THE ROLE OF THE DEEP SPAWNING GROUNDS IN CHOKKA SQUID (*LOLIGO REYNAUDI* D'ORBIGNY, 1845) RECRUITMENT

A thesis submitted in fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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by

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Declaration

Declaration submitted by a candidate presenting a thesis for examination

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Title of thesis: The role of the deep spawning grounds in chokka squid (*Loligo reynaudi* D'Orbigny, 1845) recruitment.

I certify that this thesis has not been submitted for a degree in any other university and that it is my original work except as follows:

Chapter 2: The location, extent and potential significance of the chokka squid, *Loligo reynaudi*, mid-shelf spawning grounds. Initial data analysis for this section was originally started in 2005 by Professor Michael John Roberts. However, this work was never completed. I, Nicola Downey, redid the analysis with updated data, as well additional analysis. I was responsible for drafting the manuscript for publication. Co-authors and supervisors, Prof. Michael Roberts and Prof. Warwick Sauer, oversaw this process. This chapter was *published in 2012.

Signed: NJDowney Date: 10 December 2013

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Abstract

It was previously thought that the South African chokka squid *Loligo reynaudi* is exclusively an inshore, shallow water spawner. Although spawning mostly within shallow bays (<60 m) the presence of squid eggs in trawls at depths up to 130 m indicates this species frequently makes use of deeper spawning areas on the mid-shelf. The extent of mid-shelf spawning (referred to as deep spawning) and the contribution to recruitment has yet to be assessed. Studies have shown mid-shelf bottom temperature to vary considerably from those inshore, suggesting chokka squid spawn in two very different oceanographic environments. Considering these apparent environmental differences, what leads to the mid-shelf environment becoming a suitable spawning habitat? Does a suitable benthic habitat, required for the attachment of egg pods, occur on the mid-shelf? These questions are not only important for determining the extent of deep spawning, but also to the understanding of factors “driving” deep spawning. The fate of deep spawned hatchlings is another unknown. It has been proposed that the main chokka squid inshore spawning grounds are positioned to exploit the net westward currents on the Eastern Agulhas Bank, i.e. paralarvae would be transported west from the hatching site to the cold ridge, an area of high primary and secondary productivity on the Central Agulhas Bank. This concept has come to be known as the Western Transport Hypothesis. Lagrangian ROMS-IBMs (regional ocean model system – individual-based model) predict the net westward transport of paralarvae from both the inshore and deep spawning grounds, to the cold ridge. These simulations were used to investigate the transport of hatchlings to the cold ridge feeding grounds before the exhaustion of yolk reserves. The fate of paralarvae on reaching the feeding grounds has not yet been investigated.

This work has contributed new knowledge to our understanding of deep spawning and its role in recruitment. Specific aims of this study were to (1) determine the extent, range and importance of the deep spawning grounds relative to those inshore; (2) investigate the deep spawning ground habitat (Agulhas Bank mid-shelf) morphology and oceanographic environment; (3) determine the transport and survival of deep spawned hatchlings; and (4) investigate the origin and distribution of chokka squid paralarvae on the Agulhas Bank.

The extent, depth range and importance of the deep spawning grounds, relative to those inshore was assessed using 23 years of demersal trawl survey data. Data for both the west and south coasts of South Africa 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. The majority of deep spawned eggs however, were found in the depth range 71-130 m. Squid egg density markedly decreased beyond 70 m, suggesting delineation between the inshore and deep 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 chokka squid is an inshore spawner and redefine the spawning grounds to extend across the shelf.

Apart from an initial study investigating bottom temperature on the mid-shelf, very little is known about the deep spawning habitat. St Francis Bay, a commonly used spawning location, was chosen as a demonstration area for further study. The deep spawning grounds (71-130 m) were mapped and benthic habitat described from underwater video footage. A study investigating cross-shelf bottom conditions was undertaken off Thys Bay. CTD data were used to compare seasonal bottom temperature and oxygen on the St Francis Bay inshore and deep spawning grounds. Squid movement between the two spawning habitats was assessed using filament tagging. Predation and fishing pressure across the spawning grounds was reviewed. The mid-shelf benthic habitat was found to be similar to that inshore and available for spawning. Despite the generally colder bottom temperatures on the mid-shelf, this study showed that bottom temperature in deeper waters can at times be warmer than inshore. Although mid-shelf warming events lasted from a few hours to a number of days, they resulted in similar conditions to those on the inshore spawning grounds. It is likely these events act to expand or shift spawning habitat. The movement of squid between the two spawning habitats makes it possible for them to seek patches of warm bottom water with appropiate substrate. This suggests they are spawning habitat opportunists. Predation and fishing pressure appear to be higher on the inshore spawning grounds. It is feasible that this also forces spawners to seek out more favourable habitat offshore.

An individual-based model was used to predict the fate of mid-shelf and inshore hatched paralarvae. Within the model, both the highly productive cold ridge and inshore spawning grounds were considered feeding or nursery areas. Paralarvae were released from six inshore and six deep spawning sites, spanning the coast between Port Alfred and Knysna. All paralarvae not reaching the feeding areas before the exhaustion of yolk-reserves (≤5 days), not retained within the feeding grounds (≥14 days), and not retained on the Agulhas Bank after exiting the feeding grounds were considered lost. This work illustrated the dependence of paralarval transport success on both spawning location and time of hatching, as established in earlier studies. The current IBM has expanded on initial work, emphasizing the importance of the cold ridge and inshore spawning grounds as nursery areas for deep and inshore spawned paralarvae, respectively. This work has highlighted the complex interactions between processes influencing recruitment variability for chokka squid. Possible relationships between periods of highest recruitment success and spawning peaks were identified for both spawning habitats. Based on the likely autumn increase in deep spawning off Tsitsikamma, and the beneficial currents during this period, it can be concluded deep spawning may at times contribute significantly to recruitment. This is particularly true for years where the cold ridge persists into winter.

Data on chokka squid paralarval distribution are scarce. Paralarval distribution and abundance, in relation to Agulhas Bank oceanography, was investigated using bongo caught paralarvae and corresponding oceanographic data. Individual-based models (IBMs) were used to predict the origin or spawning site of the wild caught paralarvae, with reference to inshore versus deep spawning. Although failing to predict realistic points of origin, this study provided evidence to support a number of scenarios previously assumed to influence chokka squid recruitment. First is the possible influence of coastal upwelling on the retention, and hence spatial distribution, of paralarvae on the inshore spawning grounds. The second factor thought to impact recruitment is the loss of paralarvae from the Agulhas Bank ecosystem. This study confirmed the removal of paralarvae from the Eastern Agulhas Bank due to Agulhas Current boundary phenomena and resultant offshelf leakage. In addition, data suggested that the formation of the cold ridge could enhance retention on the Central Agulhas Bank, and so prevent offshelf leakage from the Central and Western Agulhas Bank.

A synthesis of the main conclusions is presented. Implications of the findings and directions for future research are discussed.

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CHAPTER 1: General Introduction

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Deep spawning and its potential importance

It was previously thought that the South African chokka squid *Loligo reynaudi* is exclusively an inshore, shallow water spawner, with the greater Agulhas Bank shelf region serving as feeding grounds (Augustyn, 1991). Although spawning mostly within shallow bays (<60 m), the presence of squid eggs in trawls at depths of up to 130 m indicates that this species frequently makes use of deeper spawning areas on the Agulhas Bank mid-shelf (Augustyn and Roel, 1998; Augustyn *et al.*, 1992, 1994; Olyott *et al.*, 2007; Roberts and Sauer, 1994; Roberts *et al.*, 2002). The extent of deep spawning on the mid-shelf and contribution to recruitment had yet to be determined.

The South African squid fishery undergoes marked catch fluctuations, both monthly and annually. Short-term monthly fluctuations have been attributed to variable oceanographic conditions (Roberts and van den Berg, 2002) and have been studied in some detail. The more long-term, annual fluctuations in the availability of squid, and hence commercial catches, are thought to be influenced by recruitment strength (Roberts and van den Berg, 2002). It is assumed by resource managers and scientists that deep spawning creates a buffer against intense fishing pressure inshore, providing a reservoir of recruits. This needs to be validated by investigating the dispersal and survival of deep spawned hatchlings.

Studies have shown mid-shelf bottom temperatures to be colder (averages of 10 °C) than inshore (averages of 15.3 °C) (Oosthuizen, 1999; Roberts and Sauer, 1994; Roberts, 2005). In addition the range of bottom temperatures on the mid-shelf is narrow (9–14 °C) compared to the extensive fluctuations occurring inshore (11–22 °C) (Oosthuizen, 1999; Roberts and Sauer, 1994; Roberts, 2005). Evidently, chokka squid spawn in two very different oceanographic environments. Considering these apparent environmental differences, what leads to the mid-shelf environment becoming favourable spawning habitat? Does suitable benthic habitat, required for the attachment of egg pods, occur on the mid-shelf? These questions are not only important for determining the extent of deep spawning, but also for our understanding of factors “driving” deep spawning.

Chokka squid research to date

The distribution, abundance, biology and ecology of chokka squid were first addressed during three joint Japanese–South Africa south coast trawl surveys (Hatanaka *et al.*, 1983; Uozumi *et al.*, 1984, 1985). During these initial surveys and the regular stratified random sampling surveys that followed (Augustyn and Roel, 1998), the presence of chokka squid egg capsules in mid-shelf trawls provided the first indication that deep spawning occurred frequently. Despite knowing of the existence of deep spawning for almost 30 years, a review of relevant published literature clearly illustrates research has been focused primarily on inshore spawning behaviour and the inshore spawning grounds. These studies have investigated numerous aspects of inshore spawning, and the South African chokka squid could be considered one of the world's best studied squid species. Some 27 publications have investigated topics such as chokka squid distribution, biology and lifecycle (Augustyn, 1986; Lipiński, 1994; Sauer and Lipiński, 1990); stock assessment (Augustyn and Roel, 1998; Augustyn, 1986); the inshore spawning grounds and spawning behaviour (Downey *et al.*, 2010; Hanlon *et al.*, 1994, 2002; Lipiński *et al.*, 1998; Melo and Sauer, 1999; Sauer and Smale, 1993; Sauer *et al.*, 1997, 2000; Sauer, 1995a, 1995b; Sauer *et al.*, 1992, 1993; Shaw and Sauer, 2004; Shaw *et al.*, 2010); predation on spawning squid (Lipiński and Soule, 2007; Sauer and Smale, 1991; Smale *et al.*, 1995, 2001); and the oceanographic environment and links to spawning behaviour and squid catches (Downey *et al.*, 2010; Roberts and Sauer, 1994; Roberts, 1998, 2005; Sauer *et al.*, 1991; Schön *et al.*, 2002).

The research focus on inshore spawning is largely a result of the difficulty in conducting studies at depths greater than ~40 m; and in general, a paucity of knowledge exists in terms of the mid-shelf benthic environment off South Africa (Booth, 1998). Although many research trawl surveys have been undertaken, large areas of the mid-shelf consist of untrawlable hard ground and cannot be surveyed. Knowledge of offshore reef environments is therefore scarce (Smale, 1992). In terms of mid-shelf oceanography, the majority of environmental data available have been collected during ships surveys, providing only snapshots of water column conditions and surface currents. The collection of long-term, continuous data through the deployment of environmental moorings is more costly and labour intensive beyond divable depths. Fewer such datasets are therefore available. In comparison, intensive localized studies are possible inshore. Spawning concentrations can be found with relative ease, are often at divable depths, and long-term environmental moorings can be deployed and maintained at a significantly lower cost.

Routine stratified random sampling trawl surveys have enabled the investigation of some biological and ecological aspects of both inshore and mid-shelf caught squid (Augustyn, 1991; Augustyn *et al.*, 1994; Olyott *et al.*, 2006, 2007; Sauer and Lipiński, 1991; Sauer *et al.*, 1999). In addition, a few studies have addressed issues specific to deep spawning, such as embryonic development at low temperatures (Oosthuizen *et al.*, 2002a) and transport of mid-shelf hatched paralarvae (Martins *et al.*, 2010, 2013; Roberts and van den Berg, 2002, 2005). To date, only three publications report on research focused primarily on deep spawning in chokka squid. These studies are reviewed in detail in a later section.

Current management of the South African commercial squid fishery is based on the premise that a single population of chokka squid is found on the Agulhas Bank, and that mature individuals migrate to south coast inshore areas to spawn. Deep spawning is not taken into account, as questions regarding the extent, viability and contribution to recruitment first need to be addressed. It is crucial we answer these questions in order to understand the role of deep spawning. Deep spawning possibly has some evolutionary significance in that survival and reproductive success must have benefitted from its persistence. Also important are understanding the reasons for this alternative reproductive tactic. In order to place the current study on deep spawning into perspective, a review of our knowledge on the distribution, life cycle, reproduction and ecology of this species is provided below.

The South African chokka squid, *Loligo reynaudi*

Distribution

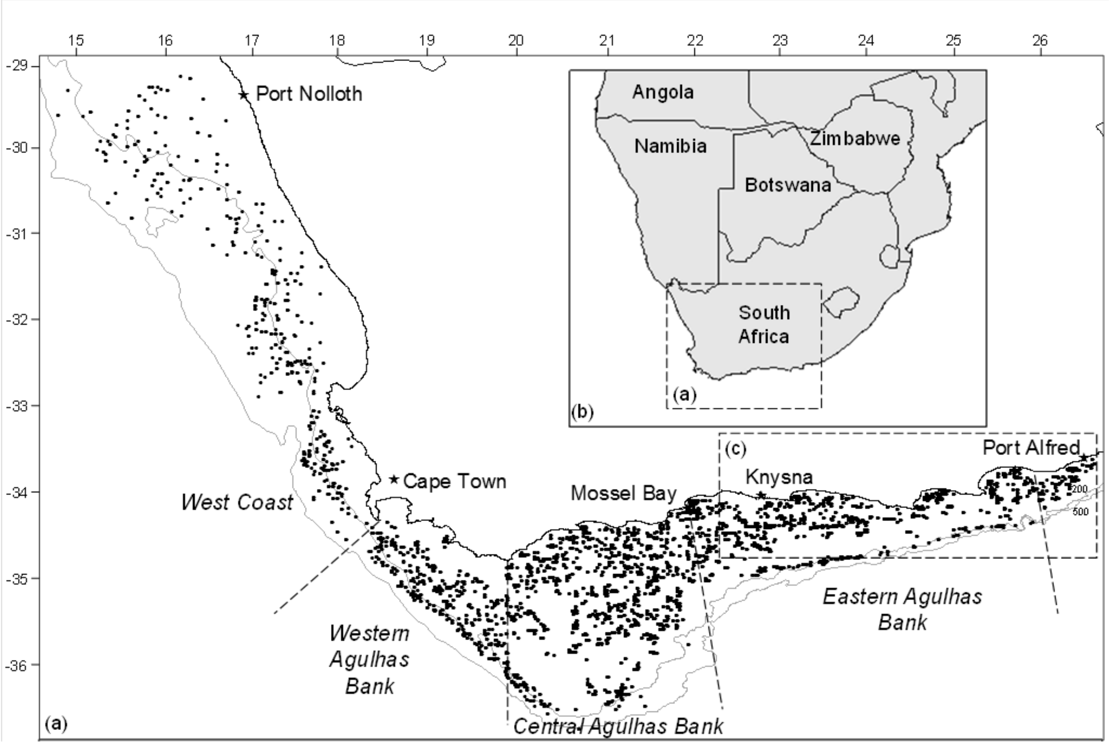

Figure 1.1: Updated from Roberts and Sauer (1994). (a) Demersal distribution (dots) from DAFF research trawls of adult (females >18 cm; males >25 cm) chokka squid *Loligo reynaudi* on the west coast and the Agulhas Bank of South Africa, (b) *Loligo reynaudi* has also been found as far north as Namibia and southern Angola but biomass appears to be low, (c) the main spawning grounds.

Adult chokka squid are distributed over most of the continental shelf off the west and south coasts of South Africa (Figure 1.1). Generally more than two thirds of the adult biomass is concentrated on the south coast on the Central and Eastern Agulhas Bank (Figure 1.1b, Augustyn (1991); Roberts and Sauer (1994); Roberts (2005)). Here they occupy the entire shelf (Figure 1.1a) (Roberts and Sauer, 1994) and their presence in almost every Department of Agriculture, Forestry and Fisheries (DAFF) research trawl shallower than 200 m (Augustyn *et al.*, 1993), confirms their widespread distribution. In contrast, squid on the west coast occupy a narrower band, avoiding both the inshore and deep outer-shelf regions (Figure 1.1a, Roberts and Sauer, 1994). The limits of adult squid distribution seen in Figure 1.1 are imposed by DAFF research trawl survey design, and are not reflective of actual distribution. DAFF research trawl surveys do not sample north of 29°S on the west coast, or east of 27°E on the south coast. However, in the west, chokka squid occur as far north as southern Angola (Figure 1.1b, Shaw *et al.* (2010)) where spawning is also known to occur (Sauer *et al.*, 2013). Interestingly, very few squid are found on the Namibian shelf between southern Angola and the west coast of South Africa. On the south coast, the eastern extent of distribution can continue beyond Port Alfred (Figure 1.1c). This eastward range extension is likely linked to sporadic shelf upwelling and cooler water that occurs between Port Alfred and East London (Lutjeharms *et al.*, 2000). What is thought to be *Loligo reynaudi* has been recorded in a joint Spanish/Mozambiquan research trawl survey off Northern Bazaruto (Mozambique, Figure 1.1b). These specimens were caught in trawls at depths of 201–400 m (see Silva *et al.* (2009)). The occurrence of chokka squid this far up the east coast of Africa still needs to be confirmed.

Spawning and life cycle

Although distributed over the greater part of the Agulhas Bank, spawning is largely confined to the south coast of South Africa . The main chokka squid spawning grounds are thought to be inshore (<60 m) between Plettenberg Bay and Port Alfred (Figure 1.1c, Augustyn (1989, 1990); Sauer *et al.* (1992)), although some spawning occurs outside of this area. The use of warm inshore areas for spawning is a common feature among loliginid squid. *Uroteuthis chinensis* (Chotiyaputta, 1997), *U. duvauceli* (Chotiyaputta, 1997; Mohamed, 1993), *L. vulgaris* (Raya *et al.*, 1999), *Doryteuthis pealeii* (McMahon and Summers, 1971) and *D. opalescens* (Fields, 1965) are all known inshore spawners. A short summary of inshore spawning in chokka squid follows.

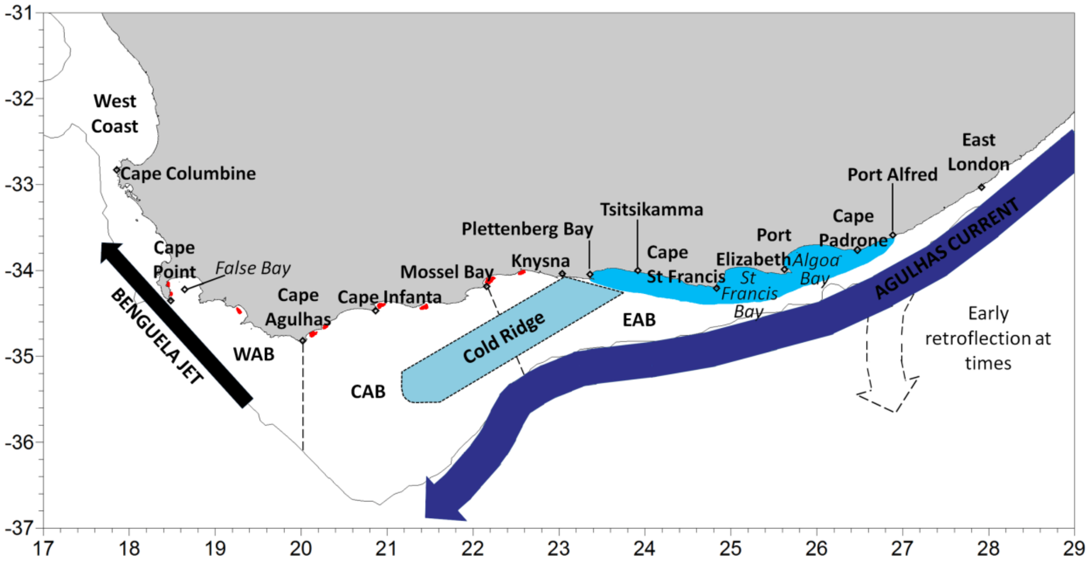

Figure 1.2: The South coast of South Africa, showing the main spawning grounds (turquoise) on the Eastern Agulhas Bank (EAB) between Plettenberg Bay and Port Alfred. Other spawning areas (red) inshore on the Western Agulhas Bank (WAB) and Central Agulhas Bank (CAB), following Sauer and Lipinski (1990), are also given. The divisions of the Agulhas Bank, the Agulhas Current, Benguela Jet and position of the cold ridge are illustrated.

Squid generally move onto the inshore spawning grounds at dawn (Sauer *et al.*, 1997). On sites with an existing egg bed, males have been found to circle the egg bed, possibly drawing in other males and females (Sauer *et al.*, 1997). This leads to the formation of a spawning aggregation (Sauer *et al.*, 1997). Pairing of squid occurs in the water column above the egg bed (Sauer *et al.*, 1992). The large consort male grasps the female from below whilst transferring spermatophores from his own to her mantle cavity (Hanlon, 1998; Hanlon *et al.*, 1994; Sauer *et al.*, 1992). In this "male-parallel" mating position the sperm is placed near the opening of the females' oviduct (Hanlon, 1998; Hanlon *et al.*, 1994). After mating, the female swims down to the egg bed, accompanied by the male, where she deposits her fertilized egg strand (Hanlon, 1998; Hanlon *et al.*, 1994; Sauer and Smale, 1993; Sauer *et al.*, 1992). "Male-sneak" mating occurs when a smaller sneaker male jets up to an already paired female and quickly deposits spermatophores onto the egg capsule held in her arms (Hanlon, 1998; Hanlon *et al.*, 1994). Another form of mating common to loliginids is "head-to-head" mating, which results in the deposition of sperm in the females' bursa copulatrix (Hanlon *et al.*, 1994, 1997). This is a sperm storage organ near the females' buccal mass (Hanlon *et al.*, 1994, 1997). Interestingly, a large proportion of chokka squid females, caught both on and off the inshore spawning grounds, contain spermatophores in their bursa copulatrix and are considered fertilised (Augustyn, 1990; Roberts *et al.*, 2002; Sauer and Smale, 1993; Sauer *et al.*, 1992). This implies the squid mating system first includes a period of offshore mating, providing sperm to most females before the onset of the inshore spawning migration (Sauer *et al.*, 1997). It has been suggested this offers an alternative tactic for females possibly not making it to the inshore spawning grounds, as well as additional sperm sources for those that do (Sauer *et al.*, 1997). This is not unique to *L. reynaudi* and has been observed in another loliginid, *Doryteuthis gahi*. In this species mating occurs in both deep water, with sperm storage within the bursa copulatrix; and in shallow waters, with sperm storage within the mantle cavity (Arkhipkin *et al.*, 2000).

Pair formation breaks down shortly after dark and the spawning aggregation disintegrates (Downey *et al.*, 2010; Hanlon *et al.*, 1994; Roberts, 1998; Sauer and Smale, 1993; Sauer *et al.*, 1997). Telemetry studies have shown squid then either remain on the inshore spawning grounds (Downey *et al.*, 2010) or disperse offshore (Sauer *et al.*, 1997). Both these behaviours have been linked to feeding. Some lone females remain on the inshore spawning grounds, depositing eggs after dark (Sauer, 1995a; Sauer *et al.*, 1992, 1993). At dawn squid aggregate in the vicinity of egg beds once again.

Chokka squid egg beds can vary in size from just a few strands, to numerous strands forming massive beds up to 4 m in diameter (Sauer *et al.*, 1992). The configuration of egg beds depends on substratum type (Sauer, 1995b). Large egg beds are usually formed on open sandy areas, whilst smaller egg mops have been observed on reefs (Roberts, 1998; Sauer, 1995b). On average egg pods deposited on the inshore spawning grounds take four weeks to hatch (Augustyn *et al.*, 1992; Oosthuizen *et al.*, 2002a).

Chokka squid hatchlings, known as paralarvae (Young and Harman, 1988), have an initial planktonic life stage. Immediately after hatching paralarvae are dependent on yolk reserves (Vidal *et al.*, 2002a, 2006), and must develop prey-capture skills before yolk is completely exhausted (Vidal *et al.*, 2005). Rearing experiments indicate that in the majority of chokka squid paralarvae, yolk reserves are depleted five days after hatching (Vidal *et al.*, 2005). Paralarvae are extremely sensitive to starvation and their survival, and hence recruitment, depends on finding sufficient food sources before internal reserves are diminished (Lipiński, 1998; Vidal *et al.*, 2006). Young squid hatchlings are not completely developed morphologically (Augustyn *et al.*, 1994), having saccular, rounded bodies and small, rudimentary fins (Bartol *et al.*, 2008). They are therefore not strong swimmers and transport to food-rich areas is largely dependent on ocean circulation (Augustyn *et al.*, 1992; Goldman and McGowan, 1991; Hanlon *et al.*, 1985; Roberts, 2005).

The currently accepted life cycle, first proposed by Augustyn (1989), postulates that chokka paralarvae are carried westwards, away from the main spawning grounds, by the Agulhas Current (Augustyn *et al.*, 1994). When the juvenile and sub-adult phase is reached, a portion of the population that remained on the south coast also moves westwards, to the rich feeding grounds on the west coast (Figure 1.1). Here they mature and grow before embarking on spawning migrations back to the south coast. Sub-adults that remained on offshore feeding grounds on the Central and Eastern Agulhas Bank (Figure 1.1) also undergo these inshore spawning migrations. The biological characteristics and distribution of paralarvae, juveniles, sub-adults and adults on the Agulhas Bank, investigated in detail by a number of authors (Augustyn, 1989, 1990, 1991; Augustyn *et al.*, 1994; Olyott *et al.*, 2006, 2007) supports this hypothesis to some degree. Recent work suggests the possibility of geographically fragmented stocks on the Agulhas Bank (Olyott *et al.*, 2006, 2007). Evidence indicates some adult squid near the western boundary of their distribution (Figure 1.1) may remain on the west coast, migrating inshore to spawn in False Bay and other shallow areas on the Western Agulhas Bank (Olyott *et al.*, 2007). Documented inshore spawning areas in this region, following Sauer and Lipinski (1990), are shown in Figure 1.2. There are also indications that a proportion of the south coast biomass does not undertake a westward migration, but rather remains in the east offshore of the spawning grounds (Olyott *et al.*, 2006). It is possible different management strategies may need to be considered for the various areas of the Agulhas Bank (Olyott *et al.*, 2006). Genetic analysis to date has yet to confirm significant genetic differentiation of populations in South African waters, although some isolation by distance is apparent, supporting the hypothesis by Olyott et al. (2006) (Shaw *et al.*, 2010).

Very evident is the importance and role of the Agulhas Bank ecosystem throughout the chokka squid life cycle. Despite the existence of fringe spawning inshore on the Western and Central Agulhas Bank, the position of the main spawning grounds on the South Coast coupled with paralarval, juvenile and adult distribution (Augustyn *et al.*, 1994) suggests different areas of the Agulhas Bank are utilized during different life-history stages. Chokka squid are inarguably environmentally driven (Roberts and Sauer, 1994) and carry out their life cycle in one the most diverse and highly variable ocean environments in the world (Roberts, 2005). A review of Agulhas Bank oceanographic conditions and the influence on various chokka squid life stages follows. Emphasis is on environmental conditions limiting suitable spawning habitat to the south coast and the transport of chokka squid hatchlings.

The Agulhas Bank

The Agulhas Bank is a triangular extension of the continental shelf off South Africa. Off the east coast the shelf is very narrow, beginning to widen towards the south. At its apex, the shelf is some 250 km wide (Hutchings, 1994). The shelf break occurs in the vicinity of the 200 m isobath, with the continental slope dropping steeply beyond 200 m (Hutchings, 1994). The Agulhas Bank is bound by two major current systems: the southwesterly flowing Agulhas Current along the eastern edge of the bank, and the northward flowing Benguela Current in the west (Figure 1.2). Regions of the Agulhas Bank can be characterized by different hydrological conditions, resulting primarily from the forcing of the Agulhas Current and wind-driven coastal upwelling (Probyn *et al.*, 1994). As such, the Agulhas Bank can be divided into three main regions: the Eastern Agulhas Bank (22–27°E), Central Agulhas Bank (20–22°E) and the Western Agulhas bank (18.5–20°E) (Figure 1.1 and Figure 1.2).

Western and Central Agulhas Bank

The Western Agulhas Bank and the west coast (west of Cape Point) – The west coast is dominated by the productive Benguela upwelling system. Here bottom temperatures range between 3.2 and 16.4 °C, with an average minimum bottom temperature of 7.7 °C (Roberts, 2005). The characteristically low temperatures in this region reflect both quasi-permanent large-scale upwelling and the deep shelf break at 400 m (Roberts, 2005). Inshore (<100 m) bottom temperatures average around 10 °C and seldom exceed 11 °C (Roberts, 2005). Roberts (2005) proposed the west coast benthic environment is too cold for successful development of chokka squid eggs, and indeed, no eggs have been found in this area (see Chapter 2). Instead, this area is important as a feeding ground. The cross-shelf variation in bottom dissolved oxygen on the west coast is large. Inshore (<150 m), average bottom dissolved oxygen levels are generally below 3 $mg.l^{-1}$, dropping to almost zero in some areas (Roberts, 2005). Beyond 150 m, bottom dissolved oxygen levels increase, with the highest levels (≥4 $mg.l^{-1}$) found on the outer shelf. The distribution of adult chokka squid has been found to be strongly linked to environmental conditions, with more than 95% of adults found in bottom waters ≥8°C and 86% in waters with oxygen levels ≥3 $mg.l^{-1}$ (Roberts and Sauer, 1994). The majority of squid tend to avoid both the coastal and deeper outer shelf regions (Figure 1.1). It is thought inshore distribution is limited by oxygen levels and offshore by bottom temperature. Bottom temperature and dissolved oxygen on the Western Agulhas Bank reflect characteristics of both the west coast and Agulhas Bank proper (Roberts, 2005). Inshore bottom temperatures range from 9–16 °C (average 10–11 °C). On the mid-shelf and outer regions temperatures are lower and range between 7–10 °C (Roberts, 2005). Average dissolved oxygen over the majority of the shelf is ≥4 $mg.l^{-1}$, with only a few inshore and mid-shelf areas having mean levels of 3–4 $mg.l^{-1}$.

The Central Agulhas Bank – This region of the Agulhas Bank is the widest in terms of distance from the coast to the shelf break. Subsequently large areas of this region can be regarded as having primarily shelf characteristics with inshore regions being dominated by forcing from wind stress, tides and radiation (Lutjeharms *et al.*, 1996). Because of the wide shelf, circulation and temperature structures on the outer regions are influenced by open ocean boundary conditions (Lutjeharms *et al.*, 1996). The dominant circulation pattern on the Central Agulhas Bank is cyclonic circulation around the cold ridge (this feature is discussed in the next section). This results in an eastward flow inshore and a south-westward flow offshore (Hutchings, 1994). The outer shelf regions of the Central Agulhas

Bank are dominated by the south-westward flow of the Agulhas Current along the shelf edge as it moves offshore in the vicinity of the Agulhas Bight (Boyd and Shillington, 1994). At times, the Agulhas Current can flow onto the shelf in this region before sweeping offshore (Boyd and Shillington, 1994). Warm surface water from the Agulhas Current regularly intrudes onto the Central Agulhas Bank from the Agulhas Bight (Boyd and Shillington, 1994). As detailed by Roberts (2005), bottom temperatures on the extensive shallow region of the Central Agulhas Bank (<100 m) can exceed 16 °C (average 12–13 °C). Generally, bottom temperatures inshore are warmer during winter as a result of storm induced isothermal mixing of the water column. Average bottom temperatures on the mid-shelf and outer regions are ~10 °C. Average bottom dissolved oxygen is ≥4 $mg.l^{-1}$ across the entire Central Agulhas Bank. Inshore, minimums below 3 $mg.l^{-1}$ can occur. Bottom dissolved oxygen levels on the outer-shelf are consistently ≥4 $mg.l^{-1}$, most likely a result of active shelf-edge upwelling along the inner boundary of the Agulhas Current. Adult chokka squid are distributed across the greater part of the Central Agulhas Bank and spawning has been known to occur inshore (see Chapter 2).

Eastern Agulhas Bank and the inshore spawning grounds

The Eastern Agulhas Bank – This region of the Agulhas Bank is the narrowest in terms of distance from the coast to the shelf edge, and continues to narrow from west to east. Hydrological conditions are strongly influenced by the fast flowing Agulhas Current, particularly near the shelf edge. Average bottom temperatures inshore vary from ~11–15 °C with temperatures generally increasing from west to east. This increase is a result of the narrowing shelf and the greater influence of the Agulhas Current inshore east of Port Elizabeth (Roberts, 2005). Maximums of above 20 °C can occur inshore (Roberts, 2005). Bottom dissolved oxygen levels in this region are consistently above 3 $mg.l^{-1}$, with St Francis Bay and Algoa Bay having levels ≥6 $mg.l^{-1}$ (Roberts, 2005). Roberts (2005) concluded, based on his detailed analysis of bottom dissolved oxygen and temperature on the Agulhas Bank, that conditions are suitable for chokka squid spawning over the Eastern Bank throughout the year, or over the inner Central Agulhas Bank in early summer, before dissolved oxygen drops.

Another characteristic of the south coast considered beneficial for spawning is the intermittent wind-driven coastal upwelling. Coastal upwelling is common in summer and initiates on the western side of prominent capes as a result of strong easterly winds (Schumann *et al.*, 1982). During extreme upwelling events, bottom temperatures inshore can drop as low as 9 °C (Downey *et al.*, 2010). The increase in intensity and frequency of upwelling events in summer coincides with the peak chokka squid spawning season (Sauer *et al.*, 1991). The abundance of squid on the inshore spawning grounds has been linked to upwelling frequency (Sauer *et al.*, 1991) and it seems either upwelling (Downey *et al.*, 2010; Roberts, 1998) or possibly a rapid temperature change (Schön *et al.*, 2002) are environmental cues or triggers for spawning.

The region also experiences frequent turbidity events, particularly during the winter months (Dorfler, 2002). It is thought turbidity events disrupt spawning due to reduced visibility (Schön *et al.*, 2002). Visual signalling using the neurally controlled chromatophore organs in the skin is integral to the mating system of squid (Hanlon *et al.*, 1994; Jantzen and Havenhand, 2003). Other important components of the visual signalling system are body posture and locomotor components (Hanlon *et al.*, 1994). Hanlon *et al.* (1994) observed and described a total of 36 components on the chokka squid inshore spawning grounds, 26 of which were related to intraspecific behaviours within the mating arena. Severe turbidity events can last for several days and possibly force squid to move offshore to spawn in colder but cleaner water (Roberts and Sauer, 1994).

The cold ridge

The cold ridge is a subsurface feature extending from the Knysna coast (Eastern Agulhas Bank), southwestward onto the Central Agulhas Bank (Figure 1.2). It is visible in SST satellite imagery as a filament or tongue of cold water extruding from the coast out onto the mid-shelf. It is believed to be formed by the doming of the thermocline, bringing cold, nutrient-rich bottom layers towards the surface (Roberts, 2005). Also visible in satellite (chlorophyll) imagery are the high levels of primary production associated with this feature (Boyd and Shillington, 1994). Although paralarvae prey (copepods) can be found in all regions of the Agulhas Bank, a great deal of spatial and temporal variability in abundance exists (Roberts and van den Berg, 2002). Numerous studies (Boyd and Shillington, 1994; Huggett and Richardson, 2000; Largier *et al.*, 1992; Peterson and Hutchings, 1995; Verheye *et al.*, 1994) have recorded high densities of copepods in the vicinity of the cold ridge. The cold ridge is a significant feature of the Agulhas Bank ecosystem, and is considered an important feeding ground or nursery area for squid paralarvae. Its formation and the consequent concentration of copepod abundance is thought to enhance paralarval survival and recruitment. The presence of the cold ridge is variable and it can last for a period of days to weeks (Roberts, 2005). The cold ridge is more prevalent in summer and in some summers appears to be a semi-permanent feature on the Agulhas Bank (Roberts, 2005).

Western Transport Hypothesis

It is apparent from the work by Roberts (2005) that chokka squid make use of a very specific environmental niche on the inshore Eastern Agulhas Bank for spawning. This author proposed that nowhere else on the Agulhas Bank are bottom temperature and dissolved oxygen levels suitable for egg development. Roberts (2005) also noted that the chokka squid spawning grounds are displaced from the high copepod biomass, in the vicinity of the cold ridge, by some 200 km. He postulated paralarvae hatching on the inshore spawning grounds, between Plettenberg Bay and Port Alfred, could be transported to the cold ridge by the net westward currents on the Eastern Agulhas Bank. This has become known as the "Western Transport Hypothesis", and is in line with the currently accepted life cycle.

Roberts (2005) calculated the passive transport of paralarvae in this net westward flow would be at average speeds of 18–25 $km.d^{-1}$, or based on actual current speeds, 35–43 $km.d^{-1}$. This indicated paralarvae as far away as Algoa Bay would take approximately 4–7 days (average speeds) or 3–5 days (actual current speeds), to reach the cold ridge. Based on findings regarding the duration of the yolk-utilisation phase in chokka squid paralarvae, it is likely hatchlings will survive the journey to the rich feeding grounds. Lagrangian dispersal simulations of paralarvae from both the inshore and deep spawning grounds have confirmed the net westward transport of particles (or paralarvae) on the Eastern Agulhas Bank (Martins, 2009). The south coast of South Africa appears to be suitable both as spawning habitat and for early life stages of the chokka squid (Roberts, 2005).

Deep spawning

Current understanding of deep spawning aggregations

Inshore, large masses of mating squid in the water column and pairs moving between this mass and the egg bed below, results in a distinct "mushroom-shaped" aggregation visible on echotraces (Lipiński *et al.*, 1998; Sauer *et al.*, 1992). In the past this definite shape has successfully been used to acoustically locate inshore spawning concentrations (Lipiński *et al.*, 1998). Unusual hydroacoustic targets were observed in November 1996, May 1998 and November 1998 during routine pelagic biomass surveys off the south coast of South Africa. These targets were recorded both on the inshore spawning grounds and offshore of these areas (Roberts *et al.* (2002), see Figure 2.1c Lines A–C). A comparison of the characteristics of just such an inshore target, confirmed to be an aggregation of spawning squid, with the deep water targets, suggested these echotraces were also spawning aggregations. Targets were similar in terms of time of observation, location adjacent to the seabed ridges, shape and size (Roberts *et al.*, 2002). A number of these observations were made in areas where bottom trawls have previously retrieved squid eggs. This combined with the knowledge of inshore squid spawning behaviour lead these authors to conclude echo-traces observed on the deep spawning grounds were in fact spawning aggregations. This study potentially confirmed the formation of large spawning aggregations on the mid-shelf as well as identifying 19 accurate deep spawning sites.

Viability of deep spawned eggs

Initial laboratory experiments by Augustyn (1989) indicated that chokka squid egg mortality occurred at temperatures <10 °C. Oosthuizen *et al.* (2002a, 2002b) 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. Only 0.45% of all eggs showed signs of abnormal embryonic development (Oosthuizen and Roberts, 2009). The collection of bottom temperature data during these mid-shelf incubation experiments revealed two important findings regarding the deep spawning environment: (1) A possible seasonal trend of warming and cooling of the bottom layer, and (2) transient intrusions of warm and cooler water onto the mid-shelf, causing “extreme” high and low temperature events. These authors suggested that the warming events combined with seasonal warming, provides frequent optimal temperature windows for egg development on the mid-shelf. It was also suggested that, based on observations during the laboratory experiments previously discussed, the very early period of development (first few days) is thought to be most critical and is when abnormal development is initiated (Oosthuizen *et al.*, 2002a). This implies that to ensure successful embryonic development, egg deposition must take place during the warm periods (Oosthuizen and Roberts, 2009). Thereafter colder temperatures on the deep spawning grounds will only extend the incubation time (Oosthuizen and Roberts, 2009).

Transport and recruitment of deep spawned hatchlings

Although net displacement of paralarvae hatching on the Eastern Agulhas Bank is westward (Western Transport Hypothesis), shelf water containing paralarvae could leak into the surrounding Indian and Atlantic oceans (Roberts and van den Berg, 2002). Due to the narrowness of the Eastern Agulhas Bank shelf and the offshore flow of the Agulhas Current in the vicinity of Algoa Bay, it follows that large paralarval losses can occur from this area (Augustyn *et al.*, 1994; Roberts and van den Berg, 2002). Other potential leakage mechanisms identified by Roberts and van den Berg (2002) are the entrainment and removal of shelf water through meander plumes and cyclonic eddies on the inshore edge of the Agulhas Current, and early retroflection of the Agulhas Current resulting in extensive offshore leakage of shelf waters. Considering the closer proximity of the deep spawning grounds to the shelf edge, this does not bode well for deep spawned hatchlings. Their survival and contribution to recruitment is therefore questionable. Using a Lagrangian individual-based model (IBM) coupled to a 3-D regional ocean model (ROMS), Roberts and Mullon (2010) investigated the removal of virtual paralarvae from the mid-shelf of the Eastern, Central and Western Agulhas Bank. The results indicated massive losses (76%) of paralarvae from the Eastern Agulhas Bank. In comparison, losses from the Central Agulhas bank were much lower (2%). A major limitation to these earlier simulations was the use of particles with neutral buoyancy and zero swimming capacity. Both buoyancy and swimming influence the position of paralarvae in the water column and hence the extent of dispersion (Roberts and Mullon, 2010).

Later IBM simulations by Martins *et al.* (2010, 2013) used a higher resolution 3-D hydrodynamic model. The purpose of these simulations was to test the Western Transport Hypothesis and assess factors influencing successful transport. These studies reported the successful transport of paralarvae from mid-shelf sites to the cold ridge to vary from 1.13–67.10% (depending on release site, month, specific gravity and diel vertical migration). Release area was found to be the most important factor determining transport success. This implies deep spawning off at least some areas of the south coast may contribute to recruitment.

Although these earlier studies have shed some light on the deep spawning phenomenon, many questions remain.

Research aims and thesis structure

The aims of this thesis are to (1) determine the extent, range and importance of the deep spawning grounds relative to those inshore; (2) investigate the deep spawning ground habitat (Agulhas Bank mid-shelf) morphology and oceanographic environment; (3) determine the transport and survival of deep spawned hatchlings; and (4) investigate the origin and distribution of chokka squid paralarvae on the Agulhas Bank.

Chapter 2 uses 23 years of Department of Agriculture, Forestry and Fisheries (DAFF, previously Department of Environmental Affairs and Tourism) demersal trawl survey data to determine the extent, depth range and importance of deep spawning.

In Chapter 3, the mid-shelf environment is described in terms of oceanographic conditions and benthic habitat. An investigation of cross-shelf bottom conditions was undertaken off Thys Bay (see Figure 3.2 for location). A demonstration area (St Francis Bay, Figure 1.2) within the main south coast spawning grounds was chosen for more detailed descriptions of the deep spawning habitat. Other questions addressed in Chapter 3 include the identification of potential deep spawning habitat (St Francis Bay) and a review of predation and fishing pressure on the inshore and deep spawning grounds. The movement of chokka squid on the Eastern Agulhas Bank, between the two habitats, was also investigated.

Chapter 4 uses an individual-based model coupled with a high resolution 3-D hydrodynamic model of the Agulhas Bank to investigate the transport of paralarvae from deep and inshore spawning sites. To determine potential paralarval survival, and hence contribution to recruitment, success was calculated based on (1) reaching areas of high productivity before the onset of starvation; (2) retention in feeding grounds; and (3) retention on the shelf once exiting feeding grounds. Data were analysed in a step-by-step approach to identify factors responsible for paralarval losses.

Chapter 5 investigates the origin, distribution and abundance of chokka squid paralarvae on the Agulhas Bank. Chokka squid paralarvae, collected during oblique bongo hauls, were identified and distribution and abundance plotted. The origin of bongo caught paralarvae under various transport scenarios was determined using a backwards run individual-based model. Spatial distribution and the potential impact of coastal upwelling and the cold ridge on transport/retention are discussed.

Chapter 6 presents a synthesis of the main findings. Implications of the findings and directions for future research are discussed.

CHAPTER 2: The location, extent and importance of the chokka squid, *Loligo reynaudi*, deep spawning grounds

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Introduction

It is well known that chokka squid, *Loligo reynaudi*, mainly spawn in the shallow (20–60 m depth) inshore regions of the south coast of South Africa (Augustyn, 1990; Roberts and Sauer, 1994; Sauer *et al.*, 1992). Areas further offshore were thought to serve as feeding grounds for juvenile and adult squid (Augustyn, 1991). However, the presence of chokka squid eggs in Department of Agriculture, Forestry and Fisheries (DAFF, previously Department of Environmental Affairs and Tourism) demersal survey trawls, indicates that spawning can take place up to a depth of 270 m (unpublished data). Although spawning intensity is known to decreases with depth on the inshore spawning grounds (Schön *et al.*, 2002), the amount and depth range of offshore spawning have yet to be investigated.

Estimates of commercial fishing effort prior to 1990 indicated the South African squid fishery targeted 90% of its effort on the inshore spawning grounds (Sauer, 1995a). This was because depths >60 m were beyond the range of hand-held jigs and vessel anchors (Augustyn and Roel, 1998; Roberts and Sauer, 1994), and for many years deep spawning aggregations were largely unexploited. More recently drift fishing using sea drogues has enabled fishermen to target squid in areas where bottom depth exceeds 60 m. Strong lights (1–2 kW) are used at night to attract squid to the surface where they can be caught by hand-held jigs. Since the advent of drift fishing, the majority of the commercial fishing fleet now moves offshore in April–May, targeting squid as they move into deeper waters. Generally, commercial catches in April–May are now higher offshore, as fewer aggregations are formed on the inshore spawning grounds. In light of the improved fishing efficiency offshore, fishing effort on the deep spawning grounds needs to be recalculated.

Also important is determining the degree or extent of offshore spawning, the depth range and the importance of the offshore grounds relative to those inshore. This would enable researchers to gauge the potential contribution of deep spawning to recruitment. As the viability of deep spawned eggs has now been confirmed (Oosthuizen and Roberts, 2009), this suggests important implications for the conservation of the stock and management of the fishery. As noted by Roberts *et al.* (2002) increased fishing activity offshore has likely resulted in the removal of possible deep spawners, and it can no longer be assumed that deep spawning provides a reservoir of recruits.

Using 23 years of demersal trawl survey data, this chapter aims to define the chokka squid spawning grounds. More specifically this chapter determines the extent, location, depth range, and importance of the deep spawning grounds relative to those inshore. The ramifications of cross-shelf spawning and implications regarding management of this resource are discussed.

Materials and Methods

Survey Data

Demersal survey data used in this study were collected by DAFF over the period 1985–2008. In total data from 61 demersal research surveys covering the west and south coasts, separately, were examined for squid eggs. All surveys were undertaken by the F.R.S. *Africana* with the exception of BE 214 and Nan 405, for which the F.R.S. *Benguela* and the *Dr Fridtjof Nansen* were used respectively. 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. Survey BE 214 was a dedicated inshore (depth range ~20–100 m) squid survey on the south coast. Survey area remained the same each year, with west coast surveys covering the shelf between 29°S (Orange River) and 20°E (Cape Agulhas) while south coast surveys extended between 20°E 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 grids of approximately 5' degrees of latitude by x 5' degrees of longitude, within strata of 0–50 m, 51–100 m, 101–200 m and 201–500 m. Trawl blocks (also referred to as stations) for each survey were selected on a semi-random basis 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 2.1). Surveys comprised of up to 109 stations. 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

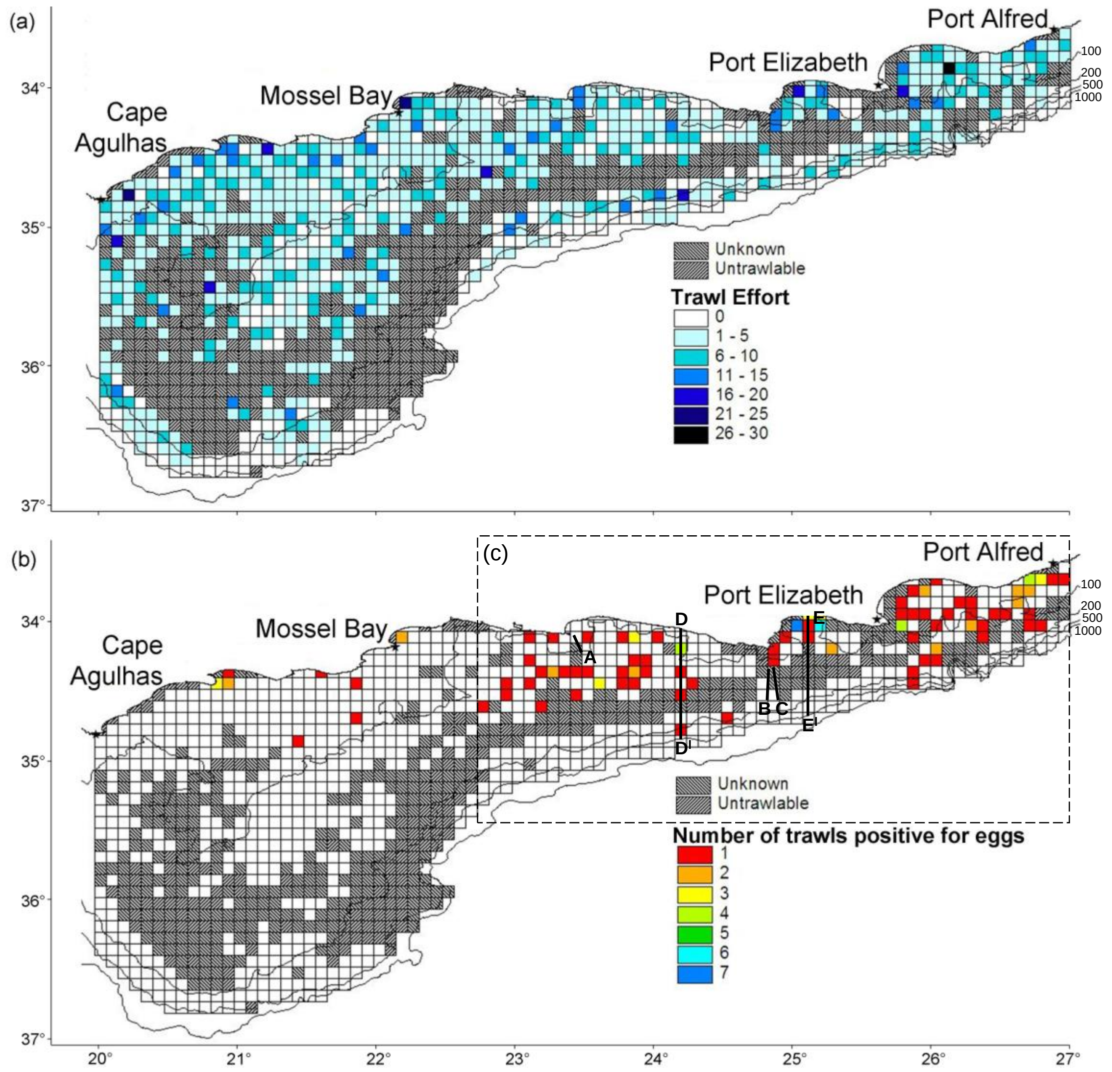

Figure 2.1: Composite maps of data between 1985 and 2008 for (a) the DAFF survey trawl effort on the Agulhas Bank and (b) the distribution of *Loligo reynaudi* eggs caught in demersal trawls. Colour codes indicate the frequency of trawls undertaken in a block or the frequency of trawled squid eggs, respectively. 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 “super” 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 2.3d.

with 27.5 mm mesh in the form of a sleeve to retain most small fish. Trawl duration was limited to 30 minutes, actual bottom time, and the data collected from trawls less than 30 minutes was standardized to 30-minute duration. This equated to a standard trawl area of ~0.0842 $km^2.trawl^{-1}$.

The processing of the trawl catch has been described in detail by Badenhorst and Smale (1991). At each station the catch was sorted into species and the total catch per species weighed to the nearest 0.5 g. During instances where the catch was too large, a sub-sample was weighed. Length frequency distributions of the weighed catch were measured using electronic fish-measuring boards.

Egg Biomass

Although the presence of squid eggs in trawls was recorded (referred to as positive or +'ve trawls in this study), before 1989 their mass was not always determined. Egg mass data from the 1989 to 2008 south coast surveys were used in a simple calculation, shown below, to estimate biomass within the 20–70 m and 71–130 m depth stratums.

For each station trawled, density was calculated using the swept area method (1) (Sparre and Venema, 1998):

$$d = C_w/a \qquad (1)$$

To calculate egg biomass for each stratum, average egg density was calculated (2) and multiplied by the area of the stratum (3):

$$đ_i = \sum d/n_i \qquad (2)$$

$$B_i = đ_i \times A_i \qquad (3)$$

Total biomass was calculated by summing the biomasses for each strata (4) (noting the total biomasses for the 20–70m and 71–130 m depth ranges); and the percentage contribution of the inshore (20–70 m) and deep (71–130 m) spawning habitats calculated (5):

$$B = B_i + B_{i+1} \qquad (4)$$

$$P_i = (B_i/B) \times 100 \qquad (5)$$

d = egg density ($kg.km^{-2}$)

C_w = Catch weight (kg)

a = area trawled (km^2)

$đ_i$ = average egg density in *i*-th stratum ($kg.km^{-2}$)

n_i = number of trawls in *i*-th stratum

B_i = egg biomass in i-th stratum (kg)

A_i = area of i-th stratum (km^2)

B = total egg biomass (kg)

P_i = Percentage contribution of each stratum to total biomass (%)

Results

Geographical egg distribution

The area surveyed on the south coast is shown in Figure 2.1. 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 2.1a). On average, each block has been trawled five times. The grey shading indicates untrawlable ground. Figure 2.1b 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 1.1a). 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 2.1c). This area, ~35 866 km^2, accounts for 37% of the total survey grid. From these data one may gain the 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.

Figure 2.2 schematically presents the data in Figure 2.1, 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 2.1). Using the total number of trawls in each depth range (20–70 m and 71–130 m), the percentage of positive trawls was calculated. 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 2.1c were used to investigate egg distribution with depth. Figure 2.3a 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 2.3d). The small number of trawls between 131 and 170 m reflects the outer band of hard ground depicted in Figure 2.1. 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 2.3b 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 a secondary peak at 101–110 m. Note in Figure 2.3d 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 probably 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 2.3d, the average egg density (kg.km^{-2}) per depth stratum was calculated, using the swept-area method (Sparre and Venema, 1998), and is given in Figure 2.3c. This provides

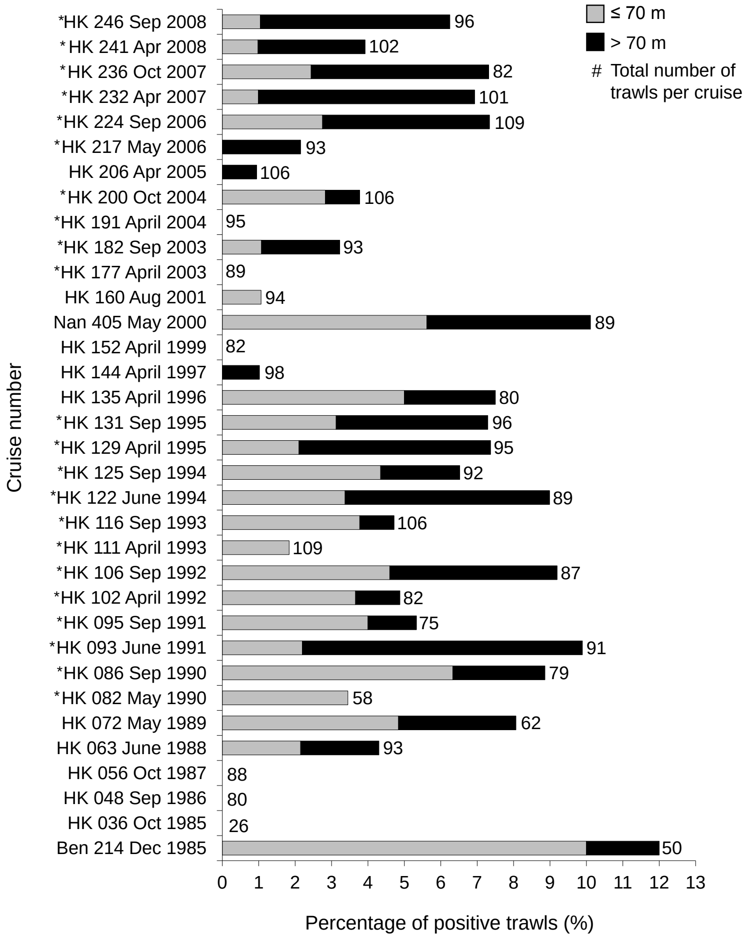

Figure 2.2: Schematic representation of the south coast 1985 to 2008 cruise data used in this study. Horizontal bars indicate the proportion of positive trawls at depths shallower ≤70 m (grey shading) and >70 m (black shading). The total number of trawls per survey is given at the end of each bar.

Table 2.1: Seasonal percentage of positive shallow (≤70 m) and deep (> 70 m) 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%

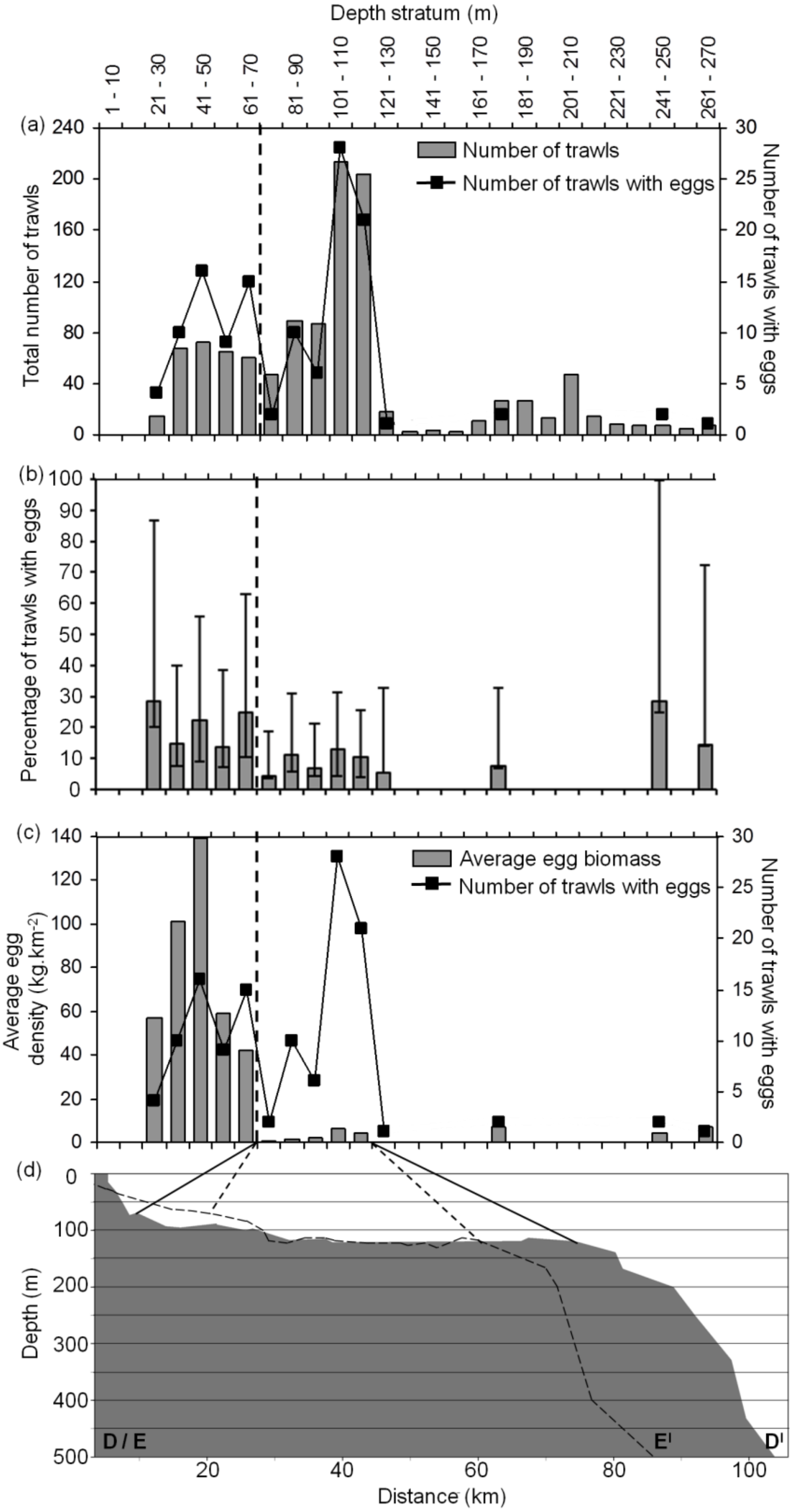

Figure 2.3: Distribution of positive trawls (squid eggs) with depth on the Agulhas Bank (a) Total number of trawls and the number of positive trawls per depth stratum. (b) Percentage of positive trawls per depth stratum with 95% confidence limits. (c) The average egg density and the number of positive trawls per depth stratum. Note: Data includes only those 5' x 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 2.1c. Notice 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.

another, possibly more relevant, view of the importance of the different depth strata as spawning grounds. The difference between the inshore average egg density 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, deep spawning is seen to be much less with the highest egg density 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 2.3a 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 m and 71–130 m strata were calculated. As detailed in Table 2.2, 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 2.1c. Spawning west of this appears to be less consistent and including the large area on the outer Central Agulhas Bank, where no eggs were found, would have provided an unrealistic estimate of egg density.

Table 2.2: Estimated chokka egg biomass for the inshore and deep spawning grounds. *Note: $*\sum d$ is the sum of egg densities, as determined by each trawl, in the relevant depth range.

	20–70 m	71–130 m
$*\sum d$	24 092 kg.km^{-2}	2 543 kg.km^{-2}
n_i	254	604
$\bar{d}_i$	94.85 kg.km^{-2}	4.21 kg.km^{-2}
A_i	3 641 km^{2}	17 490 km^{2}
B_i	345 386 kg	73 638 kg
B	419024 kg	
P_i	82%	18%

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 2.1b) 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 2.3b and c, spawning intensity markedly decreases at a depth of 70 m, suggesting delineation between the inshore and deep 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. Spawning on the mid-shelf 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.

Study limitations

When considering these results, especially the egg biomass estimates, it is important to be mindful of a few constraints inherent in the methods 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 2.3a, where trawl effort is greater in the 31–120 m depth range than in areas >121 m. In these deeper areas, rocky 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 and Smale, 1993; Sauer, 1995b; Sauer *et al.*, 1992, 1993). 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.

In addition, 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. 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 2.1). Clearly, as indicated by the inshore fishing positions in Figure 1.1c, spawning does occur east of 27°E (Port Alfred), and, moreover, it is highly probable that deep 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, and 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 chokka squid spawning grounds, they also elicit several pertinent questions. The first of these is whether cross-shelf spawning is unique to this species. The occurrence of loliginid eggs beyond what was thought to be the depth limit for spawning is not unique to *L. reynaudi*. Eggs of *Doryteuthis gahi*, *D. opalescens* and *L. forbesi* have all been found outside of the previously recorded spawning depth range. The Patagonian squid *D. gahi*, which inhabits Falkland Islands waters, is a cold water inshore spawner, attaching egg masses to algal stipes at depths <20 m (Arkhipkin and Middleton, 2003; Arkhipkin *et al.*, 2000). In 2006, a *D. gahi* egg mass was retrieved from a bottom trawl at 68–71 m (Laptikhovsky, 2007). This egg mass was attached to an empty polychaete worm tube. The Market squid *D. opalescens* is known to migrate inshore (Monterey Bay, California) to spawn, mainly within the depth range of 20–60 m (Foote *et al.*, 2006). McInnis and Broenkow (1978) however, mentioned the occurrence of *D. opalescens* eggs, in this same area, from just below the intertidal zone to a depth limit of at least 180 m whilst commercial trawlers have reported large volumes of eggs caught at 720 m (Butler *et al.*, 1999). Similar to *L. reynaudi*, inshore *L. forbesi* spawning aggregations (in the Azores) are targeted by a hand-jigging fishery (Pham *et al.*, 2008). Contrary to other loliginid species however, *L. forbesi* deposits eggs on hard structures (Pham *et al.*, 2008). The eggs of this widely distributed species 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 Agean Sea (Salman and Laptikhovsky, 2002). The greatest depth at which loliginid eggs have been found to date is 720 (*D. opalescens*, Butler et al., 1999) and 740 m (*L. forbesi*, Salman and Laptikhovsky, 2002).

This is surprising as loliginid spawning behaviour (Downey *et al.*, 2010; Iwata *et al.*, 2008) as well as egg development (Arkhipkin and Middleton, 2003; McMahon and Summers, 1971; Oosthuizen *et al.*, 2002a, 2002b) has been shown to be greatly influenced by temperature. In terms of temperature, the shallow and deep spawning grounds differ considerably. Bottom temperatures on the inshore spawning grounds are highly variable, particularly during the summer months November–January, ranging between 8–24 °C (unpublished data). Averages of 15.4–17.5 °C are found, dependent on location along the south coast (unpublished data). In contrast, bottom temperatures on the mid-shelf (~100 m) vary between 9–14 °C (Oosthuizen and Roberts, 2009; Roberts and Sauer, 1994; Roberts, 2005) with an average of 10 °C (Oosthuizen and Roberts, 2009). How this impacts embryonic development has been a topic of considerable interest. Although earlier laboratory studies showed high percentages of abnormalities in embryos incubated at low temperatures (Augustyn, 1989; Oosthuizen *et al.*, 2002a, 2002b), a recent *in situ* experiment indicated this is not the case (Oosthuizen and Roberts, 2009). Squid eggs collected on the inshore spawning grounds, and incubated in egg cages deployed on the mid-shelf, resulted in embryonic abnormalities in only 0.45% of eggs.

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; Şen, 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 deep spawning occur at all? For *D. gahi*, Laptikhovsky (2007) suggested that the offshore 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 Ninõ* might have forced squid to spawn in deeper, cooler water.

Numerous studies have mentioned the possibility that deep spawning in chokka squid is forced by unfavourable conditions inshore. According to the literature, unfavourable conditions could result from dense turbidity events inshore (Roberts and Sauer, 1994), anthropogenic influences such as disturbance caused by fishing activity (Oosthuizen *et al.*, 2002a) and temperatures >21 °C (Augustyn and Roel, 1998). However, the high number of mature eggs in the oviducts of females on the deep spawning grounds indicates chokka squid can store mature eggs for prolonged periods and are not forced to empty their oviducts (Sauer *et al.*, 1999), suggesting a further element of choice available to female squid.

Observations of deep spawning for chokka squid are many both in spring and autumn. Instead of unfavourable conditions inshore forcing spawners into deeper water, 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.

Individual variability and the existence of alternative reproduction strategies have been confirmed for this species (Hanlon *et al.*, 2002; Shaw and Sauer, 2004). Deep spawning could indicate the existence of an additional reproductive tactic. Another theory, proposed by Oosthuizen and Roberts (2009), suggests deep spawning is an aspect of a diversified life cycle strategy that strengthens recruitment. Delayed hatching on the mid-shelf could provide for a longer period of hatchlings, and hence a greater chance to encounter a survival window of food and currents suitable for their survival (Roberts, 2005).

Implications and conclusions

The results of this study have further defined the south coast (22°45–27°'E) chokka squid spawning grounds. 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, calculated to contribute 18% to total squid egg biomass, may still enhance recruitment. There is a need to revise our current understanding of the chokka squid life cycle to include deep spawning. Specifically, the original (and later popular) hypothesis by Augustyn *et al.* (1992) that chokka squid spawn in warm, protected locations along the inshore regions of the Eastern Cape Coast do not reflect the complete picture. 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.

CHAPTER 3: The deep spawning environment: What makes it possible for squid to spawn on the mid-shelf?

Unpublished

Introduction

Loliginids typically spend much of their life-span dispersed over the continental shelf until migrating to specific inshore sites to spawn (Jackson and Pecl, 2003; Sauer *et al.*, 2000). This life-history trait has been observed for the South African chokka squid, *Loligo reynaudi*, and was discussed in Chapter 1. The periodic use of particular inshore spawning areas by loliginids suggests favoured environmental conditions and specific spawning habitat requirements. Loliginids generally spawn in temperatures greater than 11–14 °C (Boletzky, 1987), although the eggs of some species have been recorded at temperatures well below this limit (e.g. *L. gahi* eggs in 6.8–8.0 °C, Arkhipkin *et al.* (2000)). For *Doryteuthis opalescens*, it appears that temperature and substrate are stronger behavioural cues than depth to stimulate spawning (Zeidberg *et al.*, 2012). An investigation of bottom conditions on the Agulhas Bank, South Africa (Figure 1.2), showed both bottom temperature and bottom dissolved oxygen to be important environmental variables determining suitable chokka squid inshore spawning habitat (Roberts, 2005). The main chokka squid spawning grounds on the Eastern Agulhas Bank are positioned where bottom temperature and bottom dissolved oxygen are optimal for embryonic development (Roberts, 2005).

The importance of substrate type, as suggested for *D. opalescens* (Zeidberg *et al.*, 2012), is not surprising as the use of substratum for the attachment of egg pods, whether sand or hard substrate, is characteristic of neritic cephalopods (Boyle and Rodhouse, 2005). Like *D. opalescens* (McGowan, 1954), chokka squid deposit their eggs on sandy substrates. Eggs have been found attached to sand grains, low profile rocky reefs partially covered with sand and reef encrusting organisms such as seaweed or soft coral outcrops (Sauer and Smale, 1993; Sauer *et al.*, 1993). Substrate types that seem to be favoured however, are open sand areas or sandy areas within low relief (<1 m) rocky reefs (Sauer, 1995b; Sauer *et al.*, 1992). Egg cluster size is dependent on substratum type. Low relief reef areas usually consist of small, dispersed clusters or egg mops (usually attached to the seabed), and open sand areas have large central egg beds surrounded by smaller egg mops (Sauer, 1995a). Egg capsules are anchored by the formation of a cement-like block of sand around the egg stalk (Sauer *et al.*, 1992). Sauer *et al.* (1992) proposed a specific grain size might be favourable to form good anchoring for the eggs. A later study found sandy bottoms with a grain size within 125–250 µm to be preferred (Sauer *et al.*, 1993). It is evident that egg deposition can occur on a variety of substrates. The only substratum apparently unsuitable for egg deposition is fine mud (Roberts, 1998).

Surprisingly, despite specific requirements for spawning, the South African chokka squid spawn both in shallow coastal waters (≤70 m) and on the mid-shelf (71–130 m). Chapter 2 demonstrated that the inshore, shallow coastal areas (≤70 m) of the Eastern Agulhas Bank between Knysna and Port Alfred (Figure 1.2) form the epicentre of the spawning grounds. Although bottom temperatures here fluctuate between 8 and 24 °C, consistently low chokka squid catches outside of the temperature range 11–21 °C (Sauer *et al.*, 1991) likely denote a decrease in spawning activity at temperatures <11 and >21 °C. Bottom temperature on the deep spawning grounds ranges between 9–14 °C (Oosthuizen and Roberts, 2009; Roberts and Sauer, 1994; Roberts, 2005) with an average of 10 °C (Oosthuizen and Roberts, 2009). Although this is outside of the temperature range preferred for spawning, it has been suggested deep spawning could be forced by dense turbidity events inshore (Roberts and Sauer, 1994). But what makes the mid-shelf benthic habitat suitable for spawning and how do the deep spawning grounds differ from inshore habitats? Very little is known about the deep spawning habitat. To date, there is no record of chokka squid eggs occurring at depths > 70 m further west of 22°45' (offshore of Knysna area, Figure 2.1c). It therefore appears that the deep spawning grounds are geographically defined, possibly a result of specific habitat requirements.

Apart from unfavourable conditions inshore, it has also been suggested that deep spawning could be forced by disturbances caused by fishing activity on the inshore spawning grounds (Oosthuizen *et al.*, 2002a). Another potential disturbance causing the termination of spawning activity is predation. Predators respond to aggregated squid and actively prey on them (Smale *et al.*, 2001), resulting in the disruption of spawning activity from a few minutes up to almost an hour (Roberts, 1998; Smale *et al.*, 2001). Increased predation levels inshore could possibly also force squid into deeper water.

The main objective of this study was to provide a first description of the deep spawning environment. Due to limited ships time, survey efforts were focused on a demonstration area within the main chokka squid spawning grounds, namely St Francis Bay (Figure 1.2). St Francis Bay has been a focal point for squid research for over three decades, and is a commonly used squid spawning area. Aims included the mapping of bathymetry and benthic habitat of the deep spawning grounds and the identification of potential deep spawning habitat. A qualitative review of predation and fishing pressure across the two habitats is also presented. Differences in the physical environment across the inshore and offshore spawning habitats were investigated using cross-shelf and seasonal comparisons of environmental conditions. The offshore-inshore movement of chokka squid on the Eastern Agulhas Bank was also examined.

Materials and Methods

Bathymetry, substrate mapping and morphology of the St Francis Bay mid-shelf

Three benthic surveys were undertaken on the St Francis Bay mid-shelf in March 2011, July 2011 and November 2011. Sounding data, underwater video footage of the benthic habitat and CTD profile data were collected. Transects for the collection of sounding data were positioned 1 nautical mile apart (dotted lines in Figure 3.1), with survey efforts concentrated on the St Francis Bay mid-shelf (Figure 3.1). Due to collection of data at only one frequency, substrate hardness could not be determined. Sounding data were collected using the RS *Algoa* SIMRAD EK60 – 38 kHz transducer and processed using SONARDATA Echoview acoustic integration and analysis software. Inshore bathymetry and sounding data for areas not surveyed were extracted from digital ships navigation charts (source: South African Navy Hydrographic Office). Data were gridded using Kriging interpolation (Surfer 8, Golden Software) and the bathymetry plotted.

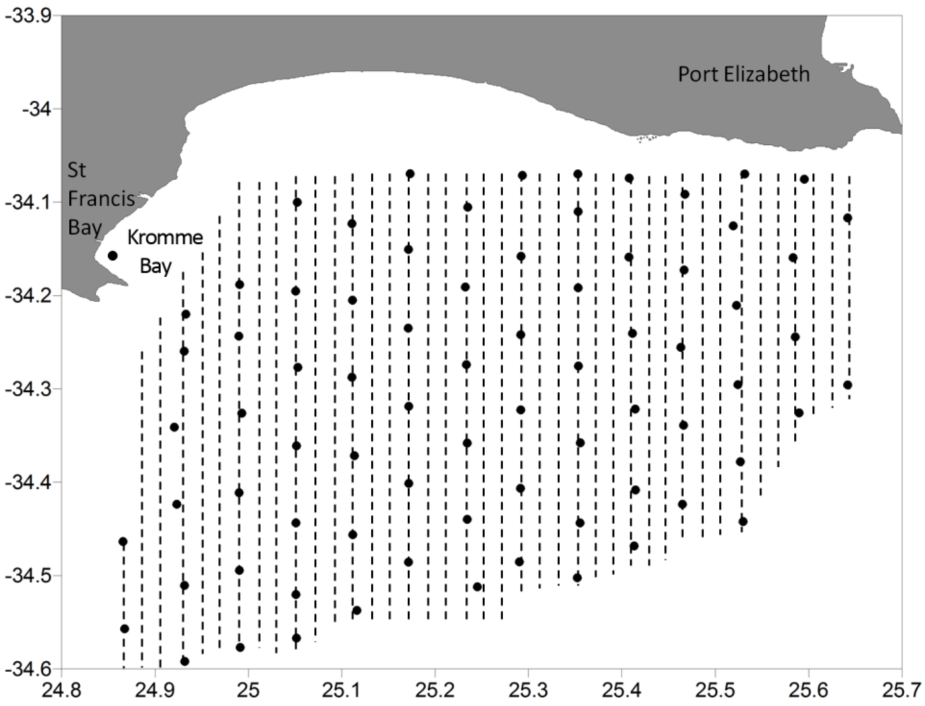

Figure 3.1: Survey design for the collection of echosounder data (dotted lines) and underwater video footage. Camera and CTD stations are indicated by dots.

The 75 stations at which underwater video footage were recorded are given in Figure 3.1. An autonomous deep sea recording system (Tritech SeaCorder), attached to a CTD frame, was deployed at each station. The video camera was deployed as close to the seabed as possible with bottom time for each deployment being 10 minutes. Video footage was analysed visually frame-by-frame and where possible substrate type categorized (sand, sand interspersed with rock or rocky reef). Poor visibility resulted in substrate type being classified for only 59 stations. This information was then used to map mid-shelf rocky reefs, areas of sand interspersed with rock and large sand areas. Similar areas were given the same numerical integer and these data interpolated using Nearest Neighbour spatial analysis techniques (ArcMap 10). Larger areas denoted by integer values only were plotted, excluding the majority of fractional values generated by this technique. This ensured the grouping and mapping of known substrate areas only. Detailed descriptions of benthic habitat type, epifauna and reef abundance are given. For comparative purposes, underwater video footage of frequently used inshore spawning sites (Figure 3.1) were collected in Kromme Bay.

Inshore and mid-shelf benthic communities

The Department of Agriculture, Forestry and Fisheries (DAFF) routinely conducts south coast demersal surveys to estimate the biomass of deep and shallow water hake, *Merluccius capensis* and *M. Paradoxus*. Information on trawl location and catch composition for the St Francis Bay area (1986–2011) was extracted from the DAFF south coast demersal survey database. These data were used to compare the chokka squid shallow and deep spawning habitats in terms of demersal assemblages and potential predation levels. Species habitat preference and depth distributions were collated from numerous publications (referenced in Appendix: Table A.2–Table A.4). Potential squid predators were identified from published diet studies and published observations of predation on the inshore chokka squid spawning grounds. Although the diet of all species listed was investigated, only those studies confirming predation on chokka squid are referenced in the Appendix: Table A.2–Table A.4.

Movement of chokka squid between shallow and deep spawning habitats

Filament tagging was used to confirm the movement of chokka squid between the mid-shelf and shallow waters of the south coast. The annual six week squid fishery closed season (October–November) was considered the ideal time to carry out the tagging study. This allowed the mixing of tagged squid back into the population by preventing their immediate capture by commercial fisherman. A commercial vessel, locally known as a chokka boat, was used to capture squid on the mid-shelf. Drift fishing using drogue anchors took place at night and strong lights were used to attract squid to the surface. Captured squid were immediately tagged with numbered double anchor filament tags and released. Although the goal was to tag 1 000 individuals, the low number of squid offshore during this time of year combined with rough sea conditions, limited the number that could be tagged within the short time period available. In 2010, 257 squid were caught and tagged south-east of Cape Recife (Figure 3.8). Bottom depth in this area was 107 m. In 2011, 149 individuals were caught and tagged off Kenton-on-Sea on the south-east coast (Figure 3.8). Bottom depth at this site was 80 m. A monetary reward was offered to commercial fishermen who captured tagged squid and submitted the filament tag, the animal, and position and date of capture.

Inshore and mid-shelf environment

Four sets of bottom temperature measurements, spanning the shallow and deep spawning grounds, were undertaken off Thys Bay (Figure 3.2). Temperature data were collected using *Starmon* mini underwater temperature recorders. The four moorings off Thys Bay were deployed over the same time period (18 September 2010–7 November 2011), enabling the cross-shelf comparison of bottom temperatures. A *Campbell Scientific* OBS (underwater turbidity recorder) was also deployed on the shallowest and deepest moorings. Turbidity was measured in nephlometric turbidity units (NTUs). Due to biofouling, severe storms, the failure of acoustic release systems and the subsequent loss of moorings, data for all moorings is only available for the first six months of deployment. This prevented the seasonal comparisons of cross-shelf environmental conditions.

An additional four sets of bottom temperature measurements off the Tsitsikamma coast (Figure 3.2) were extracted from historical datasets (unpublished and published: Oosthuizen and Roberts (2009); Roberts and van den Berg (2002)). Data for the three deeper moorings (85 m, 104 m and 205 m, Figure 3.2) were collected over different time periods. Data for the inshore 10 m mooring (Figure 3.2) was available for the better part of these time series. This environmental mooring forms part of a long term environmental monitoring network which commenced in 1991.

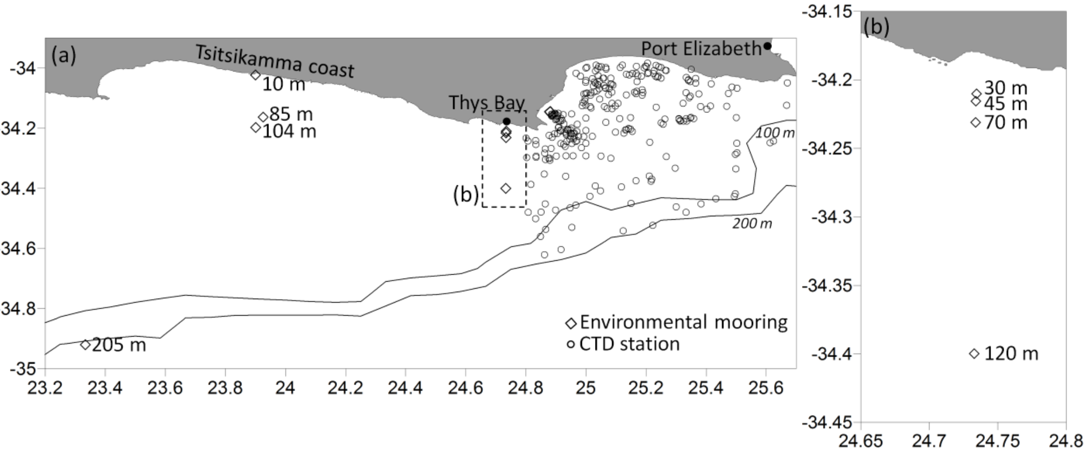

Figure 3.2: (a) A map showing the position of environmental moorings off the Tsitsikamma coast and Thys Bay, and CTD stations within St Francis Bay (from this study and SADCO database). (b) An expanded view of the environmental mooring positions off Thys Bay.

To investigate seasonal inshore and mid-shelf bottom environmental conditions in St Francis Bay, data for this area were obtained from the Southern African Data Centre for Oceanography (SADCO). CTD profile data collected during the three benthic surveys previously described (see Figure 3.1 for CTD stations) were added to this dataset. Temperature, salinity and oxygen profile data were recorded using Neil Brown Instrument Systems Mark 3 and 5 CTDs. Water samples were collected at standard depths and dissolved oxygen determined using the Winkler titration method (Strickland and Parsons, 1972). Stations were distributed fairly equally between the two areas of interest, with 150 CTD stations sampling inshore (≤70 m) and 121 the mid-shelf (71–130 m).

Results

Bathymetry, substrate and morphology of the St Francis Bay mid-shelf

Bathymetry of the St Francis Bay inshore (cartographic sources) and mid-shelf (this study) is shown in Figure 3.3. Due to differing bathymetric gradients, the St Francis Bay deep spawning ground (71–130 m) is three times larger than the inshore spawning ground (≤70 m), accounting for 75.7% of the total area between the coast and the 130 m contour. The largest area of the deep spawning grounds is within the depth range 111–130 m. The eastern portion of the mid-shelf area surveyed is shallower with the majority of this area being within the depth range 101–110 m.

Substrate category, determined in this study, and sediment texture from Wilkinson and Japp (2005) are presented in Figure 3.4. A large portion of the St Francis Bay mid-shelf consists of offshore reef, with the largest reef complexes found in the centre of the study area. Smaller and shallower reef complexes occur off Port Elizabeth. A considerable portion of the western sector of the mid-shelf is made up of large open areas of sand. In terms of sediment texture, the majority of the mid-shelf environment is classified as gravelly mud, the rest being mostly sand. Inshore, sediment texture has been classified as sand or sandy mud.

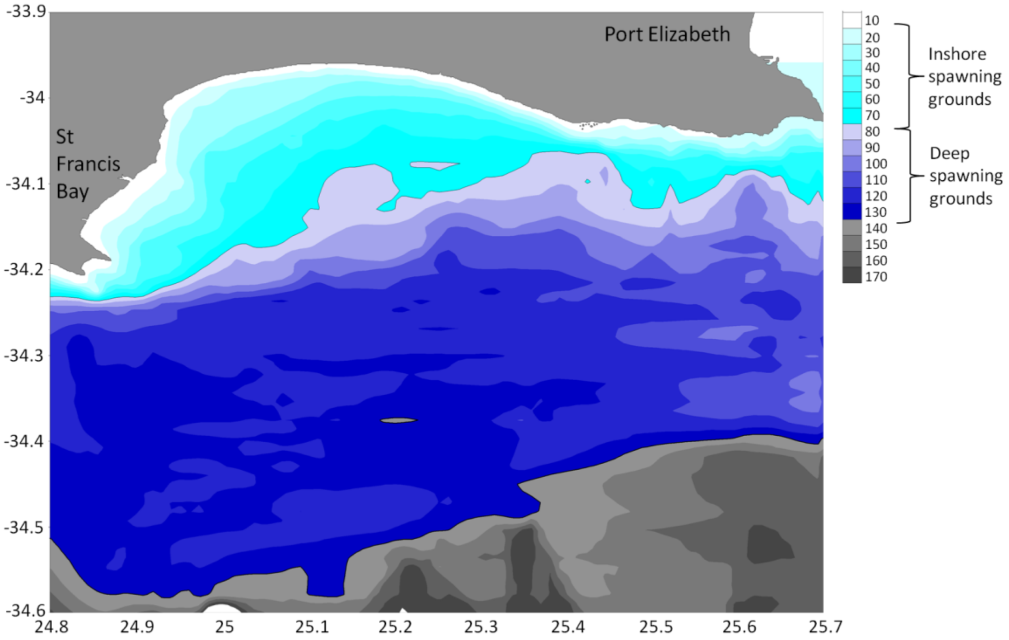

Figure 3.3: Bathymetry of the St Francis Bay mid-shelf generated using Kriging interpolation.

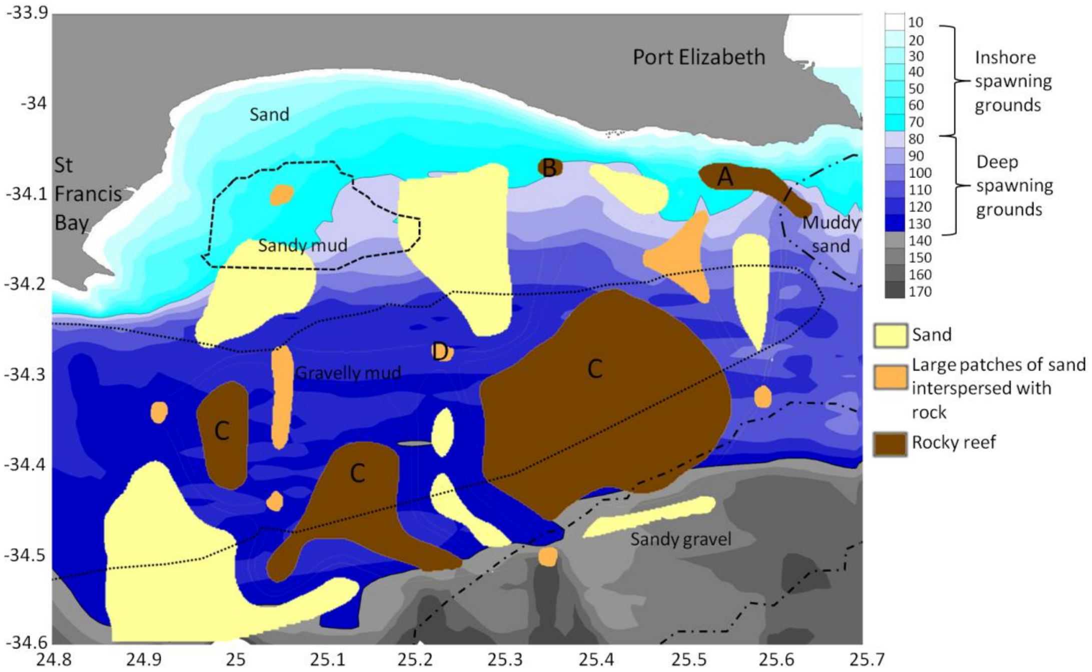

Figure 3.4: Bottom morphology of the St Francis Bay mid-shelf. Rocky reef complexes, large sand areas interspersed with rock and sand areas are indicated. Also shown is sediment texture (following Wilkinson and Japp (2005)).

Due to swell it was not always possible to maintain the underwater video camera within 1–2 m above the seabed. Consequently, the area captured in each video frame is not comparable. The drift of the ship with surface currents influenced the speed at which the camera moved over the bottom and hence the detail observed. Ships drift varied from 0.1–0.8 km, depending on sea conditions. This meant that data obtained from the video footage could not be treated statistically or used in comparative analysis. Nonetheless, this method has allowed the first broad categorizing and mapping of substrate type on the mid-shelf of St Francis Bay.

Video footage showed the inshore reef complex (A in Figure 3.4) to consist of high profile reef with many rocky overhangs (Figure 3.6a and b). The two shallowest stations (45 and 65 m) were densely populated (see Figure 3.5 for reef abundance) with porifera, bryozoa, hydroids, gorgonians, hard corals, false corals, sea pens and zoanthids (Figure 3.6a, b and d). A number of brittle stars and basket stars, (Figure 3.6c) were also observed. Abundance was sparse on the deepest reef forming this complex. Similarly, the rocky reef on the border of the shallow and deep spawning grounds (72 m, B in Figure 3.4) was also high profile reef with dense coverage (Figure 3.5) by noble corals, staghorn-like false corals, hydroids and anemones. The largest offshore rocky reef complexes in the centre of the mid-shelf (C in Figure 3.4) consisted of low to very high profile rock. Reef abundance varied from sparse to dense (Figure 3.5). It appears abundance was highest near reef fringes. Generally, larger and higher boulders and rocky outcrops were more densely populated with epifauna (Figure 3.6e). In a number of videos, unidentified fish were observed sheltering under crevices and rocky overhangs. Benthic invertebrates observed in the video footage included gorgonians, hydroids, porifera (Figure 3.6g), staghorn-like false corals, bryozoans, sea pens, tubular hydroids, lace bryozoans and what resembled lace corals. A large variety of sponges (porifera), i.e. encrusting sponges (purple, blue, red, orange), broad oval-shaped sponges, tree-like sponges and wide coral-like sponges, were noted (Figure 3.6). Other benthic invertebrates seen on these large reef complexes were unidentified starfish, raspberry stars (*Crossaster penicillatus*), long arm puffy stars (*Henricia abyssalis*), brittle stars (*Ophiura* spp.), basket stars (*Astrocladus euryale*), sheriff stars, false sheriff stars and urchins. South coast rock lobster (*Palinurus gilchristi*), one octopus and four fish species (one flatfish, horsefish and groups of panga and jacopever) were also seen on these offshore reefs.

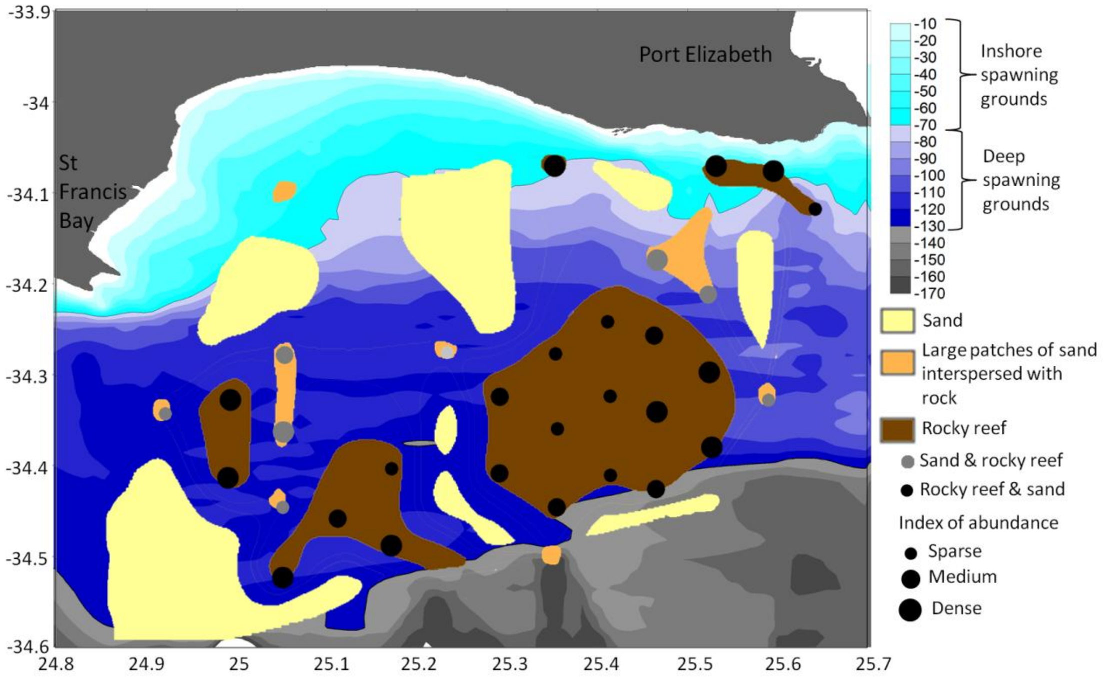

Figure 3.5: An index of reef abundance (sparse, medium, dense) of offshore rocky areas, superimposed on bottom morphology and bathymetry.

Rocky reefs with large open sandy areas were similar (in terms of epifauna) as the offshore reef complexes described above (Figure 3.6e–h and i–l). Abundance of benthic invertebrates varied from sparse to dense, again with the higher profile rock appearing to be more densely populated. Many urchins were seen on large sandy areas and at a single station (D in Figure 3.4), what resembled large pencil worms, were observed on the sand. The camera was too far from the bottom to examine these invertebrates in detail however.

Sandy areas were by comparison far less diverse than the reef complexes (Figure 3.6m–p). Invertebrates seen on the sand were yellow sea cucumbers (Figure 3.6o), urchins (Figure 3.6p), unidentified starfish, raspberry stars, red sheriff stars and radial sea pens. The only fish observed were two flatfish (on the sand) and what appeared to be spiny dogfish *Squalous megalops*, resting on the substrate. A non-exhaustive list of benthic invertebrates observed on the mid-shelf, the number of stations at which observed and the depth range of occurrence is provided in Appendix, Table A.1.

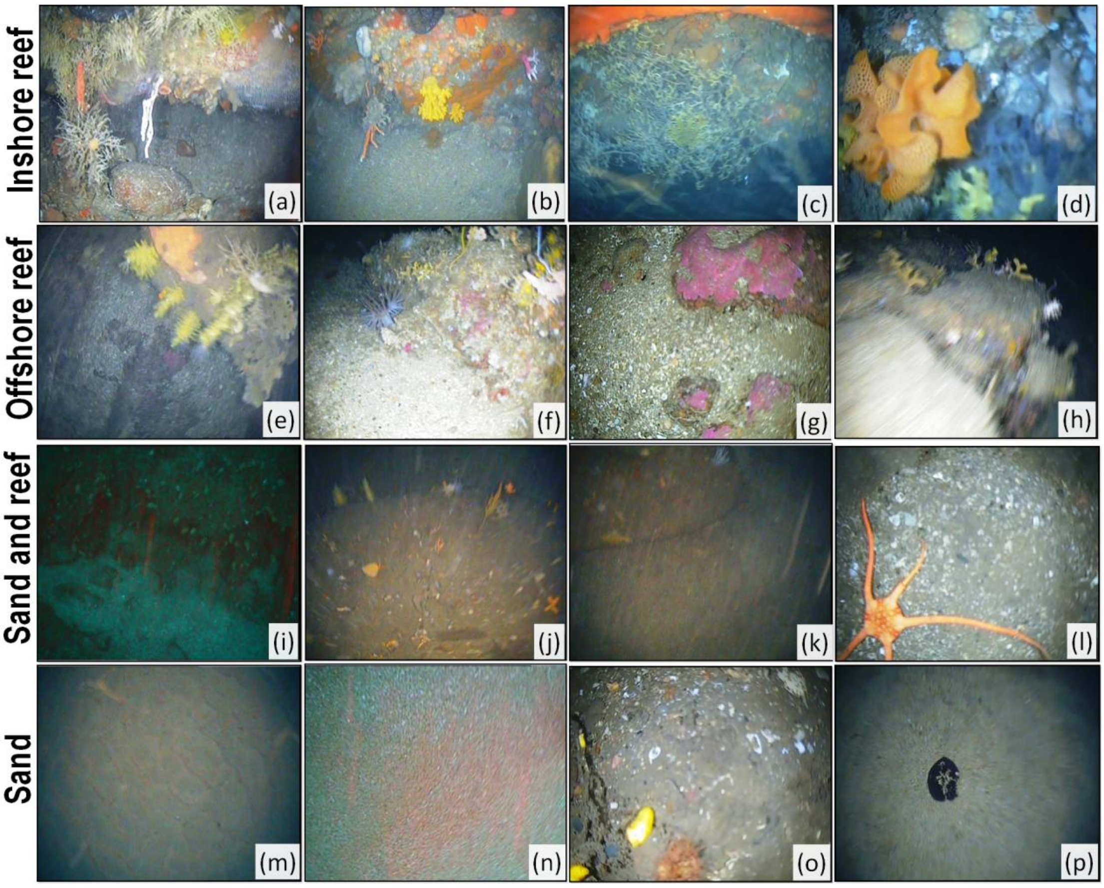

Figure 3.6: Still images captured from underwater video footage showing inshore reef, offshore rocky reefs, sandy areas interspersed with reef and sandy bottoms. Although not quantifiable, the variation in sediment texture between stations is apparent. INSHORE REEF: Images (a) and (b) show the high abundance of epifauna and high profile rocky outcrops. Also apparent are overhangs and crevices which fish use to shelter. Image (c) depicts a large basket star, and (d) a lace bryozoan. OFFSHORE REEF: Very high profile reef with dense coverage by epifauna is shown in image (e). Images (f) and (g) depict lower profile reef with coverage by epifauna and encrusting sponges. Medium coverage by epifauna is shown in image (h). SAND AND REEF: Image (i) shows medium profile reef on the edge of an open sandy area. Numerous small boulders are evident. Image (j) shows the sparse coverage of a rocky outcrop by epifauna. Image (k) again shows reef on the edge of a large open sandy area. Sandy areas at this station were not interspersed with smaller boulders. A brittle star is shown in image (l). SAND: Large open sandy areas, from which benthic invertebrates were absent, are shown in images (m) and (n). Image (m) is from the south-western most region of the St Francis Bay mid-shelf. Image (n) is from a known chokka squid spawning site inshore. A yellow sea cucumber and urchin are shown in images (o) and (p), respectively.

Inshore and mid-shelf benthic communities

A composite of DAFF demersal trawl survey effort (1986–2011) in St Francis Bay is given in Figure 3.7. In total 150 trawls have been undertaken in the bay, 98 of which sampled the inshore areas (24–70 m) and 52 the offshore areas (71–130 m). Due to untrawlable hard ground on the mid-shelf, a much larger proportion of the inshore spawning area has been sampled. Species caught in demersal survey trawls are given in the Appendix: Table A.2–Table A.4. Also provided are the number of trawls species were caught in, the depth range of catch, habitat preference and the general depth range or limit of species. Known chokka squid predators are indicated in the species column by an asterisk (*).

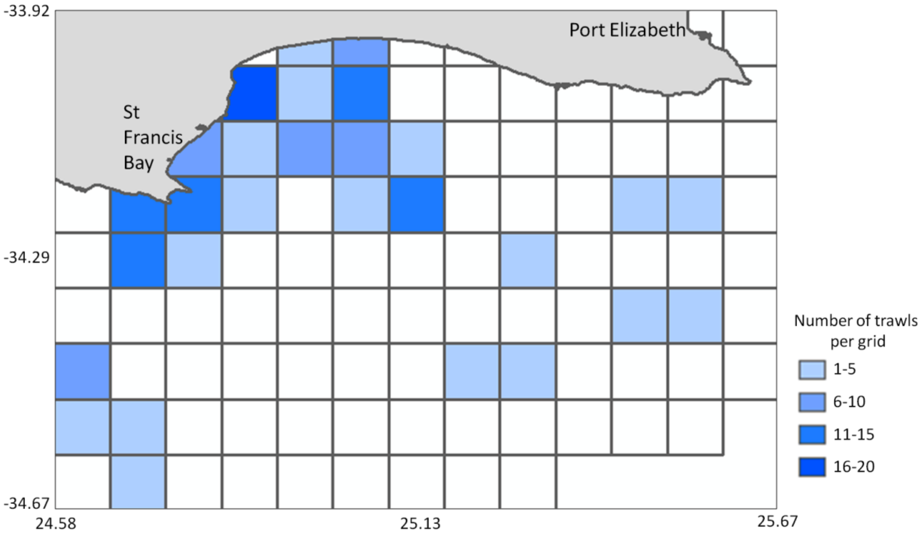

Figure 3.7: A composite of data (1986–2011) indicating DAFF demersal survey trawl effort in St Francis Bay. A total of 150 trawls were undertaken, 98 sampling the inshore spawning grounds (24–70 m) and 52 sampling the deep spawning grounds (71–130 m).

Table 3.1 shows chokka squid predator species occurring on the shallow and deep spawning grounds. Predation on chokka squid was confirmed from published diet studies and from published observations of predation on spawning squid. These studies have been referenced in Appendix: Table A.2–Table A.4. Also shown is the percentage of occurrence in inshore and offshore trawls.

Immediately evident is the higher number of predator species inshore. A total of 26 species occurred in both areas, with an additional nine species found inshore. Common to both spawning areas was the high incidence in trawls of spiny dogfish *Squalous megalops* (97% inshore trawls and 98% offshore trawls) and lesser gurnard *Chelidonichthys queketti* (96% inshore trawls and 100% offshore trawls). Other predator species most often caught inshore were the Cape gurnard *C. capensis* (94%) and the white barbel *Galeichthys feliceps* (87%).

Table 3.1: Known chokka squid, *Loligo reynaudi*, predator species occurring on the inshore (≤70 m) and deep (71–130 m) spawning grounds. The percentage of occurrence in inshore (n=98) and offshore (n=52) trawls is given. Also shown are the lower (L) and upper (U) 95% confidence limits (CL), and the number of trawls predator species occurred in (n). Diet and predator studies from which information was collated are referenced in the Appendix: Table A.2–Table A.4.

Species	**Inshore (LCL%, UCL%, n)**		**Deep Spawning ground (LCL%, UCL%, n)**	
Argyrosomus inodorus & japonicus (Kob)	50 %	(39.7, 60.3, 49)	6 %	(1.2, 15.9, 3)
Argyrozona argyrozona (Carpenter Seabream)	23 %	(15.5, 33.1, 23)	10 %	(3.2, 21, 5)
Carcharhinus brachyurus (Bronze whaler)	12 %	(6.5, 20.4, 12)		
Cheimerius nufar (Santer)	4 %	(1.1, 10.1, 4)		
Chelidonichthys capensis (Cape Gurnard)	94 %	(87.1, 97.7, 92)	58 %	(43.2, 71.3, 30)
Chelidonichthys queketti (Lesser Gurnard)	96 %	(89.9, 98.9, 94)	100 %	(93.2, 100, 52)
Chirodactylus grandis (Bank steenbras)	3 %	(0.6, 8.7, 3)	4 %	(0.5, 13.2, 2)
Chrysoblephus laticeps (Red roman)	2 %	(0.2, 7.2, 2)		
Dasyatis brevicaudata (Shorttail stingray)	2 %	(0.2, 7.2, 2)	2 %	(0, 10.3, 1)
Galeichthys feliceps (White barbel)	87 %	(78.4, 92.7, 85)	4 %	(0.5, 13.2, 2)
Galeorhinus galeus (Soupfin shark)	27 %	(18.1, 36.4, 26)	8 %	(2.1, 18.5, 4)
Genypterus capensis (Kingklip)	21 %	(13.8, 30.9, 21)	60 %	(45.1, 73, 31)
Gymnura natalensis (Diamond ray)	20 %	(12.9, 29.7, 20)		
Halaelurus natalensis (Tiger catshark)	66 %	(56.1, 75.6, 65)	6 %	(1.2, 15.9, 3)
Haploblepharus edwardsii (Puffadder shyshark)	29 %	(19.9, 38.6, 28)	19 %	(9.6, 32.5, 10)
Helicolenus dactylopterus (Jacopever)	5 %	(1.7, 11.5, 5)	75 %	(61.1, 86, 39)
Lepidopus caudatus (Buttersnoek)	2 %	(0.2, 7.2, 2)	25 %	(14, 38.9, 13)
Lophius vomerinus (Monkfish)	1 %	(0, 5.6, 1)	21 %	(11.1, 34.7, 11)
Merluccius capensis (Shallow water Cape Hake)	80 %	(70.3, 87.1, 78)	100 %	(93.2, 100, 52)
Merluccius paradoxus (Deep water Cape Hake)			8 %	(2.1, 18.5, 4)
Mustelus mustelus (Common smooth-hound)	78 %	(68, 85.4, 76)	12 %	(4.4, 23.4, 6)
Octopus vulgaris (Common octopus)	2 %	(0.2, 7.2, 2)	4 %	(0.5, 13.2, 2)
Pagellus natalensis (Red tjortjor)	66 %	(56.1, 75.6, 65)		
Pomatomus saltatrix (Elf)	40 %	(30, 50.2, 39)	4 %	(0.5, 13.2, 2)
Poroderma africanum (Pyjama shark)	9 %	(4.3, 16.7, 9)		
Poroderma pantherinum (Leopard catshark)	7 %	(2.9, 14.2, 7)		
Pterogymnus laniarius (Panga)	62 %	(51.9, 71.8, 61)	98 %	(89.7, 100, 51)
Raja alba (Spearnose skate)	64 %	(54, 73.7, 63)	8 %	(2.1, 18.5, 4)
Raja pullopunctata (Slime skate)	8 %	(3.6, 15.5, 8)	31 %	(18.7, 45.1, 16)
Raja wallacei (Yellowspot skate)	6 %	(2.3, 12.9, 6)	38 %	(25.3, 53, 20)
Scomber japonicus (Chub mackerel)	47 %	(36.8, 57.3, 46)	27 %	(15.6, 41, 14)
Sphyrna zygaena (Smooth hammerhead)	27 %	(18.1, 36.4, 26)		
Spondyliosoma emarginatum (Steentjie)	36 %	(26.3, 46, 35)		
Squalus megalops (Spiny dogfish)	97 %	(91.3, 99.4, 95)	98 %	(89.7, 100, 51)
Thyrsites atun (Snoek)	2 %	(0.2, 7.2, 2)	4 %	(0.5, 13.2, 2)
Zeus capensis (Cape dory)	52 %	(41.7, 62.2, 51)	87 %	(74.2, 94.4, 45)

These species were recorded in only 58% and 4%, respectively, of offshore trawls. Apart from the high incidence of spiny dogfish and lesser gurnard in trawls on the deep spawning areas, panga *Pterogymnus laniarius* and Cape dory *Zeus capensis* were also present in the majority of catches (98% and 87% of trawls, respectively). Inshore these species were only present in 62% (panga) and 52% (Cape dory) of trawls. Five chondrichthyan predator species were caught only on the inshore spawning grounds and nine in both areas (including the already mentioned spiny dogfish). Species caught only inshore were the smooth hammerhead *Sphyrna zygaena*, diamond ray *Gymnura natalensis*, bronze whaler

Carcharhinus brachyurus, pyjama shark *Poroderma africanum* and leopard catshark *P. pantherinum*. Of species common to both spawning habitats, the common smooth-hound *Mustelus mustelus*, tiger catshark *Halaelurus natalensis*, spearnose skate *Raja alba*, puffadder shyshark *Haploblepharus edwardsii*, and the soupfin shark *Galeorhinus galeus* were most often caught inshore. Those with the greatest number of catches offshore were the yellowspot (*R. wallacei*) and slime (*R. pullopunctata*) skates. The shorttail stingray *Dasyatis brevicaudata* was present in an equal number of inshore and offshore trawls. In terms of teleosts known to prey on chokka squid, inshore species recorded included the red tjor tjor *Pagellus natalensis*, steentjie *Spondyliosoma emarginatum*, santer *Cheimerius nufar* and red roman *Chrysoblephus laticeps*. As for chondrichthyans, although a number of teleost species were common to both spawning grounds, their abundance (as determined by presence in trawl catch), differed between the two areas. Kob (*Argyrosomus* spp.), chub mackerel *Scomber japonicus*, elf *Pomatomus saltatrix* and the carpenter seabream *Argyrozona argyrozona* were caught in a higher percentage of inshore trawls, whereas jacopever *Helicolenus dactylopterus*, kingklip *Genypterus capensis*, buttersnoek *Lepidopus caudatus* and monkfish *Lophius vomerinus* were caught mainly offshore. Bank steenbras *Chirodactylus grandis*, snoek *Thyrsites atun* and the common octopus *Octopus vulgaris* were caught in a very small percentage of trawls both inshore and offshore. *Merluccius paradoxus*, also a known chokka squid predator, was only caught offshore.

Offshore-onshore movement of chokka squid

Of the 406 animals tagged during the 2010 and 2011 squid fishery closed seasons, only 11 individuals were recaptured. Three tagged animals were caught following the 2010 study, and eight following the 2011 study. Tag returns for the two experiments were 1.2 and 5.4% respectively. All individuals tagged on the mid-shelf were recaptured on the inshore spawning grounds 8–22 days after tagging. Three animals tagged on the deep spawning grounds south-east of Cape Recife moved west and were caught inshore off Oyster Bay, The Wreck and Huisklip (Figure 3.8). These animals moved a distance of 113, 124 and 134 km respectively. Animals tagged on the south-east coast off Kenton-on-Sea remained on this part of the coast, moving inshore onto the spawning grounds where they were recaptured. One individual moved west and was caught 34.8 km from the tagging site, six moved directly inshore (8.93–11.68 km from tagging site) and one moved further east (22.61 km from tagging site) (Figure 3.8). It should be noted that although six individuals moved directly inshore of the 2011 tagging site, two animals were caught on the same day at the same location, hence only five sites are shown. The distance covered by individuals was not related to time at large, and the greatest distances travelled in both years occurred within 12–15 days after tagging. Of the returned tags, eight fishermen also returned the tagged animal. All females (n=5) were sexually mature (Stage V: see Lipinski and Underhill (1995) for descriptions of *L. reynaudi* sexual maturity stages) and fertilised. Female mantle length varied from 182–204 mm. Of the males (n=3), only one individual was sexually mature (Stage V) with the remaining two being Stage IV males. Male mantle length varied from 189–285 mm.

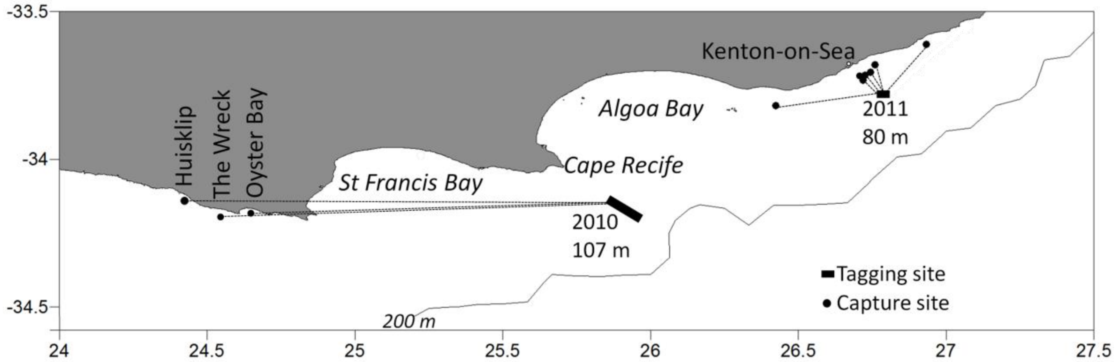

Figure 3.8: Tagging and recapture sites for two mid-shelf tagging experiments undertaken on the Eastern Agulhas Bank.

Inshore and mid-shelf environment

Mid-shelf average daily bottom temperature data for the 84 and 104 m moorings depicted in Figure 3.9 is taken from Oosthuizen and Roberts (2009). As described by these authors the time-series shows two trends: a long, possibly seasonal, trend of warming and cooling of the bottom layer over many months (dotted lines); and distinct warm (shaded numbers 1–7) and cool (shaded numbers 8 and 9) events which occurred over several days. At the shallower 84 m mooring, temperatures rose from ~10 to 15–17 °C (events 1–3), and to 11.9–13.4 °C (events 4–7) at the 104 m mooring. More pronounced and longer lasting warm events were evident at the shallower mooring (84 m) (Oosthuizen and Roberts, 2009). A comparison of bottom temperature at the 10 and 104 m mooring during mid-shelf warming events showed inshore to be warmer by 1.6–4.7 °C. Interestingly, during event 6, bottom temperatures at the shallowest mooring dropped to ~9 °C. Temperatures on the mid-shelf were 2 °C warmer. Warm and cool events were also recorded at the 205 m mooring. Warming of the bottom layer this far offshore however, was less extreme and maximum temperature reached was 11.3 °C. Average bottom temperature at this depth was 9.3 °C.

Six months of cross-shelf average daily bottom temperatures (30–120 m) off Thys Bay are given in Figure 3.10a–d. Inshore temperatures (30 and 45 m) fluctuated sharply during the months September–November with minimums of ~8.5 °C and maximums >18 °C at both sites. From December towards the end of March bottom temperature was more stable varying between 8.5–13.2 °C at 30 m, and 8.0–12.6 °C at 45 m. Average bottom temperatures at these sites were 12.1 and 11.1 °C respectively. In contrast, mid-shelf bottom temperatures were more stable varying between 8–14 °C at 70 m, and 8–15 °C at 120 m. Average bottom temperature at both mid-shelf sites was 10.5 °C. Mid-shelf warm events were also evident off Thys Bay, i.e. events 1–4 at 70 m, and event 5 at 120 m (Figure 3.10c and d). During warm events 1–4 (70 m), bottom temperatures increased to 12.5–14.0 °C. During the major warm event at 120 m, bottom temperature increased to a maximum of 15 °C. This latter event was initially associated with a major increase in turbidity to ~80 NTUs. In this case, bottom temperature rose steadily for 36 hours, from 9.6 °C to 13.6 °C, before turbidity levels increased and remained high for 10 hours. After a slight decrease, temperature then increased to 15 °C. Bottom temperature remained >13 °C for nine days during event 5.

During the first six months of deployment, turbidity levels remained low inshore (30 m) with two minor events in which levels reached 12–20 NTUs. In contrast, turbidity levels were higher and more variable during the following August–October period. While this time series of temperature is not as long as that collected on the Tsitsikamma coast (Figure 3.9), a seasonal warming and cooling trend over the months is evident. This is most marked in the mid-shelf mooring data. Inshore areas are subject to frequent and large-scale upwelling events making the analysis of seasonal warming and cooling more difficult.

A comparison of bottom temperature from the deep and shallow moorings shows, at times, temperatures to be quite similar, varying by only 1–2 °C (Figure 3.10e–g). As expected, these temperature differences increase with depth. Unexpected though was the number of times that bottom temperature at 120 m was warmer than inshore (events 1–7, Figure 3.10g). This occurred over time-spans of hours to days, e.g. during event 5, bottom temperature at 120 m was consistently warmer (average 13.9 °C) for 8.4 days.

The frequency of temperatures (0.5 °C categories) recorded at each station for the first six months of deployment are shown in Figure 3.10h. Interestingly, the summary of these data

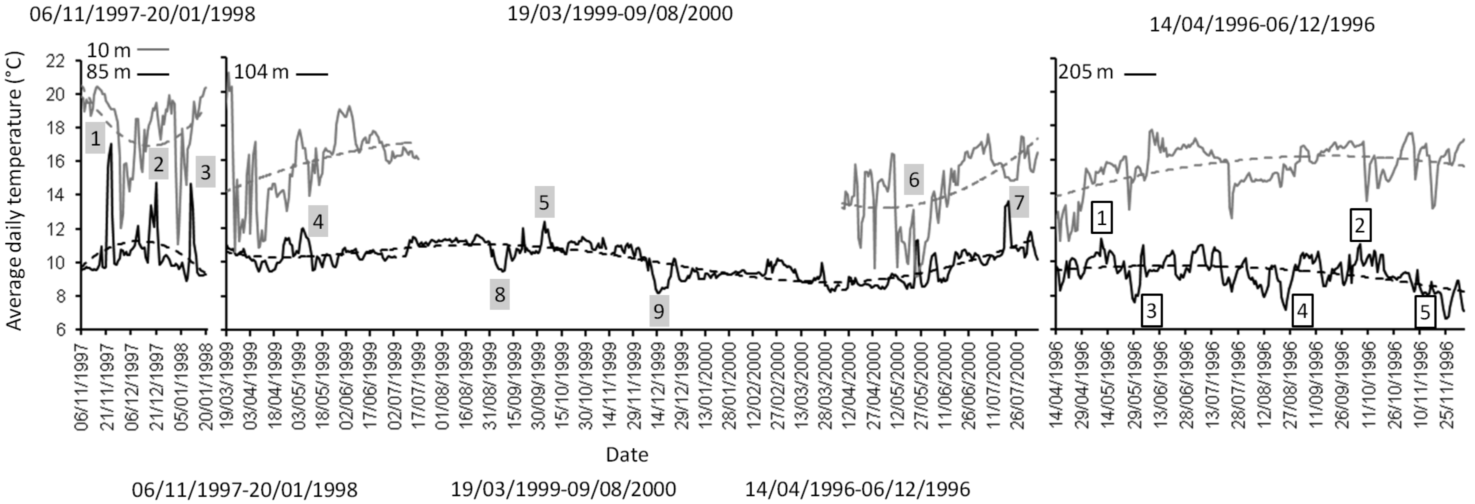

Figure 3.9: Average daily bottom temperature at depths 10 m, 85 m, 104 m and 205 m off the Tsitsikamma coast. Data for the 85 m and 104 m mooring have been published and discussed in Oosthuizen and Roberts (2009). The 10 m mooring forms part of a long-term, ongoing, environmental monitoring network commenced in 1991. The 205 m mooring was deployed along with current meters in a study known as "Project L". See Roberts and van den Berg (2002). Moorings positions are shown in Figure 3.2. Warm and cool events, as described in the text, have been numbered.

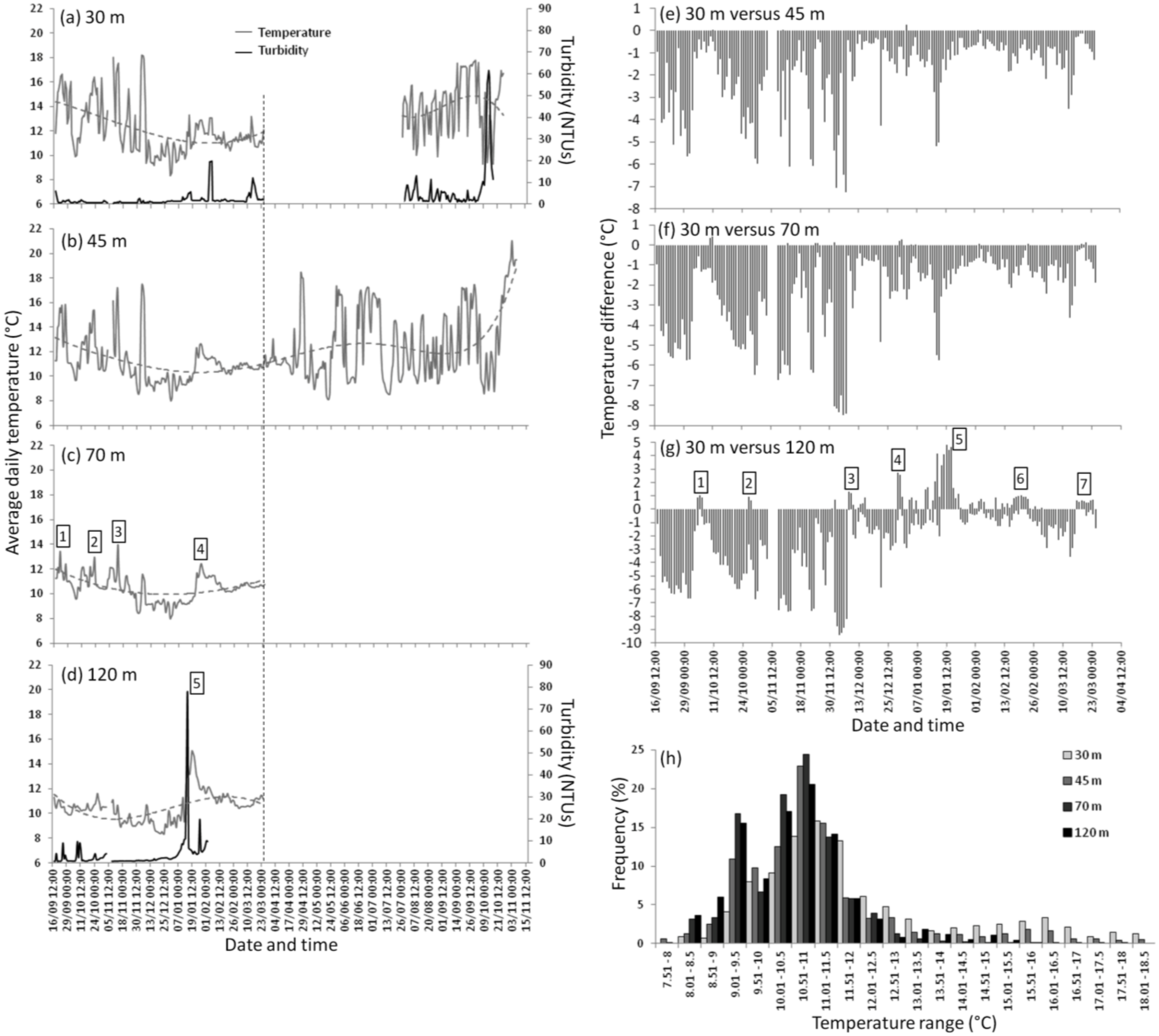

Figure 3.10: (a–d) Average daily bottom temperature off Thys Bay during the period 18 September 2010 to 7 November 2011. Data for all four moorings (30 m, 45 m, 70 m and 120 m) is only available for the first 6 months. Also shown are tubidity levels recorded at the shallowest (30 m) and deepest (120 m) moorings. Plots e–g show hourly bottom temperature difference between the shallowest mooring (30 m) and three deeper moorings (45 m, 70 m, 120 m) for the first six months of deployment. Plot h shows the frequency of temperatures (0.5 °C categories) recorded at each station for the first six months of deployment. See Figure 3.2a and b for mooring positions. Warm events, as described in the text, have been numbered.

(Table 3.2), highlights the comparability of frequencies of occurrence within the temperature range 11.01–13 °C for the 45, 70 and 120 m moorings.

Average seasonal bottom temperature and oxygen, minimums and maximums for the St Francis Bay inshore and mid-shelf are shown in Figure 3.11. Average bottom temperature appears to be warmer in autumn-winter on both spawning areas. Inshore during spring-summer the temperature range is larger and a maximum of ~4 °C warmer than the mid-shelf. During autumn-winter, maximum temperatures recorded on the mid-shelf are only ~2 °C cooler than inshore. This is a result of the much larger temperature range found offshore during autumn-winter (~9–17 °C). Bottom dissolved oxygen data indicates minimum levels in St Francis Bay are consistently >3 mg.l^{-1}. Despite the highest average bottom dissolved oxygen occurring on the inshore spawning grounds, average mid-shelf dissolved oxygen levels are also higher (>4 mg.l^{-1}).

Table 3.2: A summary of comparative temperature frequencies (Figure 3.10h) recorded at each station off Thys Bay. Similarities in the frequency of occurrence of temperatures 11.01–13 (°C) at depths 45, 70 and 120 m are evident (shaded area).

Temperature (°C)	30 m	45 m	70 m	120 m
≤10	13.7%	25.1026	30.14136	33.51573
10.01–11	23%	35.40812	43.57045	37.5057
11.01–12	29%	21.36343	19.51664	19.83584
12.01–13	10.8%	6.543548	5.221158	4.012768
>13	23.6%	11.58231	1.550388	5.129959

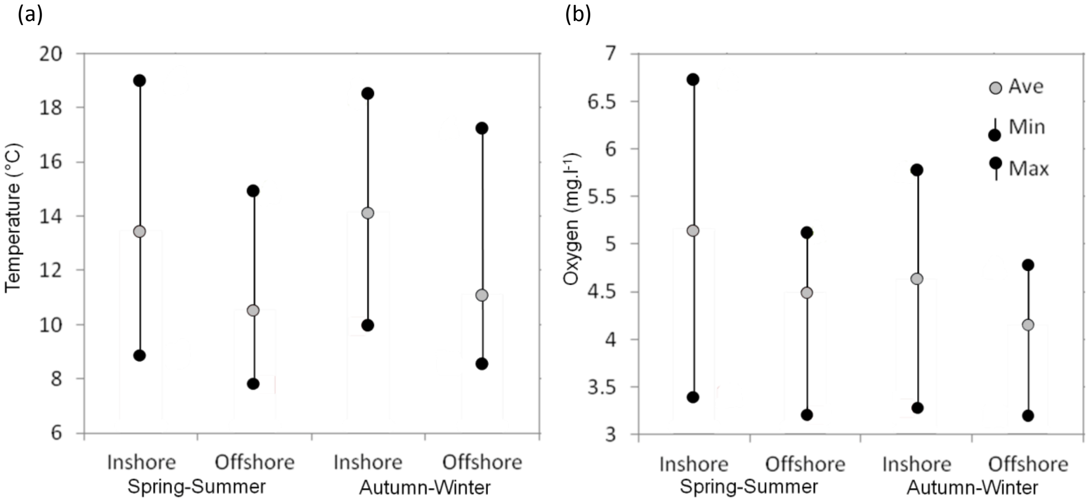

Figure 3.11: Seasonal differences between the *Loligo reynaudi* inshore and deep spawning grounds. (a) Average bottom temperature. (b) Average bottom oxygen. Data have been sourced from the SADCO database and this study. See Figure 3.2a for station positions.

Discussion

Bathymetry, substrate type and morphology of the deep spawning grounds

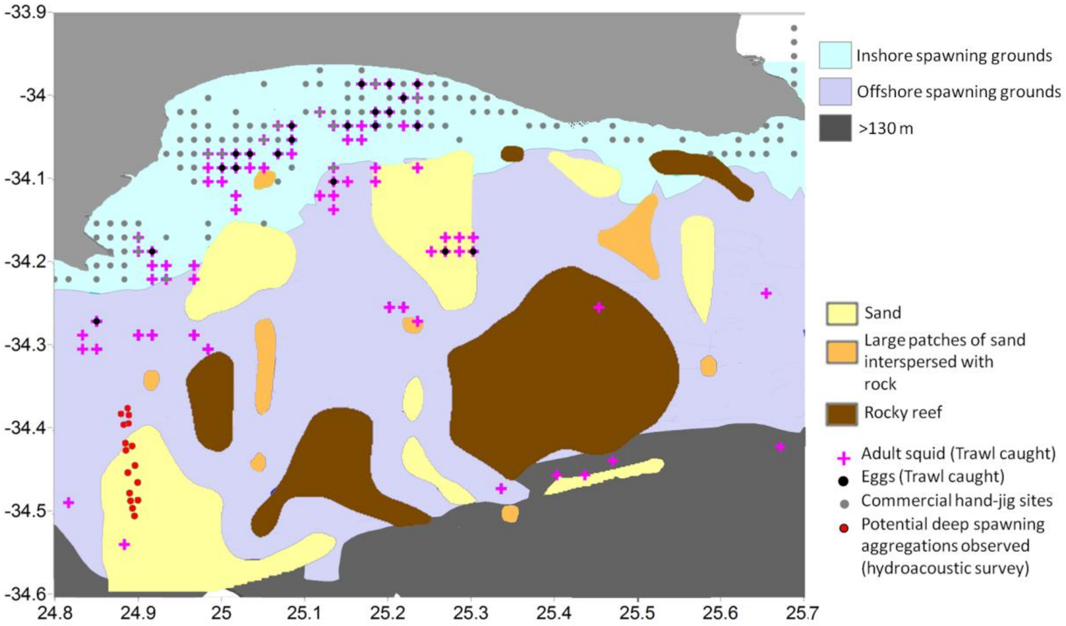

Figure 3.12: The location of trawl caught adult squid, trawl caught eggs, hydroacoustic observations of "super" spawning aggregations (Roberts *et al.*, 2002) and known inshore spawning sites (commercial jigging sites) overlaid on bathymetry and substrate type for the St Francis Bay area.

The St Francis Bay mid-shelf exhibits a great deal of variability in terms of sediment texture. According to Wilkinson and Japp (2005), this region consists of sand, gravelly mud, sandy mud, muddy sand and sandy gravel sediments (Figure 3.4). Although not classified, variation in sediment colour, grain size (when the camera came to rest on the bottom) and amount of course shelly substrate was observed in the video footage (Figure 3.6). Mid-shelf substrate type can be broadly categorized as sand, rocky reef interspersed with large open sandy areas or primarily rocky reef. This study showed approximately 22% of the mid-shelf was comprised of offshore reef habitat. Within these reef complexes much variation in reef profile (low to very high) and reef epifaunal abundance was observed. Generally, rock coverage by epifauna was most dense on the higher profile rocky outcrops and on the reef fringes. The calculated proportion of rocky reef habitat is most likely an underestimation, as poor visibility at the shallower stations prevented substrate classification. The remainder of the stations surveyed consisted of sand or rocky reef habitat with large open sandy areas. Based on known substrate types used for egg deposition inshore, these latter areas can be considered suitable chokka squid spawning habitat. The area most similar in terms of substrate type and morphology to the inshore spawning grounds was the large sand complex in the southwestern most region of the mid-shelf (Figure 3.12 and Figure 3.6m and n).

Figure 3.12 shows commercial squid fishing locations, positions at which adult squid and eggs have been caught in research trawls and sites at which deep spawning aggregations were acoustically observed (Roberts *et al.*, 2002). Dive surveys have shown that most chokka squid are caught over egg beds (Sauer *et al.*, 1991) and the commercial jigging locations are in all probability indicative of spawning sites. The large number of inshore sites highlights the optimal spawning habitat within St Francis Bay. Although inadequate visibility often prevented the categorizing of substrate type, data shows the mid-shelf eggs to be on sand (Figure 3.12). Also interesting are the sites at which deep spawning “super” aggregations were acoustically observed (Roberts *et al.*, 2002). The majority of these observations are over a large sand area similar to the inshore spawning habitat (Figure 3.12 and Figure 3.6m and n). A crude estimate of mid-shelf spawning habitat was made based on the information in Figure 3.12 and DAFF research survey ground categories (Figure 2.1: Trawlable, indicating sand or low profile reef; and untrawlable, indicating high profile reef). Excluding known areas of hard ground or rocky reef habitat, some 45% of mid-shelf is then estimated to be potential spawning habitat. This is again likely an underestimate as chokka squid could spawn amongst the low relief reef (Sauer, 1995b; Sauer *et al.*, 1992) within the larger reef complexes. Inshore, chokka squid egg beds have been recorded on open sand and, on and amongst very low relief reef (Roberts, 1998); and this study confirms the inshore-offshore continuum of these habitats in the St Francis Bay area. Not only can a large proportion of the mid-shelf be considered potential spawning habitat, but some mid-shelf areas are comparable with those spawning sites inshore.

Inshore and deep spawning ground fish communities

South coast inshore rocky reef communities, and inshore and offshore soft substrata communities, have been studied in some detail (Smale, 1992). By comparison, a paucity of information on Agulhas Bank offshore reef communities exists. Numerous studies have confirmed the distribution of fish populations to be determined by, among other factors, underlying habitat association and preferred physical conditions (see Booth (1998) for references). This is indeed the case on the South Coast of South Africa where three distinct demersal fish and cephalopod communities have been identified. These include a neritic community (<100 m), a continental-shelf community (90–190 m) and a shelf edge community (>200 m) (Smale *et al.*, 1993). Relevant to this study are the neritic and continental shelf communities. Although the depth distributions of species addressed in this study have been categorized based on the delineation of shallow and deep spawning grounds (Chapter 2), the distinction in neritic and continental-shelf communities is still evident (Appendix: Table A.2–Table A.4). These communities can be further defined as largely pelagic, reef or soft substrate associated (Appendix: Table A.2–Table A.4). A total of 86 species were recorded on the inshore spawning grounds compared to 54 offshore. Of these, 51 species were common to both spawning areas. This was expected as the deep spawning grounds overlap both community habitats. It is clear a larger number of species, and hence potential predators (Table 3.1), inhabit the shallower waters of St Francis Bay. Moving offshore the number of species present is reduced. Filament tagging has confirmed the movement of squid between the two habitats, and hence their availability to predators in both areas.

Chokka squid is an important prey to numerous marine predators on the south coast of South Africa (Lipiński *et al.*, 1992; Meyer and Smale, 1991a, 1991b; Sauer and Smale, 1991; Smale *et al.*, 2001). None of the species listed Table 3.1 are specialist cephalopod feeders and the importance of squid in the diet of predators is seasonal, coinciding with the inshore chokka squid spawning peak (Smale *et al.*, 2001). This suggests that squid are more susceptible to predation while spawning (Smale, 1996), and indeed predators have been found to respond to the aggregated squid and actively prey on them (Smale *et al.*, 2001). Squid are highly visible in the immediate vicinity of egg beds, especially while signalling by way of chromatophoric communication, and female's particularly vulnerable when moving down to the egg bed to deposit an egg strand (Smale *et al.*, 2001). Predation attempts on actively spawning squid disrupt the spawning process for time periods lasting from a few minutes to almost an hour (Roberts, 1998; Smale *et al.*, 2001). In view of the number of predators inshore versus offshore (Table 3.1), it is intuitive to assume predation pressure is greatly reduced on the deep spawning grounds. Not only because of the fewer predator species, but importantly also because of the absence of the majority of species that have been observed actively preying on or attacking spawning squid (e.g. *G. natalensis*, *P. africanum*, *P. pantherinum*, *P. natalensis*, *S. emarginatum* and *C. nufar* (Smale *et al.*, 2001)). Another aspect influencing predation pressure needs to be considered. Upwelling appears to be an environmental cue initiating the spawning process (Downey *et al.*, 2010; Roberts, 1998; Schön *et al.*, 2002). Smale *et al.* (2001) have suggested that shortly after upwelling, a window of reduced predation pressure is created from the quick temperature decrease. As temperature decreases are known to greatly affect the metabolism of poikilotherms, these authors proposed previously warm-adapted fish move away or rest-up to reduce physiological stress, and that initial predation is by cold-acclimated predators. It is possible that upwelling events inshore allow the predators from deeper waters to move into shallow coastal regions (Smale *et al.*, 2001). Can similar arguments regarding temperature increases be applied to deep spawning?

Inshore and deep spawning ground environments

Previously it was believed that in comparison to the inshore spawning grounds, offshore bottom temperature was colder (~10 °C) and more stable. Oosthuizen and Roberts (2009) have recently shown not only a seasonal trend of benthic warming and cooling on the mid-shelf, but also extreme high and low temperature events (8.2–14.6 °C). Results reported on in this chapter have confirmed the existence of high and low temperature events on the mid-shelf and shelf edge. Warming of the bottom layer near the shelf edge could explain the occasional occurrence of eggs in trawls deeper than 130 m. In addition, results have shown bottom temperature offshore (120 m) can at times be warmer than inshore (30 m). This was seen in event 5 in Figures 3.11d and g, where data indicate a large upwelling event inshore. As described by Oosthuizen and Roberts (2009), the mechanism responsible for warm and cold events on both spawning grounds is the vertical behaviour of an ever-present thermocline on the Eastern Agulhas Bank. Tilting of the thermocline upwards towards the coast allows cold water to reach both the seabed and surface in shallow coastal water. Similarly downward tilting of the coastal thermocline allows warm upper-mixed water to reach the seabed on the mid-shelf.

Another interesting aspect of the cross-shelf bottom temperature study was the comparison of temperature frequencies between 11.1–13.0 °C (Table 3.2). Within these temperature categories, the percentage of frequency of occurrence was quite similar at the depths of 45 m (inshore), 70 m (border) and 120 m (deep). Although the bottom temperature environment inshore and offshore is quite different, some similarities do exist. Inshore chokka squid are known to frequently spawn at these temperatures and evidence suggests these low temperatures may trigger spawning (Downey *et al.*, 2010; Roberts, 1998; Schön *et al.*, 2002). Perhaps, in the same manner, downwelling offshore may trigger the formation of spawning aggregations and spawning activity. This however is purely speculative.

What is almost certain is warm events provide a window of opportunity for deep spawning, as originally proposed by Oosthuizen and Roberts (2009). Sexually mature squid are found throughout the year, both inshore and offshore (Olyott *et al.*, 2006). It is therefore possible that deep spawning occurs when these windows of opportunity coincide with reproductive readiness. A similar argument has been put forward by Roberts (2005) to explain fringe spawning inshore on the Western and Central Agulhas Bank (Figure 1.2). Although oceanographic conditions in these areas are considered largely unfavourable, the high degree of environmental variability can occasionally result in spawning (Olyott *et al.*, 2007). This is further supported by the lack of spatial variability in gonadosomatic indices observed by Olyott *et al.* (2006). These authors suggest squid across the Agulhas Bank have equal reproductive potential and that in some years spawning may take place anywhere across the bank. The cross-shelf movement (Sauer *et al.* (1997); this study) and alongshore migrations (Sauer *et al.*, (2000); Sauer (1995b); this study) of adult squid on the south coast possibly increases the likelihood of encountering favourable conditions or windows of opportunity. Results of the current study support and further expand this argument, suggesting the occasional and temporary shifting of the spawning grounds to deeper water. As evidenced by event 5, favourable environmental conditions for spawning shifted offshore. Bottom temperature was ~10 °C inshore and ~14 °C offshore. After the subsiding of offshore bottom turbidity levels, the most favourable spawning environment was almost certainly the deep spawning ground. The shifting of squid spawning habitat has been observed off the coast of California (Zeidberg *et al.*, 2011). During strong *El Niño* events, depression of isotherms result in the shifting of preferred *D. opalescens* spawning habitat (9–14 °C) into deeper waters (Zeidberg *et al.*, 2011).

Data indicate St Francis Bay bottom temperatures were warmer during autumn-winter on both the inshore and deep spawning grounds (Figure 3.11). This further supports the observation by Oosthuizen and Roberts (2009) that a seasonal trend of warming and cooling occurs on the mid-shelf. It is possible that the seasonal warming of offshore bottom water also acts to either expand or shift (or both) the inshore spawning habitat. Generally, chokka squid move offshore during autumn. It is possible that deep spawning increases from April onwards. Autumn DAFF demersal research trawl catches add weight to this theory, with catches in deeper water off the Tsitsikamma coast and Plettenberg Bay (23°–24°E) consisting entirely of adult squid (Olyott *et al.*, 2007). Although this same pattern was not reflected in the seasonal analysis of average egg biomass in Chapter 2, results from some years indicated at times deep spawning increased substantially in autumn. Maximum winter mid-shelf temperature for the St Francis Bay area reveal that warming events are more intense during autumn-winter (17.2 °C). This too suggests a potential for an increase in deep spawning. Bottom dissolved oxygen levels consistently ≥3 $mg.l^{-1}$, within the range required for spawning (Roberts, 2005), indicate spawning on the mid-shelf would not be limited by oxygen levels.

Predation and fishing pressure: Drivers for deep spawning?

It has been suggested that deep spawning in chokka squid could be forced by unfavourable conditions inshore (Augustyn and Roel, 1998; Oosthuizen *et al.*, 2002a; Roberts and Sauer, 1994). Although chokka squid may well be spawning habitat opportunists, adverse conditions could still force squid to seek out suitable habitat elsewhere.

Inshore spawning aggregations are targeted by the commercial jig fishery (Sauer *et al.*, 1992), both day and night (Roberts and Sauer, 1994). Apart from removing a large proportion of the spawners, fishing also potentially disrupts spawning activity (Sauer, 1995a). In contrast, fishing in deeper waters is most effective at night when strong lights can be used to draw squid to the surface within the range of hand-held jigs. As spawning aggregations are known to disintegrate shortly after dusk (Downey *et al.*, 2010; Hanlon *et al.*, 1994; Roberts, 1998; Sauer and Smale, 1993; Sauer *et al.*, 1997), it is unlikely this method of fishing disrupts spawning activity.

Predation pressure could also be somewhat reduced on the deep spawning grounds. Spawning shortly after an increase in bottom temperature suggests predation levels may be low initially, before warm-water predators move into the area. In addition, as argued for inshore predators, changes in bottom temperature may result in cold-acclimated predators immediately moving further offshore. Smale *et al.* (1993) illustrated that depth and temperature were important in determining the cross-shelf distribution of neritic and continental-shelf species on the south coast of South Africa. These authors observed that occasionally water temperature (and oxygen) over-rode the normal depth distribution of species groups. Perhaps this provides further evidence of the variable nature of temperatures both inshore and offshore on the south coast of South Africa. During prolonged (days) mid-shelf warm events however, although fewer species, and indeed fewer squid predators are generally found on the deep spawning grounds, Smale *et al.* (1993) findings suggest predation levels could approach levels close to those observed inshore.

Although broadly descriptive, this chapter has highlighted both differences and similarities between the inshore and deep spawning grounds. The mid-shelf benthic habitat is similar to that inshore and available for spawning. It seems the “super” aggregations of spawning squid observed by Roberts *et al.*, (2002) were spawning on a large sandy area similar to spawning habitat inshore. Despite the generally colder bottom temperatures on the mid-shelf, this study has shown bottom temperature in deeper waters can at times be warmer than inshore. Mid-shelf warming events last from a few hours to a number of days, and result in similar conditions to those on the inshore spawning grounds. It is likely these events make deep spawning possible. The movement of squid between the two spawning habitats enables them to seek patches of warm bottom water with appropiate substrate. This suggests they are spawning habitat opportunists. It is also possible factors such as predation and fishing pressure inshore make this habitat unfavourable, so forcing spawners to seek out suitable habitat in deeper water. Although we cannot directly answer this, the disruption of spawning by predator activity demonstrated by Smale *et al.* (2001) suggests this could at times be applicable; especially as fewer known chokka squid predators are found on the mid-shelf.

This study has described the Agulhas Bank mid-shelf and habitat. Not only has this provided additional insight into deep spawning in chokka squid, but is also important in terms of a broad understanding of mid-shelf ecology. This is currently one of the key research focus areas of the South African Environmental Observation Network (SAEON). Future work should focus on the collection of more high resolution data, and where possible, more quantitative analysis of the Agulhas Bank mid-shelf. This has implications regarding not only the understanding of chokka squid deep spawning habitat and behaviour, but is essential to the effective resource management of other Agulhas Bank fishery species.

CHAPTER 4: Transport and survival of deep spawning ground hatchlings

Unpublished

Introduction

In Chapter 2 mid-shelf spawned eggs (71–130 m depth) were calculated to contribute 18% to total chokka squid, *Loligo reynaudi*, egg biomass. The fate of these deep spawned hatchlings and their potential contribution to recruitment is unknown. Although observations by M.R. Lipiński (as cited in Augustyn *et al.*, (1992)) indicate chokka paralarvae may undergo diel vertical migration (DVM), their limited ability to move horizontally means dispersion, transport to food-rich areas and subsequent recruitment depends on ocean currents (Augustyn *et al.*, 1992). This is not unique to chokka squid and the importance of ocean circulation to transport and recruitment of other cephalopod paralarvae has been demonstrated (Goldman and McGowan, 1991; Hanlon *et al.*, 1985). The transition from the yolk-utilization phase to exclusively prey capture is also considered a critical period (see Vidal *et al.* (2006) for citations) during the early life-history. Survival of paralarvae is dependent on numerous factors, such as predation and avoiding starvation (Lipiński, 1998; Vidal *et al.*, 2006). During the initial yolk-utilization period, paralarvae must develop prey-capture skills in order to meet metabolic requirements as yolk reserves are diminished (Vidal *et al.*, 2006). Food availability during this critical period is therefore important.

Roberts (2005) proposed that the main chokka squid inshore spawning grounds are positioned to exploit the net westward currents on the Eastern Agulhas Bank, i.e. paralarvae would be transported west from the hatching site to the cold ridge on the Central Agulhas Bank. This concept has come to be known as the Western Transport Hypothesis (WTH) and was discussed in detail in Chapter 1. Lagrangian ROMS-IBM (regional ocean model system – individual-based model) simulations have been used to investigate the transport and recruitment of chokka squid paralarvae on the Agulhas Bank. Initial models using neutrally buoyant paralarvae not only confirmed westward transport on the mid-shelf but also indicated that the potential exists for paralarvae hatched on the Eastern Agulhas Bank mid-shelf to be removed from the shelf ecosystem (Roberts and Mullon, 2010). Subsequent IBM studies have also substantiated the net westward transport of particles (or paralarvae) from both the shallow and deep spawning grounds (Martins *et al.*, 2013).

The importance of the cold ridge (Figure 4.1) as an area of high primary and secondary productivity has been discussed in relation to the Western Transport Hypothesis. The highest densities of the dominant copepod *Calanus agulhensis* occur in summer in the vicinity of this ridge (Huggett and Richardson, 2000). However, other areas of high productivity, potentially important as paralarval feeding grounds, do occur. Using a composite of satellite images showing chlorophyll concentration (mg.m^{-3}), all areas of high productivity on the Agulhas Bank are illustrated in Figure 4.1. The high productivity results from the various upwelling systems along the coast namely: (A) wind-driven coastal upwelling (Lutjeharms and Stockton, 1991) occurring between Cape Point and Cape Agulhas, (B) a quasi-permanent submerged cold ridge (described in Chapter 1) (Roberts and van den Berg, 2002; Roberts, 2005), (C) intermittent, wind-driven coastal upwelling, associated with prominent capes (Schumann *et al.*, 1982), (D) minor and sporadic upwelling along the inshore boundary of the Agulhas Current as a result of boundary phenomena (Lutjeharms *et al.*, 1989), and (E) upwelling in the vicinity of Port Alfred, known as the Port Alfred upwelling cell (Lutjeharms, 2006).

The majority of chokka squid paralarvae are found on the inshore spawning grounds (Figure 4.2b) (Augustyn *et al.*, 1994). Copepods, long thought to be a major component of chokka squid paralarval diet (Augustyn *et al.*, 1994), are found year round on the entire Agulhas Bank (Huggett and Richardson, 2000). From the knowledge of this distribution, coupled with the intermittent coastal upwelling and concomitant production in the vicinity of the main spawning grounds (C in Figure 4.1), it can be surmised that the inshore spawning grounds are likely an important feeding ground for chokka squid paralarvae.

Martins *et al.* (2013) investigated interactions between circulation, diel vertical migration and specific gravity of chokka squid paralarvae during the yolk-utilization phase. Results showed that both release area and particle buoyancy influenced the dispersal and transport of paralarvae. Within these simulations no biological attributes were assigned to the particles and the fate of particles beyond the yolk-utilisation phase (4–5 days) was not assessed. The study by Martins *et al.* (2013) also only considered the cold ridge as a nursery area/feeding grounds for young paralarvae. The aim of this chapter was to determine the transport and recruitment success of deep spawned hatchlings relative to inshore hatched paralarvae. Although driven by the same 3-D hydrodynamic model used by Martins *et al.* (2013), the IBM in the current study differs in that both the cold ridge and inshore chokka squid spawning grounds are considered feeding or nursery areas. In addition, paralarvae were given biological characteristics such as temperature related growth. Higher resolution release areas were used and the fate of paralarvae beyond the initial yolk-utilisation phase investigated (i.e. 40-day simulations).

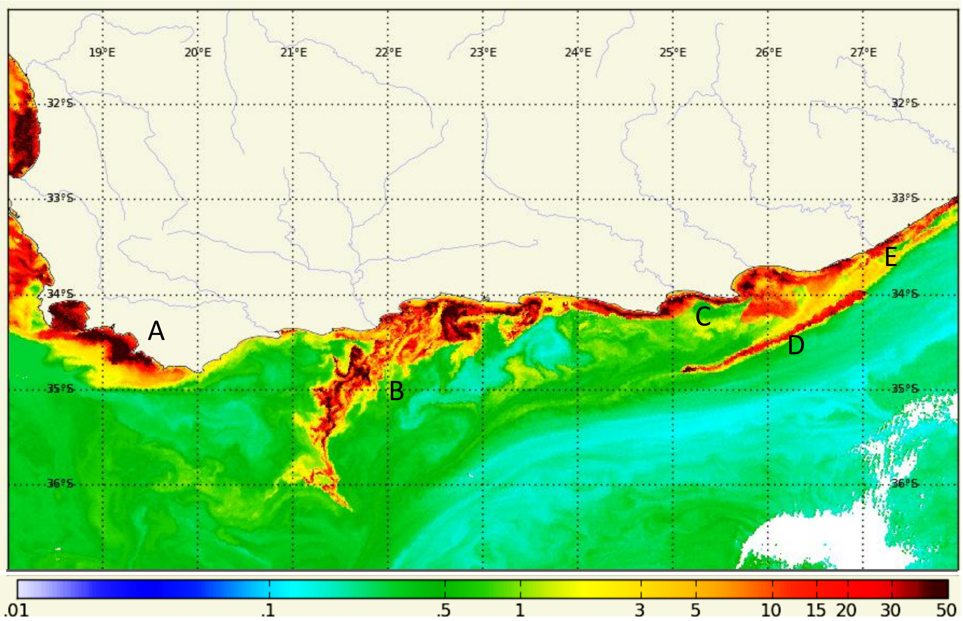

Figure 4.1: A composite of several satellite images (Marine Remote Sensing Unit http://www.afro-sea.org.za/) highlighting chlorophyll concentration (mg.m^{-3}) on the Agulhas Bank and areas of high productivity. These areas of high productivity are a result of the various upwelling systems along the coast: (A) wind-driven coastal upwelling (B) cold ridge (C) intermittent, wind-driven coastal upwelling (D) minor and sporadic upwelling along the inshore boundary of the Agulhas Current and (E) Port Alfred upwelling cell.

Materials and Methods

A Lagrangian particle-tracking IBM (*Ichthyop* Version 3.1, free software available from http://www.previmer.org/ichthyop) was used to simulate the hatching and transport of paralarvae from 12 spawning sites (Figure 4.2). Advection of paralarvae was controlled by a Forward Euler scheme and horizontal dispersion by a Lagrangian horizontal diffusion coefficient $K_h=\varepsilon^{1/3}l^{4/3}$, (Peliz et al. 2007) where $\varepsilon=10^{-9}$ m^2 s^{-3} and is the turbulent dissipation rate and l the length of the grid cell as determined by the application. *Ichthyop* has been developed to study the physical (e.g. ocean currents, temperature) and biological (e.g. growth, mortality) factors affecting ichthyoplankton dynamics (Lett *et al.*, 2008). As described by Lett *et al.* (2008), this tool uses time series of velocity, temperature and salinity fields archived from ocean model simulations. The hydrodynamic dataset used in this study was developed by Chang (2008). By embedding a higher resolution model within the courser resolution (20–25 km) parent Southern African Experiment (SAfE) model (Penven *et al.*, 2006), a 10 year high resolution (~8 km) child model was developed. The child model covers the area 27.7 to 39°S and 11.5 to 27.4°E. Bottom topography data was obtained from the General Bathymetric Chart of the Oceans (GEBCO) (Chang, 2008). Statistical equilibrium of the child model took approximately two years, indicating that the model is stable, (Chang, 2008), and model outputs from year three were used.

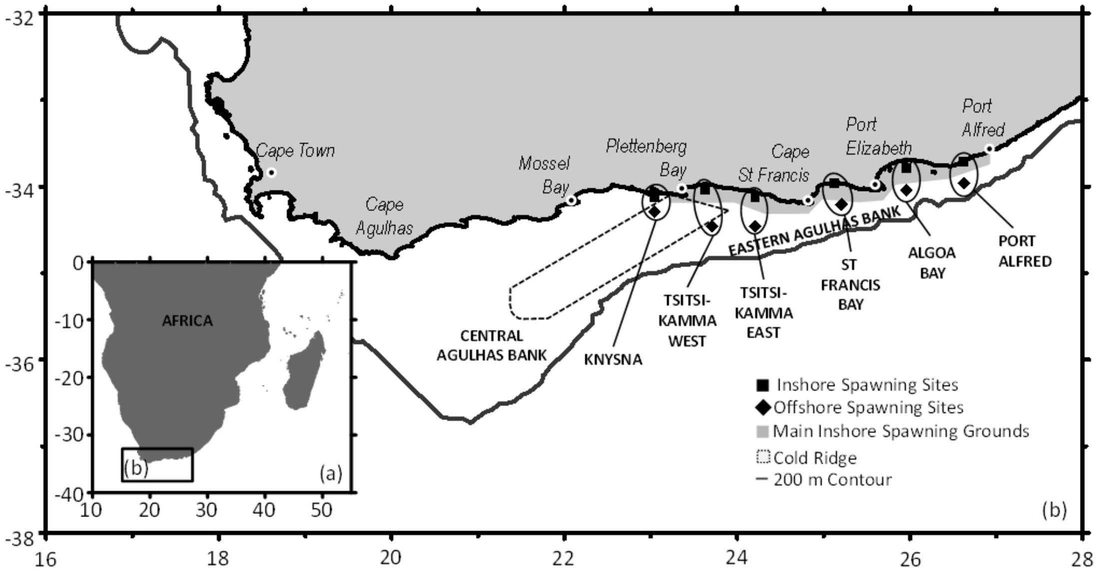

Figure 4.2: (a) The southern African continent and (b) the location of the six inshore and six offshore spawning (or release) sites used in the individual-based models. Also shown are the cold ridge (dotted line), the inshore spawning grounds (shaded grey), the Eastern Agulhas Bank, the Central Agulhas Bank and the shelf break along the 200 m isobath (dark grey line).

Due to the different coastal features dominating the inshore spawning grounds, it was expected paralarvae would be subjected to different transport trajectories, depending on release location. Subsequently, the coastline between Port Alfred (east) and Knysna (west) was divided into six areas, based on general coastal features, namely: (1) the Port Alfred area made up of the portion of the coastline with a northeast to southwest orientation; (2) the Algoa Bay area; (3) the St Francis Bay area; the Tsitsikamma coastline, which due to its length was divided into (4) Tsitsikamma East and (5) Tsitsikamma West; and lastly, (6) the Knysna area. Within each of these areas, one inshore (shallow) and one offshore (deep) spawning area were chosen as release sites for the IBMs (Figure 4.2). These spawning areas were determined from the presence of squid eggs in Department of Agriculture, Forestry and Fisheries (DAFF) Research trawl catches or from known spawning sites. Unfortunately, when using DAFF trawl catch data, it is not known exactly where in the area trawled the squid eggs were caught. It was therefore necessary to use the entire trawl block (5'X5' grids, Figure 2.1) as the release site. Co-ordinates for the 12 chosen blocks were “set” into the model. Paralarvae were then released from a random location, assigned by the modelling software, within these pre-defined grids. To determine the variability that could arise from this method, a number of simulations for the same release grid and for the same month were run and the results compared. Variations were found to be minimal and running only one simulation for each release site and for each month of the year was sufficient, making a total of 144 simulations.

Certain parameters and biological inputs remained the same for all 144 simulations. These included (1) a single release event of 5000 particles (paralarvae) from each spawning site (although chokka squid are serial spawners and spawn throughout the year, for the purpose of simplification, only one release event per month was used); (2) a thickness of each patch (egg bed) of 0.5 m; (3) a radius of each patch (egg bed) of 1 m, based on the observation by Sauer *et al.* (1993) that large egg beds are usually >2 m; (4) equal initial egg lengths and hatching lengths of 4.67 mm (total paralarval length as given by Augustyn *et al.* (1994)), to ensure the release of paralarvae and not eggs in the model; (5) a yolk-sac to feeding paralarval threshold length of 4.8 mm (personal communication, M. Lipiński); (6) a buoyancy of 1.048 g cm^{-3} for paralarvae ≤4 days old (Martins *et al.*, 2010); (7) temperature related growth with growth coefficient 1 = 0.0028 (minimum, 12 °C) and growth coefficient 2 = 0.0064 (maximum, 16 °C) (Vidal *et al.*, 2005); and a threshold temperature of 12 °C to ensure paralarvae grow with a minimum rate in cold water; (8) DVM (from age 4.01 days) with a specified depth of 90 m during the day, forcing paralarvae to remain near the seabed, and 10 m at night, simulating the movement of paralarvae into surface water at night; and (9) a 40-day paralarval transport duration, as loliginid paralarvae begin displaying schooling behaviour at ~40 days, possibly indicating the transition from the paralarvae to juvenile stage (Bigelow, 1992).

There is some indication that chokka squid paralarvae undergo DVM (M.R. Lipiński as cited in Augustyn *et al.*, (1992)) however, the vertical distribution of chokka squid paralarvae is unknown. The copepod thought to make up a large component of chokka squid paralarval diet, *C. agulhensis*, also undergoes DVM. An investigation into the DVM of this species at three sites on the Agulhas bank was undertaken by Huggett and Richardson (2000). At night, *C. agulhensis* occupied the food rich layers near the surface. During the day, the maximum depths at which this copepod occurred (determined from mean weighted depth) were ~85, ~105 and ~70 m at stations with depths of 100, 140 and 80 m respectively. The daytime depth of 90 m used in this study is therefore not unrealistic.

Within the model, two zones of high productivity were specified as feeding grounds, namely the inshore spawning grounds and the cold ridge. The area beyond the 200 m isobath was also stipulated as a zone to allow the determination of paralarval losses from the Agulhas Bank. Model outputs (paralarva number, position, depth, length and mortality; water temperature and which zone each paralarva was in were recorded every 12 hours (00:00 and 12:00).

To determine potential paralarval survival, and hence contribution to recruitment, success was calculated based on (1) reaching areas of high productivity before the onset of starvation; (2) retention in feeding grounds; and (3) retention on the shelf once exiting feeding grounds. Data were analysed in a step-by-step approach to identify factors responsible for paralarval losses. For each spawning site and for each month of the year, the following was calculated:

(1) Losses due to not reaching feeding grounds before the onset of starvation, i.e. the percentage of paralarvae not reaching the feeding grounds within five days. Rearing experiments showed the majority of chokka squid paralarvae to completely exhaust their yolk reserves five days after hatching (Vidal *et al.*, 2005).

(2) Losses due to poor retention within food-rich areas, i.e.: the percentage of paralarvae reaching the feeding grounds within five days of release that were not retained for 14 days or more. A retention time of ≥14 days was used as paralarvae become more resistant to starvation as they become older (Vidal *et al.*, 2006), and can survive longer periods without food. A laboratory study by Vidal *et al.* (2006) showed 15-day old *D. opalescens* paralarvae to be able to survive three days of starvation. Although overall survival decreased, paralarvae were able to recover after one to two days of refeeding. In addition, Huggett and Richardson (2000) showed early stages of *C. agulhensis* to be found in the vicinity of the cold ridge, whereas older stages occurred west of the cold ridge. This indicates the transport of copepods out of the cold ridge, and so paralarvae also carried out of the feeding grounds are not necessarily entering a food scarce environment.

(3) *Losses due to offshelf advection*, i.e.: the percentage of paralarvae advected off the Agulhas Bank once exiting the feeding grounds.

After factoring in paralarval losses, the percentage of successful recruits for each release site and for each month of the year was calculated. All results were expressed as the percentage of the total number of particles (hereafter referred to as paralarvae) released.

The position of recruited paralarvae, when schooling behaviour commenced (day 40), was plotted and analysed using kernel density analysis. This enabled not only distribution on the Agulhas Bank to be investigated, but also areas of highest paralarval concentration to be identified. Results were plotted on the same scale to allow monthly comparisons.

Results

IBM results are data intensive and consist of numerous animations. A composite map (Figure 4.3) shows the dispersal of particles released from the deep spawning grounds during the model month November. End positions for days 1, 10 ,20 ,30, and 40 are given to provide an impression of dispersal of the paralarvae. As can be seen, the end-points create extremely busy maps. Quantitative results are therefore given in tables.

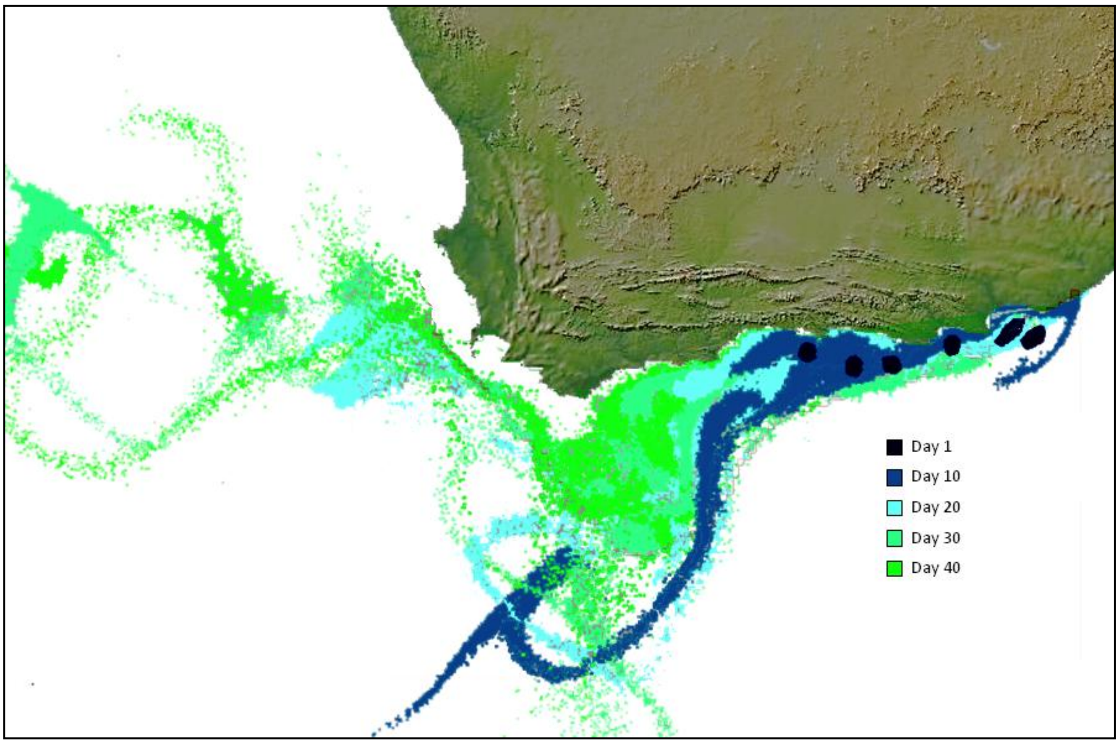

Figure 4.3: The end points of paralarvae, released from the six offshore (deep) spawning sites, during the model month of November. End points for days 1, 10, 20, 30 and 40 have been plotted.

Table 4.1 and Table 4.2 present results for offshore and inshore hatchlings, respectively. Results are given as the percentage of losses occurring due to (1) not being transported to feeding grounds within five days of hatching, (2) not being retained within food-rich areas

(≥14 days) and, (3) not being retained on the Agulhas Bank (after exiting feeding grounds). Also given is the percentage of successful recruits. Table 4.1 provides results for paralarvae released from the six offshore spawning sites, and considering both the (a) inshore spawning grounds and (b) the cold ridge, as feeding grounds. Table 4.2 provides these same results for paralarvae released from the six inshore spawning sites.

Deep spawned hatchlings and the inshore feeding grounds

The majority of paralarvae released from the offshore spawning sites were not transported to the inshore feeding grounds within five days (Table 4.1a). Those paralarvae released from the offshore Algoa Bay site which were carried inshore, were later lost by transport out of the feeding grounds and advection off the Agulhas Bank (Table 4.1a). Transport trajectories seen within the model animations showed these paralarvae were transported eastwards towards Port Alfred where they were swept off the shelf. A relatively high percentage of paralarvae released from the offshore St Francis Bay site were transported to the inshore feeding grounds during July and August only (Table 4.1a).

Deep spawned hatchlings and the cold ridge feeding grounds

Very few paralarvae released from the Port Alfred, Algoa Bay and St Francis Bay offshore spawning sites were transported to the cold ridge feeding grounds within five days of release (Table 4.1b). Transport from the two Tsitsikamma (Tsitsi) and Knysna offshore spawning sites was more successful. The greatest losses of paralarvae released from the Tsitsikamma East site resulted from slow transport and not reaching the cold ridge feeding ground within the five day window (Table 4.1b). Of secondary importance were paralarval losses due to poor retention within the cold ridge. From the offshore Tsitsikamma West and Knysna sites, which were situated closer to the cold ridge, the largest losses resulted primarily from poor retention within the cold ridge (Table 4.1b). A very small percentage of paralarvae were lost through advection from the Agulhas Bank after being transported out of the feeding grounds. The percentage of successful recruits released from the offshore Tsitsikamma West and Knysna sites was highest during autumn–winter (April to August).

Inshore spawned hatchlings and the inshore feeding grounds

As all except the Knysna inshore release sites were situated within the inshore spawning/feeding grounds, transport to this area within the five day period did not

Table 4.1: Losses (%) of mid-shelf *Loligo reynaudi* hatchlings resulting from slow transport, poor retention and advection off the Agulhas Bank. Results are given for each release site, and for both feeding grounds: (a) inshore spawning areas and (b) cold ridge. Also given is the percentage of survivors or successful recruits.

		(a) South coast inshore spawning area as feeding grounds												**(b) Cold ridge as feeding grounds**											
		Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Port Alfred	>5 days	61	100	100	100	100	100	99	100	100	99	100	100	100	100	98	100	100	100	100	100	98	85	85	95
	Not retained	38	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	2	15	15	4
	Advected off AB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
	Recruited	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Algoa Bay	>5 days	100	80	92	97	35	37	91	47	98	96	61	99	77	100	100	100	100	100	100	100	100	99	100	100
	Not retained	0	19	6	1	31	21	5	12	1	4	25	1	23	0	0	0	0	0	0	0	0	2	0	0
	Advected off AB	0	0	2	1	34	39	4	3	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0
	Recruited	0	1	1	1	0	2	0	38	0	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0
St Francis	>5 days	99	99	94	97	97	89	30	63	98	84	99	98	100	100	100	100	100	100	100	100	100	100	100	100
	Not retained	1	0	2	0	1	5	11	2	0	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Advected off AB	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Recruited	0	0	5	3	3	5	37	36	1	10	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Tsitsi East	>5 days	100	100	100	100	100	100	100	100	100	100	100	100	76	0	0	94	41	0	70	5	97	37	99	94
	Not retained	0	0	0	0	0	0	0	0	0	0	0	0	13	98	71	1	40	10	16	64	0	60	1	4
	Advected off AB	0	0	0	0	0	0	0	0	0	0	0	0	0	2	10	0	7	0	0	0	0	0	0	0
	Recruited	0	0	0	0	0	0	0	0	0	0	0	0	11	0	19	5	12	90	14	31	3	4	0	2
Tsitsi West	>5 days	100	100	100	100	100	100	100	100	100	100	100	100	15	0	0	0	8	0	2	0	3	38	56	1
	Not retained	0	0	0	0	0	0	0	0	0	0	0	0	51	89	80	1	55	42	37	100	60	57	13	69
	Advected off AB	0	0	0	0	0	0	0	0	0	0	0	0	3	11	6	0	17	0	0	0	0	1	1	0
	Recruited	0	0	0	0	0	0	0	0	0	0	0	0	31	0	14	99	21	58	61	0	37	5	30	30
Knysna	>5 days	100	100	100	100	100	100	100	100	100	100	100	100	0	3	9	0	0	0	0	0	4	4	0	0
	Not retained	0	0	0	0	0	0	0	0	0	0	0	0	80	97	90	7	4	2	34	86	94	96	98	86
	Advected off AB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0
	Recruited	0	0	0	0	0	0	0	0	0	0	0	0	20	0	1	93	92	98	66	14	2	0	2	14

Table 4.2: Losses (%) of inshore *Loligo reynaudi* hatchlings resulting from slow transport, poor retention and advection off the Agulhas Bank. Results are given for each release site, and for both feeding grounds: (a) inshore spawning areas and (b) cold ridge. Also given is the percentage of survivors or successful recruits.

		(a) South coast inshore spawning area as feeding grounds												**(b) Cold ridge as feeding grounds**											
		Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
Port Alfred	>5 days	1	16	6	69	0	1	1	1	27	2	56	53	100	100	100	100	100	100	100	100	100	100	100	100
	Not retained	42	71	74	29	50	32	58	51	52	72	39	38	0	0	0	0	0	0	0	0	0	0	0	0
	Advected off AB	36	1	10	0	34	51	30	20	5	13	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	Recruited	21	12	11	2	16	16	11	28	16	13	4	9	0	0	0	0	0	0	0	0	0	0	0	0
Algoa Bay	>5 days	0	0	0	0	0	0	0	0	0	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100
	Not retained	96	73	45	39	49	1	40	13	44	54	69	56	0	0	0	0	0	0	0	0	0	0	0	0
	Advected off AB	0	1	6	20	35	58	35	8	24	12	16	1	0	0	0	0	0	0	0	0	0	0	0	0
	Recruited	4	26	49	42	16	41	25	79	33	34	15	43	0	0	0	0	0	0	0	0	0	0	0	0
St Francis	>5 days	0	0	0	0	0	0	0	0	0	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100
	Not retained	62	7	22	8	15	11	2	4	25	46	80	33	0	0	0	0	0	0	0	0	0	0	0	0
	Advected off AB	0	1	2	13	0	25	5	3	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Recruited	38	92	76	79	85	65	93	93	68	54	20	67	0	0	0	0	0	0	0	0	0	0	0	0
Tsitsi East	>5 days	0	4	12	1	0	1	1	1	0	2	0	0	100	98	90	100	100	100	100	98	100	100	100	100
	Not retained	25	17	63	36	9	25	31	9	6	50	30	22	0	1	6	0	0	0	0	0	0	0	0	0
	Advected off AB	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Recruited	75	79	25	60	90	74	68	90	94	48	70	78	0	1	4	0	0	0	0	1	0	0	0	0
Tsitsi West	>5 days	5	14	19	6	2	5	5	10	15	18	4	4	94	42	4	94	97	95	94	85	63	17	99	95
	Not retained	86	85	77	29	9	44	21	39	65	82	40	49	4	54	60	2	1	1	2	4	19	82	0	1
	Advected off AB	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Recruited	9	1	4	65	89	51	75	52	20	0	56	46	2	4	36	4	2	4	4	10	19	0	1	4
Knysna	>5 days	100	100	100	99	100	100	96	100	100	100	100	100	43	98	100	0	1	1	0	32	42	100	25	35
	Not retained	0	0	0	0	0	0	1	0	0	0	0	0	49	3	0	61	27	16	29	20	0	0	57	16
	Advected off AB	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Recruited	0	0	0	1	0	0	3	0	0	0	0	0	8	0	0	39	73	83	71	47	58	0	18	49

determine paralarval survival. However, a few paralarvae were immediately advected after release, and were therefore not considered present. Poor retention on the inshore feeding grounds (Table 4.2a) was the major cause of paralarval losses. The degree of paralarval losses varied depending on both month and release site (Table 4.2a). Of those paralarvae successfully retained in the feeding grounds, later losses through advection off the Agulhas Bank were greatest for those hatchlings originating from the Eastern Agulhas Bank, namely Port Alfred, Algoa Bay and St Francis Bay (Table 4.2a). Losses from offshelf advection were particularly great during the autumn–winter months, May to July (Table 4.2a). No paralarvae released from the Knysna inshore site were transported to the inshore feeding grounds within five days, except for a very small percentage in July (Table 4.2a). In general, the number of successful recruits was highest for the St Francis Bay and Tsitsikamma East release sites (Table 4.2a). Survival varied between months, but did not appear to be linked to seasons.

Inshore spawned hatchlings and the cold ridge feeding grounds

No paralarvae released from the Port Alfred, Algoa Bay or St Francis Bay inshore spawning sites were transported to the cold ridge feeding grounds within the five days (Table 4.2b). Moving further west to inshore spawning sites closer to the cold ridge, successful transport increased only slightly (Table 4.2b). During February, March and October a relatively large percentage of paralarvae were transported within five days from the Tsitsikamma West inshore spawning site to the cold ridge (Table 4.2b). The majority of these paralarvae were not retained within the cold ridge (Table 4.2b) and were considered lost. Only paralarvae hatched from the inshore Knysna site during the months April–September and December showed a relatively high percentage of successful recruits (Table 4.2b).

The influence of release month and release area on recruitment

Overall paralarval survival per month and per release area is given in Figure 4.4 and Figure 4.5, respectively. Immediately evident in Figure 4.4 is the relative importance of the two feeding grounds depending on the origin of the hatchlings. The results show the cold ridge to be an important feeding area for deep spawned hatchlings, with few inshore hatchlings being transported here (Figure 4.4a). Instead, young inshore hatchlings were initially retained within the inshore feeding grounds (Figure 4.4b). Despite the evident monthly variability in recruitment success, common to both offshore and inshore hatchlings was the

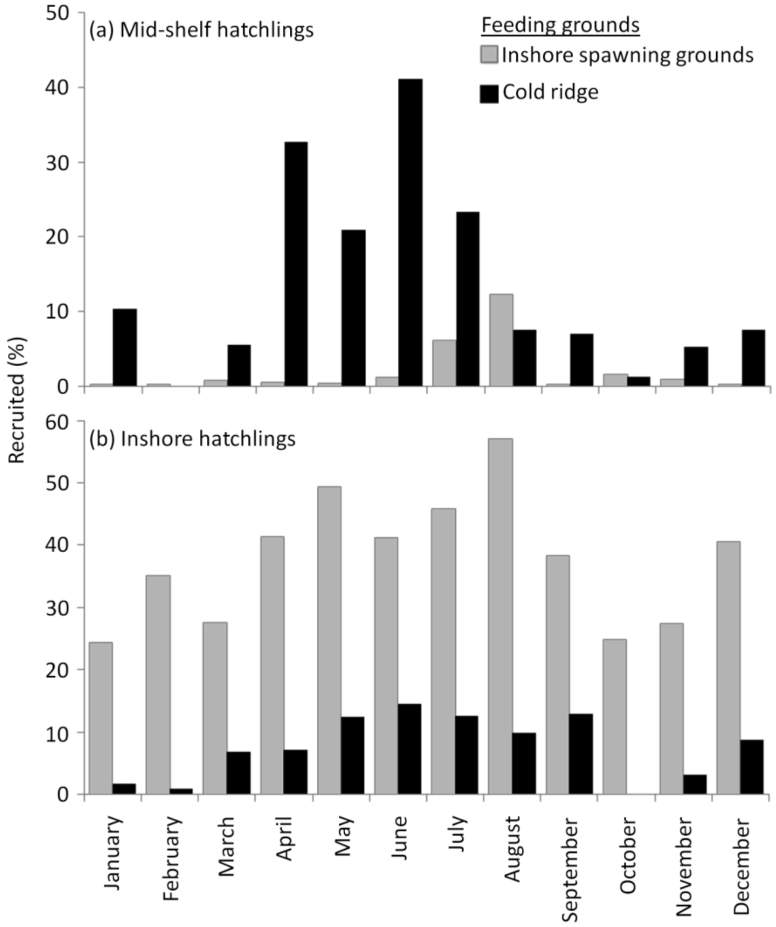

Figure 4.4: The overall monthly percentages of successful recruits released from the mid-shelf (deep) and inshore spawning grounds. Results are given for both feeding grounds: (1) inshore spawning areas and (2) cold ridge.

highest survival during the months April–August. A second peak in the number of successful recruits was observed for inshore hatchlings released in December.

Hatching site also played a role in paralarval survival (Figure 4.5). When considering the inshore spawning areas as feeding grounds, a very small number of hatchlings originating from the Port Alfred, Algoa Bay and St Francis Bay offshore sites survived (Figure 4.5a). Further west (Tsitsikamma and Knysna sites), survival was zero. Not surprising considering the proximity to the cold ridge, offshore paralarvae hatching off the Tsitsikamma and Knysna coasts, and transported to the cold ridge feeding grounds, showed the highest recruitment success (Figure 4.5a). Survival of paralarvae originating from hatching sites further east was zero to minimal. Recruitment success of inshore hatchlings, when considering the inshore spawning area as feeding grounds, was greatest for those paralarvae originating from the centre of the spawning grounds (St Francis Bay and

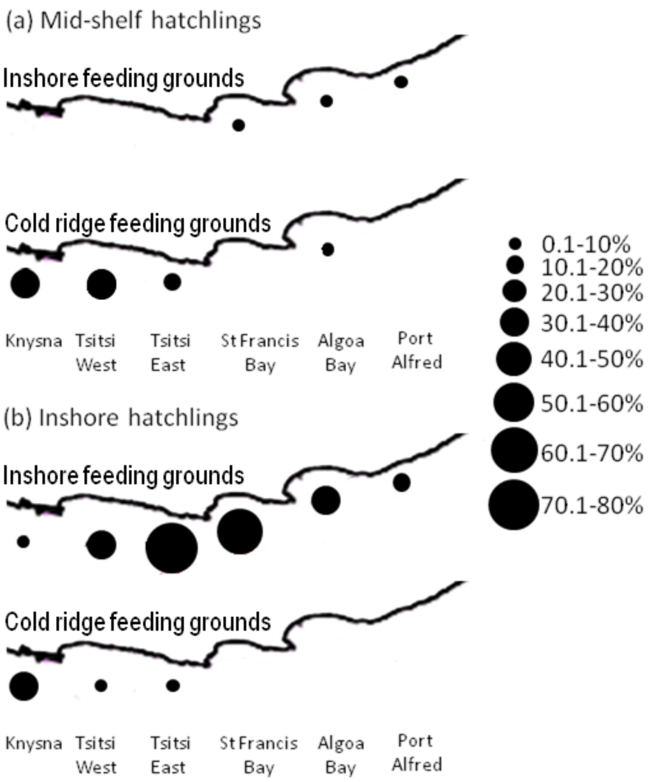

Figure 4.5: The overall percentages of successful recruits, per release area, seeded from the mid-shelf (deep) and inshore spawning grounds. Results are given for both feeding grounds: (1) inshore spawning areas and (2) cold ridge.

Tsitsikamma East) (Figure 4.5b). Further east, paralarvae were lost through offshelf advection; and further west paralarvae were quickly transported westwards out of the feeding grounds. A portion of the westward carried paralarvae did enter the cold ridge (Figure 4.5b). Transport to the cold ridge of paralarvae originating from other inshore spawning sites was minimal (Figure 4.5b).

Paralarval distribution and concentration

Figure 4.6a and b show the monthly position and areas of concentration of 40 day old paralarvae released from the offshore and inshore spawning sites, respectively. Immediately evident is the monthly variability in distribution on the Agulhas Bank, as well as areas of highest paralarval concentration. It is interesting to note that despite the large area of distribution observed in some months, paralarvae were concentrated close to the coast on the spawning grounds, the base of the cold ridge and/or just west of the cold ridge. The simulated paralarval end-points (day 40) also give some indication of transport on the Agulhas Bank. From the Eastern Agulhas Bank, offshore released paralarvae were generally transported westwards. Although the net westward transport continued over the Central

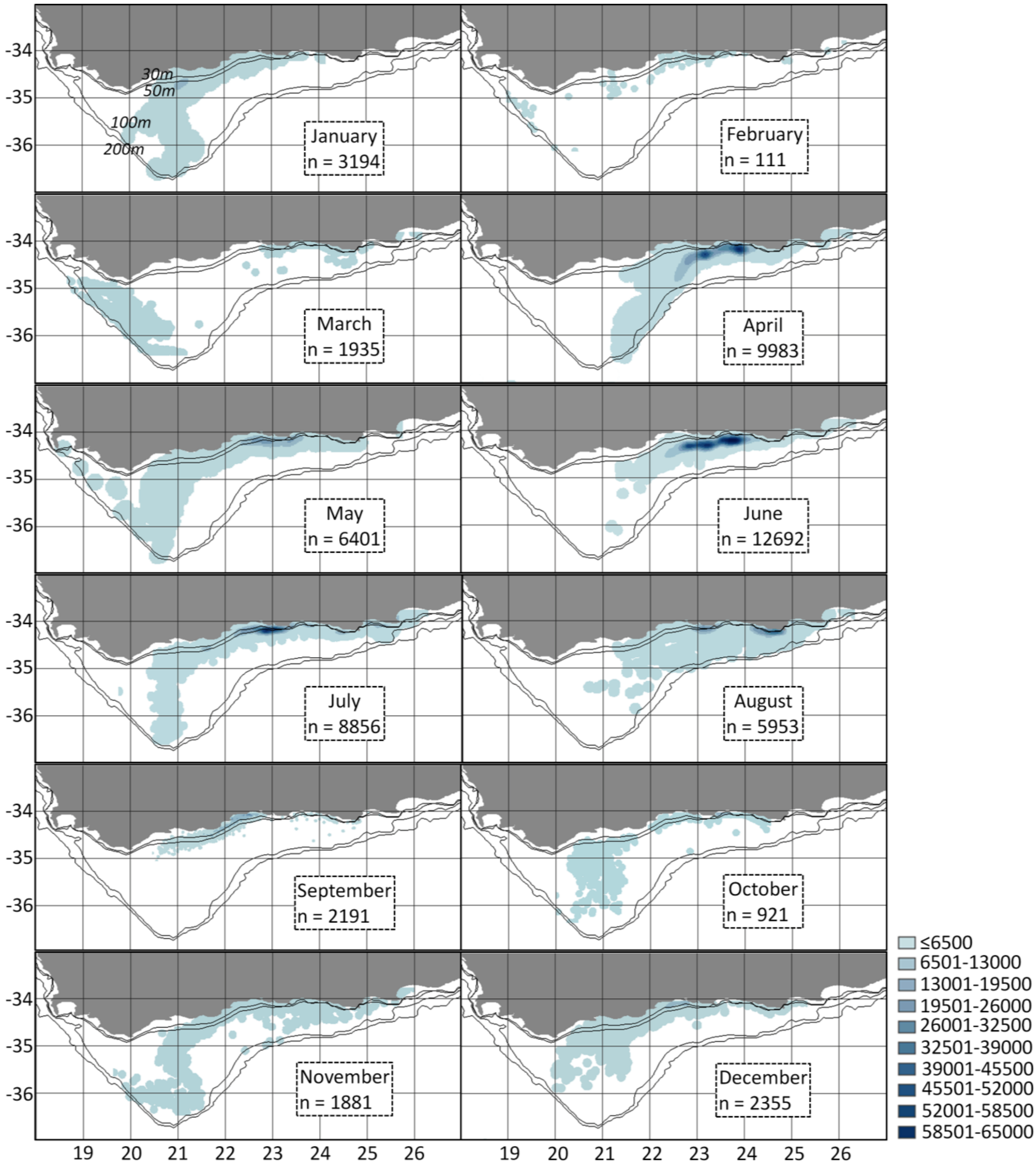

Figure 4.6a: The position of successful paralarvae, released from the offshore spawning sites, on the Agulhas Bank when schooling behaviour commences (day 40 of simulation). Also shown is the number of successful or surviving paralarvae per month (n), out of the 30 000 paralarvae released within the simulations. Values given in the index are generated by the kernel density analysis, and do not indicate paralarval numbers.

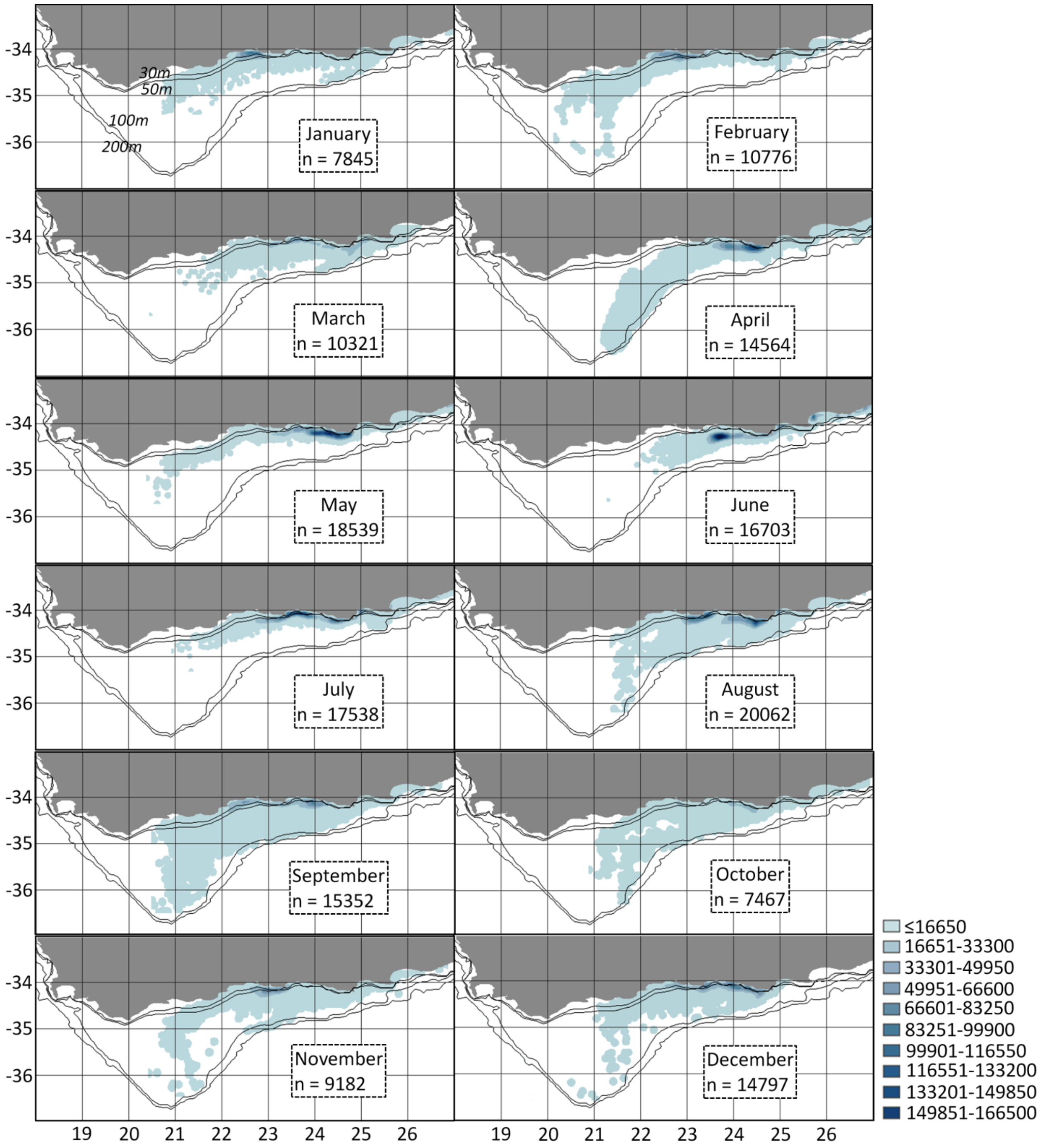

Figure 4.6b: The position of successful paralarvae, released from the inshore spawning sites, on the Agulhas Bank when schooling behaviour commences (day 40 of simulation). Also shown is the number of successful or surviving paralarvae per month (n), out of the 30 000 paralarvae released within the simulations. Values given in the index are generated by the kernel density analysis, and do not indicate paralarval numbers.

Agulhas Bank, a strong southerly component is evident. Some paralarvae were therefore transported southwestwards towards the shelf edge. The degree of southward transport varied between months, as indicated by the distance of paralarvae from the shelf edge. Although only the positions of recruited paralarvae have been plotted, the potential for removal of paralarvae from the Central and Western Agulhas Bank (Figure 4.3) is apparent. Also evident is the northwards transport of paralarvae along the shelf edge towards the west coast. The transport trajectories of paralarvae released from the inshore spawning sites was similar, although there appeared to be a higher degree of retention near the coast, and paralarvae were not transported as far westwards (Figure 4.6b).

The 3-D hydrodynamic model used in this study has been authenticated and found to simulate both the large- and meso-scale elements of the Agulhas Current system (Penven *et al.*, 2006). Although imbued with both biological and behavioural characteristics, paralarval movement within the IBMs was driven by the simulated ocean currents and represents the main circulation features influencing transport and recruitment. The detailed analysis of these specific currents, seasonal variability and their role in transport and recruitment is beyond the scope of this study. It must be noted however, early retroflection of the Agulhas Current, Natal pulses, Agulhas Current boundary phenomena, intermittent wind-driven coastal currents and the formation of cyclonic gyres all act on the particles, resulting in the monthly variability in recruitment success and distribution observed within the models.

Discussion

Transport and recruitment of deep spawned hatchlings

This study provides further evidence of the westwards transport of chokka squid paralarvae from the deep spawning grounds to the cold ridge, predicted in earlier IBMs (Martins *et al.*, 2013). Also in line with earlier findings was the dependence of transport success on spawning site. Using three offshore release areas spanning the entire Tsitsikamma coast, St Francis Bay and Algoa Bay, Martins *et al.* (2013) established paralarvae released off Tsitsikamma showed the greatest success in reaching the cold ridge before the exhaustion of yolk reserves. The current study both corroborates and further refines these findings, showing greatest transport success from the Tsitsikamma West and Knysna hatching sites specifically. Once reaching the cold ridge nursery area, the largest losses resulted from poor retention in this highly productive region.

In Chapter 1, the cold ridge was described as a subsurface feature extending from the Knysna coast (Eastern Agulhas Bank), southwestward onto the Central Agulhas Bank (Figure 4.2b). As such, both coastal and mid-shelf currents influence the retention of paralarvae within the cold ridge. Using average ship-borne ADCP data, Roberts (2005) showed the existence of a narrow eastward coastal flow between Mossel Bay and Cape Seal (Plettenberg Bay, Figure 4.2). This author proposed the eastward current would be beneficial to paralarvae hatching as a result of fringe spawning in this area. The model animations support this hypothesis. This coastal current was also observed to enhance the retention of virtual paralarvae at the base of the cold ridge. Closer to the centre of the cold ridge, westerly flow in the upper mixed layer has been recorded to vary between 15–30 cm.s^{-1} (Roberts and van den Berg, 2002). Surface and bottom currents in the region of the FA gas platform, situated in the centre of the cold ridge(~22°E, ~35°S), are reported to be southwest-southerly (CSIR report 1986, cited in Roberts and van den Berg 2002)). Although current strength varies, the greatest velocities observed were in this direction (CSIR report 1986, cited in Roberts and van den Berg (2002)). Slacking of these mid-shelf currents enhanced the retention of virtual paralarvae within the cold ridge and on the Agulhas Bank. Another feature thought to promote retention in this area, is cyclonic circulation around the ridge (Huggett and Richardson, 2000). Variation in the strength and direction of currents on the Eastern and Central Agulhas Bank resulted in monthly variability in both recruitment success and paralarval distribution.

According to Roberts and van den Berg (2002), paralarvae on the Central and Western Agulhas Bank can be “lost” in two ways. Either they can be transported to the west coast or removed from the shelf through offshore leakage. The current study indicates that offshelf advection of paralarvae, once exiting the cold ridge, can occur. In comparison to losses resulting from poor retention within the cold ridge however, additional losses through offshelf leakage are minimal. The positions of 40-day old paralarvae reveal that deep spawned hatchlings can be transported to the west coast. In model month May (Figure 4.6a), paralarvae were transported as far west as False Bay. Roberts and van den Berg (2002) suggest that due to the low temperatures, low dissolved oxygen levels, considerable offshore transport and high predation levels on the west coast, it is unlikely these paralarvae are recruited.

Despite the wide distribution of 40-day old paralarvae on the Agulhas Bank, deep spawned hatchlings were still concentrated along the south coast during autumn-winter (Figure 4.6a, April–August). This seasonal influence is also evident in the overall monthly results (Figure 4.4a), which indicate increased survival of mid-shelf hatchlings during April–July. This is interesting in light of the offshore migration of adult squid occurring around April. This movement of squid into deeper water suggests a greater potential for deep spawning during autumn. Although no seasonal differences in trawl caught egg biomass were found in Chapter 2, results from certain years show at times offshore spawning increased substantially in autumn (April/May). Findings by Olyott et al. (2007) further support the likelihood that deep spawning increases in April, particularly off the Tsitsikamma coast and Plettenberg Bay. The autumn increase in deep spawning activity off Tsitsikamma appears to take advantage of not only the ideal spawning location, but also currents beneficial for paralarval transport and recruitment. This argument stands when taking into account the increased incubation times occurring at low temperatures. The rate of embryonic development on the deep spawning grounds is 2–3 times longer than inshore (Oosthuizen and Roberts, 2009), equating to an incubation period of ~two months. This suggests that deep spawning in April enables emergent hatchlings to take advantage of the particularly beneficial currents occurring two months later in June, when over 40% of deep spawned hatchlings were recruited.

The earlier IBM study by Martins *et al.* (2013) demonstrated that between 1.13–67.10% of offshore released paralarvae were successfully transported to the cold ridge. Although also factoring in successful transport to inshore feeding areas, the inclusion of paralarval losses beyond the yolk-utilization phase in the current study resulted in lower estimates. The inclusion of temperature related growth also influenced transport to some degree (see Appendix: Figure A.1). Overall, the successful recruitment of deep spawned hatchlings varied between 0.37–42.21% (depending on release month). This equated to only 15.69% of deep spawned paralarvae being successfully recruited to the juvenile population for the entire year modelled.

Transport and recruitment of inshore spawned hatchlings

In contrast successful recruitment of inshore hatched paralarvae varied between 24.89–66.87% (depending on release month). Overall recruitment success for paralarvae released for the entire year modelled was 45.32%. For virtual paralarvae hatching from the inshore spawning grounds, this food-rich environment was the more important nursery area. Here, paralarval losses resulted mainly from poor retention within the feeding grounds and offshore leakage from the narrow Eastern Agulhas Bank. The distribution of 40-day old paralarvae (Figure 4.6), indicates the cold ridge to be an important feeding area for older paralarvae transported to the Central Agulhas Bank. The majority of paralarvae were concentrated on the inshore spawning grounds and/or at the base of the cold ridge. This corresponds to field observations of paralarval distribution on the Agulhas Bank (Augustyn *et al.*, 1994).

As for the mid-shelf hatchlings, model results indicated monthly variability in paralarval recruitment. Recruitment success was highest during the autumn and winter months (April–August), with an additional peak in December. Surprisingly, increased recruitment success was not related to decreased advection off the Eastern Agulhas Bank, initially thought to be a major concern in terms of chokka paralarval survival and recruitment (Roberts and Mullon, 2010; Roberts and van den Berg, 2002). Studies have suggested DVM aids in the retention of paralarvae in certain areas (González *et al.*, 2005; Roberts and van den Berg, 2002), as bottom currents tend to be weaker than surface currents and are often in the opposite direction (Roberts and van den Berg, 2002). The DVM incorporated into the current model combined with complex Agulhas Bank boundary currents and intermittent wind-forced coastal currents likely contributed to the observed success during these months. Coastal retention of inshore released paralarvae was greatest in the centre of the main spawning grounds (St Francis Bay and Tsitsikamma East). Both these areas are used frequently by inshore spawners, as is indicated by the high commercial catches reported from this part of the coast (personal observation).

This study has provided insight into the potential advantage of the two inshore spawning peaks observed for this species (Augustyn *et al.*, 1994; Olyott *et al.*, 2006). The major summer peak (September to December) could enable hatchlings to benefit from the seasonal high productivity resulting from upwelling on the south coast and in the vicinity of the cold ridge. Spawning and/or hatching peaks coinciding with upwelling and planktonic blooms have been observed in other cephalopods, such as *Octopus vulgaris* (Katsanevakis and Verriopoulos, 2006), *L. vulgaris* (Rocha *et al.*, 1999) and *L. forbesi* (Rocha *et al.*, 1999). Also evident in the model is the higher paralarval survival for inshore spawned hatchlings during the period April–August. It is possible this second minor peak (March–July) takes advantage of autumn-winter circulation patterns and their positive role in transport to, or retention in, areas of highest productivity. The year round presence of the copepod *C. agulhensis* on the Agulhas Bank (Huggett and Richardson, 2000) indicates this could indeed be a viable spawning strategy. Just as intermittent flow patterns appear to concentrate chokka squid paralarvae in certain areas (Figure 4.6b), so could their food source be similarly concentrated. This is a strategy believed to have evolved for fish species. It is thought that the spawning time and location of fish species has evolved to ensure that early life larval stages emerge into an environment suitable for their survival (Cushing, 1969 as cited by Somarakis *et al.*, 2002). The suitability of this environment is dependent not only on food availability, but also circulation regimes promoting transport to, and retention in, food-rich areas (Heath, 1992 as cited by Somarakis *et al.*, 2002).

Model limitations and implications

Using statoliths growth increments, Gonzalez et al. (2010) estimated the instantaneous rate of total mortality for wild caught *L. vulgaris* paralarvae over three consecutive years (2003–2005). The estimated instantaneous rate of total mortality (first 90 days) was 9.6, 5.3, and 4.8%.d^{-1} for 2003, 2004, and 2005, respectively. This equates to 1.95–14.68 % of paralarvae surviving to day 40, and gives some indication of the influence of biotic and abiotic factors on loliginid paralarval survivorship. Apart from poor retention on feeding grounds and loss from the shelf ecosystem, no other mortality factors (predation, unfavourable oceanographic conditions) are included in the IBMs used here. The percentages of paralarval survival predicted from the IBMs are therefore unrealistically high. However, considering the values obtained in relation to one another still provides valuable insight.

The overall successful recruitment of deep spawned paralarvae was found to be much lower (15.69%) than for inshore hatched paralarvae (45.32%). The IBM used assumed the year round presence of food-rich areas, and seasonal variation is not taken into account. In reality, both the formation of the cold ridge and upwelling on the inshore spawning grounds is more prevalent in summer (Roberts and van den Berg, 2002; Roberts, 2005; Schumann *et al.*, 1982), although the cold ridge can persist into early winter (June) (Hutchings, 1994). Also not numerically factored into the models is the major summer and minor autumn inshore spawning peaks; nor the probable autumn peak in deep spawning. Furthermore, as suggested by the IBM results, is the importance of spawning location to successful recruitment. As a west to east sequence of inshore spawning is common (Augustyn and Roel, 1998; Augustyn, 1990), the current IBM results indicate the interaction between spawning site and hatching month will also influence recruitment. What is highlighted is the complex interplay between seasonal spawning intensity, spawning site (alongshore), time of hatching, spawning depth (inshore vs. deep), ocean currents on the Agulhas Bank and the presence and persistence of food-rich areas. Considering these complex interactions, it is not surprising that links between chokka squid biomass/catches and environmental conditions (Roberts and Sauer, 1994; Roberts, 1998, 2005) are difficult to establish.

In order to move towards more predictive models, the temporal and spatial aspects of spawning intensity need to be quantified. The effect of the ocean environment on paralarvae, also known to impact recruitment (Challier *et al.*, 2005; Jackson *et al.*, 2008) too needs to be addressed. The influence of environmental conditions on paralarval distribution and abundance needs to be investigated and factored into future models. More realistic IBMs with stronger predictive capabilities could then be developed.

Martins *et al.*, (2013) examined food availability on the Agulhas Bank in relation to the results of the IBM developed in that study. Based on plankton survey results, these authors concluded zooplankton concentrations on the Agulhas Bank can approach the minimum threshold feeding concentration (50 prey.L^{-1}, Vidal *et al.*, 2002b) required for loliginid paralarval survival and growth. It was suggested that a complete absence of food on the Agulhas Bank is probably not often the case, implying a number of good condition paralarvae could reach the cold ridge area beyond the yolk-utilization phase. The importance of this to paralarvae hatching on the easternmost reaches of the Eastern Agulhas Bank was noted. This same argument could be applied to paralarvae exiting the feeding grounds earlier than 14 days, but still retained on the Agulhas Bank. The percentage of paralarvae successfully recruited to the juvenile stage, based solely on food availability, is therefore likely an underestimation.

Does deep spawning contribute to recruitment?

Temperature, food and predation are likely the most important factors affecting paralarval survival, although it is thought that for young hatchlings, sufficient food sources are the most critical (Augustyn *et al.*, 1992). Despite fewer deep spawned hatchlings surviving to the end of the paralarval life-stage, deep spawning could contribute substantially to recruitment. A number of aspects need to be considered. First is the evidence pointing towards an autumn (Chapter 2, Chapter 3 and Olyott *et al.*, 2007) increase in deep spawning off the Tsitsikamma coast. Second is the model predicted successful autumn-winter transport and retention of deep spawned paralarvae hatching from the Tsitsikamma West and Knysna sites (this study). In years where the cold ridge persists until June (Hutchings, 1994), deep spawning would contribute significantly to recruitment. A third aspect to consider is the advantages of embryonic development in the cold mid-shelf environment.

Hatching size is inversely correlated with incubation temperature (Vidal *et al.*, 2006). A laboratory study by Villanueva *et al.* (2003), showed the incubation of *L. vulgaris* at low temperatures to result in significantly larger and longer hatchlings. These authors suggested the larger hatching size confers a competitive advantage due to greater swimming power enhancing food-searching and prey capture abilities, as well as making them less vulnerable to their smaller predators. Larger hatchlings are also less vulnerable to starvation (Vidal *et al.*, 2006). In addition, the ability to withstand periods of starvation is increased at lower temperatures (Vidal *et al.*, 2006), presumably due to lower metabolic rates. Another advantage of lower metabolic rates would be the slower utilization of yolk. This would allow more time for transport to food-rich areas, further reducing vulnerability to starvation. The prolonging of the yolk-utilization phase would allow more time for the development of prey capture abilities (Martins *et al.*, 2010). As *C. agulhensis* is present throughout the year (Huggett and Richardson, 2000), even in the absence of the cold ridge these advantages could prolong paralarval survival until sufficient food sources are encountered.

In conclusion, this work lends weight to the dependence of paralarval transport success on both spawning location and time of hatching, as shown in earlier IBM studies. The current IBM has expanded on initial work, emphasizing the possible importance of the cold ridge and inshore spawning grounds as nursery areas for deep and inshore spawned paralarvae, respectively. Although the significance of ocean currents to transport and recruitment of cephalopod paralarvae is well-known, this work has highlighted the complex interactions between processes influencing recruitment variability for chokka squid. Possible relationships between periods of highest recruitment success and spawning peaks have been identified for both spawning habitats. Based on the likely autumn increase in deep spawning off Tsitsikamma, and the beneficial currents during this period, it can be concluded deep spawning may at times contribute significantly to recruitment. This is particularly true for years where the cold ridge persists into winter.

CHAPTER 5: The origin and distribution of *Loligo reynaudi* paralarvae on the Agulhas Bank, South Africa

Unpublished

Introduction

Chapter 4 illustrated the important role of currents in the transport and survival of chokka squid *Loligo reynaudi* paralarvae. Another factor, equally important in influencing recruitment, is the environment that early life-stages encounter (Challier *et al.*, 2005; Jackson *et al.*, 2008). Distribution of cephalopod paralarvae is generally associated with distinct oceanographic features (González *et al.*, 2005; Moreno *et al.*, 2009; Rocha *et al.*, 1999; Rodhouse *et al.*, 1992; Vidal *et al.*, 2010) and consequently, interannual variability in oceanic conditions can influence recruitment (Rodhouse *et al.*, 1992). This is also true for a number of loliginid species, such as *L. forbesi* (Challier *et al.*, 2005; Rocha *et al.*, 1999), *L. vulgaris* (Rocha *et al.*, 1999) and *Doryteuthis opalescens* (Koslow and Allen, 2011). The main environmental variable found to influence distribution and/or recruitment in these studies was sea surface temperature (SST), particularly with regards to upwelling.

Data on chokka squid paralarval distribution are scarce. A single study by Augustyn *et al.* (1994) showed the majority of chokka paralarvae to be found on the main spawning grounds. Fewer paralarvae have been recorded on the Central Agulhas Bank and shelf edge (Augustyn *et al.*, 1994). In this chapter, the author aimed to investigate the spatial distribution of paralarvae, in relation to the cold ridge; and paralarval abundance in relation to the Agulhas Bank oceanographic environment. Individual-based modelling was used to determine the origin or spawning site of these paralarvae, with reference to inshore versus deep spawning.

Materials and Methods

A survey of environmental conditions on the Central and Eastern Agulhas Bank was undertaken during 3–16 March 2011. This survey was designed to investigate the cold ridge and the spatial distribution of chokka squid paralarvae in relation to this oceanographic feature. Survey design and stations at which CTD profile data and oblique bongo samples were collected are shown in Figure 5.1. CTD profile data were collected in the same manner as described in Chapter 3 using a Neil Brown Instrument Systems Mark 5 CTD. Water samples were collected at standard depths and dissolved oxygen determined using the Winkler titration method (Strickland and Parsons, 1972). At each station, a double bongo net sampler (300 µm mesh) was lowered 5 m from the bottom and then towed obliquely through the water to the surface at a speed of ~2 $m.s^{-1}$. At stations deeper than 200 m, the bongo net was lowered to a maximum depth of 200 m before towing to the surface. Plankton samples were preserved with 10% buffered formalin. Cephalopod paralarvae were removed and chokka squid paralarvae identified based on the morphological descriptions by Vecchione and Lipinski (1995). The distribution and abundance of chokka squid paralarvae on the Agulhas Bank were plotted. Other cephalopod paralarvae were not identified but their presence in samples was noted (Figure 5.1.). Chokka squid paralarvae mantle length was measured to the nearest 0.5 mm and the number of paralarvae caught at each station recorded. CTD data (temperature, dissolved oxygen and salinity) were plotted using Ocean Data View (ODV) 3.4.0. Surface chlorophyll concentration for the survey period (3–16 March 2011) was obtained from the Marine Remote Sensing Unit (MRSU: http://www.afro-sea.org.za/) and averages plotted in ODV. Although the intention was to carry out additional surveys, the cessation of research cruises due to Government Departmental matters, prevented this.

Backwards individual-based model (IBM) simulations (Ichthyop 3.2b) were used to determine the origin or hatching site of bongo caught paralarvae. Model inputs were (1) location of capture, (2) paralarvae mantle length (3) and growth coefficients of 0.0028, to ensure minimum growth within the model. One simulation was run for each bongo caught paralarvae. The model month chosen for the simulations was March of model year three (see Chapter 4 for greater detail). Sixteen paralarvae were released during each simulation. A release schedule was used to seed one individual per day (over a 16-day period), to determine origin under various transport scenarios. Chokka squid paralarvae undergo an initial period of weight loss after hatching (Vidal *et al.*, 2005). By day five however, weight lost is recovered resulting in a “no-net-growth” phase (Vidal *et al.*, 2005). To incorporate this “no-net-growth” phase, models were run for an additional four days once hatching size (2.5 mm mantle length) was reached within the model. It was assumed bongo caught paralarvae measuring 2.5 mm mantle length were at the end of the “no-net-growth” phase and these simulations were run for four days. Model determined origin was overlaid on a digital chart (source: South African Navy Hydrographic Office) of the Agulhas Bank. Bottom depth for each point of origin was determined by the nearest plotted sounding (m). Model days resulting in paralarval origins at bottom depths >130 m were excluded as least likely (see Chapter 2). Most likely origins were plotted.

The abundance of chokka paralarvae in relation to Agulhas Bank (≤200 m depth) surface and bottom environmental conditions (temperature, oxygen, salinity) were analysed.

Results

The majority of chokka squid paralarvae were found on the Eastern Agulhas Bank (Figure 5.1). Paralarvae did not appear to be concentrated along the coast, but were relatively spread out across the shelf. Fewer paralarvae were found on the Central Agulhas Bank and there was little evidence of any accumulation in the vicinity of the cold ridge. No paralarvae were found at stations shallower than 84 m.

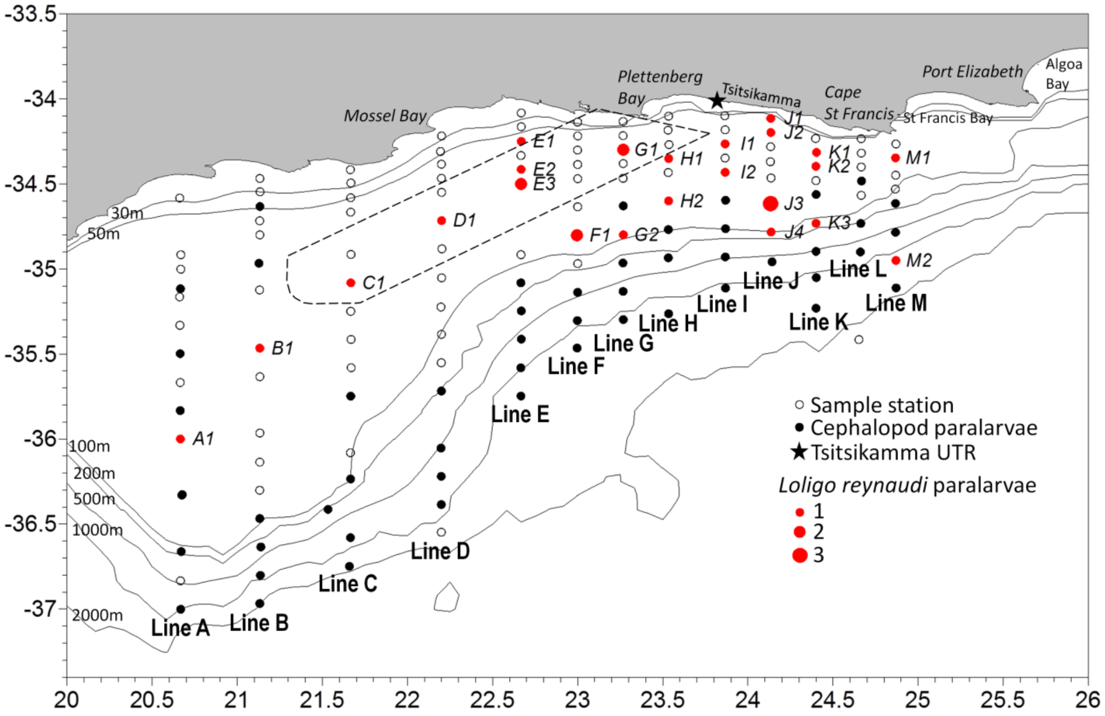

Figure 5.1: Distribution and abundance of *Loligo reynaudi* paralarvae on the Agulhas Bank (red circles). Black circles indicate stations at which other cephalopod paralarvae were found, and empty circles stations at which cephalopod paralarvae were absent. Also shown is the approximate position of the cold ridge (dotted line) and the position of long-term environmental mooring off the Tsitsikamma coast (star). CTD transect lines have been named Line A–Line M (west to east).

Very surprising was the presence of a 2.5 mm (Table 5.1) chokka squid paralarva at station M2 (Figure 5.1). Bottom depth at this station was 1 441 m. The mantle length of chokka squid paralarvae varied from hatching size (2.5 mm) to 4.5 mm, with the majority of paralarvae having mantle lengths of 2.5 or 3 mm (Table 5.1). Apart from *L. reynaudi*, no other cephalopods were identified to species level. It is likely the squid paralarvae found in samples from the shelf edge and beyond (Figure 5.1) were ommastrephids. The smaller paralarvae in these samples still had what appeared to be a proboscis i.e. fused feeding tentacles. This is a common trait in paralarvae belonging to the family Ommastrephidae. Further inshore on the Agulhas Bank, a small number of samples (1–2) contained octopus or *Sepia* sp. hatchlings (Figure 5.1).

Table 5.1: The number and size (mantle length) of paralarvae caught in bongo hauls on the Agulhas Bank (n=28).

Station	**Number of paralarvae**	**Mantle length (nearest 0.5 mm)**
A1	1	4 mm
B1	1	4 mm
C1	1	3 mm
D1	1	2.5 mm
E1	1	2.5 mm
E2	1	3 mm
E3	2	3 mm (2)
F1	2	2.5 mm (2)
G1	2	4 mm and 3.5 mm
G2	1	3.5 mm
H1	1	3 mm
H2	1	3 mm
I1	1	2.5 mm
I2	1	3 mm
J1	1	4.5 mm
J2	1	2.5 mm
J3	3	2.5 mm (2) and 3 mm
J4	1	3 mm
K1	1	2.5 mm
K2	1	3 mm
K3	1	3 mm
M1	1	2.5 mm
M2	1	2.5 mm

Backwards IBM simulations showed large variation in spawning site or origin as a result of release day (Figure 5.2a). Considering what we now know about the depth limits of the deep spawning grounds (71–130 m, Chapter 2), the most likely depth of the origin sites could be determined (model release days 10–12, Figure 5.2b). Origin or spawning sites were categorized as either inshore (≤70 m) or offshore (71–130 m). These simulations showed

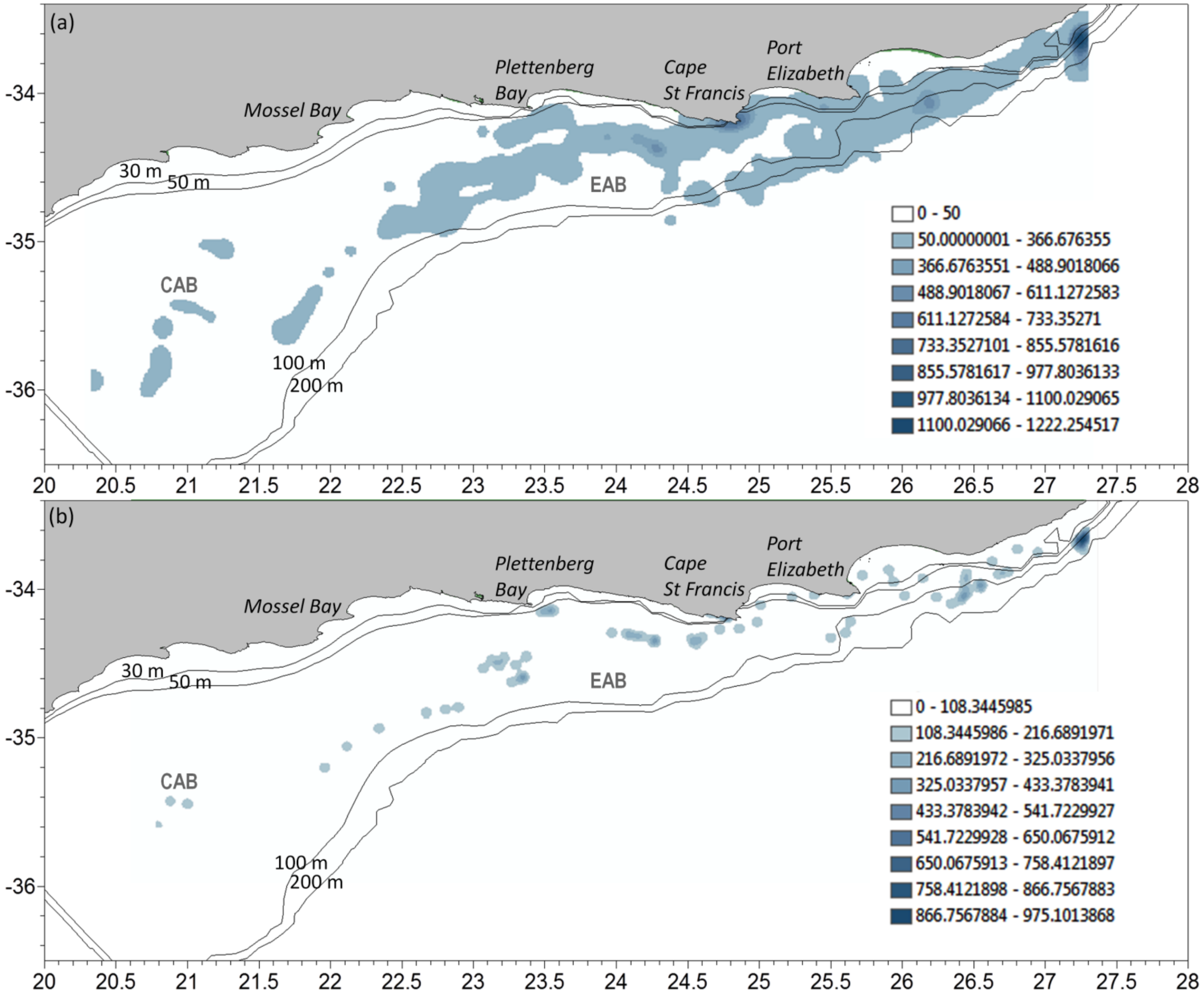

Figure 5.2: (a) Backwards run model predicted spawning sites for 28 captured paralarvae (Figure 5.1) under 16 different transport scenarios. (b) The most likely model predicted spawning sites (sites >130 m deep excluded) for these 28 paralarvae under three different transport scenarios (model days Y3 M3 D14–16). Values given in the index are generated by the kernel density analysis, and do not indicate paralarval numbers.

only 16–20% of paralarvae originated from the inshore spawning grounds, and 72–76% from deep spawning areas. Remaining paralarvae (8%) originated east of Port Alfred beyond the limits of the hydrodynamic model. Possible inshore spawning sites were confined to the Eastern Agulhas Bank, namely Algoa Bay, St Francis Bay and off Plettenberg Bay (see Figure 5.1 and Figure 5.2 for places named). Possible deep spawning sites were found on the east coast mid-shelf, offshore of Algoa Bay, Port Elizabeth, Tsitsikamma and Plettenberg Bay. Two paralarvae were predicted to originate from the mid-shelf in the eastern regions of the Central Agulhas Bank, and surprisingly, one from the centre of the Central Agulhas Bank.

Conditions on the Agulhas Bank during March 2011 were somewhat typical for this time of year. A strong thermocline was evident in the near surface waters (Appendix Figure A.2). Large temperature differences in the upper 50 m of water are common on the Agulhas Bank during summer (Schumann and Beekman, 1984). This thermal stratification results from the warming of surface water (solar radiation) and minimal wind-induced mixing (Schumann and Beekman, 1984). During the transition from summer to autumn, this strong stratification is still evident due to continued warming of the surface layer and shelf edge upwelling of Indian Ocean Central water onto the shelf (Swart and Largier, 1987). The temperature and salinity characteristics of autumn Agulhas Bank surface and bottom water correspond to those of Subtropical Surface water and Indian Ocean Central water, respectively (Swart and Largier, 1987). The latter is evident in Figure 5.7.

Noteworthy was the absence of surface upwelling along the south coast. Sea surface temperature (SST) satellite imagery indicates coastal upwelling before (Figure 5.4a) and after (Figure 5.4d) the March survey. Satellite images of SST during the survey period confirm the lack of wind-driven upwelling. Examples from early on (7 March 2011) and towards the end (15 March 2011) of the survey are given in Figure 5.4b and c. Corresponding chlorophyll concentrations are shown in Figure 5.5. An analysis of bottom temperature data (Figure 5.6), collected at a depth of 10 m off the Tsitsikamma coast (Figure 5.1), indicates a brief upwelling event on the 8 March 2011. Although bottom temperature decreased to ~12 °C, SST satellite data for the same date suggests the cold bottom layer did not penetrate surface waters. Survey CTD data for this region of the Agulhas Bank were only collected from 12 March onwards.

Also absent during this survey was the formation of the cold ridge. Cross-shelf CTD transects (Appendix Figure A.2: Lines A–C) show bottom water to be just below 10 °C on parts of the

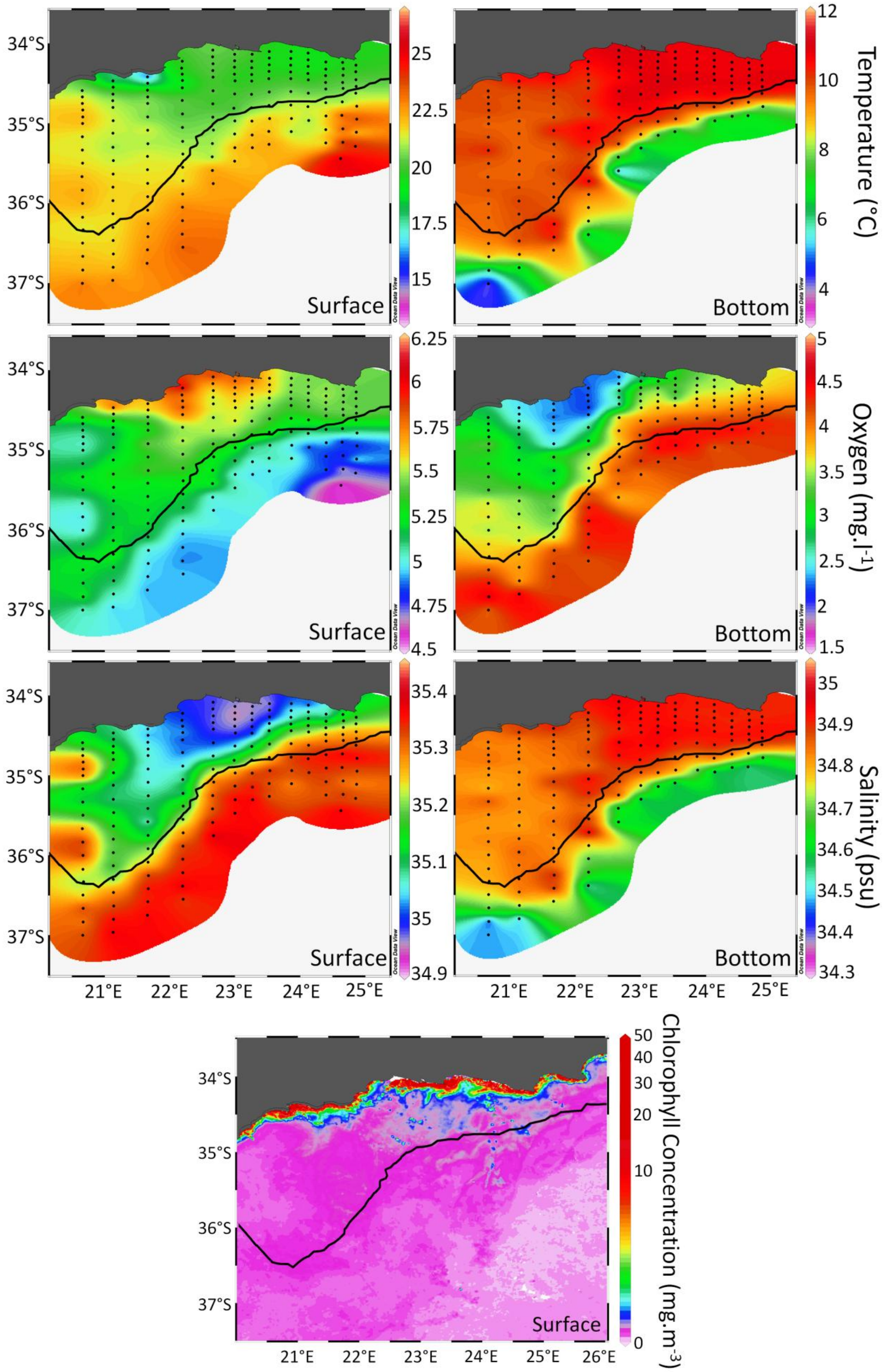

Figure 5.3: Surface and bottom oceanographic conditions on the Agulhas Bank during March 2011. CTD sampling stations are indicated by dots. The 200 m isobath, denoting the shelf edge, is also illustrated.

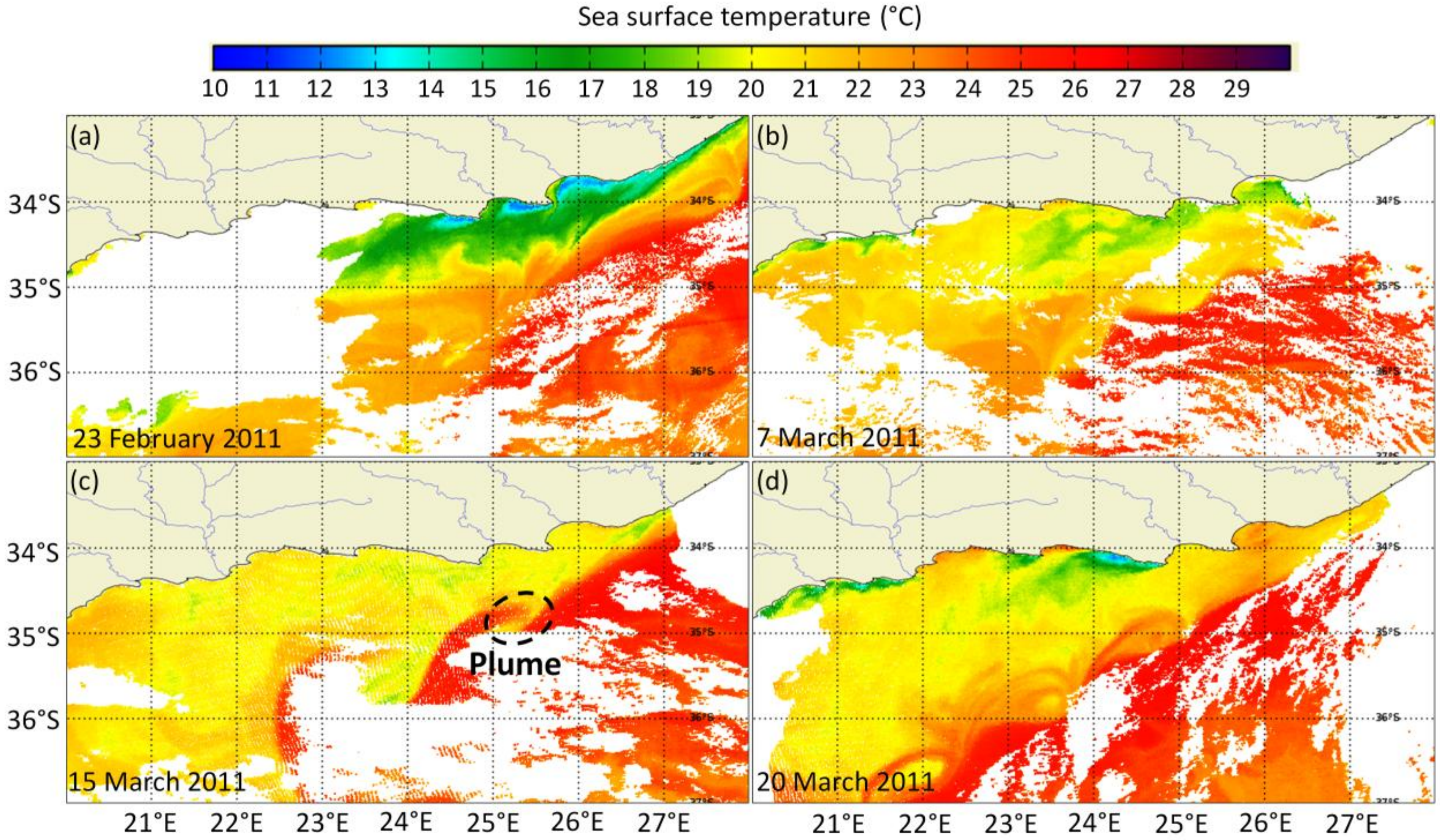

Figure 5.4: Satellite sea surface temperature (MRSU: http://www.afro-sea.org.za/) (a) before (23 February 2011), (b and c) during (7 and 15 March 2011), and (d) after (20 March 2011) the March 2011 Agulhas Bank oceanographic survey. Evident on the 15 March 2011 is a plume of shelf water being drawn off the Eastern Agulhas Bank.

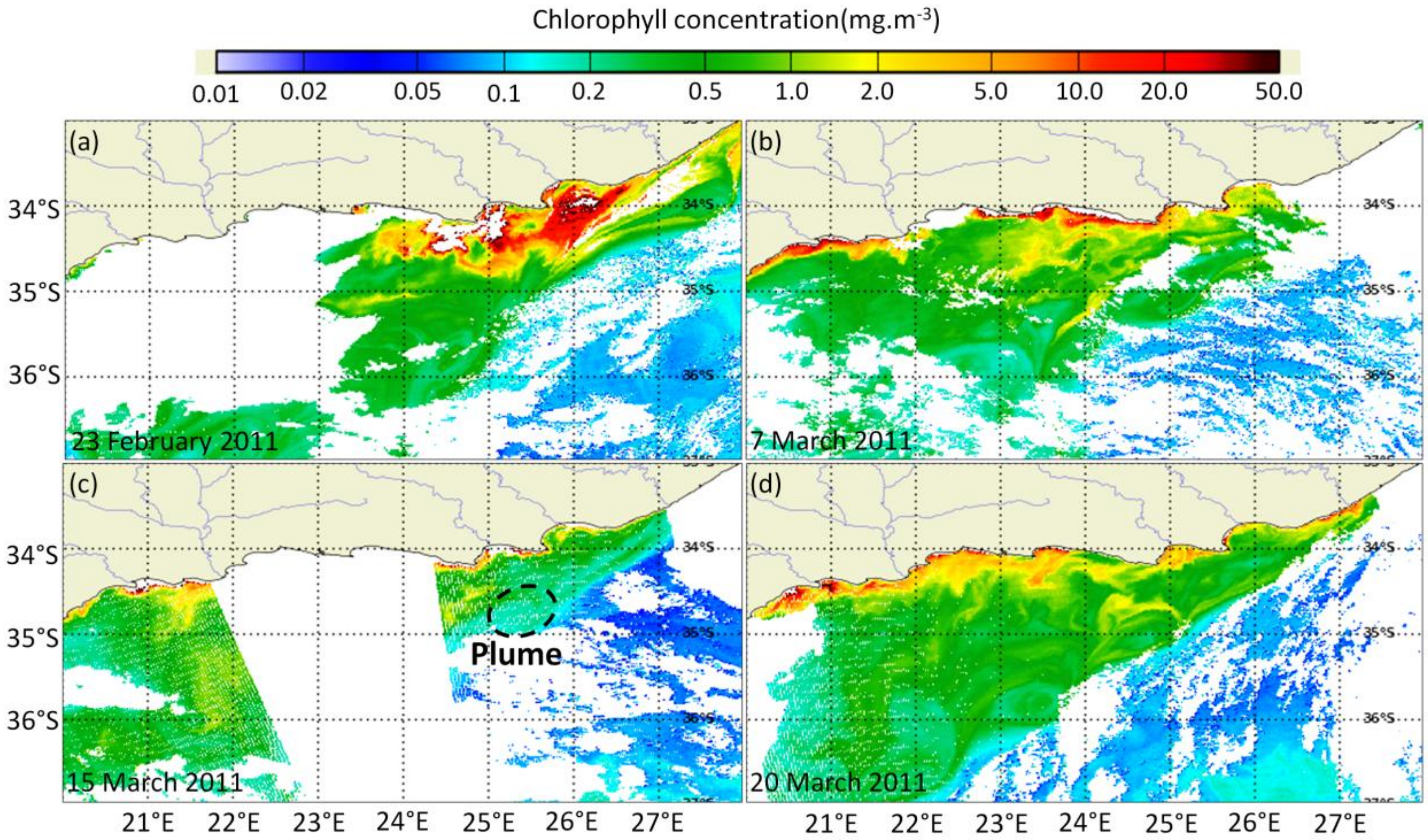

Figure 5.5: Satellite surface chlorophyll concentration (MRSU: http://www.afro-sea.org.za/) (a) before (23 February 2011), (b and c) during (7 and 15 March 2011), and (d) after (20 March 2011) the March 2011 Agulhas Bank oceanographic survey. Evident on the 15 March 2011 is a plume of shelf water being drawn off the Eastern Agulhas Bank.

Central Agulhas Bank and the thermocline positioned 20–30 m beneath the surface. The cross-shelf transects show strong shelf edge upwelling.

Surface temperatures on the Eastern Agulhas Bank (Figure 5.3) and inshore of the Central Agulhas Bank ranged between 18 and 21.25 °C. Only a small area of the south coast had surface temperatures ~15–17 °C. Temperatures on the Central Agulhas Bank and area beyond the 200 m isobath were slightly higher ~22.5°C. Bottom temperatures on the shelf of the Agulhas Bank ranged between 10 and 12°C. Beyond the shelf edge bottom temperatures were <10°C. Surface dissolved oxygen levels were relatively high (≥4.5 mg.l^{-1}) across the entire survey area. Bottom dissolved oxygen levels increased from ~2 mg.l^{-1} at the coast in the centre of the survey area, east towards the main spawning grounds (~4 mg.l^{-1}) as well as south towards the shelf edge (4.5 mg.l^{-1}). Surface salinity levels increased in a similar manner as described for bottom dissolved oxygen (increase from 35 psu to 35.4 psu both eastwards and south towards the shelf edge). Bottom salinity was lowest inshore on the Central Agulhas Bank, increasing slightly towards the eastern region of the survey area and offshore towards the shelf edge. On the Agulhas Bank itself, bottom salinity did not exceed 35 psu. Average surface chlorophyll concentrations during the survey period were highest inshore, corresponding with satellite chlorophyll concentration for the same period (Figure 5.5b and c). The majority of the Agulhas Bank had levels <1 mg.m^{-3}.

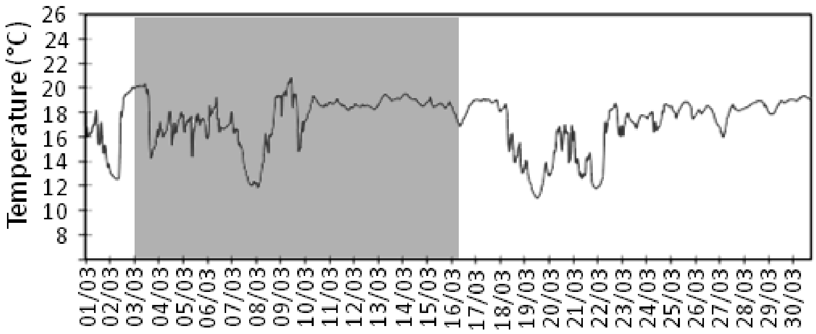

Figure 5.6: Surface temperature data for a long-term environmental mooring off Tsitsikamma (see Figure 5.1 for position) deployed at an inshore site with a bottom depth of 10 m. The shaded area indicates the March 2011 oceanographic survey period.

As paralarvae samples were collected using a bongo net lowered close to the bottom and then hauled obliquely to the surface, it is impossible to determine where in the water column paralarvae were. Nonetheless, chokka squid paralarvae were present throughout the surface temperature range plotted in Figure 5.7. Stations with the highest number of chokka paralarvae had surface temperatures <21 °C. In terms of bottom temperature, chokka paralarvae were present at temperatures <11.5 °C, with the greatest abundance found at stations with bottom temperatures between 10.5–11.5 °C. Chokka paralarvae were present across the surface salinity range 34.9–35.4 psu, but no relationship concerning abundance is evident. Chokka paralarvae were only found at stations with a bottom salinity of <35 psu. Surface and bottom dissolved oxygen did not appear to influence the presence of chokka paralarvae. Samples with the highest abundance however were collected at stations with surface dissolved oxygen levels >5.2 mg.l^{-1} and bottom dissolved oxygen levels >3.9 mg.l^{-1}.

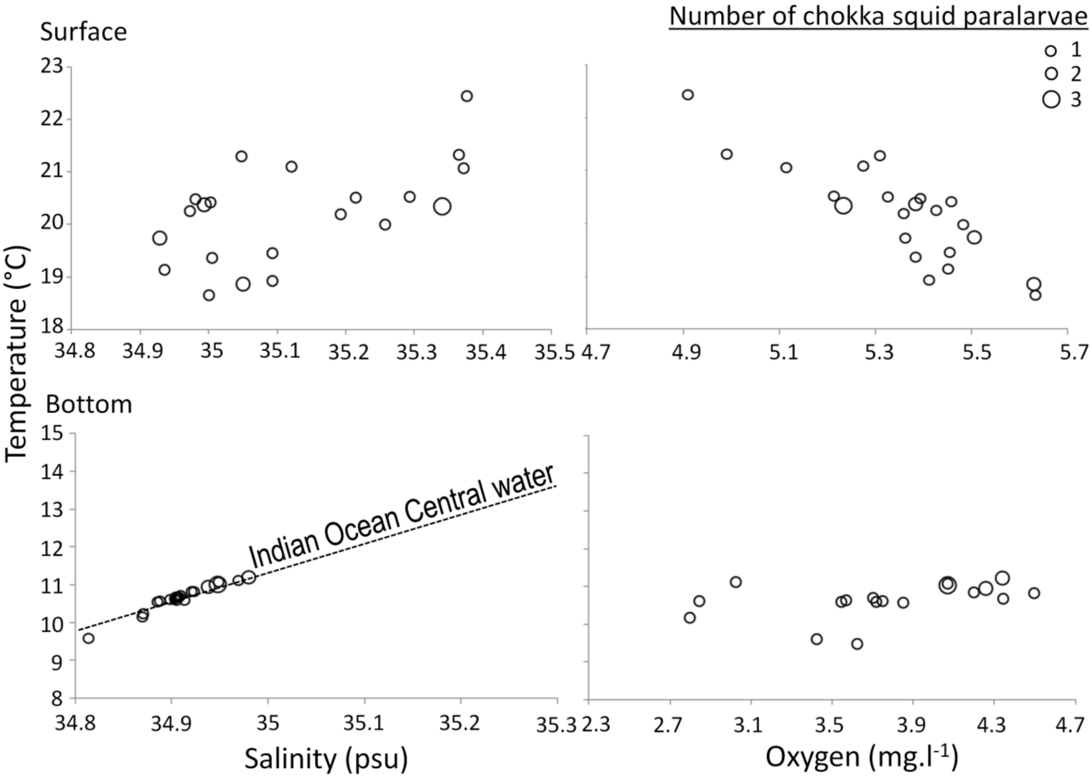

Figure 5.7: The presence and abundance (indicated by circle size) of *Loligo reynaudi* paralarvae in relation to surface and bottom temperature, salinity and oxygen. The temperature-salinity characteristics of Indian Ocean Central water are indicated by a dotted line.

Discussion

Spatial distribution and meso-scale features/circulation

The distribution of chokka squid paralarvae during the survey period corresponds with early observations by Augustyn *et al.* (1994). That is, the majority of paralarvae occur on the Eastern Agulhas Bank in the vicinity of the main spawning grounds. One obvious disparity found during the current survey was the absence of paralarvae from shallow stations. Two possible explanations for the observed paralarval distribution exist.

Upwelling has been shown to greatly influence both paralarval abundance and spatial distribution (González *et al.*, 2005; Moreno *et al.*, 2009; Rocha *et al.*, 1999). The effect of upwelling on paralarvae is two-fold. Firstly, upwelling draws cold nutrient rich water upwards into the euphotic zone. The resultant primary and secondary production creates an area of high food abundance, and hence ideal conditions for the growth and survival of paralarvae (Vidal *et al.*, 2010). Secondly, upwelling could enhance the retention of paralarvae in coastal areas. On the south coast of South Africa, wind-driven coastal upwelling is frequent in summer (November–February) (Schumann *et al.*, 1982). Strong easterly winds results in the offshore transport of the surface layer of water. This surface layer is then replaced by cold subsurface water drawn inshore and upwards (Schumann *et al.*, 1982). Under such conditions, the diel vertical migration of paralarvae might result in their retention in coastal areas (González *et al.*, 2005; Moreno *et al.*, 2009). The prevalence of wind-driven coastal upwelling in summer suggests retention of paralarvae along the coast will be greatest during this period. A comparison of early spring (September) and late spring/early summer (October–December) paralarval distribution on the Agulhas Bank, (see Augustyn *et al.*, (1994) for distribution plots) indicates this could be the case. Moreno *et al.* (2009) observed a similar seasonal distribution of loliginid paralarvae off the coast of Portugal. During winter paralarvae were found over the whole sample area with higher abundances over the 100 m isobath. During summer paralarvae were concentrated in coastal waters. This variation in seasonal distribution was attributed to, amongst other factors, low temperature and upwelling. The absence of wind-driven coastal upwelling during the March survey could explain to some extent the dispersed distribution of chokka squid paralarvae over the mid-shelf and their absence from areas with high surface chlorophyll concentration (Figure 5.3 and Figure 5.5b and c).

Meso-scale circulation during the sample period could explain the distribution of paralarvae on the Central Agulhas Bank. Roberts and van den Berg (2002) proposed paralarvae on the Central Agulhas Bank could be removed from the shelf through offshore leakage. As shown in Chapter 4: Figure 4.6a, the modelled paralarval end points indicate at times transport on the Central Agulhas Bank is southwestward. The position of paralarvae D1, C1, B1 and A1 on the Central Agulhas Bank certainly suggests southwestward transport towards the shelf edge. When the cold ridge forms on the Central Agulhas Bank, cyclonic circulation around the ridge is thought to enhance the local retention of copepods (Huggett and Richardson, 2000). The high summer densities of the copepod *Calanus agulhensis* within the vicinity of the cold ridge supports this suggestion (Huggett and Richardson, 2000). Despite the retention however, the net westward movement of eggs and larvae across the Central Agulhas Bank still occurs (Huggett and Richardson, 2000). It is likely that when the cold ridge is formed, the westward transport of chokka squid paralarvae is similarly impeded. As well as creating an area of high primary and secondary production, the cold ridge may also enhance paralarval survival by retarding the southwestward transport suggested by the positions of paralarvae D1, C1, B1 and A1.

It should be noted that a large portion of the main spawning grounds were not sampled during the current survey (east of Cape St Francis, Figure 5.1). It is possible there was retention of paralarvae within the bays beyond the survey area (St Francis Bay and Algoa Bay), indicating inshore spawning, or transport of inshore hatched paralarvae to the adjacent mid-shelf. An analysis of satellite SST data (http://www.afro-sea.org.za/) shows no upwelling within these areas during the survey period (3–16 March 2011) and so decreases the likelihood of retention.

Paralarval loss from the Agulhas Bank

Already mentioned was the presence of a chokka squid paralarva beyond the shelf edge, at a station with a bottom depth of 1 441 m (Figure 5.1 and Table 5.1). Model results indicate this paralarva originated from the east coast (beyond or close to the eastern boundary of the model), and was then advected from the shelf off St Francis Bay. Satellite imagery of SST and chlorophyll concentrations on the 15 March (Figure 5.4c and Figure 5.5c), show a plume of shelf water being drawn off the Eastern Agulhas Bank near Cape St Francis. It is highly likely paralarva M2 was entrained in this filament of water and advected off the shelf. The removal of biological material from the shelf edge of the Eastern Agulhas Bank has been demonstrated by Roberts and van den Berg (2002). According to regional ocean modelling systems (ROMS) and IBM simulations, numerous chokka squid paralarvae are lost as a result of advection from the Eastern Agulhas Bank (Roberts and Mullon, 2010; Chapter 4). The leakage of shelf waters evident in the satellite images, and the presence of a chokka squid paralarvae so far beyond the shelf edge, confirm this. The mantle length size (2.5 mm) indicated the paralarva to still be within the period of “no-net-growth” and hence yolk-utilisation phase. Once yolk reserves are exhausted it is likely young hatchlings transported off the shelf die of starvation.

Wild caught paralarval origins

Model results predicted that the majority of paralarvae originated from deep spawning sites on the Eastern Agulhas Bank (Figure 5.2b). Paralarvae within the simulations were transported for 4–19 days, depending on input size (2.5–4 mm). The minimum growth coefficient used within the IBM equated to a growth rate of 0.1 mm.day^{-1}, and 40-day old simulated paralarvae reached a mantle length of ~6 mm (data from Chapter 4 IBM). Market squid *D. opalescens* paralarvae, which have a similar hatching size to *L. reynaudi* (Vidal et al 2005), have a dorsal mantle length of 6.1 mm when schooling begins 35-40 days after hatching (Vidal *et al.*, 2009). It is therefore unlikely the offshore origin estimates are the result of too short a transport duration (in terms of paralarval growth). Instead, it appears that overall, the backwards run simulations failed to predict realistic spawning sites. As highlighted in Chapter 1, the Agulhas Bank ocean environment is highly variable. This variability is also evident in the hydrodynamic model used to drive the IBMs (see Chapter 4). It is clear however, that in the majority of cases the model days used to run the backwards simulations did not accurately simulate the localized circulation patterns prior to and during the survey. Although backwards run simulations have been used to predict the origin of wild caught hake larvae (Garavelli *et al.*, 2012), that simulation was run for 30 days. The longer time period likely allowed the masking of localized short-term variability within the hydrodynamic model and origin was largely dependent on the dominant circulation patterns.

Paralarval abundance and oceanographic conditions

As yet, no specific inferences can be made regarding the abundance of chokka squid paralarvae in relation to oceanographic conditions, and a comparative analysis is not possible due to sampling being limited to one survey. Regarding observed oxygen concentration, levels both in the surface and bottom waters where above those known to impact chokka squid (Roberts, 2005). There is some indication that paralarvae were more abundant at stations with surface temperatures between 18 and 21.5 °C, (Figure 5.7). However, this was the temperature range of surface waters on the Eastern Agulhas Bank (Figure 5.3). It follows that this is almost certainly a result of the position of the main spawning grounds on the Eastern Agulhas Bank and not indicative of a relationship with temperature. In terms of bottom conditions, paralarvae where more abundant at stations with temperatures between 10.5–11.5 °C (Figure 5.7). Observations by M. Lipiński (as cited in Augustyn *et al.* (1992)) indicate chokka paralarvae move into surface waters at night whilst inhabiting deeper depths during the day (on or near the bottom). Day-time depths and the age at which diel vertical migration commences are as yet unknown. The specific gravity of newly hatched chokka squid paralarvae has been assessed by Martins (2009). Results revealed paralarvae are negatively buoyant during the initial yolk-utilisation phase, regardless of yolk content. This does not imply young paralarvae are confined to bottom waters, as certain planktonic larvae have a similar specific gravity (Martins, 2009). Conclusions with regard to abundance and bottom conditions should therefore be made with great caution.

Summary and conclusions

This study has emphasized a critical knowledge gap and the necessity of further studies of this nature. Understanding the distributional ecology of cephalopod paralarvae is essential to furthering knowledge of the life cycles of this group (Vidal *et al.*, 2010). The profound influence of current regimes, spawning location and time of hatching on recruitment was discussed in Chapter 4. Moreno *et al.* (2009) established significant relationships between month, latitude and depth, and loliginid paralarval distribution in western Iberia. Further studies of this nature could not only substantiate the findings of individual-based models developed for chokka squid paralarvae; but knowledge of distribution and abundance in relation to oceanographic conditions will enable the refinement of the these models. Environmental variables, such as temperature, are known to influence recruitment due to effects on early life stages (Rodhouse *et al.*, 1992). This has implications for modelling the potential effects of climate change during the environmentally sensitive early life-history stages.

This chapter has highlighted a number of scenarios likely contributing to recruitment variability in chokka squid. First is the possible influence of coastal upwelling on the retention of paralarvae on the inshore spawning grounds. Similarly the formation of the cold ridge may aid in retention on the Agulhas Bank. The second factor impacting recruitment is the loss of paralarvae from the Agulhas Bank ecosystem due to offshelf advection. This study has confirmed the loss of paralarvae from the Eastern Agulhas Bank, previously observed in IBMs, due to Agulhas Current boundary phenomena and resultant offshelf leakage. Some data supporting the loss of paralarvae from the Central and Western Agulhas Bank, observed in IBMs (Chapter 4), has also been provided. Furthermore, this work has brought to light the unreliability of short (in terms of model days), backwards run simulations and their use in determining wild caught paralarvae origins.

CHAPTER 6: Synthesis and conclusions

Unpublished

Although spawning mostly within shallow bays, the South African chokka squid *Loligo reynaudi* frequently makes use of deeper spawning areas. Previous research has: (1) confirmed the viability of deep spawned eggs (Oosthuizen and Roberts, 2009), (2) confirmed the westward transport of deep spawned hatchlings to the cold ridge nursery area/feeding grounds (Martins *et al.*, 2010, 2013; Roberts and Mullon, 2010), (3) provided evidence of the formation of large spawning aggregations offshore, and (4) illustrated that frequent windows of opportunity exist for deep spawning as a result of mid-shelf warming events. Despite these findings, many questions remained unanswered. How the deep spawning environment differs from the inshore spawning habitat; the extent, range and potential importance of deep spawning; and the fate of deep spawned hatchlings and their role in recruitment were unknown. This study has expanded on initial research, supporting previous findings and providing new knowledge. We can now begin to answer a number of questions about deep spawning and its role in chokka squid recruitment.

How is deep spawning on the cold mid-shelf possible?

In Chapter 3 it was established that an inshore-offshore continuum of suitable chokka squid spawning habitat exists in St Francis Bay. A large proportion of the mid-shelf can not only be considered suitable spawning habitat, but some mid-shelf areas are comparable with spawning sites inshore. Chapter 3 has provided evidence substantiating: (1) a seasonal trend of warming and cooling of the mid-shelf bottom layer, and (2) transient intrusions of warm and cooler water onto the mid-shelf, causing “extreme” high and low temperature events. Although mid-shelf warming events last from a few hours to a number of days, they result in similar conditions to those on the inshore spawning grounds. Results have also demonstrated that mid-shelf bottom temperatures can at times be warmer than on the inshore spawning grounds (~14 vs ~10 °C). These data indicate warming events combined with seasonal warming, create frequent optimal temperature conditions for spawning (Oosthuizen and Roberts, 2009) and can also temporarily expand or shift spawning habitat into deeper water (Chapter 3).

Where and when does deep spawning occur?

There is little doubt that the inshore, shallow coastal areas (≤70 m) of the Eastern Agulhas Bank, between Knysna and Port Alfred, form the epicentre of the chokka squid spawning grounds. This has been linked to specific spawning habitat requirements (Roberts, 2005). The lack of squid eggs on the mid-shelf west of 22°45' (offshore of the Knysna area, Figure 2.1c), suggests the deep spawning grounds to also be geographically defined (Chapter 2). This too is likely linked to suitable spawning habitat. Data indicated not only is deep spawning largely confined to the Eastern Agulhas Bank, but appears to mostly occur within a distinct depth range (70-130 m). Based on the findings in Chapter 3, it is thought that this is related to the frequency and magnitude of mid-shelf warming events. Substantial increases in bottom temperature were found to occur at a depth of 120 m. Although warm events were still evident in deeper waters (205 m), warming of the bottom layer this far offshore was less extreme.

As chokka squid are known to spawn inshore throughout the year (Augustyn *et al.*, 1994), it is plausible that some deep spawning will occur year round. Observations of deep spawning, as evidenced by trawl caught eggs, have been many in both spring and autumn (Chapter 2). As Department of Agriculture, Forestry and Fisheries (DAFF) south coast research trawl surveys are only undertaken in spring and autumn (see Chapter 2), the year round occurrence of deep spawning could not be substantiated. There is mounting evidence however, suggesting an increase in deep spawning activity in autumn (April). Generally, chokka squid move offshore around April, as is reflected by the higher offshore catches (commercial) during this period. Autumn DAFF demersal research trawl catches add weight to this theory. Olyott *et al.* (2007) report autumn catches in deeper water off the Tsitsikamma coast and Plettenberg Bay (23°–24°E) to consist entirely of adult squid. The seasonal warming of mid-shelf bottom temperature (Chapter 3) and the greater intensity of warming events in autumn-winter (Chapter 3), also suggests the potential for an increase in deep spawning. The seasonal analysis of average egg biomass in Chapter 2, did not support this theory. Results from certain years however, indicated at times deep spawning increased substantially in autumn. If deep spawning is indeed made possible by warming of the mid-shelf bottom layer, variability in the oceanographic environment on the Eastern Agulhas Bank could explain this to some extent.

Why does deep spawning occur?

Based on the premise that deep spawning on the cold mid-shelf is made possible by warming of the bottom layer (Chapter 3), it would appear chokka squid are spawning habitat opportunists. Sexually mature squid are found throughout the year, both inshore and offshore (Olyott *et al.*, 2006). The cross-shelf movement (Sauer *et al.* (1997); Chapter 3) and alongshore migrations (Sauer *et al.*, (2000); Sauer (1995b); Chapter 3) of squid on the south coast possibly increases the likelihood of encountering favourable conditions or windows of opportunity. This does not imply that deep spawning cannot be “forced” by adverse conditions inshore. It has been suggested that dense turbidity events (Roberts and Sauer, 1994), anthropogenic influences such as disturbance caused by fishing activity (Oosthuizen *et al.*, 2002a) and temperatures >21 °C (Augustyn and Roel, 1998), could force squid to spawn in deeper waters. The high number of mature eggs in the oviducts of females on the deep spawning grounds indicates chokka squid can store mature eggs for prolonged periods, and are not forced to empty their oviducts (Sauer *et al.*, 1999). It is more likely then that unfavourable conditions inshore promote deep spawning, by forcing squid to seek out suitable habitat on the deep spawning grounds.

Although at this stage still purely speculative, it would appear that both predation and fishing pressure are indeed greater on the inshore spawning grounds, possibly forcing squid into deeper waters. Not only are there fewer predators offshore, but there is an absence of the majority of species that have been observed actively preying on or attacking spawning squid (Smale *et al.*, 2001). The disruption of spawning by predator activity demonstrated by Smale *et al*. (2001) suggests this argument could at times be applicable. However, based on the observations of deep spawning in other loliginid species, i.e. *Doryteuthis gahi* (Laptikhovsky, 2007) and *D. opalescens* (Butler *et al.*, 1999; Zeidberg *et al.*, 2011), and links to ambient temperature; it would seem warming of the mid-shelf bottom layer is the main driver behind deep spawning.

Does deep spawning contribute to recruitment?

This study has underlined a number of factors influencing paralarval survivorship and recruitment. Chapter 4 demonstrated the effect of spawning site (alongshore), time of hatching, spawning depth (inshore vs. deep) and ocean currents on survival and recruitment success. In Chapter 5 the loss of paralarvae from the Eastern Agulhas Bank due to Agulhas Current boundary phenomena and resultant offshore leakage of shelf waters was confirmed. The potential role of wind-induced coastal upwelling and the cold ridge in paralarval distribution and retention in food-rich areas was discussed (Chapter 5). Also evident in the individual-based model (IBM) developed in Chapter 4, was the complex interaction between these factors and paralarval transport and survival.

The IBM indicated that overall 15.69% of deep spawned hatchlings would be recruited into the juvenile population (Chapter 4). Deep spawning was found to contribute 18% to total chokka squid egg biomass (Chapter 2). In light of the distribution of egg biomass between the two spawning habitats, and the survival of these hatchlings, deep spawning can be calculated to contribute 7.6% to the total percentage of paralarvae recruited (inshore: 92.4%). This calculation is based on overall results, and does not take into account monthly variation in spawning depth, intensity or paralarval survival.

When considering the evidence pointing towards: (1) an autumn (Chapter 2, Chapter 3 and Olyott *et al.*, 2007) increase in deep spawning off the Tsitsikamma coast (Olyott *et al.*, 2007); and (2) the model predicted successful autumn-winter transport and retention of deep spawned paralarvae hatching from the Tsitsikamma West and Knysna sites (Chapter 4), it can be concluded that deep spawning may contribute significantly to recruitment at certain times. Deep spawning may indeed create a buffer to intense fishing pressure inshore, by providing a reservoir of recruits.

Future research

This study has contributed new knowledge to our understanding of deep spawning and its role in chokka squid recruitment. Important knowledge gaps have also been identified. Future studies should focus on:

(1) Substantiating and quantifying, where possible, the seasonal variability of deep spawning. In light of the IBM results, deep spawning could not only provide a reservoir of recruits, but also strengthen recruitment in certain years. Annually quantifying both inshore and offshore spawning, could also aid in the prediction and/or estimation of annual recruitment strength.

(2) Estimate fishing effort inshore versus offshore. Prior to 1990, the South African commercial squid fishery was estimated to focus 90% of its effort on the inshore spawning grounds. Since the use of sea drogues and strong lights, fishing efficiency offshore has improved considerably. The offshore movement of the commercial fleet in autumn suggests the substantial removal of potential deep spawners.

(3) Investigate the distributional ecology of paralarvae. The distribution of paralarvae in relation to oceanographic features and environmental variables needs further study. This has important implications for both paralarval growth and recruitment success. This knowledge will also enable the refinement of IBMs and the development of climate change models.

(4) Another important focus for future research is the ground-truthing of predicted results of the IBM developed in this and previous studies.

References

Arkhipkin, A. I., Laptikhovsky, V. V., and Middleton, D. A. J. 2000. Adaptations for cold water spawning in loliginid squid: *Loligo gahi* in Falkland waters. Journal of Molluscan Studies, 66: 551–564.

Arkhipkin, A. I., and Middleton, D. A. J. 2003. In-situ monitoring of the duration of embryonic development in the squid *Loligo gahi* (Cephalopoda: Loliginidae) on the Falkland shelf. Journal of Molluscan Studies, 69: 123–133.

Augustyn, C. J. 1986. The squid jigging fishery on the South African south coast. South African Shipping News and Fishing Industry Review.

Augustyn, C. J. 1989. Systematics, life cycle and resource potential of the chokker squid *Loligo vulgaris reynaudii*. Ph.D. thesis, University of Port Elizabeth, 378 pp.

Augustyn, C. J. 1990. Biological studies on the chokker squid *Loligo vulgaris reynaudii* (Cephalopoda; Myopsida) on spawning grounds off the south-east coast of South Africa. South African Journal of Marine Science, 9: 11–26.

Augustyn, C. J. 1991. The biomass and ecology of chokka squid *Loligo vulgaris reynaudii* off the West Coast of South Africa. South African Journal of Zoology, 26: 164–181.

Augustyn, C. J., Lipiński, M. R., and Roeleveld, M. A. C. 1995. Distribution and abundance of sepioidea off South Africa. South African Journal of Marine Science, 16: 69–83.

Augustyn, C. J., Lipiński, M. R., and Sauer, W. H. H. 1992. Can the *Loligo* squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. South African Journal of Marine Science, 12: 903–918.

Augustyn, C. J., Lipiński, M. R., Sauer, W. H. H., Roberts, M. J., and Mitchell-Innes, B. A. 1994. Chokka squid on the Agulhas Bank: life history and ecology. South African Journal of Science, 90: 143–153.

Augustyn, C. J., and Roel, B. A. 1998. Fisheries biology, stock assessment, and management of the chokka squid (*Loligo reynaudii*) in South African waters: An overview. California Cooperative Oceanic Fisheries Investigations Reports, 39: 71–80.

Augustyn, C. J., Roel, B. A., and Cochrane, K. 1993. Stock assessment in the chokka squid *Loligo vulgaris reynaudii* fishery off the coast of South Africa. *In* Recent Advances in Fisheries Biology, pp. 3–14. Ed. T. Okutani, R. K. O'Dor, and T. Kubodera. Tokai University Press, Tokyo.

Badenhorst, A., and Smale, M. J. 1991. The distribution and abundance of seven commercial trawlfish from the Cape south coast of South Africa, 1986-1990. South African Journal of Marine Science, 11: 377–393.

Bartol, I. K., Krueger, P. S., Thompson, J. T., and William, J. S. 2008. Swimming dynamics and propulsive efficiency of squids throughout ontogeny. Integrative and Comparative Biology, 48: 720–733.

Bianchi, G., Carpenter, K. E., Roux, J.-P., Molloy, F. J., Boyer, D., and Boyer, H. J. 1999. FAO species identification field guide for fishery purposes. The living marine resources of Namibia. FAO, Rome.

Bigelow, K. A. 1992. Age and growth in paralarvae of the mesopelagic squid *Abralia trigonura* based on daily growth increments in statoliths. Marine Ecology Progress Series, 82: 31–40.

Boletzky, S. 1987. Embryonic phase. *In* Cephalopod life cycles, Vol. II, pp. 5–31. Ed. P. R. Boyle. Academic Press, London.

Booth, A. J. 1998. Spatial analysis of fish distribution and abundance patterns : A GIS approach. Fishery Stock Assessment Models: Alaska Sea Grant College Program, AK-SG-98-0: 719–740.

Boyd, A. J., and Shillington, F. A. 1994. Physical forcing and circulation patterns on the Agulhas Bank. South African Journal of Science, 90: 114–122.

Boyle, P. R., and Rodhouse, P. G. 2005. Cephalopods. Ecology and Fisheries. Blackwell Science Ltd. Oxford, U.K.

Branch, G. M., Griffiths, C. L., Branch, M. L., and Beckley, L. E. 2010. Two Oceans: A guide to the marine life of southern Africa. Struik Nature, Cape Town.

Butler, J., Fuller, D., and Yaremko, M. 1999. Age and growth of market squid (*Loligo opalescens*) off California during 1998. California Cooperative Oceanic Fisheries Investigations Reports, 40: 191–195.

Challier, L., Royer, J., Pierce, G. J., Bailey, N., Roel, B., and Robin, J. 2005. Environmental and stock effects on recruitment variability in the English Channel squid *Loligo forbesi*. Aquatic Living Resources, 18: 353–360.

Chang, N. 2008. Numerical ocean model study of the Agulhas Bank and the Cool Ridge. Ph.D. thesis, University of Cape Town, 164 pp.

Chotiyaputta, C. 1997. Distribution, abundance, reproductive biology, age and growth of *Loligo chinensis* and *Loligo duvauceli* in the western Gulf of Thailand. *In* Second World Fisheries Congress: Proceedings: Developing and Sustaining World Fisheries Resources: the State of Science and Management, pp. 614–619. Ed. D. A. Hancok, D. C. Smith, A. Grant, and J. P. Beumer. CSIRO Publishing, Collingwood.

Downey, N. J., Roberts, M. J., and Baird, D. 2010. An investigation of the spawning behaviour of the chokka squid *Loligo reynaudii* and the potential effects of temperature using acoustic telemetry. ICES Journal of Marine Science, 67: 231–243.

Fields, W. 1965. The structure, development, food relations, reproduction and life history of the squid *Loligo opalescens* Berry. Fish Bulletin, 131: 1–108.

Foote, K. G., Hanlon, R. T., Iampietro, P. J., and Kvitek, R. G. 2006. Acoustic detection and quantification of benthic egg beds of the squid *Loligo opalescens* in Monterey Bay, California. The Journal of the Acoustical Society of America, 119: 844.

Garavelli, L., Gruss, a., Grote, B., Chang, N., Smith, M., Verley, P., Stenevik, E. K., *et al.* 2012. Modeling the dispersal of Cape hake ichthyoplankton. Journal of Plankton Research, 34: 655–669.

Goldman, D. A., and McGowan, M. F. 1991. Distribution and abundance of Ommastrephid squid paralarvae off the Florida Keys in August 1989. Bulletin of Marine Science, 49: 614–622.

Gonzalez, F., Otero, J., Pierce, G. J., and Guerra, A. 2010. Age , growth , and mortality of *Loligo vulgaris* wild paralarvae: implications for understanding of the life cycle and longevity. ICES Journal of Marine Science, 67: 119–1127.

González, A. F., Otero, J., Guerra, A., Prego, R., Rocha, F. J., and Dale, A. W. 2005. Distribution of common octopus and common squid paralarvae in a wind-driven upwelling area (Ria of Vigo, northwestern Spain). Journal of Plankton Research, 27: 271–277.

Hanlon, R. T. 1998. Mating systems and sexual selection in the squid *Loligo*: How might commercial fishing on spawning grounds affect them? California Cooperative Oceanic Fisheries Investigations Reports, 39: 92–100.

Hanlon, R. T., Hixon, R. F., and Turk, P. E. 1985. Behaviour, feeding and growth of young *Loligo forbesi* (Cephalopoda: Myopsida) reared in the laboratory. Vie Milieu, 35: 1–247.

Hanlon, R. T., Maxwell, M. R., and Shashar, N. 1997. Behavioural dynamics that would lead to multiple paternity within egg capsules of the squid *Loligo pealei*. Biology Bulletin, 193: 212–214.

Hanlon, R. T., Smale, M. J., and Sauer, W. H. H. 2002. The mating system of the squid *Loligo vulgaris reynaudii* (Cephalopoda, Mollusca) off South Africa: Fighting, guarding, sneaking, mating and egg laying behavior. Bulletin of Marine Science, 71: 331–345.

Hanlon, R. T., Smale, M., and Sauer, W. 1994. An ethogram of body patterning behavior in the squid *Loligo vulgaris reynaudii* on spawning grounds in South Africa. Biology Bulletin, 187: 363–372.

Hatanaka, H., Sako, T., Augustyn, C. J., Payne, A., and Leslie, R. 1983. Report on the Japan/South Africa Joint Trawling Survey on the Agulhas Bank, November/December 1980. Japan Marine Fishery Resource Research Center, Japan.

Heemstra, P., and Heemstra, E. 2004. Coastal fishes of southern Africa. NISC and SAIAB, Grahamstown.

Huggett, J., and Richardson, A. 2000. A review of the biology and ecology of *Calanus agulhensis* off South Africa. ICES Journal of Marine Science, 57: 1834–1849.

Hutchings, L. 1994. The Agulhas Bank a synthesis of available information and a brief comparison with other east-coast shelf regions. South African Journal of Science, 90: 179–185.

Ikeda, Y., Ito, K., and Matsumoto, G. 2004. Does light intensity affect embryonic development of squid (*Heterololigo bleekeri*)? Journal of the Marine Biological Association of the UK, 84: 1215–1219.

Iwata, Y., Ito, K., and Sakurai, Y. 2008. Effect of low temperature on mating behavior of squid *Loligo bleekeri*. Fisheries Science, 74: 1345–1347.

Jackson, G. D., Meekan, M. G., Wotherspoon, S., and Jackson, C. H. 2008. Distributions of young cephalopods in the tropical waters of Western Australia over two consecutive summers. ICES Journal of Marine Science, 65: 140–147.

Jackson, G. D., and Pecl, G. 2003. The dynamics of the summer-spawning population of the loliginid squid (*Sepioteuthis australis*) in Tasmania, Australia—a conveyor belt of recruits. ICES Journal of Marine Science, 60: 290–296.

Jantzen, T. M., and Havenhand, J. N. 2003. Reproductive behavior in the squid *Sepioteuthis australis* from South Australia: ethogram of reproductive body patterns. The Biological Bulletin, 204: 290–304.

Jooste, K. 2007. Eastern Cape Development Corporation 2007. Strategic environmental assessment of potential mariculture sites in the Woody Cape to Cape St Francis area. A report for the Eastern Cape Development Corporation.

Katsanevakis, S., and Verriopoulos, G. 2006. Modelling the effect of temperature on hatching and settlement patterns of meroplanktonic organisms : the case of the octopus. Scientia Marina, 70: 699–708.

King, D. 1996. Reef fishes and corals. Struik Nature, Cape Town.

Koslow, J. A., and Allen, C. 2011. The influence of the ocean environment on the abundance of market squid, *Doryteuthis* (*Loligo*) *opalescens*, paralarvae in the southern California Bight. California Cooperative Oceanic Fisheries Investigations Reports, 52: 205–213.

Laptikhovsky, V. 2007. New data on spawning and bathymetric distribution of the Patagonian squid, *Loligo gahi*. JMBA2-Biodiversity Records.

Largier, J. L., Chapman, P., Peterson, W., and Swarts, V. 1992. The Western Agulhas Bank: Circulation, stratification and ecology. South African Journal of Marine Science, 12: 319–339.

Le Clus, F., and Roberts, M. J. 1995. Topographic and hydrographic effects on catch rates of *Austroglossus pectoralis* (Soleidae) on the Agulhas Bank. South African Journal of Marine Science, 16: 321–332.

Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P., and Blanke, B. 2008. A Lagrangian tool for modelling ichthyoplankton dynamics. Environmental Modelling & Software, 23: 1210–1214.

Lipiński, M. R. 1994. Differences among basic biological parameters in a population of chokka squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) sampled by three methods. South African Journal of Marine Science, 14: 281–286.

Lipiński, M. R. 1998. Cephalopod life cycles: Patterns and exceptions. South African Journal of Marine Science, 20: 439–447.

Lipiński, M. R., Hampton, I., Sauer, W. H. H., and Augustyn, C. J. 1998. Daily net emigration from a spawning concentration of chokka squid (*Loligo vulgaris reynaudii* d'Orbigny, 1845) in Kromme Bay, South Africa. ICES Journal of Marine Science, 55: 258–270.

Lipiński, M. R., Payne, A. I. L., and Rose, B. 1992. The importance of cephalopods as prey for hake and other groundfish in South African waters. South African Journal of Marine Science, 12: 651–662.

Lipiński, M. R., and Soule, M. A. 2007. Disintegration of a large concentration of loliginid squid as a response to predation. Reviews in Fish Biology and Fisheries, 17: 477–485.

Lipiński, M. R., and Underhill, L. G. 1995. Sexual maturation in squid: Quantum or continuum? South African Journal of Marine Science, 15: 207–223.

Lordan, C., and Casey, J. 1999. The first evidence of offshore spawning in the squid species *Loligo forbesi*. Journal of the Marine Biological Association of the UK, 79: 379–381.

Lutjeharms, J., Meyer, A. A., Ansorge, I., Eagle, G., and Orren, M. 1996. The nutrient characteristics of the Agulhas Bank. South African Journal of Marine Science, 17: 253–274.

Lutjeharms, J. R. E. 2006. The ocean environment off southeastern Africa: a review. South African Journal of Science, 102: 419–426.

Lutjeharms, J. R. E., Catzel, R., and Valentine, H. R. 1989. Eddies and other boundary phenomena of the Agulhas Current. Continental Shelf Research, 9: 597–616.

Lutjeharms, J. R. E., Cooper, J., and Roberts, M. J. 2000. Upwelling at the inshore edge of the Agulhas Current. Continental Shelf Research, 20: 737–761.

Lutjeharms, J. R. E., and Stockton, P. L. 1991. Aspects of the upwelling regime between Cape Point and Cape Agulhas, South Africa. South African Journal of Marine Science, 10: 91–102.

Mann, B. Q. 2000. Southern African marine linefish status reports. In Oceanographic Research Institute, Special Report. Durban.

Mann, B. Q. (Ed.). 2013. Southern African marine linefish species profiles. South African Association for Marine Biological Research, Durban.

Martins, R. S. 2009. Some factors influencing the transport of chokka squid (*Loligo reynaudii* D'Orbigny, 1839) paralarvae off the Eastern Cape, South Africa. University of Cape Town, 131 pp.

Martins, R. S., Roberts, M. J., Chang, N., Verley, P., Moloney, C. L., and Vidal, É. A. G. 2010. Effect of yolk utilization on the specific gravity of chokka squid (*Loligo reynaudii*) paralarvae: implications for dispersal on the Agulhas Bank, South Africa. ICES Journal of Marine Science, 67: 1323–1335.

Martins, R. S., Roberts, M. J., Lett, C., Chang, N., Moloney, C. L., Camargo, M. G. D., and Vidal, É. A. G. 2013. Modelling transport of chokka squid (*Loligo reynaudii*) paralarvae off South Africa: reviewing, testing and extending the “Westward Transport Hypothesis”. Fisheries Oceanography: doi: 10.1111/fog.12046.

McGowan, J. A. 1954. Observation on the sexual behaviour and spawning of the squid *Loligo opalescens* at La Jolla, California. Californian Fish and Game, 40: 47–54.

McInnis, R. R., and Broenkow, W. W. 1978. Correlations between squid catches and oceanographic conditions in Monterey Bay, California. Fisheries Bulletin of California, 169: 161–170.

McMahon, J. J., and Summers, W. C. 1971. Temperature effects on the developmental rate of squid (*Loligo pealei*) embryos. Biology Bulletin, 141: 561–567.

Melo, Y., and Sauer, W. H. H. 1999. Confirmation of serial spawning in the chokka squid *Loligo vulgaris reynaudii* off the coast of South Africa. Marine Biology, 135: 307–313.

Meyer, M., and Smale, M. 1991a. Predation patterns of demersal teleosts from the Cape South and West coasts of South Africa. 2. Benthic and epibenthic predators. South African Journal of Marine Science, 11: 409–442.

Meyer, M., and Smale, M. 1991b. Predation patterns of demersal teleosts from the Cape South and West coasts of South Africa. 1. Pelagic predators. South African Journal of Marine Science, 10: 173–191.

Mohamed, K. 1993. Spawning congregations of Indian squid *Loligo duvauceli* (Cephalopoda: Loliginidae) in the Arabian Sea off Mangalore and Malpe. Indian Journal of Marine Sciences, 22: 172–175.

Moreno, A., Dos Santos, A., Piatkowski, U., Santos, A. M. P., and Cabral, H. 2009. Distribution of cephalopod paralarvae in relation to the regional oceanography of the western Iberia. Journal of Plankton Research, 31: 73–91.

Olyott, L. J. H., Sauer, W. H. H., and Booth, A. J. 2006. Spatio-temporal patterns in maturation of the chokka squid (*Loligo vulgaris reynaudii*) off the coast of South Africa. ICES Journal of Marine Science, 63: 1649–1664.

Olyott, L. J. H., Sauer, W. H. H., and Booth, A. J. 2007. Spatial patterns in the biology of the chokka squid, *Loligo reynaudii* on the Agulhas Bank, South Africa. Reviews in Fish Biology and Fisheries, 17: 159–172.

Oosthuizen, A. 1999. The effects of temperature on embryonic development and hatching success of squid (*Loligo vulgaris reynaudii*) eggs. M.Sc. thesis, University of Port Elizabeth.

Oosthuizen, A., and Roberts, M. J. 2009. Bottom temperature and in situ development of chokka squid eggs (*Loligo vulgaris reynaudii*) on mid-shelf spawning grounds, South Africa. ICES Journal of Marine Science, 66: 1967–1971.

Oosthuizen, A., Roberts, M. J., and Sauer, W. H. H. 2002a. Temperature effects on the embryonic development and hatching success of the squid *Loligo vulgaris reynaudii*. Bulletin of Marine Science, 71: 619–632.

Oosthuizen, A., Roberts, M. J., and Sauer, W. H. H. 2002b. Early post-cleavage stages and abnormalities identified in the embryonic development of chokka squid eggs *Loligo vulgaris reynaudii*. South African Journal of Marine Science, 24: 379–382.

Paulij, W. P., Herman, P. M. J., Van Hannen, E. J., and Denucé, J. M. 1990. The impact of photoperiodicity on hatching of *Loligo vulgaris* and *Loligo forbesi*. Journal of the Marine Biological Association of the UK, 70: 597–610.

Peliz, A., Marchesiello, P., Dubert, J., Marta-Almeida, M., Roy, C., and Queiroga, H. 2007. A study of crab larvae dispersal on the Western Iberian Shelf: Physical processes. Journal of Marine Systems, 68: 215–236.

Penven, P., Chang, N., and Shillington, F. 2006. Modelling the Agulhas Current using SAfE (Southern Africa Experiment). Geophysical Research Abstracts, 8: Abstract 04225.

Peterson, W. T., and Hutchings, L. 1995. Distribution, abundance and production of the copepod *Calanus agulhensis* on the Agulhas Bank in relation to spatial variations in the hydrography and the chlorophyll concentration. Journal of Plankton Research, 17: 2275–2294.

Pham, C. K., Carreira, G. P., Porteiro, F. M., Gonçalves, J. M., Cardigos, F., and Martins, H. R. 2008. First description of spawning in a deep water loliginid squid, *Loligo forbesi*. Journal of the Marine Biological Association of the UK, 89: 171–177.

Pillar, S. C., and Wilkinson, I. 1995. The diet of Cape hake *Merluccius capensis* on the south coast of South Africa. South African Journal of Marine Science, 15: 225–239.

Probyn, T., Mitchell-Innes, B., Brown, P., Hutchings, L., and Carter, R. 1994. A review of primary production and related processes on the Agulhas Bank. South African Journal of Science, 90: 166–173.

Raya, C. P., Balguerías, E., Fernández-Núñez, M. M., and Pierce, G. J. 1999. On reproduction and age of the squid *Loligo vulgaris* from the Saharan Bank (north-west African coast). Journal of the Marine Biological Association of the UK, 79: 111–120.

Roberts, M. J. 1998. The influence of the environment on chokka squid *Loligo vulgaris reynaudii* spawning aggregations: Steps towards a quantified model. South African Journal of Marine Science, 20: 267–284.

Roberts, M. J. 2005. Chokka squid (*Loligo vulgaris reynaudii*) abundance linked to changes in South Africa's Agulhas Bank ecosystem during spawning and the early life cycle. ICES Journal of Marine Science, 62: 33–55.

Roberts, M. J., Barange, M., Lipiński, M. R., and Prowse, M. R. 2002. Direct hydroacoustic observations of chokka squid *Loligo vulgaris reynaudii* spawning activity in deep water. South African Journal of Marine Science, 24: 387–393.

Roberts, M. J., and Mullon, C. 2010. First Lagrangian ROMS – IBM simulations indicate large losses of chokka squid *Loligo reynaudii* paralarvae from South Africa's Agulhas Bank. African Journal of Marine Science, 32: 71–84.

Roberts, M. J., and Sauer, W. H. H. 1994. Environment: the key to understanding the South African chokka squid (*Loligo vulgaris reynaudii*) life cycle and fishery? Antarctic Science, 6: 249–258.

Roberts, M. J., and van den Berg, M. 2002. Recruitment variability of chokka squid (*Loligo vulgaris reynaudii*)–Role of currents on the Agulhas Bank (South Africa) in paralarvae distribution and food abundance. Bulletin of marine Science, 71: 691–710.

Roberts, M. J., and van den Berg, M. 2005. Currents along the Tsitsikamma coast, South Africa, and potential transport of squid paralarvae and ichthyoplankton. African Journal of Marine Science, 27: 375–388.

Roberts, M. J., van der Lingen, C. D., Whittle, C., and van den Berg, M. 2010. Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: their relevance to the KwaZulu-Natal sardine run. African Journal of Marine Science, 32: 423–447.

Rocha, F., Guerra, Á., Prego, R., and Piatkowski, U. 1999. Cephalopod paralarvae and upwelling conditions off Galician waters (NW Spain). Journal of Plankton Research, 21: 21–33.

Rodhouse, P. G., Symon, C., and Hatfield, E. M. C. 1992. Early life cycle of cephalopods in relation to the major oceanographic features of the southwest Atlantic Ocean. Marine Ecology Progress Series, 89: 183–195.

Salman, A., and Laptikhovsky, V. 2002. First occurrence of egg masses of *Loligo forbesi* (Cephalopoda: Loliginidae) in deep waters of the Aegean Sea. Journal of the Marine Biological Association of the UK, 82: 925–926.

Sauer, W. H. H. 1995a. The impact of fishing on chokka squid *Loligo vulgaris reynaudii* concentrations on inshore spawning grounds in the South-eastern Cape, South Africa. South African Journal of Marine Science, 16: 185–193.

Sauer, W. H. H. 1995b. South Africa's Tsitsikamma National Park as a protected breeding area for the commercially exploited chokka squid *Loligo vulgaris reynaudii*. South African Journal of Marine Science, 16: 365–371.

Sauer, W. H. H., Downey, N. J., Lipiński, M. R., Roberts, M. J., Smale, M. J., Glazer, J., and Melo, Y. C. 2013. *Loligo reynaudi*. *In* Advances in Squid Biology, Ecology and Fisheries. Ed. R. Rosa, G. Pierce, and R. K. O'Dor. Nova Science Publishers, Inc.

Sauer, W. H. H., Goschen, W. S., and Koorts, A. S. 1991. A preliminary investigation of the effect of sea temperature fluctuations and wind direction on catches of chokka squid

Loligo vulgaris reynaudii off the Eastern Cape, South Africa. South African Journal of Marine Science, 11: 467–473.

Sauer, W. H. H., and Lipiński, M. R. 1990. Histological validation of morphological stages of sexual maturity in chokker squid *Loligo vulgaris reynaudii* D'Orb (Cephalopoda: Loliginidae). South African Journal of Marine Science, 9: 189–200.

Sauer, W. H. H., and Lipiński, M. R. 1991. Food of squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) on their spawning grounds off the Eastern Cape, South Africa. South African Journal of Marine Science, 10: 193–201.

Sauer, W. H. H., Lipiński, M. R., and Augustyn, C. 2000. Tag recapture studies of the chokka squid *Loligo vulgaris reynaudii* d'Orbigny, 1845 on inshore spawning grounds on the south-east coast of South Africa. Fisheries Research, 45: 283–289.

Sauer, W. H. H., McCarthy, C., Smale, M. J., and Koorts, A. S. 1993. An investigation of the egg distribution of the chokka squid, *Loligo vulgaris reynaudii*, in Krom Bay, South Africa. Bulletin of Marine Science, 53: 1066–1077.

Sauer, W. H. H., Melo, Y. C., and de Wet, W. 1999. Fecundity of the chokka squid *Loligo vulgaris reynaudii* on the southeastern coast of South Africa. Marine Biology, 135: 315–319.

Sauer, W. H. H., Roberts, M. J., Lipiński, M. R., Smale, M. J., Hanlon, R. T., Webber, D. M., and O'Dor, R. K. 1997. Choreography of the squid's "nuptial dance". Biology Bulletin, 192: 203–207.

Sauer, W. H. H., and Smale, M. 1991. Predation patterns on the inshore spawning grounds of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Loliginidae) off the South-eastern Cape, South Africa. South African Journal of Marine Science, 11: 513–523.

Sauer, W. H. H., and Smale, M. J. 1993. Spawning behaviour of *Loligo vulgaris reynaudii* in shallow coastal waters of the South-eastern Cape, South Africa. *In* Recent Advances in Fisheries Biology, pp. 489–498. Ed. T. Okutani, R. O'Dor, and T. Kubodera. Tokai University Press, Tokyo.

Sauer, W. H. H., Smale, M. J., and Lipiński, M. R. 1992. The location of spawning grounds, spawning and schooling behaviour of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Myopsida) off the Eastern Cape coast, South Africa. Marine Biology, 114: 97–107.

Schumann, E. H., and Beekman, L. 1984. Ocean temperature structures on the Agulhas Bank. Transactions of the Royal Society of South Africa, 45: 191–203.

Schumann, E. H., Perrins, L.-A., and Hunter, I. T. 1982. Upwelling along the south coast of the Cape Province, South Africa. South African Journal of Science, 78: 238–242.

Schön, P.-J., Sauer, W. H. H., and Roberts, M. J. 2002. Environmental influences on spawning aggregations and jig catches of chokka squid *Loligo vulgaris reynaudii*: a "black box" approach. Bulletin of Marine Science, 71: 783–800.

Şen, H. 2004. A preliminary study on the effects of different light intensities on hatching of European squid (*Loligo vulgaris* Lamarck, 1798) eggs. Turkish Journal of Fisheries and Aquatic Sciences, 4: 1–4.

Shaw, P. W., Hendrickson, L., McKeown, N. J., Stonier, T., and Sauer, W. H. H. 2010. Discrete spawning aggregations of loliginid squid do not represent genetically distinct populations. Marine Ecology Progress Series, 408: 117–127.

Shaw, P. W., and Sauer, W. H. H. 2004. Multiple paternity and complex fertilisation dynamics in the squid *Loligo vulgaris reynaudii*. Marine Ecology Progress Series, 270: 173–179.

Silva, L., Balguerías, E., Afonso, P. S., Sobrino, I., Gil, J., and Burgos, C. 2009. Cephalopod species in Mozambican waters caught in the "Mozambique 0307" survey: Distribution, abundance and assemblages. Western Indian Ocean Journal of Marine Science, 8: 37–48.

Smale, M. 1996. Cephalopods as prey. IV. Fishes. Philosophical Transactions of the Royal Society B: Biological Sciences, 351: 1067–1081.

Smale, M. J. 1992. Predatory fish and their prey - An overview of trophic interactions in the fish communities of the west and south coasts of South Africa. South African Journal of Marine Science, 12: 803–821.

Smale, M. J., and Cowley, P. D. 1992. The feeding ecology of skates (Batoidea: Rajidae) off the Cape South Coast, South Africa. South African Journal of Marine Science, 12: 823–834.

Smale, M. J., Roel, B. A., Badenhorst, A., and Field, J. 1993. Analysis of the demersal community of fish and cephalopods on the Agulhas Bank, South Africa. Journal of Fish Biology, 43: 169–191.

Smale, M. J., Sauer, W. H. H., and Hanlon, R. T. 1995. Short communication: Attempted ambush predation on spawning squids *Loligo vulgaris reynaudii* by benthic pyjama sharks, *Poroderma africanum*, off South Africa. Journal of the Marine Biological Association of the UK, 75: 739–742.

Smale, M. J., Sauer, W. H. H., and Roberts, M. J. 2001. Behavioural interactions of predators and spawning chokka squid off South Africa: towards quantification. Marine Biology, 139: 1095–1105.

Somarakis, S., Drakopoulos, P., and Filippou, V. 2002. Distribution and abundance of larval fish in the northern Aegean Sea—eastern Mediterranean—in relation to early summer oceanographic conditions. Journal of Plankton Research, 24: 339–357.

Sparre, P., and Venema, S. C. 1998. Introduction to tropical fish stock assessment. Part 1. Manual. Rome.

Strickland, J. D. H., and Parsons, T. R. 1972. A practical handbook of seawater analysis. 2nd edn. Bulletin of the Fisheries Research Board of Canada, 167:

Swart, V. P., and Largier, J. L. 1987. Thermal structure of Agulhas Bank water. South African Journal of Marine Science, 5: 243–253.

Uozumi, Y., Hatanaka, H., Payne, A., and Augustyn, C. J. 1985. Report on the Japan/South Africa joint trawl survey of groundfish resources on the Agulhas Bank in June 1982. Publ. Far Seas Fish. Res. Lab., S Series 13, 78 pp.

Uozumi, Y., Hatanaka, H., Sato, T., Augustyn, C. J., Payne, A. I. L., and Leslie, K. W. 1984. Report on the Japan/South Africa joint trawling survey on the Agulhas Bank in November/December 1981. Publ. Far Seas Fish. Res. Lab., S Series 11, 91 pp. Japan.

Vecchione, M., and Lipiński, M. R. 1995. Descriptions of the paralarvae of two loliginid squids in Southern African waters. South African Journal of Marine Science, 15: 1–7.

Verheye, H. M., Hutchings, L., Huggett, J., Carter, R. A., Peterson, W. T., and Painting, S. J. 1994. Community structure, distribution and trophic ecology of zooplankton on the Agulhas Bank with special reference to copepods. South African Journal of Science, 90: 154–165.

Vidal, É. A. G., DiMarco, F. P., Wormuth, J. H., and Lee, P. G. 2002a. Influence of temperature and food availability on survival, growth and yolk utilization in hatchling squid. Bulletin of Marine Science, 71: 915–931.

Vidal, É. A. G., DiMarco, F. P., Wormuth, J. H., and Lee, P. G. 2002b. Optimizing rearing conditions of hatchling loliginid squid. Marine Biology, 104: 117–127.

Vidal, É. A. G., DiMarco, P., and Lee, P. 2006. Effects of starvation and recovery on the survival, growth and RNA/DNA ratio in loliginid squid paralarvae. Aquaculture, 260: 94–105.

Vidal, É. A. G., Haimovici, M., and Hackbart, V. C. S. 2010. Distribution of paralarvae and small juvenile cephalopods in relation to primary production in an upwelling area off southern Brazil. ICES Journal of Marine Science, 67: 1346–1352.

Vidal, É. A. G., Roberts, M. J., and Martins, R. S. 2005. Yolk utilization, metabolism and growth in reared *Loligo vulgaris reynaudii* paralarvae. Aquatic Living Resources, 18: 385–393.

Vidal, É. A. G., Zeidberg, L. D., and Buskey, E. J. 2009. Swimming behavior in fed and starved squid paralarvae. *In* CIAC 2009 Symp. Abstracts, pg 61, 3–11 September, Vigo, Spain.

Villanueva, R., Arkhipkin, A., Jereb, P., Lefkaditou, E., Lipiński, M. R., Perales-Raya, C., Riba, J., *et al.* 2003. Embryonic life of the loliginid squid *Loligo vulgaris*: comparison between statoliths of Atlantic and Mediterranean populations. Marine Ecology Progress Series, 253: 197–208.

Walmsley, S. A., Leslie, R. W., and Sauer, W. H. H. 2005. The biology and distribution of the monkfish *Lophius vomerinus* off South Africa. African Journal of Marine Science, 27: 157–168.

Wilkinson, S., and Japp, D. W. 2005. Description and evaluation of hake-directed trawling intensity on benthic habitat in South Africa. Fisheries and oceanographic support services CC, Cape Town.

Young, R. E., and Harman, R. F. 1988. `Larva’, `paralarva', and `sub-adult' in cephalopod terminology. Malacologia, 29: 201–207.

Zeidberg, L. D., Butler, J. L., Ramon, D., Cossio, A., Stierhoff, K. L., and Henry, A. 2012. Estimation of spawning habitats of market squid (*Doryteuthis opalescens*) from field surveys of eggs off Central and Southern California. Marine Ecology, 33: 326–336.

Zeidberg, L. D., Isaac, G., Widmer, C. L., Neumeister, H., and Gilly, W. F. 2011. Egg capsule hatch rate and incubation duration of the California market squid, *Doryteuthis* (*Loligo*) *opalescens*: insights from laboratory manipulations. Marine Ecology: doi:10.1111/j.1439–0485.2011.00445.x.

van der Elst, R. 2012. A guide to the common sea fishes of southern Africa. Struik Nature, Cape Town.

Appendix

Table A.1: Benthic invertebrates observed on the mid-shelf. Also given is the number of stations at which species were observed and the depth range of occurrence (according to underwater video footage).

Class	Species		Stations	Depth (m)
Bryozoa				
Gymnolaemata		False coral	3	44.5-72.2
Gymnolaemata		False coral (staghorn-like)	3	44.5-107.3
Gymnolaemata		False coral (pore-plated like)	1	44.5
Gymnolaemata		Lace bryozoan	9	44.5-126.9
Cnidaria				
Alcyonaria	*Capnella* spp.	Grey cauliflower coral	1	44.5
Anthozoa		Anemone	23	44.5-131.9
Anthozoa	*Homophyton verrucosum*	Finger sea fan	4	44.5-131.9
Anthozoa	*Eunicella albicans*	Flagellar sea fan	2	44.5-109
Anthozoa	*Eunicella papillosa*	Nippled sea fan	4	44.5-125
Anthozoa	*Leptogorgia palma*	Palmate sea fan	1	44.5
Anthozoa		Sea fan	23	72.2-136.9
Anthozoa	*Actinoptilum molle*	Radial sea pen	1	105
Anthozoa		Sea pen	5	44.5-125.7
Anthozoa		Zoanthid (yellow)	1	107.6
Hydrozoa	*Solanderia procumbens*	Fan hydroid	6	72.2-118
Hydrozoa	*Allopora nobilis*	Noble coral	3	44.5-72.2
Hydrozoa		Planar-like hydroid	1	44.5
Hydrozoa		Tubular hydroid	2	125.7-131.9
Hydrozoa	*Aglaophenia pluma*	Tooth-feather hydroid	2	44.5-72.2
Hydrozoa	*Eudendruim* spp.	Bushy hydroid	2	44.5-65.3
Hydrozoa	Hydroid	Hydroid	26	44.5-136.9
Echinodermata				
Asteriodea	*Crossaster penicillatus*	Raspberry Star	4	114-129.5
Asteroidea	*Henricia abyssalis*	Orange long arm puffy star	5	111.7-136.9
Asteroidea	*Toraster tuberculatus*	Red sheriff star	6	107.6-131.9
Asteroidea		Unidentified starfish (red, orange, white)	24	105-171.9
Crinoidea		Feather star	1	105
Echinoidea		Urchin	22	82.2-152.5
Holothuroidea		Sea cucumber (yellow)	2	63.2-82.2
Ophiuroidea	*Astrocladus euryale*	Basket Star	4	44.5-107.6
Ophiuroidea	*Ophiura* spp.	Brittle Star	7	44.5-136.9
Mollusca				
Gastropoda	*Turitella* spp.	Snail	1	107.3
Porifera				
Demospongiae	*Clathria dayi*	Broad-bladed tree sponge	6	44.5-131.9
		Sponge (Encrusting, some with visible turrets-red, purple, orange, blue)	15	44.5-131.9
		Sponges, other	19	44.5-136.9

Table A.2: Species caught in DAFF demersal survey trawls found only on the inshore (≤70 m) chokka squid spawning grounds. Also shown are the number of trawls species were caught in, the depth range of catch, habitat preference and the general depth range or limit of species. Known chokka squid predators are indicated in the species column by an asterisk (*****).

		Trawls				
Family	**Species**	**Number**	**Depth**	**Habitat**	**Depth range/limit**	**Reference**
Cephalopoda						
Loliginidae	*Lolliguncula mercatoris*	4	45-65			
Sepiidae	*Sepia vermiculata*	1	56	Sheltered lagoons and estuaries		(Branch *et al.*, 2010)
Chondrichthyes						
Carcharhinidae	**Carcharhinus brachyurus* (Bronze whaler)	12	33-57	Neritic, occurs over the continental shelf from the surfline to at least 100 m, either close to the surface or near the bottom	100 m	(Mann, 2013)
Dasyatidae	*Dasyatis chrysonota* (Blue stingray)	53	24-73	Summer: sandy beaches, sand and mud flats. Winter: offshore	110 m	(Mann, 2013)
Gymnuridae	**Gymnura natalensis* (Diamond ray)	20	24-70	Benthic, sandy beaches	75 m	(Heemstra and Heemstra, 2004)
Scyliorhinidae	**Poroderma africanum* (Pyjama shark)	9	37-63	Reefs	100 m	(Mann, 2013)
Scyliorhinidae	**Poroderma pantherinum* (Leopard catshark)	7	29-61	Benthic, rocky reefs		(Smale *et al.*, 2001)
Sphyrnidae	**Sphyrna zygaena* (Smooth hammerhead)	26	30-63	Benthic and pelagic feeder	200 m	(van der Elst, 2012)
Teleosts						
Ariidae	*Galeichthyes ater* (Black barbel)	3	26-30	Shallow offshore reefs	60 m	(Mann, 2013)
Carangidae	*Lichia amia* (Garrick)	1	35	Nearshore surface waters	0-50 m	(Mann, 2013)
Cheilodactylidae	*Chirodactylus brachydactylus* (Twotone fingerfin)	5	34-67	Benthic, shallow rocky reefs	55-146 m	(King, 1996)
Fistulariidae	*Fistularia commersonii* (Bluspotted cornetfish)	1	44	Reefs and seagrass beds	128 m	(Heemstra and Heemstra, 2004; King, 1996)
Fistulariidae	*Fistularia petimba* (Red cornetfish)	2	45-55	Reef-associated	200 m	(Heemstra and Heemstra, 2004)
Haemulidae	*Pomadasys olivaceum* (Olive grunter)	15	34-63	Large dense shoals around edges of reefs, offshore reefs or soft banks	10-110 m	(Mann, 2013)
Oplegnathidae	*Oplegnathus conwayi* (Cape knifejaw)	1	64	Inshore reefs	5-32 m	(Mann, 2013)
Ostraciidae	*Tetrosomus gibbosus*(Humpback turretfish)	1	30	Reef-associated		http://www.guppies.za.net
Priacanthidae	*Priacanthus hamrur* (Moontail bullseye)	1	39	Shallow coral reefs and deeper rocky reefs	5-250 m	(King, 1996)

Table A.2 continued.

		Trawls				
Family	**Species**	**Number**	**Depth**	**Habitat**	**Depth range/limit**	**Reference**
Sciaenidae	*Umbrina canariensis* (Baardman)	18	30-77	Sand and rubble bottoms, but also inhabit subtidal reef		(Mann, 2000)
Sciaenidae	*Umbrina robinsoni* (Baardman)	1	55	Sand, mixed rock and sand surf zone, subtidal reefs	30 m	(Mann, 2013)
Serranidae	*Acanthistius sebastoides* (Common koester)	1	30	Rocky bottoms	25 m	(Heemstra and Heemstra, 2004)
Sparidae	*Argyrops filamentosus* (Soldier Bream)	1	38	Reef-associated	20-40 m	(Heemstra and Heemstra, 2004)
Sparidae	*Boopsoidea inornata* (Fransmadam)	1	37	Scattered high and low relief reefs	5-30 m	(Mann, 2013)
Sparidae	**Cheimerius nufar* (Santer)	4	36-51	Loose shoals primarily over low relief reefs	130 m	(Mann, 2013)
Sparidae	*Chrysoblephus gibbiceps* (Red stumpnose)	1	50	Offshore reefs	150 m	(Mann, 2013)
Sparidae	**Chrysoblephus laticeps* (Red roman)	2	42-51	Deeper high-profile inshore and offshore reefs	100 m	(Mann, 2013)
Sparidae	*Lithognathus mormyrus* (Sand steenbras)	11	30-51	Sandy substrate	0-50 m	(Mann, 2013)
Sparidae	*Pachymetopon aeneum* (Blue hottentot)	11	32-72	High profile inshore and offshore reefs	20-80 m	(Mann, 2013)
Sparidae	*Pachymetopon grande* (Bronze bream)	11	32-72	Shallow intertidal rocky shores and reefs	0-25 m	(Mann, 2013)
Sparidae	**Pagellus natalensis* (Red tjortjor)	65	24-70	Shallow sandy substrates, particularly in inshore bays, reef associated	<100 m	(Mann, 2013)
Sparidae	*Rhabdosargus globiceps* (White stumpnose)	23	24-70	Shallow reefs (south coast)	50 m	(Mann, 2013)
Sparidae	*Rhabdosargus holubi* (Cape stumpnose)	5	36-44	Sandy areas and shallow reefs, deep reefs	<50 m	(Mann, 2013)
Sparidae	*Sarpa salpa* (Strepie)	1	24	Subtidal gullies and shallow rocky reefs	<15 m	(Mann, 2013)
Sparidae	**Spondyliosoma emarginatum* (Steentjie)	35	30-72	Shallow reefs	50 m	(Mann, 2000)
Tetraodontidae	*Amblyrhynchotes honkenii* (Evileye blaasop)	40	24-70	Shallow sandy areas, also reefs and estuaries	1-50 m	(Jooste, 2007)
Tetraodontidae	*Arothron hispidus* (White spotted puffer)	2	33	Coral and rocky reefs, silty sand	1-50 m	(King, 1996; van der Elst, 2012)

Table A.3: Species caught in DAFF demersal survey trawls found on both the inshore (≤70 m) and deep (71-130 m) chokka squid spawning grounds. Also shown are the number of trawls species were caught in, the depth range of catch, habitat preference and the general depth range or limit of species. Known chokka squid predators are indicated in the species column by an asterisk (*).

		Trawls				
Family	**Species**	**Number**	**Depth**	**Habitat**	**Depth range/limit**	**Reference**
Cephalopoda						
Loliginidae	**Loligo reynaudi* (Chokka squid)	149	24-260	Demersal spawner, otherwise pelagic	200 m	(Augustyn *et al.*, 1994; Olyott *et al.*, 2007; Sauer and Lipiński, 1991)
Octopodidae	*Enteroctopus megalocyathus* (Giant octopus)	16	55-260	Benthic		(Branch *et al.*, 2010)
Octopodidae	**Octopus vulgaris* (Common octopus)	4	35-112	Benthic	200 m	(Branch *et al.*, 2010; Smale *et al.*, 2001)
Sepiidae	*Sepia australis*	71	24-171	Benthic	60-240 m	(Augustyn *et al.*, 1995)
Sepiidae	*Sepia hieronis*	10	42-199	Benthic	30-420 m	(Augustyn *et al.*, 1995)
Sepiidae	*Sepia officinalis vermiculata*	2	63-111	Benthic		
Sepiidae	*Sepia papillata*	24	33-116	Benthic		
Sepiidae	*Sepia simoniana*	19	29-115	Benthic		
Sepiidae	*Sepia typica*	9	37-160	Weedbeds, sheltered bays		(Branch *et al.*, 2010)
Ommastrephidae	*Todaropsis eblanae* (Lesser flying squid)	15	65-260			
Chondrichthyes						
Dasyatidae	**Dasyatis brevicaudata* (Shorttail stingray)	2	35-114	Benthic, sandy beaches	109 m	(Heemstra and Heemstra, 2004; Sauer and Smale, 1991)
Rajidae	**Raja alba* (Spearnose skate)	54	24-121	Benthic sand or mud	450 m	(Heemstra and Heemstra, 2004; Lipiński *et al.*, 1992; Sauer and Smale, 1991; Smale and Cowley, 1992; van der Elst, 2012)
Rajidae	**Raja miraletus* (Twineye skate)	68	29-77	Benthic sand or mud	50 m	(Heemstra and Heemstra, 2004; Smale and Cowley, 1992)
Rajidae	**Raja pullopunctata* (Slime skate)	17	34-120	Benthic sand or mud	50-150 m	(Heemstra and Heemstra, 2004; Lipiński *et al.*, 1992; Smale and Cowley, 1992)
Rajidae	**Raja wallacei* (Yellowspot skate)	25	35-239	Benthic sand or mud	80-200 m	(Heemstra and Heemstra, 2004; Smale and Cowley, 1992)
Rhinobatidae	*Rhinobatos annulatus* (Lesser sandshark)	75	24-111	Shallow coastal water, sandy habitat	73 m (SEC)	(Mann, 2013)
Scyliorhinidae	**Halaelurus natalensis* (Tiger catshark)	65	24-115	Benthic	172 m	(Heemstra and Heemstra, 2004; Lipiński *et al.*, 1992; Sauer and Smale, 1991)

Table A.3 continued.

		Trawls				
Family	**Species**	**Number**	**Depth**	**Habitat**	**Depth range/limit**	**Reference**
Scyliorhinidae	*_Haploblepharus edwardsii_ (Puffadder shyshark)	35	24-116	Benthic, soft substrate near rocks	3-15 m	(Heemstra and Heemstra, 2004; Sauer and Smale, 1991)
Squalidae	*_Squalus megalops_ (Spiny dogfish)	91	29-260	Benthic	500 m	(Heemstra and Heemstra, 2004; Sauer and Smale, 1991)
Triakidae	*_Galeorhinus galeus_ (Soupfin shark)	22	34-110	Benthic	2-471 m	(Mann, 2013; Sauer and Smale, 1991)
Triakidae	*_Mustelus mustelus_ (Common smooth-hound)	61	24-117	Shallow water over sand or shale plains and on rocky reefs	100 m	(Mann, 2013; Sauer and Smale, 1991)
Teleosts						
Ariidae	*_Galeichthys feliceps_ (White barbel)	87	24-111	Muddy and sandy substrata and reef fringes	100 m	(Mann, 2013; Sauer and Smale, 1991)
Batrachoididae	_Chatrabus hendersoni_ (Chocolate toadfish)	3	34-114	Shallow rocky reefs with sandy patches	20-160 m	http://www.easterncapescubadiving.co.za
Bothidae	_Arnoglossus capensis_ (Sole)	26	30-117	Soft substrate		
Carangidae	_Trachurus trachurus capensis_ (Horse mackerel)	146	30-253	Pelagic	surface to 400 m	(van der Elst, 2012)
Cheilodactylidae	_Cheilodactylus fasciatus_ (Red fingers)	6	34-114	Rocky shores and reefs	25 m	(van der Elst, 2012)
Cheilodactylidae	*_Chirodactylus grandis_ (Bank steenbras)	5	32-108	Demersal, soft substrate (mud banks) and reef associated	20-150 m	(Mann, 2013; Meyer and Smale, 1991a)
Clupeidae	_Etrumeus whiteheadi_ (Round herring)	94	24-160	Pelagic	100-400 m	(Heemstra and Heemstra, 2004)
Clupeidae	_Sardinops sagax ocellatus_ (Sardine)	24	24-112	Pelagic		
Congiopodidae	_Congiopodus spinifer_ (Horsefish)	109	29-253	Demersal, soft substrate and reef associated	10-146 m	(Bianchi _et al._, 1999)
Congiopodidae	_Congiopodus torvus_ (Smooth horsefish)	36	34-260	Demersal, soft substrate and reef associated	1-110 m	(Bianchi _et al._, 1999)
Cynoglossidae	_Cynoglossus zanzibarensis_ (Redspotted tonguesole)	127	29-260	Flat, soft substrata	10-430 m	(van der Elst, 2012)
Engraulidae	_Engraulis japonicus capensis_ (Cape anchovies)	19	35-112	Pelagic	200 m	(van der Elst, 2012)
Gempylidae	*_Thyrsites atun_ (Snoek)	4	50-115	Pelagic, near continents, islands and seamounts		(Lipiński _et al._, 1992; van der Elst, 2012)
Merlucciidae	*_Merluccius capensis_ (Shallow water Cape Hake)	130	29-253	Demersal, rocky bottom and sandy substrates	300 m	(Lipiński _et al._, 1992; Mann, 2013; Pillar and Wilkinson, 1995)
Ophidiidae	*_Genypterus capensis_ (Kingklip)	54	29-199	Demersal	50-500 m	(Lipiński _et al._, 1992; van der Elst, 2012)

Table A.3 continued.

Family	Species	Trawls Number	Trawls Depth	Habitat	Depth range/limit	Reference
Pomatomidae	**Pomatomus saltatrix* (Elf)	41	24-111	Sandy and rocky substrata	0-100 m	(Mann, 2013; Sauer and Smale, 1991; Smale *et al.*, 2001)
Sciaenidae	**Argyrosomus inodorus* and *Japonicus* (Kob)	52	30-105	moderate/low profile reef	20-120 m (<60m summer, offshore winter)	(Heemstra and Heemstra, 2004; Mann, 2013)
Sciaenidae	*Atractoscion aequidens* (Geelbek)	11	36-115	Over sandy and rocky substrata	150 m	(Mann, 2013)
Scombridae	**Scomber japonicus* (Chub mackerel)	62	24-253	Coastal pelagic, shoaling (and meso and epipelagic over shelf and slope up to 300m)	200 m	(Mann, 2013)
Sebastidae	**Helicolenus dactylopterus* (Jacopever)	53	35-260	Benthic, soft substrate and reef associated	55-550 m	(Meyer and Smale, 1991a)
Soleidae	*Austroglossus pectoralis* (East Coast Sole)	89	24-104	Muddy seabed	10-100 m	(van der Elst, 2012)
Sparidae	**Argyrozona argyrozona* (Carpenter Seabream)	28	32-136	Bentho-pelagic, high profile reef	50-200 m	(Mann, 2013; Sauer and Smale, 1991)
Sparidae	**Pterogymnus laniarius* (Panga)	115	30-148	Deep low and high profile reef, lesser extent over mud and sand	120 m	(Mann, 2013; Sauer and Smale, 1991)
Synodontidae	*Saurida undosquamis* (Brushtooth lizardfish)	4	55-105	Sandy and mud bottoms	200 m	(Heemstra and Heemstra, 2004)
Triglidae	**Chelidonichthys capensis* (Cape gurnard)	123	24-140	Flat, often soft substrata	10-390 m	(Meyer and Smale, 1991a; Sauer and Smale, 1991)
Triglidae	**Chelidonichthys queketti* (Lesser gurnard)	146	24-160	Flat, often soft substrata	0-150 m	(Mann, 2000; Meyer and Smale, 1991a)
Zeidae	**Zeus capensis* (Cape dory)	105	29-260	Benthic	35-200 m	(Sauer and Smale, 1991)
Centracanthidae	*Spicara axillaris* (Windtoy)	3	58-111	Benthic		
Trichiuridae	**Lepidopus caudatus* (Buttersnoek)	20	51-253	Benthic	400 m	(Mann, 2000; Meyer and Smale, 1991b)
Lophiidae	**Lophius vomerinus* (Monkfish)	18	63-260	Benthic	67-485 m	(Lipiński *et al.*, 1992; Mann, 2000; Walmsley *et al.*, 2005; van der Elst, 2012)

Table A.4: Species caught in DAFF demersal survey trawls found on only the deep (71-130 m) chokka squid spawning grounds. Also shown are the number of trawls species were caught in, the depth range of catch, habitat preference and the general depth range or limit of species. Known chokka squid predators are indicated in the species column by an asterisk (*).

		Trawls				
Family	**Species**	**Number**	**Depth**	**Habitat**	**Depth range/limit**	**Reference**
Cephalopoda						
Sepiidae	*Sepia tuberculata*	2	73-113	Mainly shallow water		(Branch *et al.*, 2010)
Sepiolidae	*Rossia enigmatica* (Bobtail squid)	3	113-260			
Teleosts						
Merlucciidae	**Merluccius paradoxus* (Deep water Cape Hake)	12	103-253	Benthic		(Lipiński *et al.*, 1992)

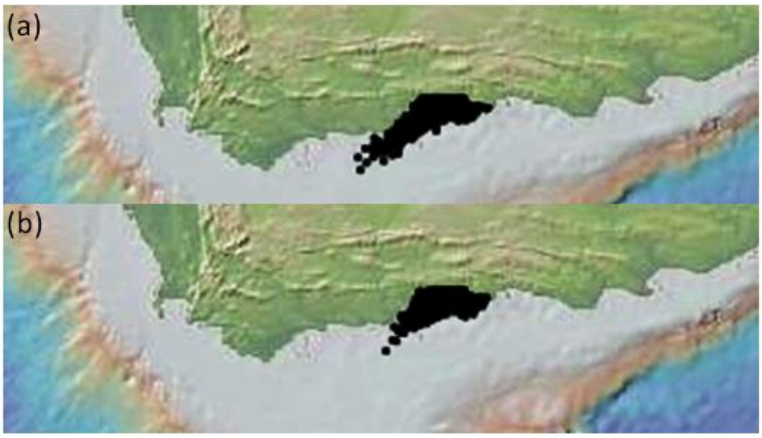

Figure A.1: An example of different individual-based model (IBM) particle transport trajectories resulting from the (a) inclusion and (b) exclusion of temperature related growth. All other inputs in these IBMs are the same.

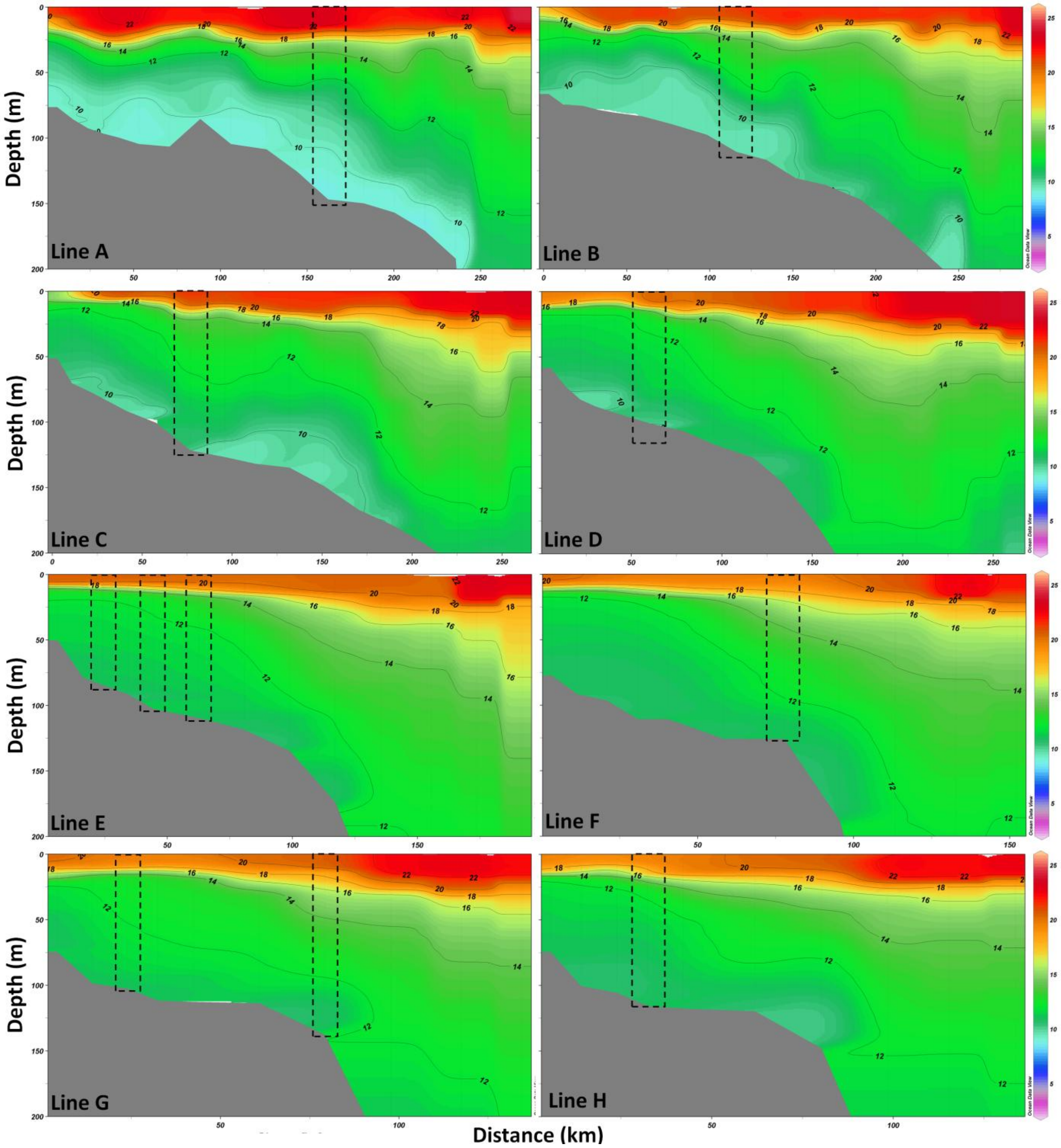

Figure A.2: Cross-shelf transects of temperature conditions on the Central and Eastern Agulhas Bank during March 2011. See Figure 5.1 for station positions (Line A-M, west-east). Vertical sections boxed by dotted lines indicate stations at which *Loligo reynaudi* paralarvae were collected.

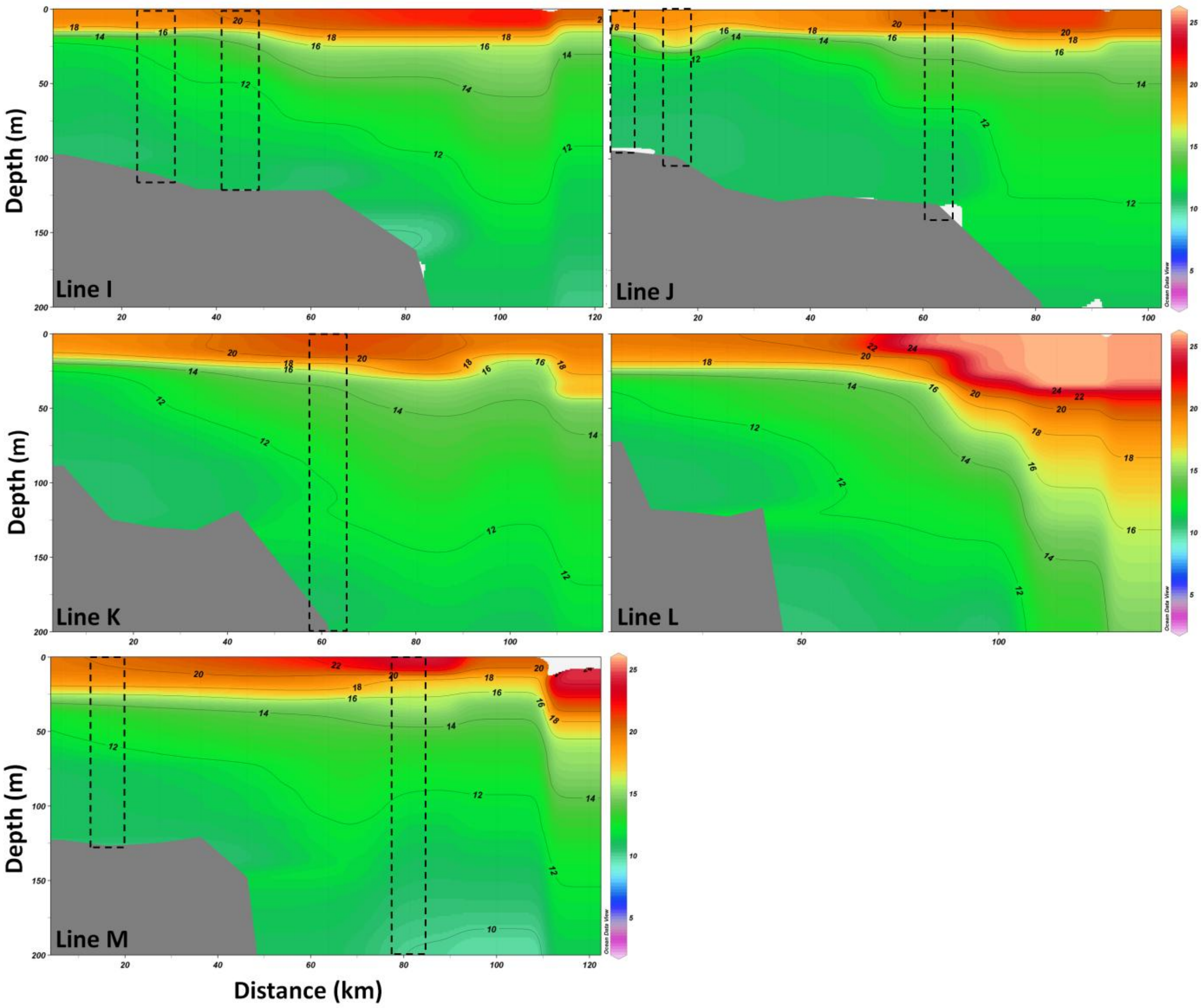

Figure A.2 continued: Cross-shelf transects of temperature conditions on the Central and Eastern Agulhas Bank during March 2011. See Figure 5.1 for station positions (Line A-M, west-east). Vertical sections boxed by dotted lines indicate stations at which *Loligo reynaudi* paralarvae were collected.

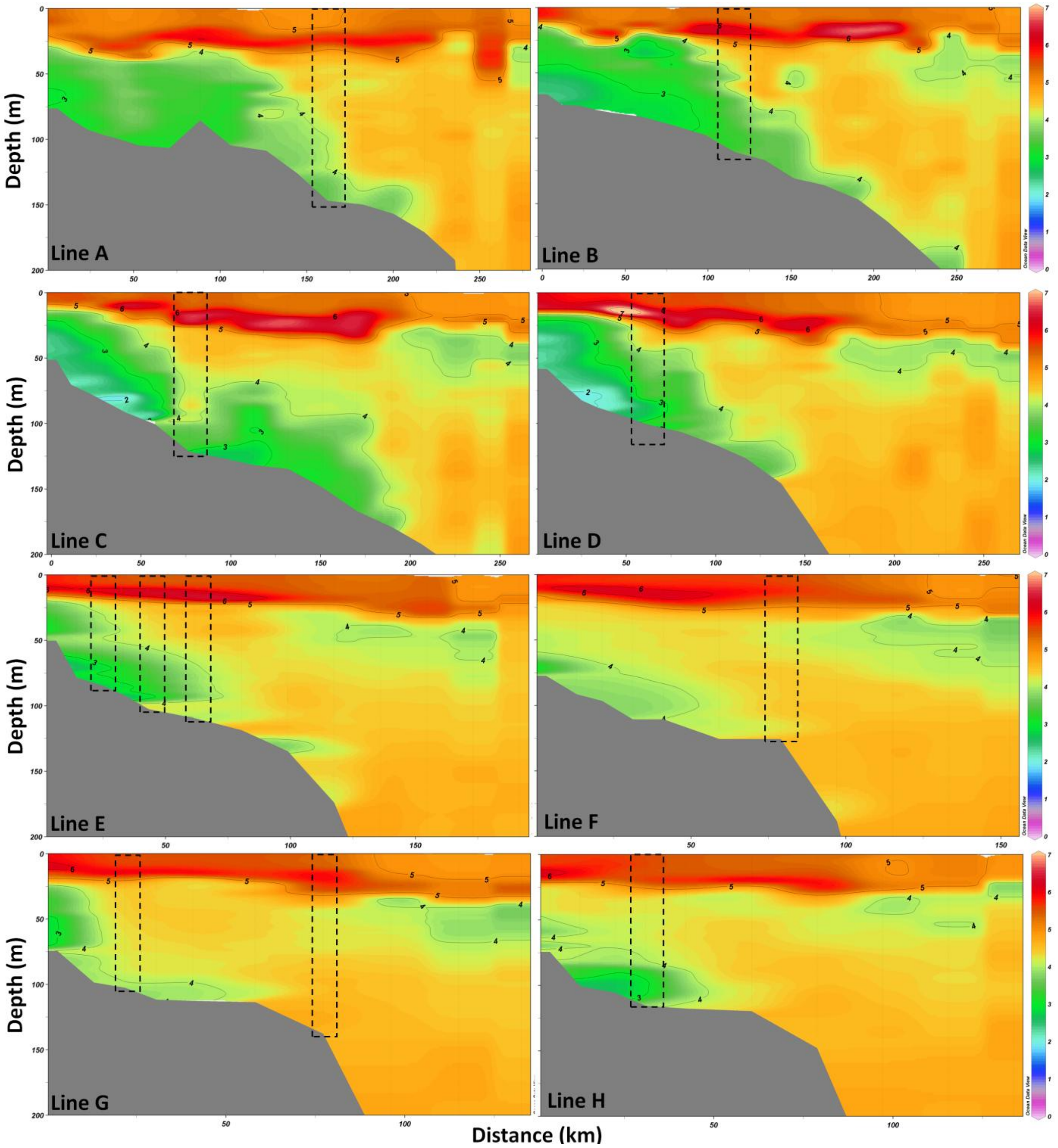

Figure A.3: Cross-shelf transects of dissolved oxygen conditions on the Central and Eastern Agulhas Bank during March 2011. See Figure 5.1 for station positions (Line A-M, west-east). Vertical sections boxed by dotted lines indicate stations at which *Loligo reynaudi* paralarvae were collected.

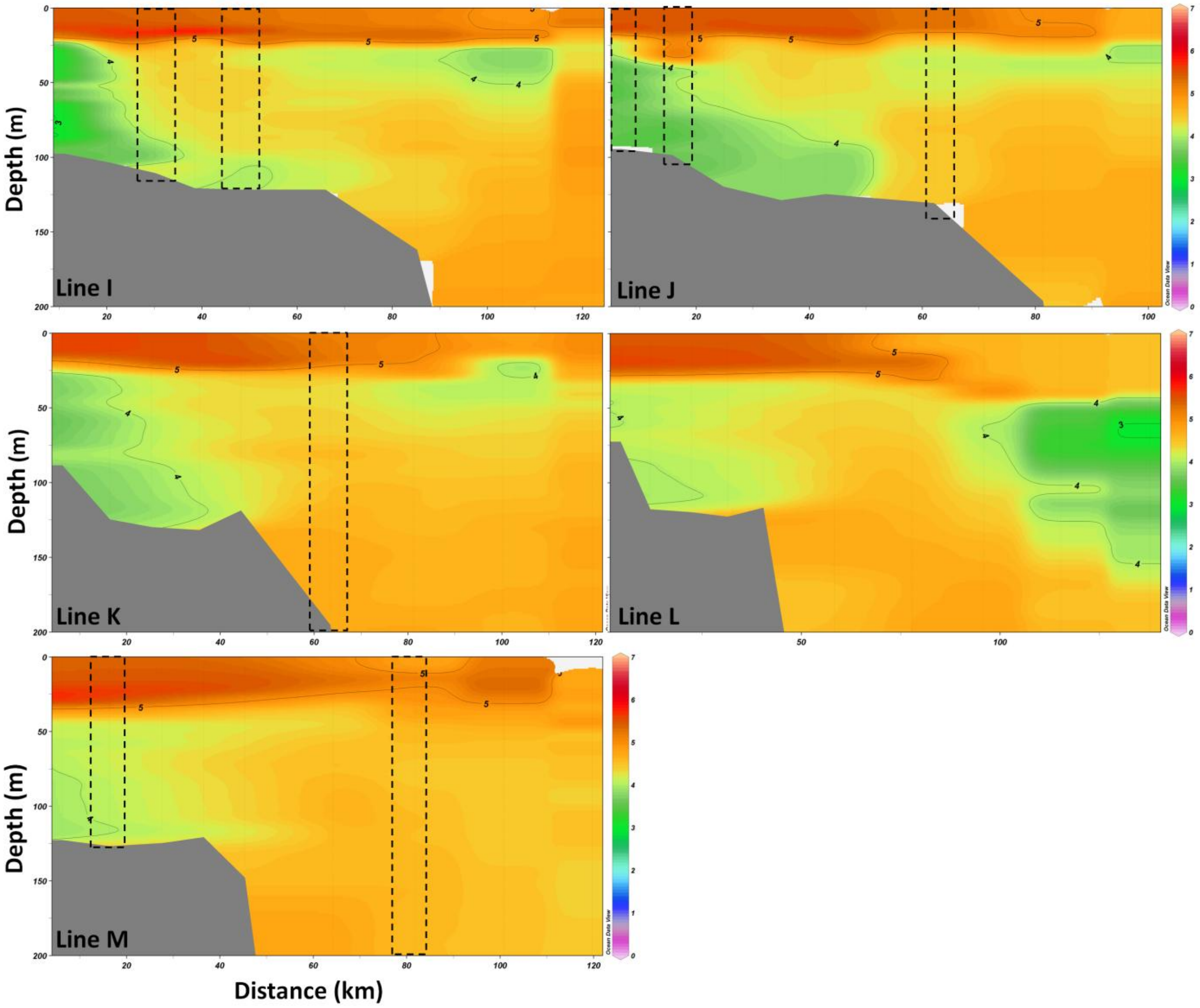

Figure A.3 continued: Cross-shelf transects of dissolved oxygen conditions on the Central and Eastern Agulhas Bank during March 2011. See Figure 5.1 for station positions (Line A-M, west-east). Vertical sections boxed by dotted lines indicate stations at which *Loligo reynaudi* paralarvae were collected.

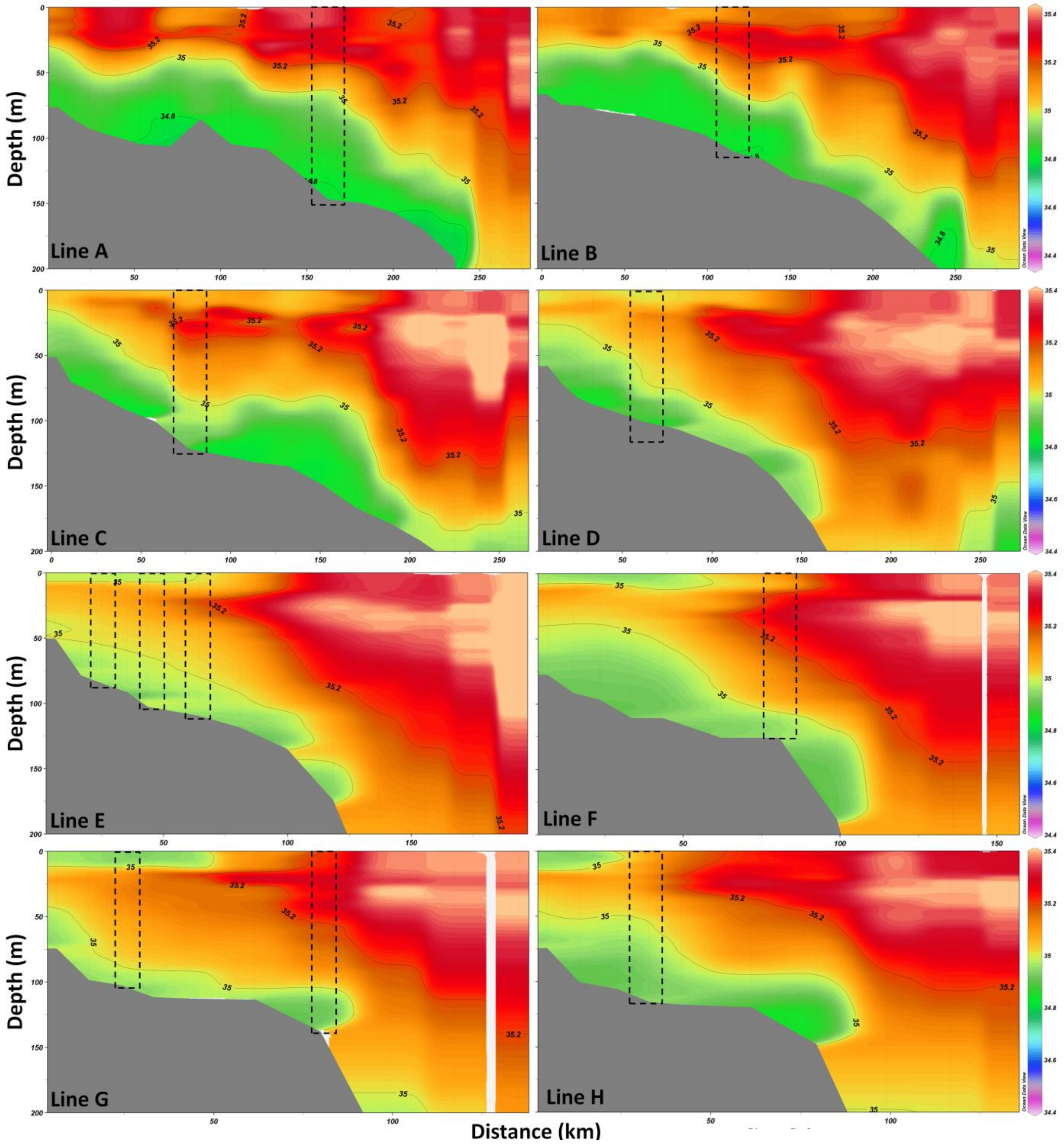

Figure A.4: Cross-shelf transects of salinity conditions on the Central and Eastern Agulhas Bank during March 2011. See Figure 5.1 for station positions (Line A-M, west-east). Vertical sections boxed by dotted lines indicate stations at which *Loligo reynaudi* paralarvae were collected.

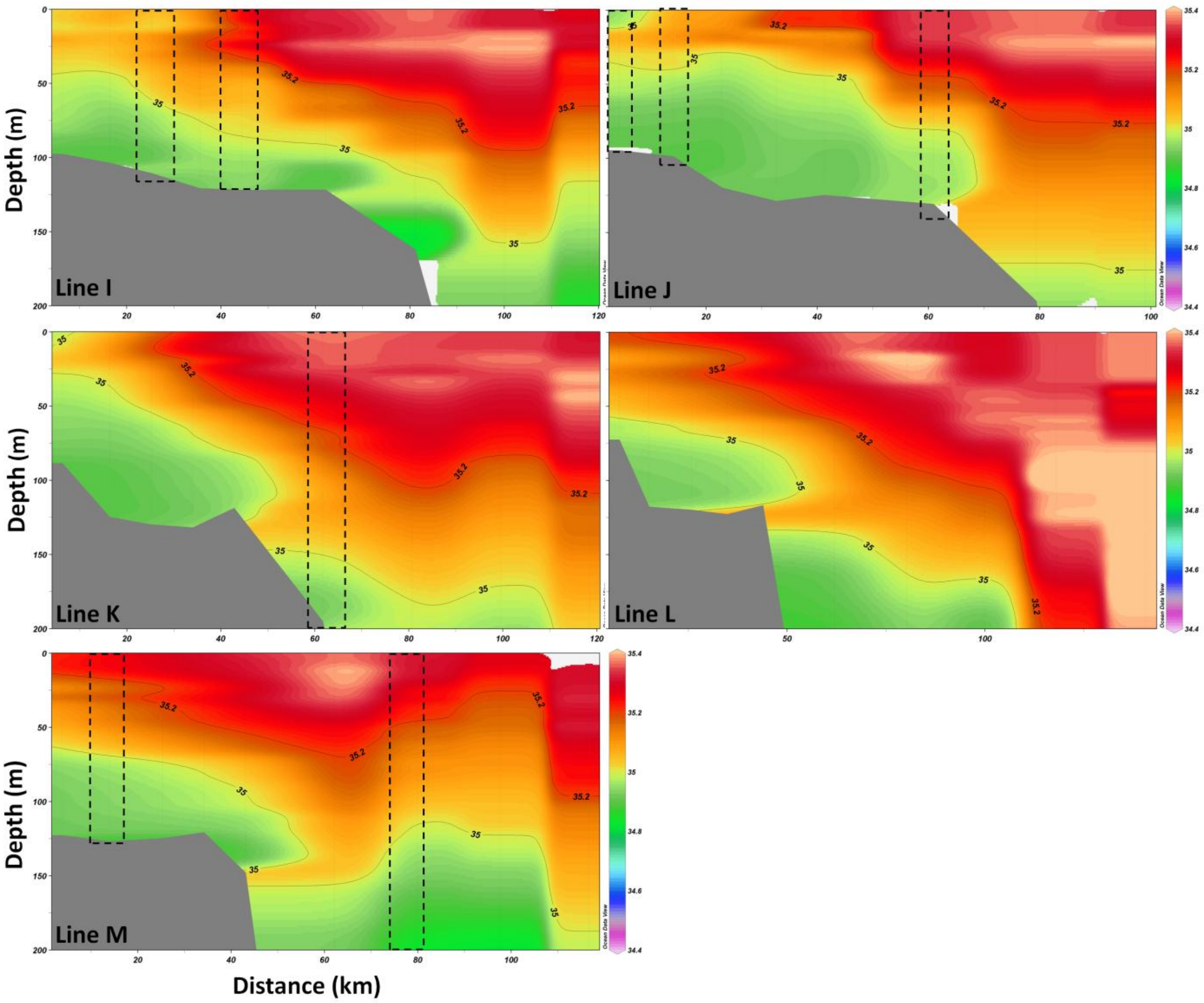

Figure A.4 continued: Cross-shelf transects of salinity conditions on the Central and Eastern Agulhas Bank during March 2011. See Figure 5.1 for station positions (Line A-M, west-east). Vertical sections boxed by dotted lines indicate stations at which *Loligo reynaudi* paralarvae were collected.