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The relative importance of shallow and deep shelf spawning habitats for the South African chokka squid (*Loligo reynaudii*)

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It is well known that the spawning grounds of chokka squid *Loligo reynaudii* lie along the shallow inshore regions of South Africa's south coast. However, egg masses have been found in deeper water on the Agulhas Bank, and hydroacoustic targets deemed to be large aggregations of spawning squid have been identified. The aim of this study was to investigate the extent, depth range, and importance of deep spawning. Trawl data collected during demersal research surveys between Port Nolloth on the west and Port Alfred on the south coast were examined for egg capsules. No spawning was found on the west coast. Data showed that chokka squid preferred the eastern Agulhas Bank for spawning. Spawning occurred not only inshore but also on the mid-shelf extending to depths of 270 m near the shelf edge. Squid egg biomass markedly decreased beyond 70 m, suggesting delineation between the inshore and offshore spawning grounds. Total egg biomass calculations for depths shallower and deeper than 70 m indicated the coastal area to be strongly favoured, i.e. 82 vs. 18%. These results contest the commonly accepted notion that *L. reynaudii* is an inshore spawner and redefine the spawning grounds to extend across the shelf.

Keywords: Agulhas Bank, chokka squid, deep spawning grounds, egg biomass, *Loligo reynaudii*, temperature.

Introduction

Research trawl surveys indicate that chokka squid *Loligo reynaudii* adults are found over most of the continental shelf off the west and south coasts of South Africa, with the greater part of the biomass on the latter (Figure 1a; Roberts, 2005). Seldom has this species been found deeper than 350 m on the west coast and 200 m on the south coast (Augustyn, 1991). The extreme geographical limits of the distribution shown in Figure 1a, however, should not be seen as definitive as these are imposed by the trawl survey design, which primarily targets South African hake. In fact, it is now known that *L. reynaudii* also occurs in Namibia and even farther north into southern Angola (Figure 1b; Shaw *et al.*, 2010). At the other extreme, on the south coast, commercial jig catches occur at times east of Port Alfred (Figure 1c). This eastward range extension is likely to be linked to sporadic shelf upwelling and cooler water that occurs between Port Alfred and East London (Lutjeharms *et al.*, 2000). On the west coast, the distribution of chokka squid tends to be limited to the mid-shelf as a result of low bottom dissolved oxygen levels on the inner shelf and low temperatures (i.e. <7°C) on the outer shelf (Augustyn, 1991; Roberts and Sauer, 1994).

Chokka squid spawn along the shallow, 20–60 m (Roberts and Sauer, 1994), inshore regions of the coast between Plettenberg Bay and Port Alfred (Figure 1c; Augustyn, 1989, 1990; Sauer *et al.*, 1992), although occasionally eggs have been reported by fishers as far west as False Bay (18°30′E) and East London (27°52′E) in the east. The use of warm inshore areas for spawning is a common trait among loliginid squid. For example, *L. chinensis* (Chotiyaputta, 1997), *L. duvauceli* (Mohamed, 1993; Chotiyaputta, 1997), *L. vulgaris* (Raya *et al.*, 1999), and *L. pealei* (McMahon and Summers, 1971) are all known inshore spawners. Many scuba diving observations show that good commercial catches take place in the immediate vicinity of spawning sites (Sauer *et al.*, 1991), many of which are indicated in Figure 1c. Spawning is most intense in spring and early summer (Augustyn, 1989; Augustyn, 1990; Sauer *et al.*, 1992; Roberts and Sauer, 1994).

In the early years of research, it was thought that the greater shelf region served as the feeding grounds for adult and juvenile chokka and that this species was exclusively an inshore spawner (Augustyn, 1991). However, the discovery of egg capsules in depths >60 m during three joint Japanese-South African south

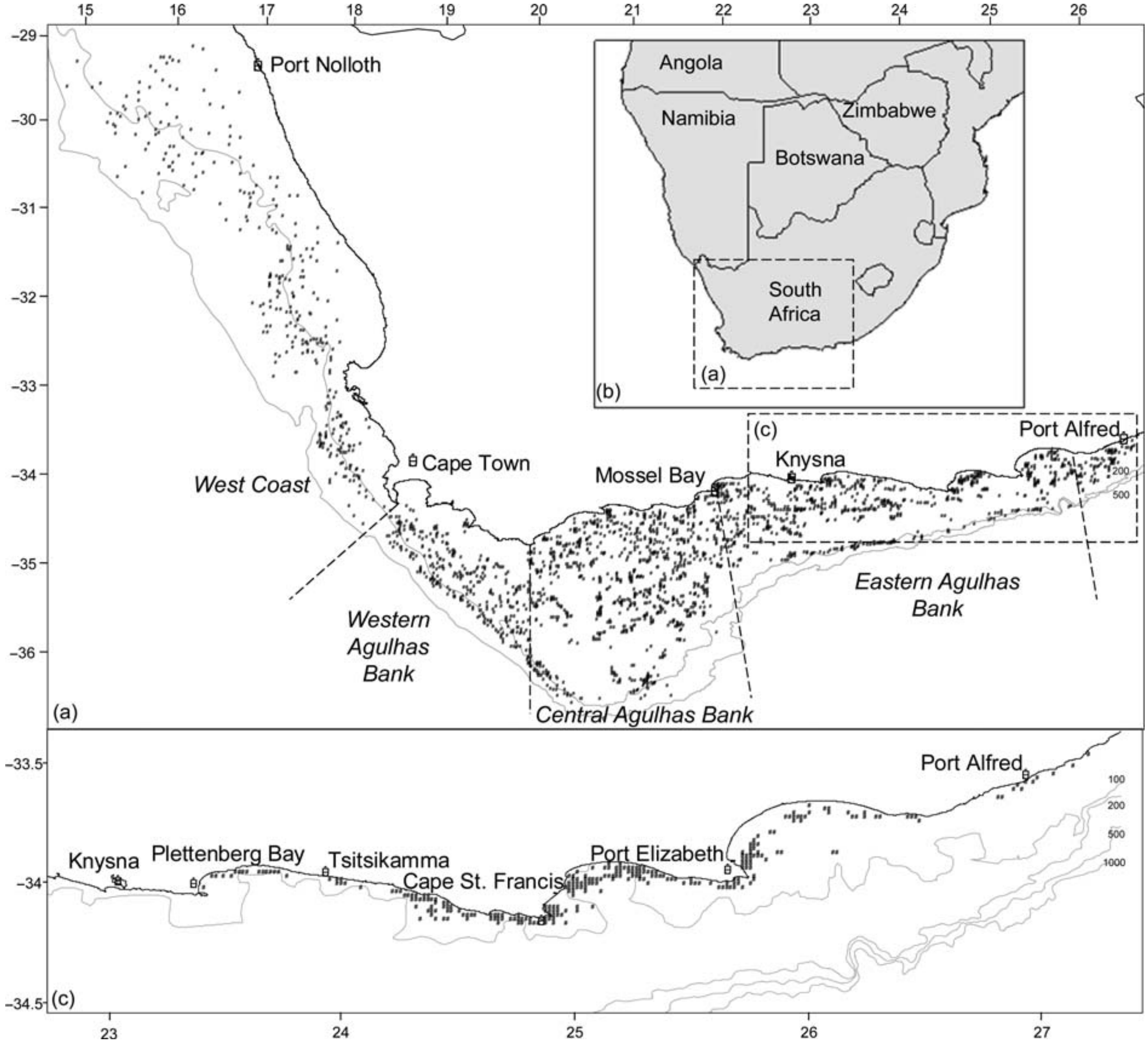

Figure 1. Updated from Roberts and Sauer (1994). (a) Demersal distribution (dots) from DAFF research trawls of adult (females >18 cm; males >25 cm) chokka squid *L. reynaudii* on the west coast and the Agulhas Bank of South Africa, (b) *L. reynaudii* has also been found as far north as Namibia and southern Angola but the biomass appears to be low, (c) commercial hand-jig fishing positions (dots) for *L. reynaudii* indicate commonly used spawning sites in <60 m along the inshore region of the eastern Agulhas Bank.

coast demersal trawl surveys (Hatanaka *et al.*, 1983; Uozumi and Suisancho En'yo Suisan Kenkyujo, 1984, 1985) challenged this view. Since then, chokka egg capsules have been caught in trawls during many south coast demersal surveys and occurrences deeper than 60 m documented (Augustyn *et al.*, 1992, 1994; Roberts and Sauer, 1994; Augustyn and Roel, 1998; Roberts *et al.*, 2002). Hydroacoustic evidence of large spawning aggregations on the mid-shelf, directly off Cape St Francis and Plettenberg Bay (Figure 2b), has been reported, further corroborating the existence of deeper spawning of this species (Roberts *et al.*, 2002).

The aim of this paper is to define the chokka squid spawning grounds, specifically, to determine the extent, depth range, and importance of the deep spawning grounds relative to those inshore. This has important implications not only for documenting the life cycle but also for the conservation of the stock and management of the fishery.

Material and methods

Survey data

Demersal survey data used in this study were collected over the period 1985–2008 by the Department of Agriculture, Forestry and Fisheries (DAFF), formerly Marine and Coastal Management. In total, trawl data from 61 demersal surveys, covering the west and south coasts separately, were examined for egg capsules. The primary aim of these surveys was to estimate the biomass of deep and shallow water hake, *Merluccius capensis* and *M. paradoxus*, over the depth range 20–500 m. The surveys were undertaken twice a year (January and July on the west coast; April and September on the south coast). All surveys were performed by the "F.R.S. Africana" except BE 214 and Nan 405, for which the "F.R.S. Benguela" and the "Dr Fridtjof Nansen" were used, respectively. Survey BE 214 was a dedicated inshore (<100 m) squid survey on the south coast but otherwise used the same sampling protocol. The survey area remained the same

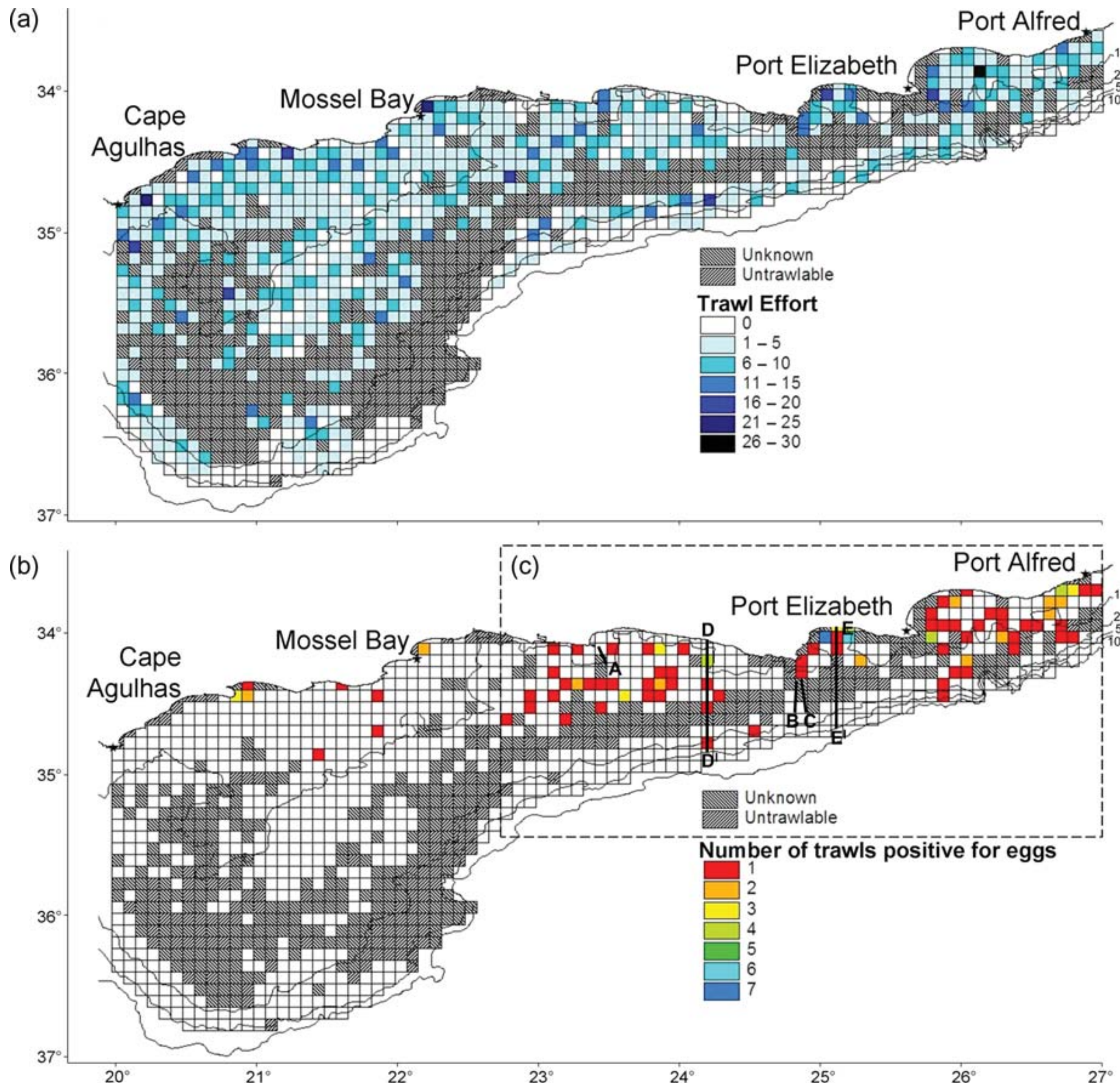

Figure 2. Composite maps of data between 1985 and 2008 for (a) the DAFF survey trawl effort on the Agulhas Bank and (b) the distribution of *L. reynaudii* eggs caught in demersal trawls. Colour codes indicate the frequency of trawls undertaken in a block or the frequency of trawled squid eggs, respectively. Grey shaded blocks indicate untrawlable or not yet trawled areas, (c) highlights the main spawning grounds for chokka squid and therein the data used to calculate the egg biomass in the shallow (≤70 m) and deep (>70 m) spawning areas. Line segments A, B, and C off Plettenberg Bay and Cape St Francis represent hydroacoustic transects that showed large aggregations of spawning squid near the seabed (Roberts *et al.*, 2002). Trans-shelf lines D–D′ and E–E′ indicate the positions of the bottom topography profiles in Figure 4d.

with the west coast surveys covering the shelf between 29°S (Orange River) and 20°E (Cape Agulhas) and the south coast surveys between 20 and 27°E (Port Alfred).

Survey design and the gear used have been described in detail by Augustyn *et al*. (1995), Badenhorst and Smale (1991), and Le Clus and Roberts (1995). The survey area was divided into 5′ × 5′ grids within depth bands of 0–50, 51–100, 101–200, and 201–500 m. Trawl blocks (also referred to as stations) for each survey were selected on a semi-random basis (according to the ratio of blocks per depth band) at intervals along the coast, the number of stations per depth and longitude stratum being directly proportional to the number of trawlable blocks in each stratum. Known areas of hard ground were avoided (Figure 2). Surveys ranged from 26 to 109 stations (Figure 3). A 150-ft (1986 and prior) or a 180-ft (since 1987) German trawlnet with V doors was used. The 75-mm codend mesh was lined with a 27.5-mm mesh in the form of a sleeve to retain most small fish. Trawl duration was limited to actual bottom time of 30 min, and the data collected from trawls <30 min was standardized to a 30-min duration. This equated to a standard trawl area of ~0.0842 km^2 trawl^{-1}.

Egg biomass

Although the presence of egg capsules in trawls was recorded (referred to as positive trawls in this study) before 1989, their mass was not always determined. Therefore, only egg mass data from the south coast surveys between 1989 and 2008 were used in the simple calculation, shown below, to estimate the total biomass

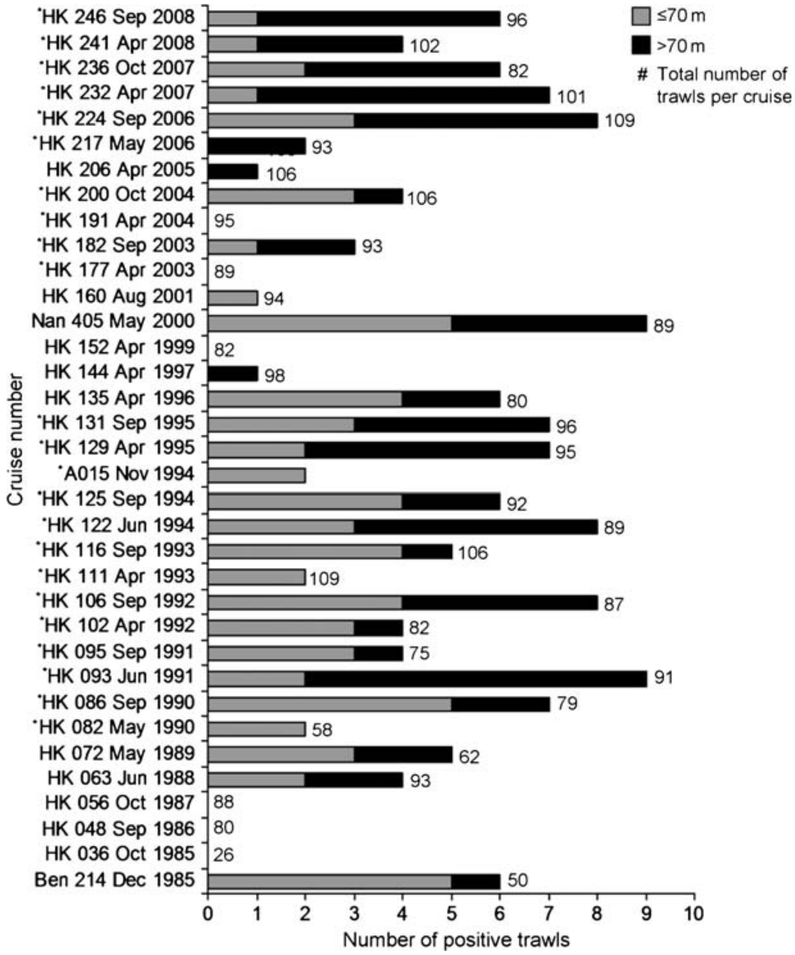

Figure 3. Schematic representation of the south coast 1985–2008 cruise data used in this study. Horizontal bars indicate the number of positive trawls at depths ≤70 m (grey shading) and <70 m (black shading). The total number of trawls per survey is given at the end of each bar.

within the 20–70- and 71–130-m depth strata. This calculation is the same as that used to estimate the biomass of hake in these surveys—referred to as the swept-area method (Sparre and Venema, 1998).

For each station,

$$d = \frac{C_w}{a}.$$

For each depth stratum,

$$\bar{d}_i = \frac{\Sigma d}{n_i}, \quad B_i = \bar{d}_i \times A_i.$$

Percentage contribution of each stratum to total biomass,

$$B = B_i + B_{i+1}, \quad P_i = \frac{B_i}{B} \times 100.$$

Here, d is the egg density (kg km^{-2}), C_w the catch weight (kg), a the area trawled (km^2), $\bar{d}_i$ the average egg density in the ith stratum (kg km^{-2}), n_i the number of trawls in the ith stratum, B_i the egg biomass in the ith stratum (kg), A_i the area of the ith stratum (km^2), B the total egg biomass (kg), and P_i the percentage contribution of each stratum to total biomass (%).

Results

Geographical egg distribution

The area surveyed on the south coast is shown in Figure 2. The west coast survey area is not shown as no egg capsules were found there despite similar trawl effort. It is evident that the demersal surveys have covered a considerable portion of the Agulhas Bank, ~96 455 km^2, with some blocks having been trawled as many as 27 times (Figure 2a). On average, each block has been trawled five times. The grey shading indicates untrawlable ground. Figure 2b shows those blocks where chokka egg capsules were caught in the trawlnet as well as the frequency (colour key) of occurrence. Immediately noticeable is the lack of egg capsules on the western and outer-central Agulhas Bank (area >100 m), despite the presence of adult squid near the bottom over this entire area (Figure 1a). Most eggs west of Mossel Bay were trawled at depths between 38 and 58 m, with only three batches of eggs found deeper than 71 m. The majority of eggs (spawning) were found on the eastern Agulhas Bank between Knysna and Port Alfred (highlighted area in Figure 2c). This area, ~35 866 km^2, accounts for 37% of the total survey grid. The data also give the

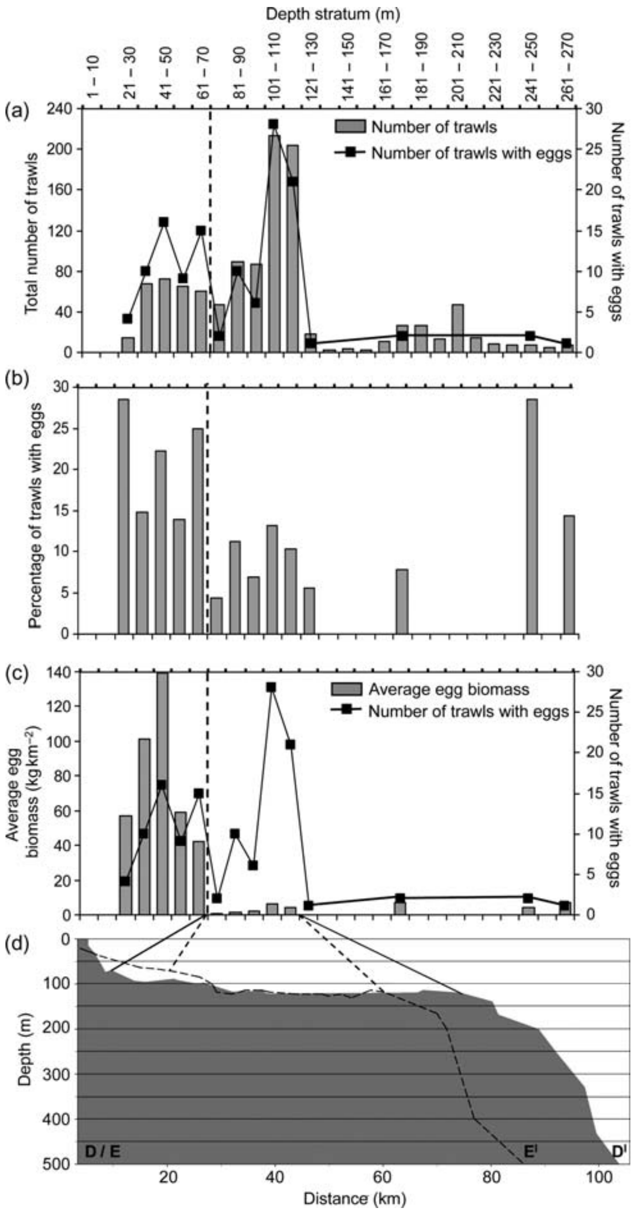

Figure 4. Distribution of positive trawls (squid eggs) with depth on the Agulhas Bank. (a) Total number of trawls and the number of positive trawls per depth stratum. (b) Percentage of positive trawls per depth stratum. (c) The average egg biomass and the number of positive trawls per depth stratum. Note: Data include only those $5' \times 5'$ survey grids east of 22°45′. (d) Trans-shelf profiles of bottom topography along lines D–D′ (shaded) and E–E′ (dotted line) in Figure 2c. Note that the area ≤70 m in the bays (E–E′) is much greater than off the Tsitsikamma coast (D–D′) where the coastal bathymetry is rocky and steep.

impression that most of the deep spawning is found off the Tsitsikamma coast and Algoa Bay, but, in reality, it is more likely that spawning does occur between these two areas too, i.e. between 24.3 and 25.7°E. The lack of data here is due to the narrowing of the shelf and extensive hard ground (10 271 km^2, 29% of the total study area) making demersal trawling impossible. Note that this hard ground forms a band along the outer shelf which is closer to the coast in the region of St Francis Bay.

Table 1. Seasonal percentage of positive inshore and offshore trawls.

	Autumn (%)		Spring (%)	
Year	**≤70 m**	**>70 m**	**≤70 m**	**>70 m**
1990	13.33	0.00	20.00	4.17
1991	8.00	10.61	12.50	1.96
1992	16.67	1.56	12.50	7.27
1993	10.53	0.00	13.33	1.33
1994	13.64	7.58	11.76	3.45
1995	11.76	6.41	11.11	5.80
2003	0.00	0.00	6.67	2.56
2004	0.00	0.00	23.08	1.08
2006	0.00	2.47	15.79	5.62
2007	7.14	6.90	16.67	5.71
2008	8.33	3.33	7.14	6.10
Average	8.13	3.53	13.69	4.10
s.d.	±5.90	±3.76	±4.97	±2.15

Figure 3 schematically presents the data in Figure 2, on a cruise basis, and depicts the number of positive shallow water (≤70 m) and deep-water (>70 m) trawls per survey. The total number of trawls for each survey is indicated at the end of the bar graphs. In total, 35 surveys were conducted on the south coast between 1985 and 2008, of which 29 trawled egg capsules. Of these 29 surveys, 22 (75.9%) trawled both shallow and deep spawned eggs, 4 (13.8%) trawled only shallow spawned eggs, and 3 (10.6%) trawled only deep spawned eggs. Data from years where there was a spring and autumn survey were used to investigate seasonality (Table 1). In both seasons, this showed a small bias of positive trawls on the shallow spawning grounds with little seasonal difference (i.e. positive trawls in ≤70 and >70 m made up 13.7 and 4.1% of the total number of spring trawls, respectively, compared with 8.1 and 3.5% for the autumn trawls).

Egg distribution with depth

Only data from the main spawning area highlighted in Figure 2c were used to investigate egg distribution with depth. Figure 4a simply depicts the total number of trawls vs. the number of positive trawls per depth stratum. Trawl effort is seen to be mostly concentrated in the depth range 101–120 m, followed by the depth ranges 81–100 and 31–70 m. From 121 to 270 m not only were there fewer trawls, but also fewer blocks compared with the shallower areas ≤120 m. This is due to the steep shelf edge gradient which starts at ~120 m (Figure 4d). The extremely small number of trawls between 131 and 170 m reflects the outer band of hard ground depicted in Figure 2. The absence or small number of trawls in areas <30 m was due to depth limitations of the vessel. Positive trawls tended to follow the trawl effort trend, with greatest numbers occurring in the depth range 101–120 m, followed by the ranges 41–50 and 61–70 m. Of interest is that eggs were found on more than one occasion at depths between 241 and 270 m.

Figure 4b shows these data expressed as the percentage of positive trawls in each stratum. A clear distinction is seen at 70 m whereby the greater spawning intensity found inshore of this depth, i.e. 14–18% positive trawls, rapidly decreases to 4% in the next depth stratum of 71–80 m. This distinct decrease possibly indicates the 70-m mark being the deepest extent of the inshore spawning ground. Beyond the 71–80-m stratum, spawning intensity increased to peak at 101–110 m. Note in Figure 4d that a small step in the bathymetry profiles exists at the depth of 110 m, beyond which, lies the greater mid-shelf plain. Little spawning occurred at depths between 131 and 270 m, although, as indicated previously, the high percentage of positive trawls near the shelf edge (241–250 and 261–270 m) is caused by the very small number of trawls undertaken here.

To account for the differing stratum areas as a result of the bathymetric gradients depicted in Figure 4d, the average egg biomass (kg km^{-2}) per depth stratum was calculated, using the swept-area method (Sparre and Venema, 1998), and is given in Figure 4c. This provides another, possibly more relevant, view of the importance of the different depth strata as spawning grounds. The difference between the inshore average egg biomass estimates (i.e. spawning intensity) and that >70 m is striking, again highlighting the delineation at a depth of 70 m. On the inshore spawning grounds, egg intensity peaked midway at 140 kg km^{-2} in the 41–50-m depth stratum, with values decreasing either side to 57 kg km^{-2} inshore (21–30 m) and 42 kg km^{-2} in the outer 61–70-m stratum.

In comparison, offshore spawning is seen to be much less with the highest egg biomass of only 6.3 kg km^{-2} in the 101–110-m depth stratum. Similarly, spawning intensity tapered off either side of this peak. The dilution effect of the large shelf area between the 71- and 120-m isobaths, calculated to be 4.8 times larger than the inshore spawning area, is patent when comparing these values with those in Figure 4a or b.

Egg biomass distribution

To gain an overall realistic impression of the importance of deep spawning relative to inshore, the total egg biomass in the 21–70- and 71–130-m strata were calculated. As detailed in Table 2, the contribution of inshore spawned eggs and deep spawned eggs to total biomass is estimated at 82 vs. 18%, respectively. Note that owing to the small number of samples and egg masses in each survey and that the aim of this paper was to estimate the relative importance of the deep spawning grounds, total egg biomass estimates B_i were calculated for each of these broader strata using data combined from all 29 surveys. Similarly, only eggs caught east of 22°45′E were used in this calculation, i.e. on the main spawning grounds highlighted in Figure 2c. Spawning west of this appears to be less consistent and the large area on the outer central Agulhas Bank, in which no eggs were found (i.e. >100 m, east of 22°45′ E), would have a strong dilution effect on the stratum egg densities.

Discussion

Extent, depth range, and importance

There is little doubt from these data that chokka squid prefer the eastern Agulhas Bank for spawning, regardless of the wide distribution of adults over the Agulhas Bank and west coast (Figure 2b) and that the area of greatest spawning intensity lies between 23 and 27°E (i.e. Knysna and Port Alfred). Previously, based on inshore fishing positions, Roberts (2005) suggested that this preference was due to higher benthic temperatures and levels of dissolved oxygen compared with those on the west coast.

These data further demonstrate that spawning occurs not only inshore but also on the mid-shelf, extending to depths of at least 270 m near the shelf edge. As shown in Figure 4b and c, spawning intensity markedly decreases at a depth of 70 m, suggesting delineation between the inshore and offshore spawning grounds. This may be linked to a change in the environment (i.e. temperature, light, turbidity). Very little spawning occurs deeper than 130 m. Within the inshore area there appears to be a preferred depth range for spawning between 41 and 50 m, with egg densities three times greater than that found in strata on either side. Mid-shelf spawning appears to peak between 101 and 110 m. Despite this trans-shelf spawning, the calculation of total egg biomass in strata shallower and deeper than 70 m indicates the former to be much more strongly favoured, i.e. 82 vs. 18%, respectively.

Table 2. Estimated chokka egg biomass for the inshore and deep spawning grounds.

	20–70 m	71–130 m
$\sum d$ (kg km^{-2})	24 092	2 543
n_i	254	604
$\bar{d}_i$ (kg km^{-2})	94.85	4.21
A_i (km^2)	3 641	17 490
B_i (kg)	345 386	73 638
B (kg)	419 024	
P_i (%)	82	18

Study limitations

When considering these results, especially the egg biomass estimates, it is important to be mindful of a few constraints inherent in the methodology used here. The first is sampling efficiency where the effectiveness of a trawlnet in collecting egg capsules and retaining these during net retrieval is unknown. This is especially relevant on the mid- and outer shelf where the net retrieval time is longer and there is a greater possibility of eggs being washed from the net.

There is also a strong sampling bias, as seen in Figure 4a, where trawl effort is greater in the 31–120-m depth range than in areas >121 m. In these deeper areas, low profile reef results in untrawlable ground. A number of studies have found that low relief reef on the inshore spawning grounds is a favoured substratum type for egg deposition (Sauer *et al.*, 1992, 1993; Sauer and Smale, 1993; Sauer, 1995). It is likely then that areas with a similar substratum, at depths >70 m, are also used for egg deposition. Consequently, this could lead to an underestimation of egg biomass in depths >70 m.

Counter to this, however, is that the egg biomass ratio for the inshore and shelf regions, i.e. 82 and 18%, respectively, was based on surveys undertaken in autumn and spring only, which missed the main inshore spawning period between November and January. This could mean that these results have underestimated the egg density for the inshore spawning grounds and hence their importance. Given these counter arguments, the ratio of 82 vs. 18% should be taken as an approximation.

Another constraint is that the surveys stopped at 27°E, artificially delineating the eastern boundary of the spawning grounds (Figure 2). Clearly, as indicated by the inshore fishing positions in Figure 1c, spawning does occur east of 27°E (Port Alfred), and, moreover, it is highly probable that deeper spawning will also be found here given the fact that the shelf extending to 28°E (East London) commonly experiences upwelling with bottom temperatures of 13–15°C (Lutjeharms *et al.*, 2000). The upwelling here is caused by the Agulhas Current moving farther offshore (Lutjeharms *et al.*, 2000; Roberts *et al.*, 2010) and is sporadic in nature. Between upwelling events, bottom temperatures can rise to 20°C, which in all likelihood will preclude this area from the main (intense) spawning ground.

To overcome these constraints and improve the results of this study will not be simple given the difficulty to determine the efficiency of a trawlnet to retain egg capsules, the near impossibility to change the time schedule of the demersal biomass surveys, then to re-establish a long-term (30-year) data record.

Ramifications of cross-shelf spawning

Although these results clearly define the spawning grounds for *L. reynaudii*, they also elicit several pertinent questions. The first of these is whether cross-shelf spawning is unique to this species. Although limited, there is evidence to suggest that this is not the case. For example, eggs of *Doryteuthis* (formerly *Loligo*) *gahi*, *D. opalescens*, and *L. forbesi*, all are inshore spawners, have recently been found in deeper areas of the shelf. For *D. gahi* found around the Falkland Islands, egg masses usually deposited in depths of <20 m (Arkhipkin *et al.*, 2000; Arkhipkin and Middleton, 2003) were found in a bottom trawl retrieved from a depth of 68–71 m (Laptikhovsky, 2007). Eggs of *D. opalescens*, a species known to migrate into Monterey Bay (California) to spawn in depths of 20–60 m (Foote *et al.*, 2006), were found in large numbers at depths around 720 m by commercial trawlers (Butler *et al.*, 1999). Eggs of the widely distributed *L. forbesi* have been discovered at depths up to 134 m in the Azores (Pham *et al.*, 2008), 135 m in France (Lordan and Casey, 1999), 302 m in Ireland (Lordan and Casey, 1999), 507 m in the Celtic Sea (Lordan and Casey, 1999), and 720–740 m in the Aegean Sea (Salman and Laptikhovsky, 2002).

Spawning across a wide depth range does, however, indicate that *L. reynaudii* spawns across differing environments, i.e. within the cold bottom boundary layer on the shelf, typically 9–11°C, and the generally warmer inshore region where bottom temperatures range between 13 and 17°C (Roberts and Sauer, 1994; Oosthuizen, 1999). How this impacts embryonic development has been a topic of considerable interest.

Initial experiments by Augustyn (1989) found that chokka squid egg mortality occurred at temperatures <10°C. Oosthuizen *et al.* (2002a, b) continued this research using environmentally controlled laboratory studies and demonstrated that embryonic development time increased with decreasing temperature and that a high incidence (>50%) of embryonic abnormalities occurred at temperatures <12°C. Hatching times ranged from 93 d at 9°C to 25 d at 18°C. Importantly, both sets of results implied that eggs deposited in the deeper regions of the shelf are not viable.

Inspection of deep trawled eggs at various stages proved otherwise, contradicting the laboratory studies. To resolve this, Oosthuizen and Roberts (2009) undertook *in situ* experiments using cages, temperature recorders, and acoustic releases off St Francis Bay. Eggs were deployed at 112–126 m and exposed to temperatures of 8.2–13.7°C for periods of 6–8 weeks. Interestingly, only 0.45% of the eggs showed embryonic abnormalities, indicating that the deep spawning grounds are indeed viable. The colder water at these depths would result in longer incubation times (up to 8 weeks), which can be an advantageous in spreading hatching times, and potentially offset conditions unfavourable to the paralarvae. Another advantage would be the slower utilization of yolk by the hatched paralarvae, due to the lower temperatures, providing more time for the development of predatory skills (Martins *et al.*, 2010).

But temperatures are not always low on the mid-shelf. Oosthuizen and Roberts (2009) showed that downwelling occurs off the Tsitsikamma–Cape St Francis coast as a result of westerly winds and the Ekman transport of the warm surface layer towards the coast. This results in downward tilting of the thermocline next to the coast and consequently warm water reaching the bottom mid-shelf habitat. Oosthuizen and Roberts (2009) demonstrated that warm-water intrusions can extend as deep as 120 m and that bottom temperatures of ≥10°C occurred 62 and 56% of the time at 84 and 104 m, respectively, from September to February. The chokka squid peak spawning season, November–January, falls within this period.

Of particular interest on the deep spawning grounds is the level of light near the seabed, as *in situ* observations using ROVs indicate dark conditions at depths >100 m. Only a few studies have investigated the effect of light intensity on embryonic development and hatching success, but none is conclusive (Ikeda *et al.*, 2004; Sen, 2004). Another study on the impact of photoperiodicity on hatching of *L. vulgaris* and *L. forbesi* (Paulij *et al.*, 1990) indicates that light and dark periods affect the timing of hatching, with most embryos hatching shortly after the sunset. Presumably, this stimulus does not play a role at great depth.

Of course, the question also arises that if embryonic development is optimal on the shallow inshore spawning grounds, then why does mid-shelf spawning occur at all? For *D. gahi* cited above, Laptikhovsky (2007) suggested that the deeper spawning was due to warmer (inshore) shelf water during an abnormally warm autumn and early winter. Similarly, for the 1998 observations of deep spawning (~720 m) of *D. opalescens*, Butler *et al.* (1999) concluded that warm water experienced inshore as a result of the 1997–1998 *El Niño* might have forced squid to spawn in deeper, cooler water.

Observations of deep spawning for *L. reynaudii* are many both in spring and autumn. Instead of warmer inshore water forcing spawners to seek cooler conditions, it might be that the frequent benthic warm-water intrusions emanating from the coast (i.e. downwelling during westerly winds), in fact, expand spawning habitat and therefore promote spawning on the mid-shelf, as do warm-water events frequently found in 200 m on the shelf edge: a 9-month time-series from a bottom-mounted current meter deployed in 200 m directly off Cape St Francis indicated temperatures to regularly reach 12°C and in one long-lasting event, even attaining 16°C (M. J. Roberts, unpublished data). This would explain egg capsules at ~200 m where temperatures are ordinarily ~9–10°C.

But equally possible is the hypothesis proposed by Roberts and Sauer (1994), which suggests that commonly experienced benthic turbidity events on the inshore spawning grounds could force spawners into deeper, clear water, the motivation being that visual chromatophoric patterns play an important role in the spawning process (mating) and that turbidity will therefore disrupt spawning behaviour. However, for the deep spawning grounds where light levels are very low, it may be possible that deposition of fertilized egg strands by solitary females can occur.

Implications

The results of this study have clearly defined the spawning grounds of chokka squid and demonstrated that the inshore, shallow coastal areas ≤70 m of the eastern Agulhas Bank between Knysna and Port Alfred form the epicentre of the spawning grounds. But deeper spawning on the mid-shelf still provides a meaningful contribution to recruitment, and hence there is a need to revise our understanding of the chokka squid life cycle to include deep spawning. Specifically, the original (and later popular) hypothesis by (Augustyn *et al.*, 1992) that *L. reynaudii* spawns in warm, protected locations along the inshore regions of the Eastern Cape Coast is not altogether correct. From a management perspective, confirmation of deeper spawning implies that jig catch data do not necessarily gauge spawner biomass abundance, or indicate overall spawning activity, and consequently cannot be used alone to forecast recruitment. The deeper spawning area also adds a further element of conservation to the fishery in that spawning takes place year round with reduced (there is some drift fishing at night using large drogue anchors and 2 kW lights) fishing pressure. This reinforces the annual 5-week closed fishing season designed to totally remove the fishing pressure during the height of spawning between November and January. In fact, the deeper spawning grounds can be included in the operational management procedure for this fishery as the fifth component of conservation along with effort limitation, closed areas (Tsitsikamma National Marine Park), closed season, and size limits (Augustyn *et al.*, 1992).

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