring. The *x*-axis scale differs for males and females and the scale of the *y*-axis is dependent on the sample size (*n*)

the eastern bays, between the coast and the 60 m isobath particularly near Cape St Francis and Port Elizabeth. Spring caught females (Fig. 7) seemed to match the distribution pattern of the males, particularly in the adults (Fig. 7c), which were virtually absent from the western region.

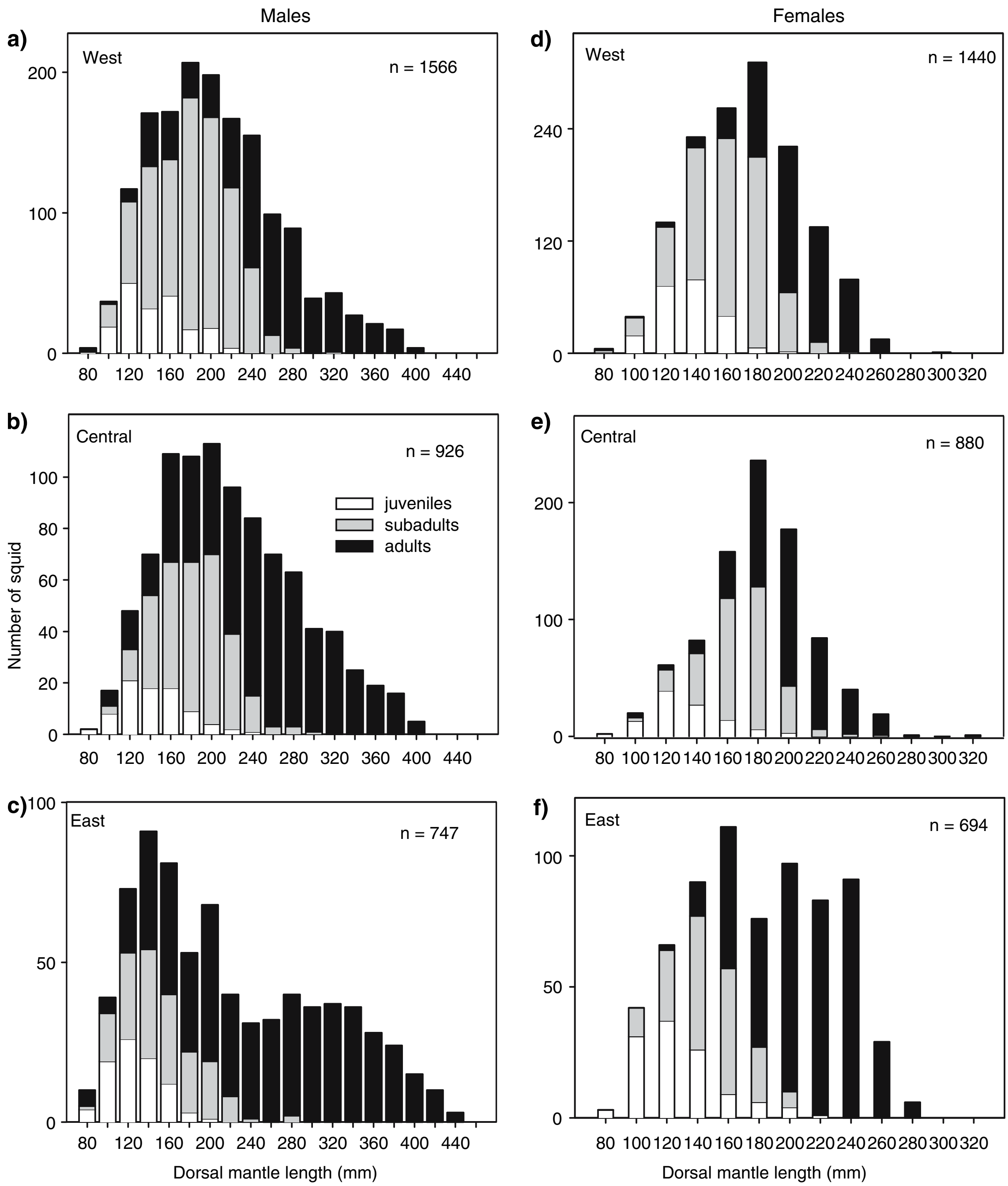
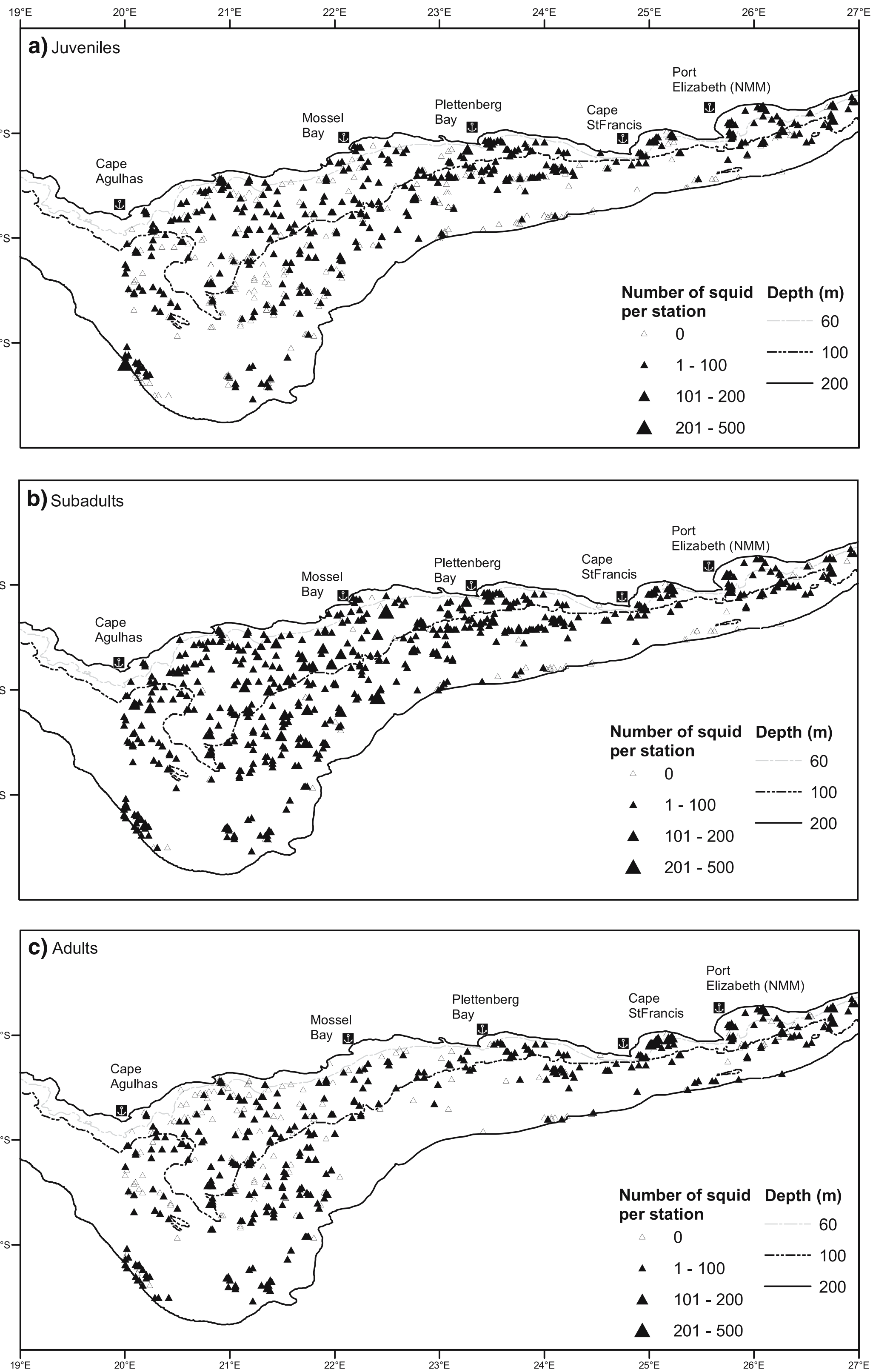


Fig. 3 Number of squid sampled in each maturity stage in 20 mm interval size classes in autumn. The *x*-axis scale differs for males and females and the scale of the *y*-axis is dependent on the sample size (*n*)

Discussion

Defining the size range of various life history stages is essential information for determining

Fig. 4 Distribution of male chokka in three life history ▶ stages caught in autumn research cruises on the Agulhas Bank


19°E
20°E
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24°E
25°E
26°E
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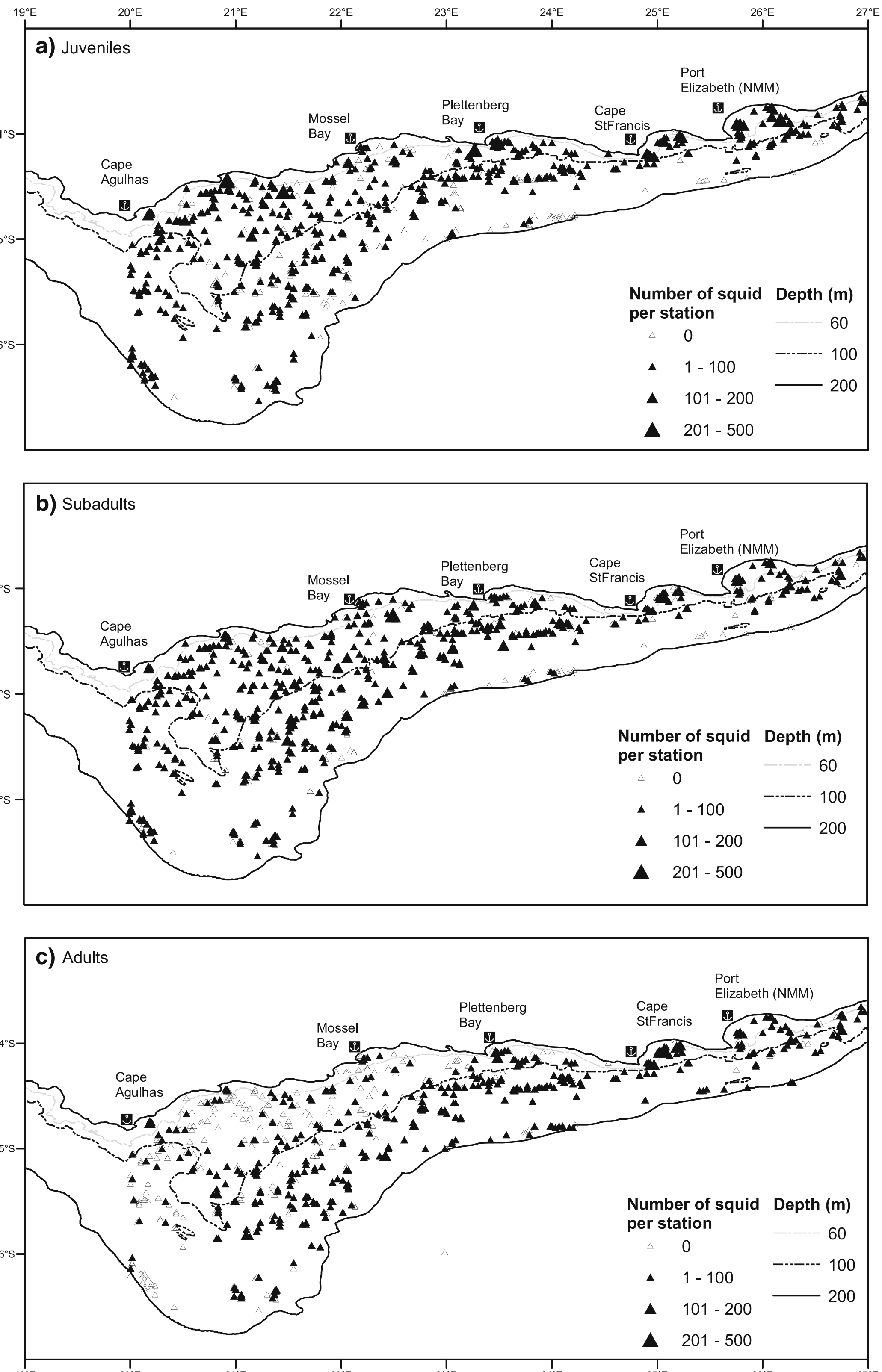
34°S
35°S
36°S
a) Juveniles
b) Subadults
c) Adults
Cape Agulhas
Mossel Bay
Plettenberg Bay
Cape StFrancis
Port Elizabeth (NMM)
Number of squid per station
0
1 - 100
101 - 200
201 - 500
Depth (m)
60
100
200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201 - 500
Depth (m)
60
100
200

◀ **Fig. 5** Distribution of female chokka in three life history stages caught in autumn research cruises on the Agulhas Bank

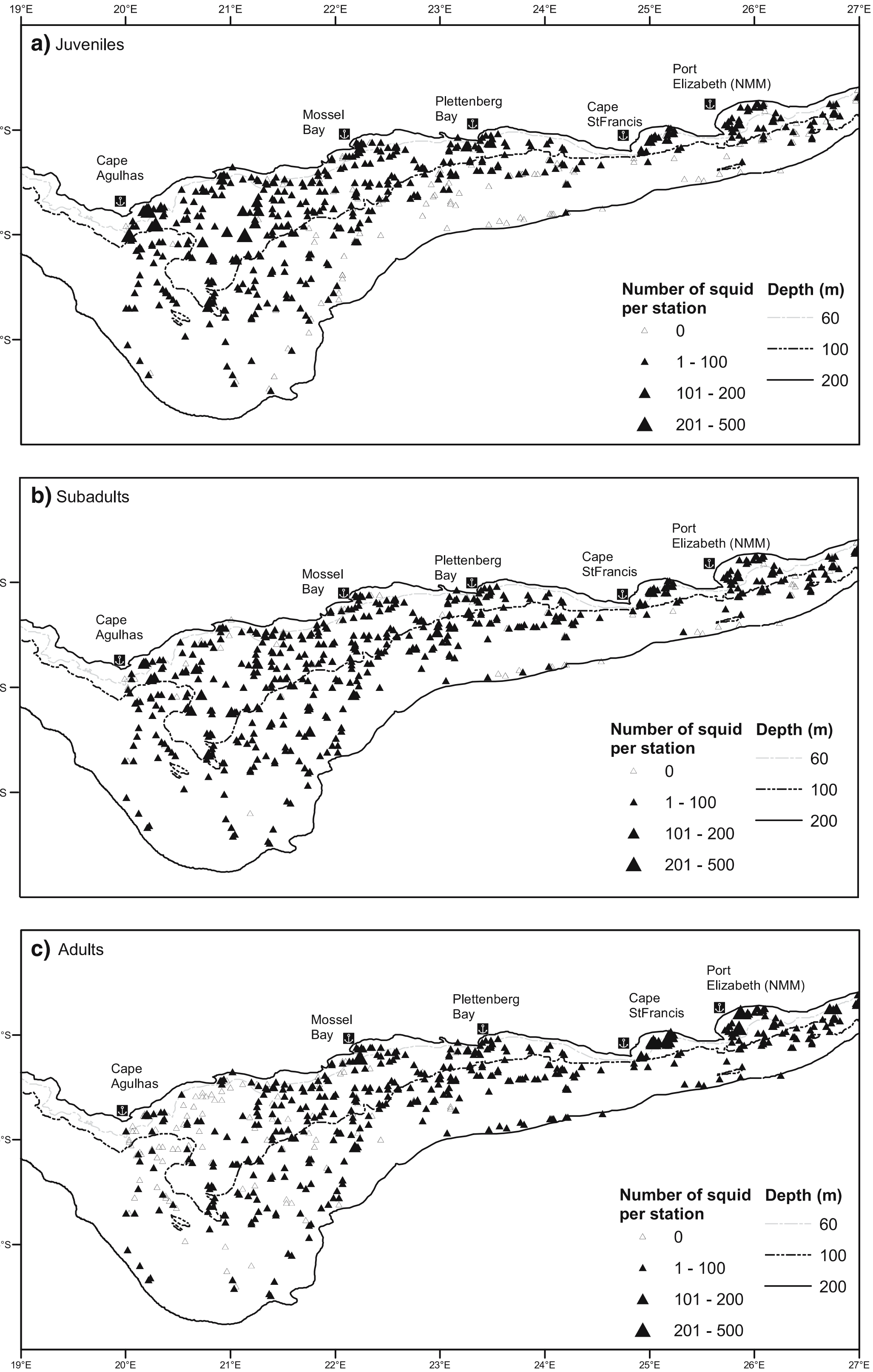
abundance and distribution patterns of cephalopod populations (Pierce et al. 1998). Due to highly variable individual growth rates in cephalopods e.g. Pecl (2004), the overlap of size ranges is great, particularly in males, which can be mature at 80 mm and immature at 200 mm. Previously published size ranges of various maturity stages for chokka have been broad scale although spatial and temporal influences have been recognized (Augustyn et al. 1994). As mentioned in the methods it was necessary to take the differences in the size ranges between eastern, central and western regions as a consequence of differences in size at maturity into consideration when defining the size ranges of juveniles, subadults and adults used in this study.

The bulk of the results appear to largely support the current acceptance of the life cycle with 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. 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. This is a fairly typical life history pattern shared with other loliginid squid such as *Loligo gahi* (Hatfield and Rodhouse 1994) and *Loligo pealeii* (Brodziak 1998; Hatfield and Cadrin 2002).

Contrasting this pattern, however, were catches of adult animals in deeper water, particularly in autumn in the central study area. These deep-water samples also seemed to consist entirely of adult squid and probably represent squid spawning in deeper waters and over a greater area than is currently targeted by the fishery. Hydro-acoustic evidence (Roberts et al. 2002) together with chokka squid eggs recovered from trawls in deeper water (Roberts in press) provides irrefutable proof that in addition to the shallow, inshore spawning grounds, chokka squid routinely utilise deeper spawning locations. Spawning grounds on the western Agulhas Bank are also not unusual and the originally hypothesised spawning grounds were thought to lie in False Bay (approximately 18°38′W 34°10′S) (Augustyn 1989). Inshore spawning areas in the west were also identified by Lipiński (1998; Fig. 2). Roberts (2005) suggests however, that the western Agulhas Bank is generally unsuitable as a spawning location due to low and variable bottom dissolved oxygen (≤3 ml l^{-1}) and temperatures that are too low (<12°C) for egg development. The Agulhas Bank is however, subject to such a high level of oceanographic variability that spawning can occasionally occur in these "fringe" areas. There is therefore a need to further address the abundance of spawners spatially and to determine whether squid hatching in variable environments manifest these differences through different life history traits.

The distribution pattern of juveniles and subadults seems to match the area of high zooplankton productivity (food source for paralarvae) described by Augustyn et al. (1992; Fig. 9) and possibly an associated abundance of other food items for the larger squid. Similarly, the more western areas, 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). The assumed process of paralarvae being passively advected in westward flowing currents is, however, challenged by Roberts and van den Berg (2002) who suggest that, based on new evidence, the predominant current on the inshore spawning grounds is a clockwise gyre that retains passive, neutrally buoyant biological material (i.e. paralarvae) in inshore waters. Similarly, the low dissolved oxygen and temperatures of the west coast may not make it an optimal environment for growth, despite the high levels of primary and secondary productivity found there. In the same paper, the authors concede that paralarvae arising from deep spawning could potentially be transported passively to the west coast which would explain the variable and smaller biomass found

Fig. 6 Distribution of male chokka in three life history stages caught in spring research cruises on the Agulhas Bank ▶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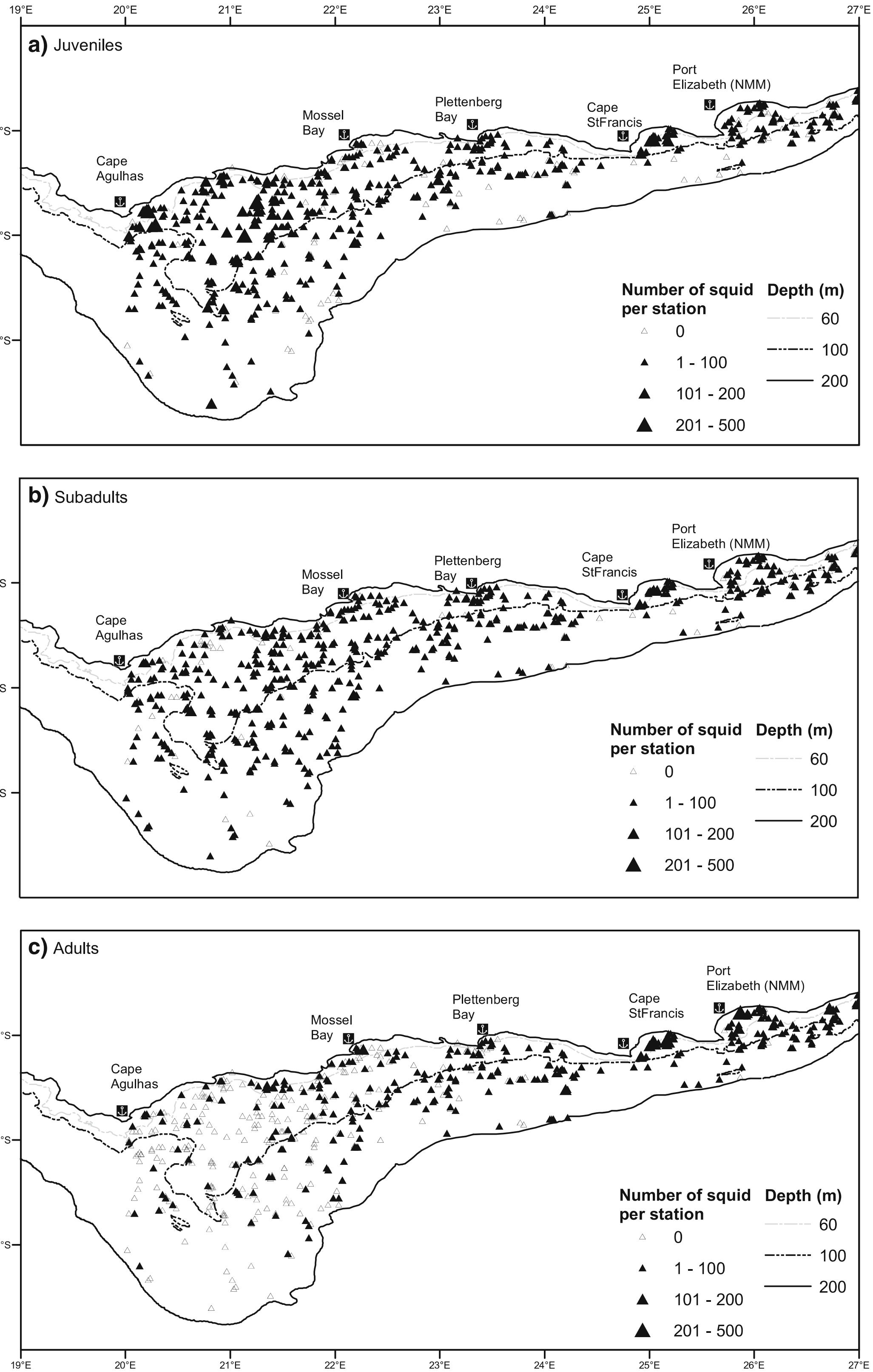
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Depth (m)
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100
200
19°E
20°E
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25°E
26°E
27°E

◀ **Fig. 7** Distribution of female chokka in three life history stages caught in spring research cruises on the Agulhas Bank

there. These contrasting early life histories with paralarvae and hence, juveniles growing under such diverse environmental conditions could result in discrete subpopulations of *L. reynaudii* with different biological characteristics inhabiting the western and eastern regions of the Agulhas Bank, respectively. In this hypothesis, some mixing of the populations does occur but generally squid from the western Agulhas Bank grow slower and mature at a larger size. Spawning may occur on the western portion of the Agulhas Bank, and juveniles grow and mature on the west coast and the Central Agulhas Bank. The larger eastern population, by contrast, matures at a smaller size and spend most of their lives in the inshore and offshore waters adjacent to the spawning grounds between Plettenberg Bay and Port Elizabeth and sometimes further east (Fig. 8).

The theory of multiple stocks or subpopulations is not unique to cephalopod fisheries but proving the existence using genetic methods has yielded mixed results. Recently, Buresch et al. (2006) utilised innovative techniques to study five microsatellite loci in *Loligo pealeii* and identified several genetically discrete spawning stocks. Using similar techniques, Shaw et al. (2004) were, however, unable to demonstrate that discrete spawning cohorts in *Loligo gahi* were genetically distinct subpopulations. The technique is however, certainly attractive and should be investigated for chokka.

For fisheries that are dependent on these species, stability and predictability are real concerns that challenge effective fisheries management. It is hoped that by having a better understanding of the dynamics of the chokka squid population and by focusing on the research needs highlighted here, this paper will prove a valuable contribution towards the management of the South African chokka squid fishery. It is possible that within-season forecasting of the recruitment strength for a particular fishing season can be made by measuring the number of subadults prior to spawning. It will be first

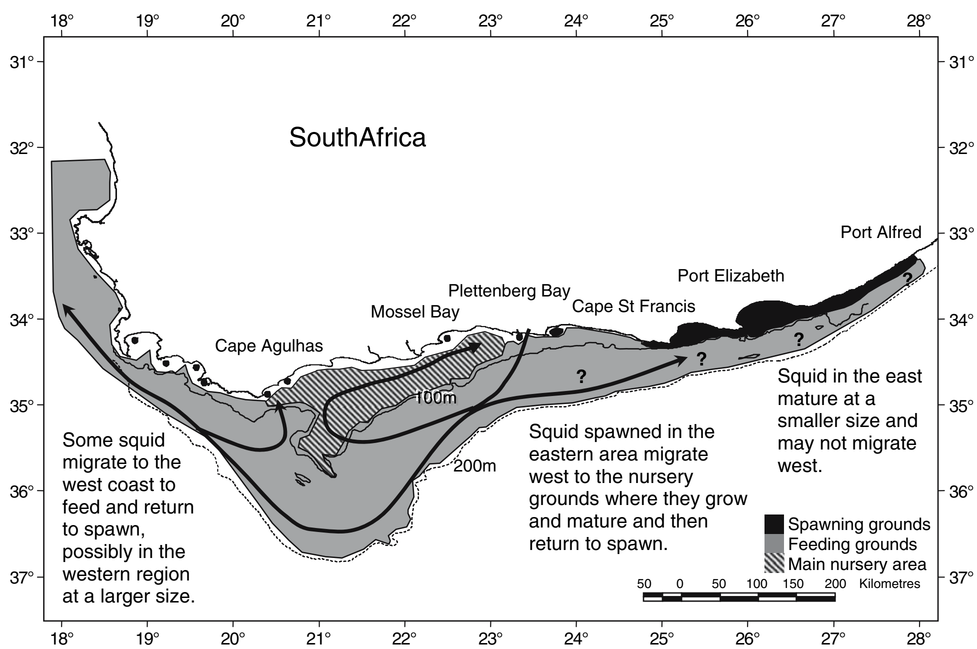

Fig. 8 Schematic overview of the chokka squid lifecycle incorporating hypotheses based on new data in this study. Question marks relate to possible feeding areas in the eastern region (24–27°E) where squid may grow and mature offshore of the spawning grounds. Arrows indicate proposed migration patterns

necessary to answer the question of geographically separate stocks with more certainty. The most obvious of these must be to understand the age structure of chokka squid both spatially and temporally. Investigations into the chemistry of statoliths may also yield valuable information about the environment in which individuals are growing and provide a means of separating the two populations. The role of deeper spawning squid also remains to be quantified and may yield some interesting results.

It seems then, that as our understanding of loliginids increases so too does appreciation of the apparent complexity of their lifecycles. What at first, seemed to be a simple pattern of annual maturation and migration now resembles an intricate matrix where subtle changes in temperature, dissolved oxygen, food supply and a host of biotic and environmental conditions combine to create populations that are highly variable through time and space.

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