



# Modelling transport of inshore and deep-spawned chokka squid (*Loligo reynaudi*) paralarvae off South Africa: the potential contribution of deep spawning to recruitment

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## ABSTRACT

The South African chokka squid, *Loligo reynaudi*, spawns both inshore ( $\leq 70$  m) and on the mid-shelf (71–130 m) of the Eastern Agulhas Bank. The fate of these deep-spawned hatchlings and their potential contribution to recruitment is as yet unknown. Lagrangian ROMS-IBM (Regional Ocean Modelling System-Individual-Based Model) simulations confirm westward transport of inshore and deep-spawned hatchlings, but also indicate that the potential exists for paralarvae hatched on the Eastern Agulhas Bank deep spawning grounds to be removed from the shelf ecosystem. Using a ROMS-IBM, this study determined the transport and recruitment success of deep-spawned hatchlings relative to inshore-hatched paralarvae. A total of 12 release sites were incorporated into the model, six inshore and six deep-spawning sites. Paralarval survival was estimated based on timely transport to nursery grounds, adequate retention within the nursery grounds and retention on the Agulhas Bank shelf ( $< 200$  m). Paralarval transport and survival were dependent on both spawning location and time of hatching. Results suggest the importance of the south coast as a nursery area for inshore-hatched paralarvae, and similarly the cold ridge nursery grounds for deep-hatched paralarvae. 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 the Tsitsikamma coast, and the beneficial currents during this period (as indicated by the model results) it can be concluded that deep spawning may at times contribute significantly to recruitment.

**Key words:** deep spawning, *Loligo reynaudi*, paralarval transport, recruitment, Regional Ocean Modelling System-Individual-Based Model

## INTRODUCTION

The South African chokka squid, *Loligo reynaudi*, is classified as a neritic, shallow-water spawner ( $\leq 70$  m). The presence of chokka squid eggs in demersal trawl catches beyond this depth, however, has long indicated spawning also occurs on the Agulhas Bank mid-shelf (Augustyn *et al.*, 1992, 1994; Roberts and Sauer, 1994; Augustyn and Roel, 1998; Olyott *et al.*, 2007). Results of a recent study by Roberts *et al.* (2012) suggest the majority of mid-shelf or ‘deep spawning’ occurs within the depth range 71–130 m (although there are records of eggs as deep as 270 m); deep spawning is confined to the Eastern Agulhas Bank; and contributes ~18% to total egg biomass. Although deep-spawned hatchlings are viable (i.e., the cold bottom temperatures do not cause abnormal embryonic development, Oosthuizen and Roberts, 2009), the fate of hatchlings and their potential contribution to recruitment is as yet unknown.

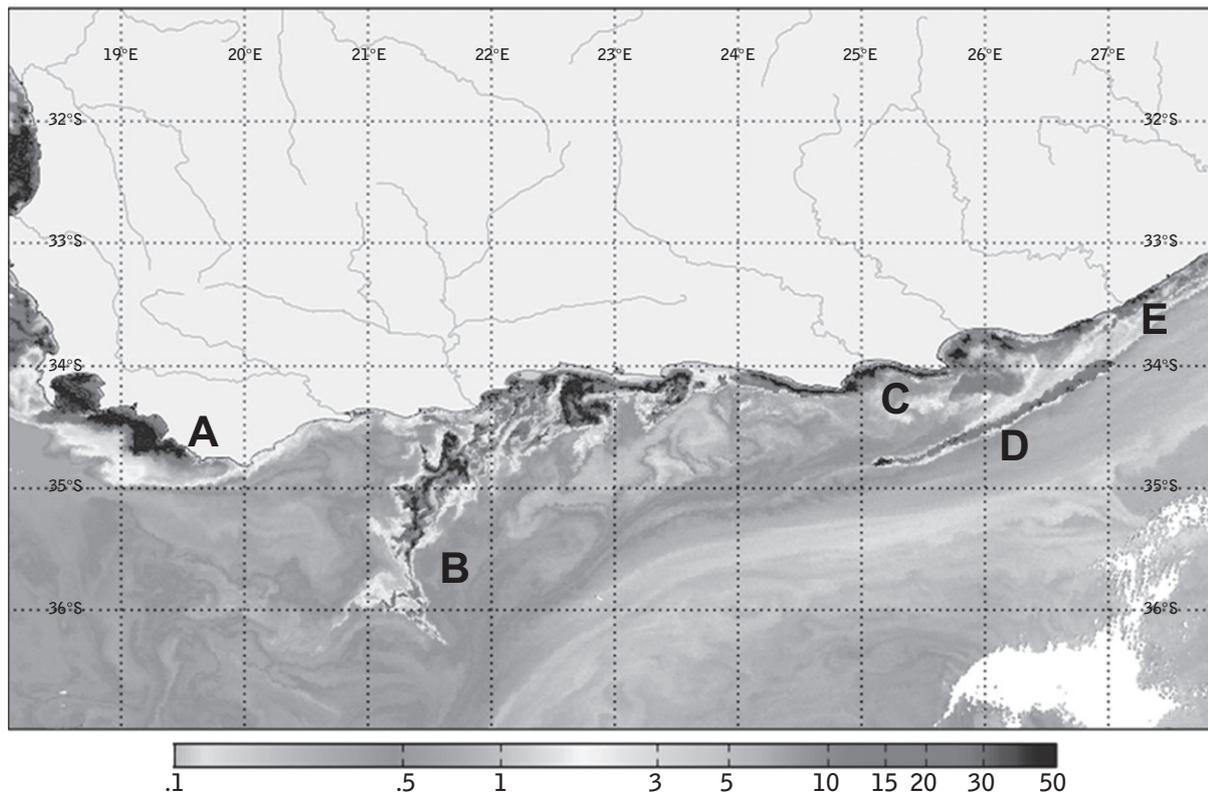
Roberts (2005) noted that chokka squid makes use of a very specific environmental niche on the inshore Eastern Agulhas Bank for spawning. This author proposed that nowhere else on the Agulhas Bank are bottom temperature and dissolved oxygen levels suitable for egg development. He also noted that the chokka squid spawning grounds are displaced from the high copepod biomass, in the vicinity of the cold ridge (Figs 1 and 2), by some 200 km. He postulated paralarvae hatching on the inshore spawning grounds,

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**Figure 1.** A composite of several satellite images (Marine Remote Sensing Unit <http://www.afro-sea.org.za/>) highlighting the chlorophyll concentration  $\text{mg m}^{-3}$  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.



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.

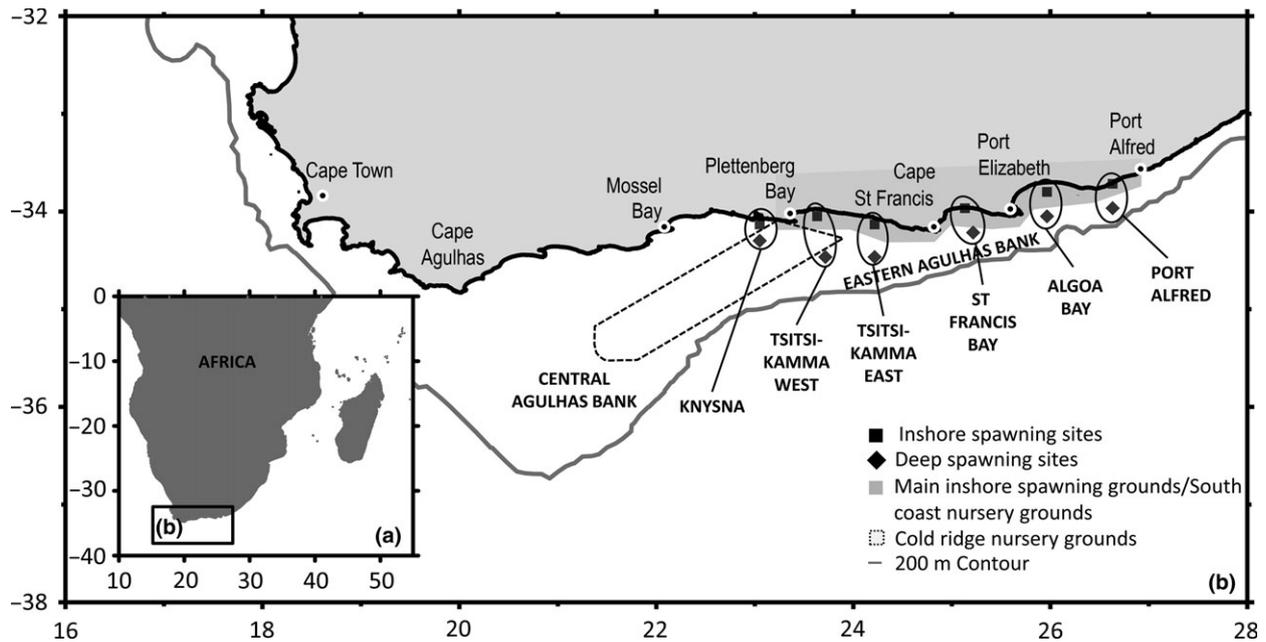
Lagrangian ROMS-IBM (Regional Ocean Modelling System-Individual-Based Model) simulations have previously been used to investigate the transport and recruitment of chokka squid paralarvae on the Agulhas Bank. Initial models using neutrally buoyant paralarvae not only confirmed westward transport on the mid-shelf but also indicated that the potential exists for paralarvae hatched on the Eastern Agulhas Bank deep-spawning grounds 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.*, 2014).

Martins *et al.* (2014) investigated interactions between circulation, diel vertical migration and the

specific gravity of chokka squid paralarvae during the yolk-utilization phase. Results showed that both the release area and particle buoyancy influenced the dispersal and transport of paralarvae. Within these simulations, the fate of particles beyond the yolk-utilization phase (4–5 days) was not assessed. The study by Martins *et al.* (2014) considered the cold ridge only (Fig. 1) as a nursery area for young paralarvae.

The cold ridge is a subsurface feature extending from the Knysna coast (Eastern Agulhas Bank), southwestward onto the Central Agulhas Bank (Fig. 1). It is visible in sea surface temperature 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). Numerous studies (Largier *et al.*, 1992; Boyd and Shillington, 1994; Verheye *et al.*, 1994; Peterson and

**Figure 2.** (a) The southern African continent and (b) the location of the six inshore and six deep-spawning (or release) sites used in the Individual-Based Models. Also shown are the cold ridge (dotted line), the inshore spawning grounds/south coast nursery grounds (shaded grey), the Eastern Agulhas Bank, the Central Agulhas Bank and the shelf break along the 200-m isobath (dark grey line).



Hutchings, 1995; Huggett and Richardson, 2000) have recorded high densities of copepods in the vicinity of the cold ridge. This ridge is a significant feature of the Agulhas Bank ecosystem and is considered an important nursery ground for squid paralarvae. Its formation and the consequent concentration of copepod abundance is thought to enhance paralarval survival and recruitment. However, other areas of high productivity, potentially important as paralarval nursery grounds, do occur and are highlighted in Figure 1.

Of importance to this study is the intermittent wind-driven upwelling and concomitant production typical of the south coast region (Fig. 1c). This is not only in the vicinity of the main chokka squid spawning grounds (Fig. 2), but also the majority of chokka squid paralarvae are found here (Augustyn *et al.*, 1994). It can be surmised that the inshore spawning grounds are, therefore, likely also an important nursery area for chokka squid paralarvae.

The aim of this study was to determine the transport and recruitment success of deep-spawned hatchlings relative to inshore-hatched paralarvae. This work is the next step to the Martins *et al.* (2014) study in that, although driven by the same 3-D hydrodynamic model, the current IBM (i) considers both the cold ridge and south coast as nursery areas; (ii) a greater number of release areas were used; and

(iii) the fate of paralarvae beyond the initial yolk-utilization phase was investigated (i.e., 40-day simulations).

## MATERIALS AND METHODS

A Lagrangian particle-tracking IBM (ICHTHYOP Version 3.1 [www.ichthyop.org/](http://www.ichthyop.org/)) was used to simulate the hatching and transport of paralarvae from 12 spawning sites (Fig. 2). *Ichthyop* has been developed to study the physical (e.g., ocean currents and temperature) and biological (e.g., growth and mortality) factors affecting ichthyoplankton dynamics (Lett *et al.*, 2008). As described by Lett *et al.* (2008), this tool uses a time series of velocity, temperature and salinity fields archived from ocean model simulations.

This study used the 2-day outputs of a high-resolution (~8 km) child model, developed by Chang (2008), embedded within the coarser resolution (20–25 km) parent Southern African Experiment (SAfE) model (Penven *et al.*, 2006). The child model covers the area of the Agulhas Bank and the Southern Benguela: 27.7–39°S and 11.5–27.4°E. Bottom topography data were obtained from General Bathymetric Chart of the Oceans (GEBCO) (Chang, 2008). Statistical equilibrium of the child model took approximately 2 yr (Chang, 2008), therefore, model outputs

from year three were used. The main modelled current features of the Agulhas Bank were analysed by Chang (2008). Along much of the south coast and on the mid-Agulhas Bank, currents are weak, generally below  $0.1 \text{ m s}^{-1}$ , and westward, whereas the outer Agulhas Bank shows oceanic influence as a result of the Agulhas Current. Seasonal changes are also evident within the child model.

Owing to the different coastal features dominating the inshore spawning grounds, it was expected paralarvae would be subjected to different transport trajectories, depending on the release location. Subsequently, the coastline between Port Alfred (east) and Knysna (west) was divided into six areas, based on general coastal features, namely: (i) Port Alfred; (ii) Algoa Bay area; (iii) St Francis Bay; the Tsitsikamma coastline, which as a result of its length was divided into (iv) Tsitsikamma East and (v) Tsitsikamma West; and lastly, (vi) Knysna. Within each of these areas, one inshore and one deep spawning area was chosen as release sites for the IBMs (Fig. 2). Spawning areas were determined from the presence of squid eggs in the Department of Agriculture, Forestry and Fisheries (DAFF) Research trawl catches or from known spawning sites. Certain parameters and biological inputs remained the same for all simulations. These included (i) a single release event of 5000 particles (paralarvae) from each spawning site; (ii) a thickness of each patch (egg bed) of 0.5 m; (iii) a radius of each patch (egg bed) of 1 m (Sauer *et al.*, 1993); (iv) a buoyancy of  $1.048 \text{ g cm}^{-3}$  for paralarvae  $\leq 4$  days old (Martins *et al.*, 2010); (v) Diel vertical migration (DVM), from age 4.01 days, with a specified depth of 90 m during the day and 10 m at night. Although the vertical distribution of chokka squid paralarvae is unknown, there is some indication that chokka squid paralarvae undergo DVM (M.R. Lipiński as cited in Augustyn *et al.*, 1992), occupying deeper waters during the day and moving towards the surface at night. The depths used here were based on the day and night time depth distribution of *Calanus agulhensis* on the Agulhas Bank (see Huggett and Richardson, 2000). This copepod is thought to make up a large component of the chokka squid paralarvae diet (Venter *et al.*, 1999). Lastly, a (vi) 40-day paralarval transport duration, as loliginid paralarvae begin displaying schooling behaviour at  $\sim 40$  days, possibly indicating the transition from the paralarvae to the juvenile stage (Bigelow, 1992). Within the IBM, the highly productive inshore spawning grounds (hereafter referred to as the south coast nursery grounds) and cold ridge were classified as nursery grounds. The area beyond the 200-m isobath was also defined as a zone to allow the determination of

paralarval losses from the Agulhas Bank. The computational time step within the IBM was set at 1800 s, with model outputs recorded every 12 h (00:00 and 12:00 h).

To determine potential paralarval survival, and hence contribution to recruitment, success was calculated based on (i) reaching areas of high productivity before the onset of starvation, i.e., within 5 days (Vidal *et al.*, 2005); (ii) Retention in nursery grounds, i.e.,  $\geq 14$  days was used as paralarvae become more resistant to starvation as they become older and can survive longer periods without food (Vidal *et al.*, 2006); and (iii) retention on the shelf (inshore of 200-m isobath) once exiting nursery 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:

- losses due to failure in reaching nursery grounds before the onset of starvation,
- losses due to poor retention within food-rich areas, and
- losses due to off shelf advection.

After factoring in paralarval losses, the percentage of successful recruits for each release site and for each month and season was calculated. All results were expressed as the percentage of the total number of particles (hereafter referred to as paralarvae) released. The effect of the release site, locality (inshore versus deep) and season (month) on successful recruitment to the south coast and cold ridge nursery grounds was analysed using a nested ANOVA. Data were arcsine-transformed to correct for heteroskedasticity of the percentage data.

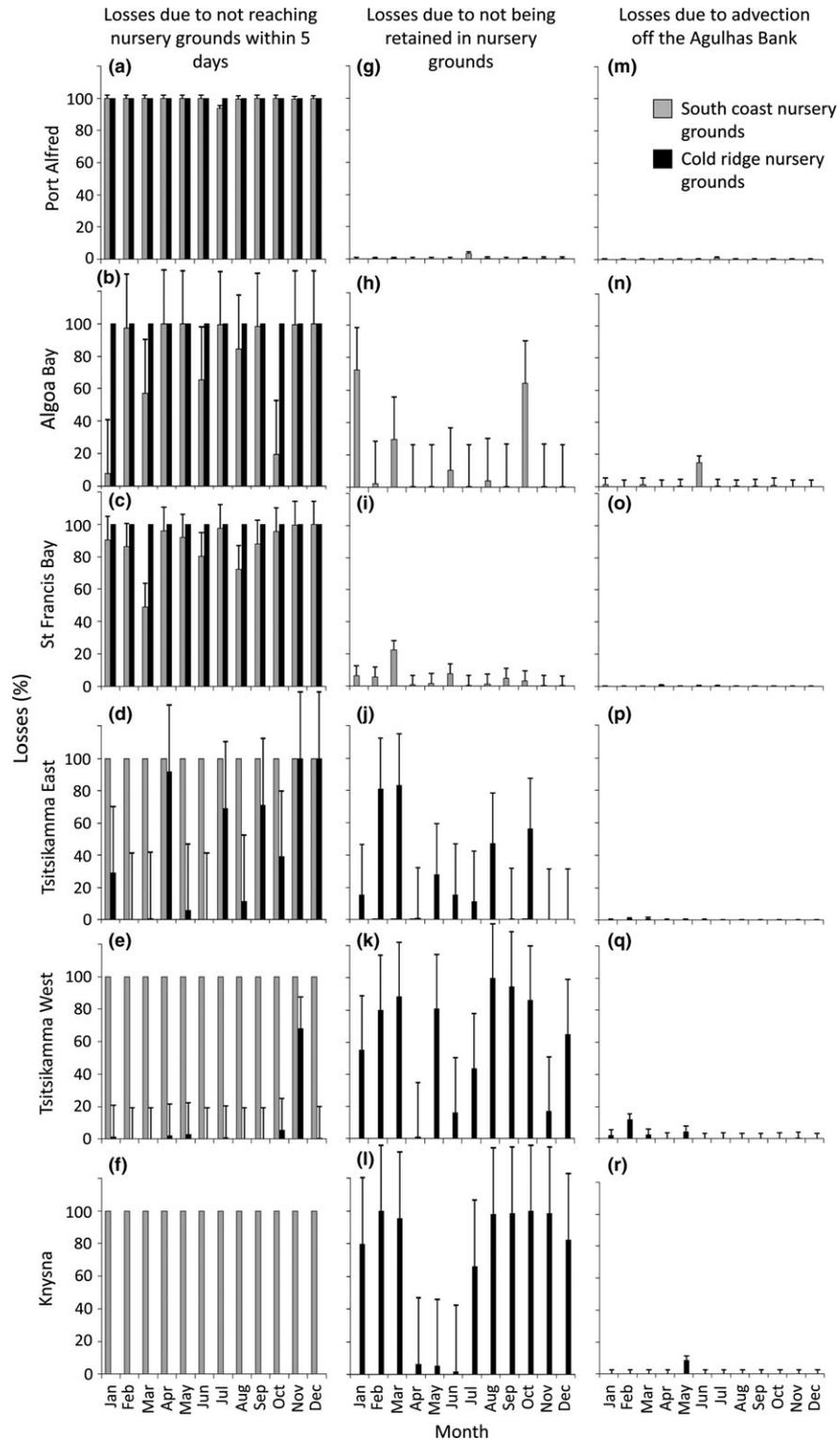
The position of recruited paralarvae, when schooling behaviour commenced (day 40), was plotted and analysed using kernel density analysis. This enabled not only distribution on the Agulhas Bank to be investigated, but also areas of highest paralarval concentration to be identified. Results were plotted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

## RESULTS

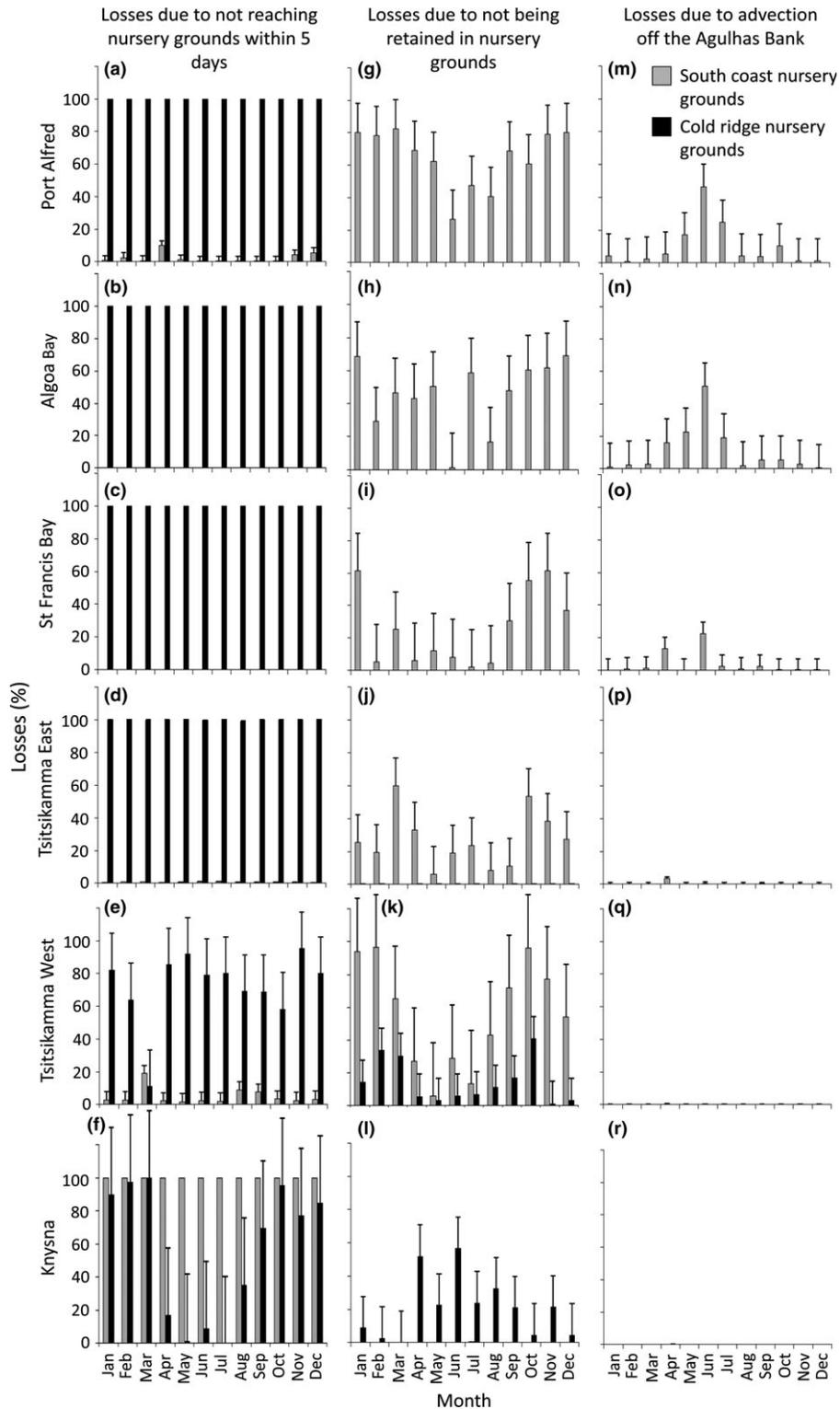
### Modelled mortality

Figures 3 and 4 show the modelled percentage of losses occurring as a result of (i) not being transported to nursery grounds within 5 days of hatching, (ii) not being retained within food-rich areas ( $\geq 14$  days), and (iii) not being retained on the Agulhas Bank (after exiting nursery grounds). Figure 3 provides results for paralarvae released from the six deep-spawning sites, and considering both the south coast and the cold

**Figure 3.** Monthly losses (%) of deep-spawned *Loligo reynaudi* hatchlings resulting from slow transport (a–f), poor retention (g–l) and advection off the Agulhas Bank (m–r). Results are given for both nursery grounds: south coast (grey bars) and cold ridge (black bars), and each release site: Port Alfred, Algoa Bay, St Francis Bay, Tsitsikamma East, Tsitsikamma West and Knysna. Error lines denote standard deviation.



**Figure 4.** Monthly losses (%) of inshore-spawned *Loligo reynaudi* hatchlings resulting from slow transport (a–f), poor retention (g–l) and advection off the Agulhas Bank (m–r). Results are given for both nursery grounds: south coast (grey bars) and cold ridge (black bars), and each release site: Port Alfred, Algoa Bay, St Francis Bay, Tsitsikamma East, Tsitsikamma West and Knysna. Error lines denote standard deviation.



ridge, as nursery grounds. Figure 4 provides these same results for paralarvae released from the six inshore-spawning sites.

*Deep-spawned hatchlings and the south coast nursery grounds.* The majority of paralarvae released from the deep-spawning sites were not transported inshore to the south coast nursery grounds within 5 days (Fig. 3a–f). Those paralarvae released from the deep Algoa Bay and St Francis Bay sites which were carried inshore were later lost by transport out of the nursery ground or advection off the Agulhas Bank (Fig. 3h,i,n). Transport trajectories seen within the model animations showed these paralarvae were transported eastwards towards Port Alfred where they were swept off the shelf.

*Deep-spawned hatchlings and the cold ridge nursery grounds.* No paralarvae released from the Eastern Agulhas Bank deep-spawning sites were transported to the cold ridge nursery grounds within 5 days of release (Fig. 3a–c). Transport from the two Tsitsikamma and Knysna deep-spawning sites was more successful (Fig. 3d–f). The greatest losses of paralarvae released from the Tsitsikamma East site resulted from slow transport and not reaching the cold ridge nursery grounds within the 5-day window (Fig. 3d). Of secondary importance were paralarval losses owing to poor retention within the cold ridge (Fig. 3j). From the deep 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 (Fig. 3k,l). A very small percentage of paralarvae were lost through advection from the Agulhas Bank after being transported out of the nursery grounds (Fig. 3q,r).

*Inshore spawned hatchlings and the south coast nursery grounds.* As all except the Knysna inshore release sites were situated within the south coast nursery grounds, paralarval survival did not depend on transport to this area within the 5-day period. However, a few paralarvae were immediately advected after release, and were, therefore, not considered present (Fig. 4a,e). Poor retention on the south coast nursery grounds (Fig. 4g–k) was the major cause of paralarval losses. The degree of paralarval losses varied depending on both month and release site (Fig. 4g–k). Of those paralarvae successfully retained in the nursery grounds, later losses through advection off the Agulhas Bank were greatest for those hatchlings originating from the Eastern Agulhas Bank (Fig. 4m–o). Losses from off shelf advection were particularly great during the autumn–winter

months, May to July (Fig. 4m–o). No paralarvae released from the Knysna inshore site were transported to the south coast nursery grounds within 5 days (Fig. 4f).

*Inshore-spawned hatchlings and the cold ridge nursery grounds.* Zero to very few paralarvae released from the Port Alfred, Algoa Bay, St Francis Bay or Tsitsikamma East inshore spawning sites were transported to the cold ridge nursery grounds within 5 days (Fig. 4a–d). Moving further west to inshore spawning sites closer to the cold ridge, successful transport increased slightly and losses were lower (Fig. 4e,f). During March, only a relatively small percentage of paralarvae from the Tsitsikamma West site were lost, with most reaching the cold ridge within 5 days (Fig. 4f). Losses by way of not reaching the cold ridge feeding grounds in the 5-day window were also low for paralarvae hatched from the inshore Knysna site during the months April–August (Fig. 4f). Overall, the largest losses resulted from slow transport to cold ridge nursery grounds (Fig. 4a–f), followed by poor retention within the nursery ground (Fig. 4k,l). Losses through advection off the Agulhas Bank once exiting the nursery ground were minimal (Fig. 4q,r).

*The influence of release area, locality and season on mortality.* For all three factors contributing to paralarval losses considered, both release area and locality (inshore versus deep) had a significant influence (Table 1a–c). In general, when considering the south coast nursery grounds, losses through not reaching the nursery ground within 5 days were greatest for deep-spawned hatchlings (Table 1a, Figs 3 and 4). The release area and season had a significant influence on retention within the south coast nursery grounds, with the greatest losses resulting from poor retention of paralarvae hatching from the eastern and westernmost release areas, particularly during the spring and summer months (Table 1b, Fig. 4). Retention on the Agulhas Bank after exiting the south coast nursery grounds was significantly influenced by all factors considered in the ANOVA analysis (Table 1c). Losses through advection off the Agulhas Bank were greatest for paralarvae hatching on the Eastern Agulhas Bank, particularly during the winter months (Table 1c, Fig. 4).

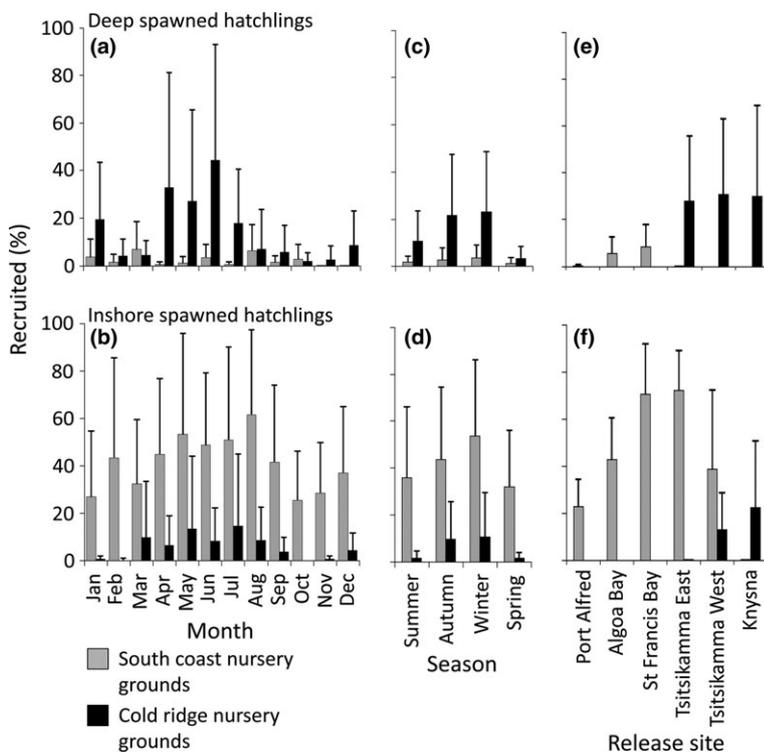
The release area and locality (inshore versus deep) were the only factors significantly affecting paralarval losses when considering the cold ridge as nursery grounds (Table 1d–f). The season did not affect transport or retention within the cold ridge or on the

**Table 1.** Results of the nested ANOVA applied to the IBM simulation results, indicating the effects and interactive effects of release area, locality (inshore versus deep) and season (month) on paralarval mortality. \*Significant.

	d.f.	South coast nursery grounds					Cold ridge nursery grounds				
		SS	MS	F	P		SS	MS	F	P	
Release area	5	(a)	17.099	3.420	115.953	<2.2E-16*	(d)	39.088	7.818	123.464	<2.2E-16*
Locality	1		45.671	45.671	1548.551	<2.2E-16*		6.051	6.051	95.557	<2.2E-16*
Season (Month)	11		0.409	0.037	1.260	0.272		0.953	0.087	1.368	0.214
Release area × Locality	5		10.392	2.078	70.469	<2.2E-16*		6.272	1.254	19.811	<2.2E-16*
Release area × Season (Month)	55		1.663	0.030	1.025	0.464		4.026	0.073	1.156	0.296
Locality × Season (Month)	11		0.438	0.040	1.351	0.223		0.448	0.041	0.643	0.784
Error	55		1.622	0.029				3.483	0.063		
Release area	5	(b)	2.494	0.499	16.062	<2.2E-16*	(e)	7.749	1.550	25.483	<2.2E-16*
Locality	1		4.907	4.907	157.977	<2.2E-16*		2.637	2.637	43.365	<2.2E-16*
Season (Month)	11		1.434	0.130	4.196	1.65E-04*		1.222	0.111	1.827	0.071
Release area × Locality	5		2.269	0.454	14.611	<2.2E-16*		3.164	0.633	10.405	<2.2E-16*
Release area × Season (Month)	55		1.491	0.027	0.873	0.692		2.426	0.044	0.725	0.882
Locality × Season (Month)	11		0.717	0.065	2.097	0.036*		1.376	0.125	2.057	0.040*
Error	55		1.708	0.031							
Release area	5	(c)	0.096	0.019	8.609	4.49E-06*	(f)	1.73E-03	3.46E-04	2.434	0.046*
Locality	1		0.056	0.056	25.144	5.88E-06*		8.13E-04	8.13E-04	5.724	0.020*
Season (Month)	11		0.140	0.013	5.713	4.74E-06*		2.28E-03	2.07E-04	1.456	0.175
Release area × Locality	5		0.069	0.014	6.165	1.33E-04*		1.68E-03	3.36E-04	2.366	0.051
Release area × Season (Month)	55		0.199	3.62E-03	1.626	0.037*		8.01E-03	1.46E-04	1.025	0.464
Locality × Season (Month)	11		0.090	8.18E-03	3.674	6.06E-04*		2.23E-03	2.03E-04	1.426	0.188
Error	55		0.123	2.23E-03				7.81E-03	1.42E-04		

**Table 2.** Results of the nested ANOVA applied to the IBM simulation results, indicating the effects and interactive effects of release area, locality (inshore versus deep) and season (month) on successful recruitment. \*Significant.

	d.f.	South coast nursery grounds				Cold ridge nursery grounds				
		SS	MS	F	P	SS	MS	F	P	
Release area	5 (a)	3.664	0.733	30.877	<2.2E-16*	(b)	2.261	0.452	12.937	<2.2E-16*
Locality	1	7.073	7.073	298.024	<2.2E-16*		0.414	0.414	11.846	1.11E-03*
Season (Month)	11	0.813	0.074	3.116	2.53E-03*		1.401	0.127	3.643	6.55E-04*
Release area × Locality	5	2.949	0.590	24.848	<2.2E-16*		0.509	0.102	2.914	0.021*
Release area × Season (Month)	55	1.590	0.029	1.218	0.234		3.205	0.058	1.667	0.030*
Locality × Season (Month)	11	0.779	0.071	2.985	3.56E-03*		0.886	0.081	2.305	0.021*
Error	55	1.305	0.024				1.923	0.035		

**Figure 5.** The overall monthly percentages of successful recruits per month, season and release site, released from the deep- and inshore-spawning grounds. Results are given for both nursery grounds: south coast (grey bars) and cold ridge (black bars). Error lines denote standard deviation.

Agulhas Bank. Overall, losses through slow transport were greatest for paralarvae hatching on the Eastern Agulhas Bank, particularly those inshore (Table 1d, Figs 3 and 4), whereas losses through poor retention were greatest for paralarvae hatching from the western release areas (Table 1e,f, Figs 3 and 4).

#### Modelled recruitment

*The influence of release area, locality and season on recruitment.* Successful recruitment considering the south coast as nursery grounds was most significantly dependent on the release area, locality (inshore versus

deep) of the hatching sites and the interaction of these two factors (Table 2a). Of lesser importance was the influence of season (Table 2a). When considering the cold ridge nursery grounds, successful recruitment was mostly influenced by release area, followed by season and locality (Table 2b). The interactive effect of factors were also significant, but to a lesser degree (Table 2b).

Overall paralarval survival per month, season and release site is given in Figure 5. Immediately evident is the relative importance of the two nursery grounds depending on the origin of the hatchlings. The results show the cold ridge to be an important nursery area for

**Figure 6.** (a) The position of successful paralarvae, released from the deep-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. (b) 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.

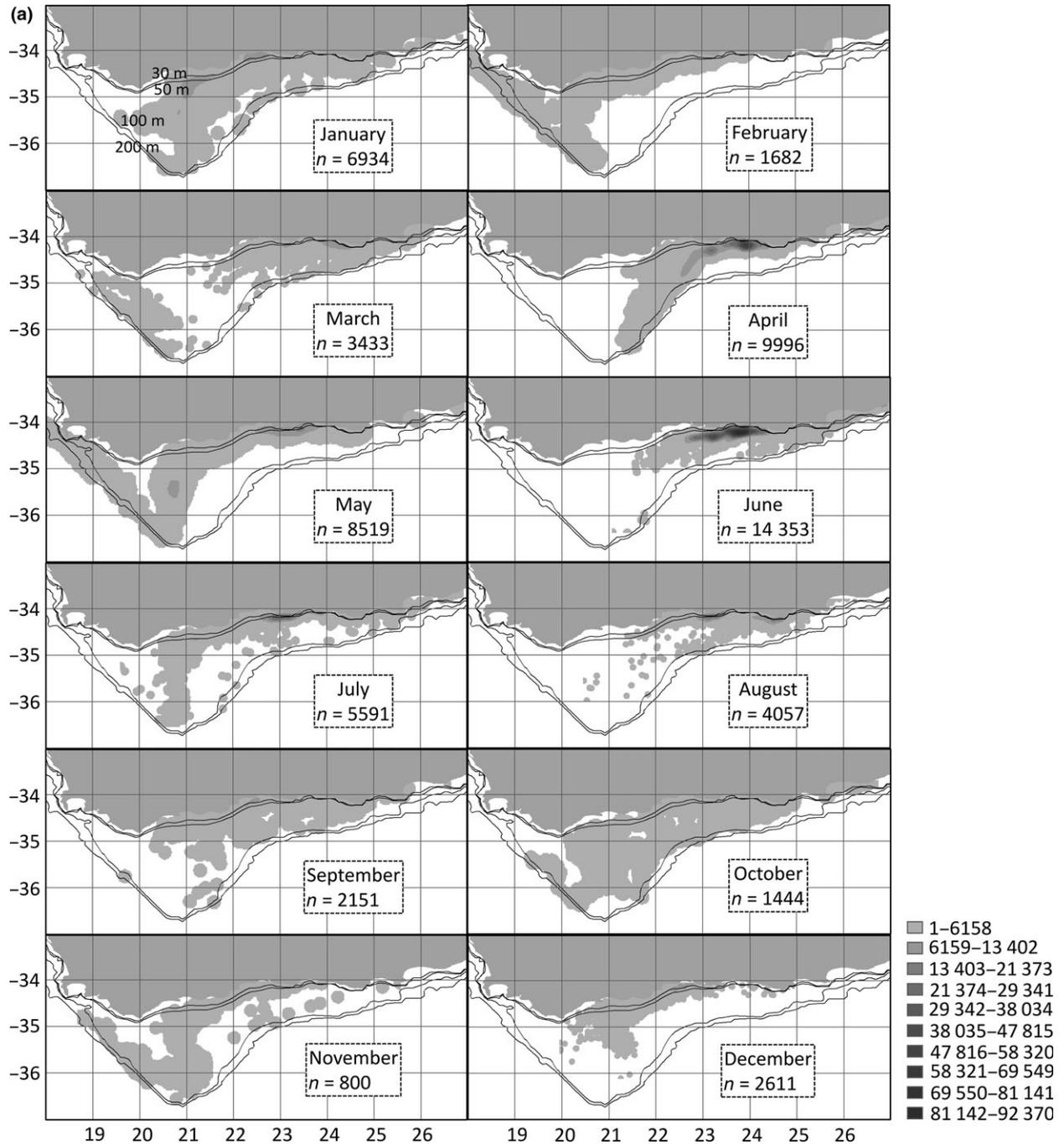
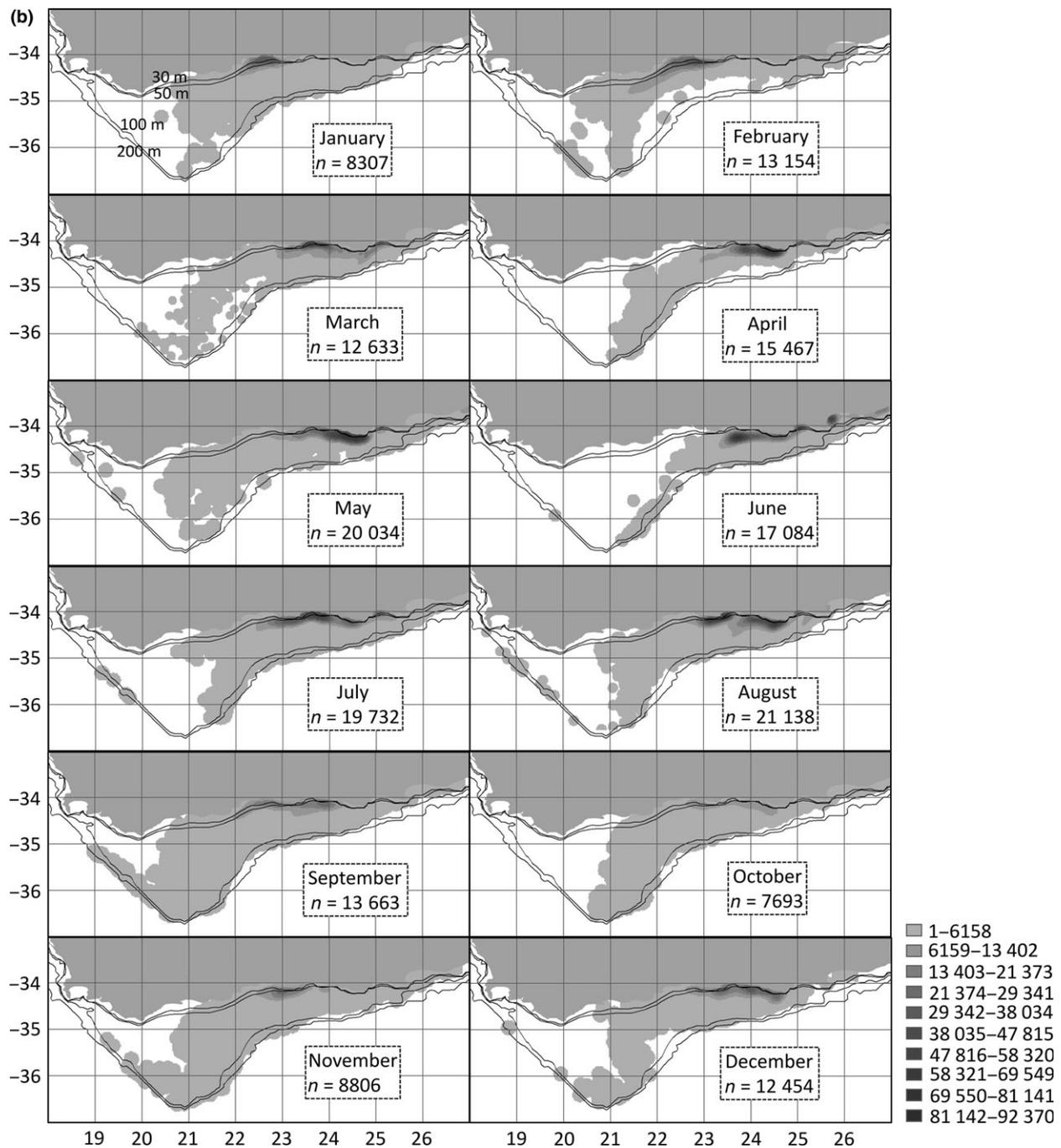


Figure 6. Continued.



deep-spawned hatchlings (Fig. 5a), with fewer inshore hatchlings being transported here (Fig. 5b). Instead, young inshore hatchlings were initially retained in the south coast nursery grounds, leading to the high recruitment levels observed (Fig. 5b). Despite the evident monthly variability in recruitment success,

common to both deep and inshore hatchlings was the highest survival during the autumn–winter (Fig. 5c,d) months April–August (Fig. 5a,b). A second peak in the number of successful recruits was observed for inshore hatchlings released in December and February (Fig. 5b).

Hatching site also played a significant role in paralarval survival (Table 2 and Fig. 5). When considering the south coast nursery grounds, a very small number of hatchlings originating from the Port Alfred, Algoa Bay and St Francis Bay deep sites survived (Fig. 5e). Further west (Tsitsikamma and Knysna sites), survival was zero. Not surprising considering the proximity to the cold ridge, paralarvae hatching on the deep-spawning grounds off the Tsitsikamma and Knysna coasts, and transported to the cold ridge nursery grounds, showed the highest recruitment success (Fig. 5e). Survival of paralarvae originating from hatching sites further east was zero. The recruitment success of inshore hatchlings, when considering the south coast nursery grounds, was greatest for those paralarvae originating from the centre of the spawning grounds (St Francis Bay and Tsitsikamma East) (Fig. 5f). Further east, paralarvae were lost through off shelf advection; and further west paralarvae were quickly transported westwards out of the nursery grounds. A portion of the westward carried paralarvae did enter the cold ridge (Fig. 5f). The successful transport of paralarvae originating from other inshore spawning sites was minimal (Fig. 5f).

*Paralarval distribution and concentration.* Figure 6a,b show the monthly position and areas of concentration of 40-day-old paralarvae released from the deep and inshore spawning sites, respectively. Immediately evident is the monthly variability in the distribution on the Agulhas Bank, as well as the 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, paralarvae released from the deep spawning grounds were generally transported westwards (Fig. 6a). Although the net westward transport continued over the Central 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 (Fig. 2) 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 were similar, although there appeared to be a higher degree of concentration near the coast, and paralarvae were not transported as far westwards (Fig. 6b).

## 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.*, 2014). Also in line with earlier findings was the dependence of transport success on spawning site. Using three deep release areas spanning the entire Tsitsikamma coast, St Francis Bay and Algoa Bay, Martins *et al.* (2014) established paralarvae released off Tsitsikamma showed the greatest success in reaching the cold ridge before the exhaustion of yolk reserves. The present study both corroborates and further refines these findings, showing the greatest transport success from the Tsitsikamma West hatching site specifically. Once reaching the cold ridge nursery area, the largest losses resulted from poor retention in this highly productive region.

The cold ridge extends from the Knysna coast (Eastern Agulhas Bank), southwestward onto the Central Agulhas Bank (Fig. 2b). As such, both coastal and mid-shelf currents influence the retention of paralarvae within the cold ridge. Using average shipborne ADCP data, Roberts (2005) showed the existence of a narrow eastward coastal flow between Mossel Bay and Cape Seal (Plettenberg Bay, Fig. 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 and 30 cm s<sup>-1</sup> (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, N.J. Downey-Breedt).

According to Roberts and van den Berg (2002), paralarvae on the Central and Western Agulhas Bank can be removed from the shelf through offshore leakage. The present study indicates that off shelf 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 off shelf leakage are minimal. The positions of 40-day-old paralarvae reveal that deep-spawned hatchlings can be transported to the west coast. In model months February and May (Fig. 6a), paralarvae were transported as far west as False Bay.

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 (Fig. 6a, April–August). This seasonal influence is also evident in the overall monthly and seasonal results (Fig. 5a,c), which indicate increased survival of deep-spawned 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 Roberts *et al.* (2012), results from certain years show at times deep 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 ~2 months. This suggests that deep spawning in April enables emergent hatchlings to take advantage of the particularly beneficial currents occurring 2 months later in June (Fig. 5a), when over 40% of deep-spawned hatchlings were recruited.

The earlier IBM study by Martins *et al.* (2014) demonstrated that between 1.13–67.10% of deep-hatched paralarvae were successfully transported to the cold ridge. In the present study, although also factoring in successful transport to the south coast nursery grounds, the inclusion of paralarval losses beyond the

yolk-utilization phase resulted in lower estimates. Overall, the successful recruitment of deep-spawned hatchlings varied between 2.67 and 47.84% (depending on release month). This equated to only 17.1% 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 25.64 and 70.46% (depending on release month). The overall recruitment success for paralarvae released for the entire year modelled was 47.27%. For virtual paralarvae hatching from the inshore spawning grounds, this food-rich environment was the more important nursery area, as first proposed by Martins *et al.* (2014). Considering the high productivity of this region, model results and *in situ* observations, these authors suggested that the cold ridge was not used as a nursery area by at least part of the inshore-spawned hatchlings.

Here, paralarval losses resulted mainly from poor retention within the south coast nursery grounds and offshore leakage from the narrow Eastern Agulhas Bank. The distribution of 40-day-old paralarvae (Fig. 6b), indicates the cold ridge to be an important nursery 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).

Model results indicated significant seasonal variability in paralarval recruitment. Recruitment success was highest during the autumn and winter months (April–August) (Fig. 5a–d), with an additional peak in December and February. 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 van den Berg, 2002; Roberts and Mullon, 2010). Studies have suggested DVM aids in the retention of paralarvae in certain areas (Roberts and van den Berg, 2002; González *et al.*, 2005), 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 probably 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, N.J. Downey-Breedt).

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 the second minor spawning 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 copepod *C. agulhensis* dominates the zooplankton biomass on the Agulhas Bank (Verheye *et al.*, 1994). The year-round presence of this species 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 (Fig. 6b), so could their food sources be similarly concentrated. This is a strategy believed to have evolved for fish species, with spawning time and location ensuring 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, González *et al.* (2010) estimated the instantaneous rate of total mortality (first 90 days) for wild-caught *L. vulgaris* paralarvae to be 9.6, 5.3 and 4.8% day<sup>-1</sup> 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 nursery grounds and loss from the shelf ecosystem, no other mortality factors (predation and 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 (17.1%) than for inshore-hatched paralarvae (47.27%). 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 the summer (Schumann *et al.*, 1982; Roberts and van den Berg, 2002; Roberts, 2005), 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, 1990; Augustyn and Roel, 1998), 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 versus 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.

Martins *et al.* (2014) 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<sup>-1</sup>, Vidal *et al.*, 2002) 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 nursery 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 (Olyott *et al.*, 2007) increase in deep spawning off the Tsitsikamma coast. Second is the model predicted successful autumn–winter recruitment of deep-spawned paralarvae hatching from the Tsitsikamma West site. 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 owing 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 as a result of lower metabolic rates. Another advantage of lower metabolic rates would be the slower utilization of the 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 also allow more time for the development of prey capture abilities (Martins *et al.*, 2010). Considering zooplankton is present on the Agulhas Bank throughout the year, in particular, the copepod *C. agulhensis* (Huggett and Richardson, 2000), 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 south coast region 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, deep spawning may at times contribute significantly to recruitment.

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