Drift routes of Cape hake eggs and larvae in the southern Benguela Current system

ERLING KÅRE STENEVIK[1]*, HANS M. VERHEYE[2], MAREK R. LIPINSKI[2], MAREK OSTROWSKI[1] AND TORE STRØMME[1]

[1]INSTITUTE OF MARINE RESEARCH, PO BOX 1870, NORDNES 5817, BERGEN, NORWAY AND [2]MARINE AND COASTAL MANAGEMENT, PRIVATE BAG X2, ROGGEBAAI 8012, CAPE TOWN, SOUTH AFRICA

*CORRESPONDING AUTHOR: erling.stenevik@imr.no

The aim of this study was to combine observed circulation pattern with data on distribution of hake eggs and larvae in the southern Benguela from a survey in September/October 2005 to investigate drift routes of hake eggs and larvae. Genetic information enabled species-specific information about drift routes of the two hake species (Merluccius capensis and M. paradoxus) to be established. The results showed that both species were transported from spawning areas to nursery areas in the jet current, but differential cross-shelf distribution would most likely lead to species-specific drift routes which could explain why the two species seem to have different nursery areas.

INTRODUCTION

Most hake species of the world are important both ecologically and commercially, supporting large fisheries (Alheit and Pitcher, 1995). Two of the three southern African species, *Merluccius capensis* Castelnau, 1861 and *M. paradoxus* Franca, 1960—referred to as Cape hakes—are dominant components of the northern and southern Benguela upwelling sub-systems and the Agulhas Bank system (Crawford *et al.*, 1987; Japp *et al.*, 1994). The third species, *M. polli* Cadenat, 1950 is not so abundant and is not found in waters south of the border between Angola and Namibia in any significant numbers (Martos and Peralta, 1995). Despite their recognized importance, knowledge of the life cycles of *M. capensis* and *M. paradoxus* is relatively poor, or spread unevenly over various aspects including age and growth, sexual maturation, spawning, migrations, stock structure and identity and early-life history among others. In particular, their early-life history in the southern Benguela has received very little research attention, as is evident from specific biological (Payne and Punt, 1985; Gordoa *et al.*, 1995) and topical reviews (Hutchings *et al.*, 2002). The main reason for this stems from a lack of distinct morphological characters that may help identification of eggs and larvae of both Cape hake species, which have a sympatric distribution and intertwined life cycles.

Whereas substantial collections of hake eggs and larvae have been made in Namibian (Sundby *et al.*, 2001) and South African waters (Shelton, 1986; Grote *et al.*, 2007), species-specific considerations were based merely on circumstantial evidence. Most recently, species-specific mitochondrial DNA PCR was used, which for the first time allowed the distinction of eggs and larvae between the two Cape hake species (von der Heyden *et al.*, 2007a).

The aim of the present paper is to describe the horizontal and vertical distribution of eggs and larvae of the two hake species using data collected during a survey in September/October 2005, and to combine this information with the observed circulation pattern in order to suggest possible drift routes for the two species' spawning products.

MATERIAL AND METHODS

Sampling was carried out between 27 September and 17 October 2005 aboard the Norwegian research vessel

"Dr Fridtjof Nansen" covering the shelf and slope between Cape Agulhas on the South African south coast and southern Namibia on the west coast (Figs 1 and 3).

Data on water column temperature, salinity, and dissolved oxygen were collected with a Seabird 9+ CTD probe between the surface and 10 m off the bottom. Casts were made at each station prior to ichthyoplankton net sampling. The CTD probe was fitted with a set of factory-calibrated sensors, installed in December 2004. In addition, water bottle samples for dissolved oxygen and salinity calibrations were taken at almost all CTD stations.

Current measurements were carried out using a hull-mounted RD Instruments Acoustic Doppler Current Profiler (ADCP), operated at 150 kHz in broad-band mode with 5 m vertical cells. Currents were measured from a depth of 20 m down to ~30 m above the bottom. Only the bottom-tracked data were used in the data analysis.

Hake eggs and larvae were sampled with a multiple opening–closing Hydrobios Multinet® plankton sampler (type Midi, 0.25 m^2 mouth area), equipped with five nets of 405 μm mesh size. Net depth was monitored using a Scanmar depth recorder mounted on top of the Multinet, with acoustic transmission to the vessel. The sampler was towed in an oblique mode, and samples were collected during ascent over five standard depth intervals: 10 m above bottom–200 m, 200–150 m, 150–100 m, 100–50 m and 50–0 m. At stations where the water depth was <200 m, the upper depth intervals were kept to the standard 50 m layers,
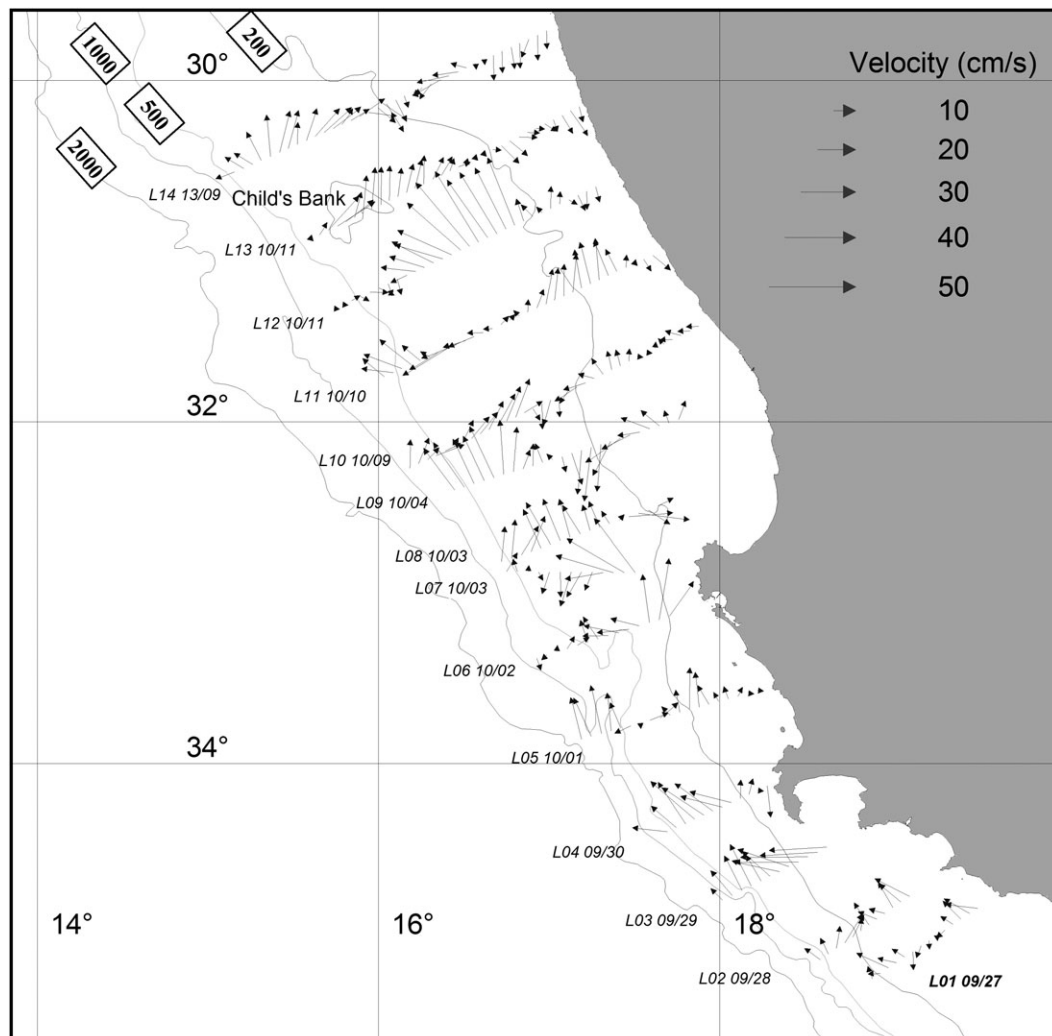

Fig. 1. ADCP-derived current vectors averaged between 20 and 80 m, 27 September to 14 October 2005. Only the transects perpendicular to the coast are shown. Transect numbers referred to in the text and their approximate dates (mm/dd) are labelled to the left of each transect. Bottom contours are also shown with labels in the top part of the figure.
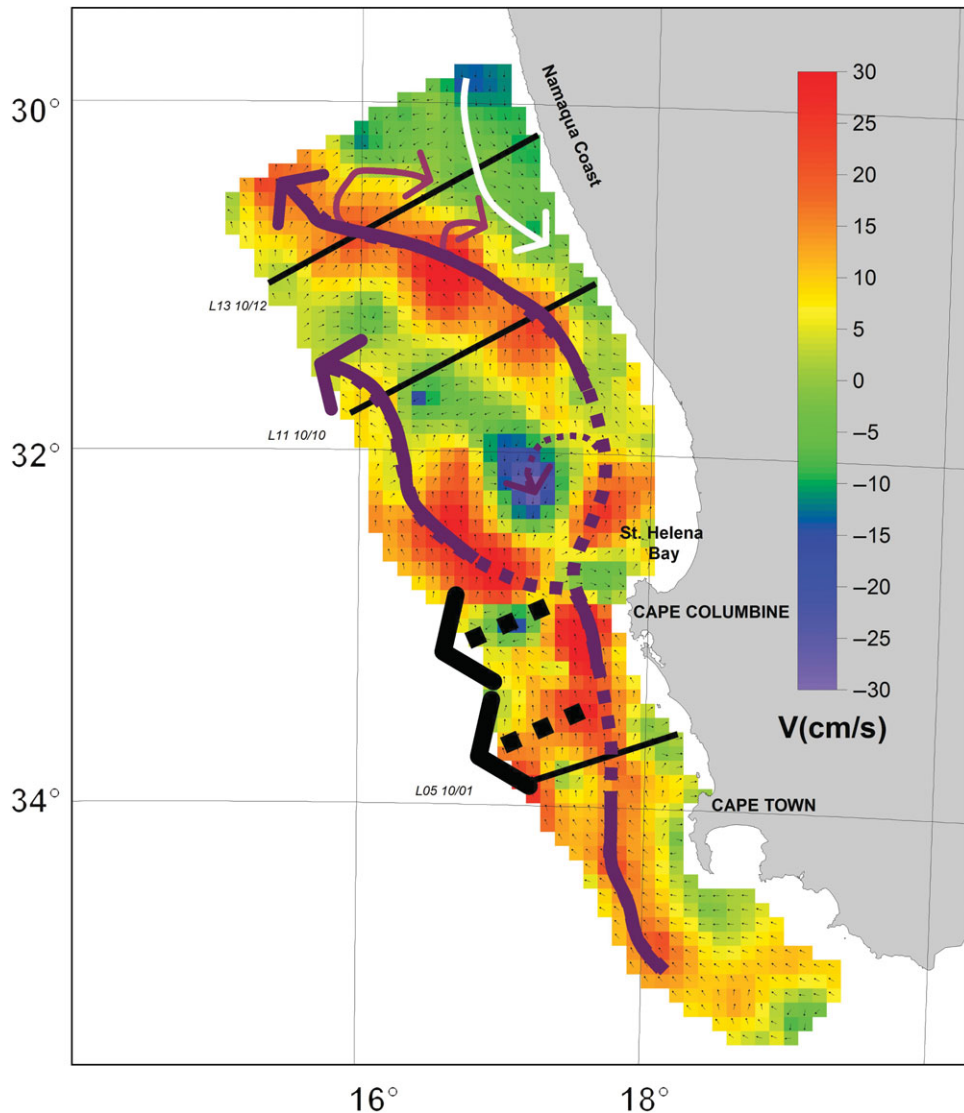
Fig. 2. Gridded distribution of ADCP-derived currents. The color scale describes the northward component of the flow while the vectors show the net direction of the total current. Conceptual drift paths are superimposed onto the current distribution: (—) convergent flow, fully supported by data from this study; (- - -) diffusive flow, drift routes are assumed based on this study's data and historical observations. The two black arrows pointing offshore near Cape Columbine denote tentative locations of largest advective losses. The white arrow shows a southward flowing current.

whereas the deepest net sampled from 10 m above the bottom to the nearest standard depth interval.

The Multinet was hauled at $0.5 \, \mathrm{m \, s^{-1}}$ while the vessel maintained a speed of two knots. A mechanical flowmeter mounted inside each net recorded water flow through the net within each depth interval, from which the volume of water filtered by each net was calculated. Immediately after collection, hake eggs and larvae from each net were sorted on board based on descriptions by Olivar and Fortuño (Olivar and Fortuño, 1991) and enumerated, and all larvae were measured [standard length (SL)]. Since it was not possible to distinguish

between the two hake species at the egg and larval stages at sea, all hake eggs and larvae sorted from the net samples were preserved in either liquid nitrogen or 96% denatured ethanol until subsequent genetic analysis. The methods for genetic analyses are described by von der Heyden *et al.* (von der Heyden *et al.*, 2007a) and will only be briefly described here. Species-specific polymerase chain reaction (PCR) primers have been designed against a large number of mtDNA control regions by von der Heyden *et al.* (von der Heyden *et al.*, 2007a). These have been tested using DNA extracted from previously species-identified adult hake by von der
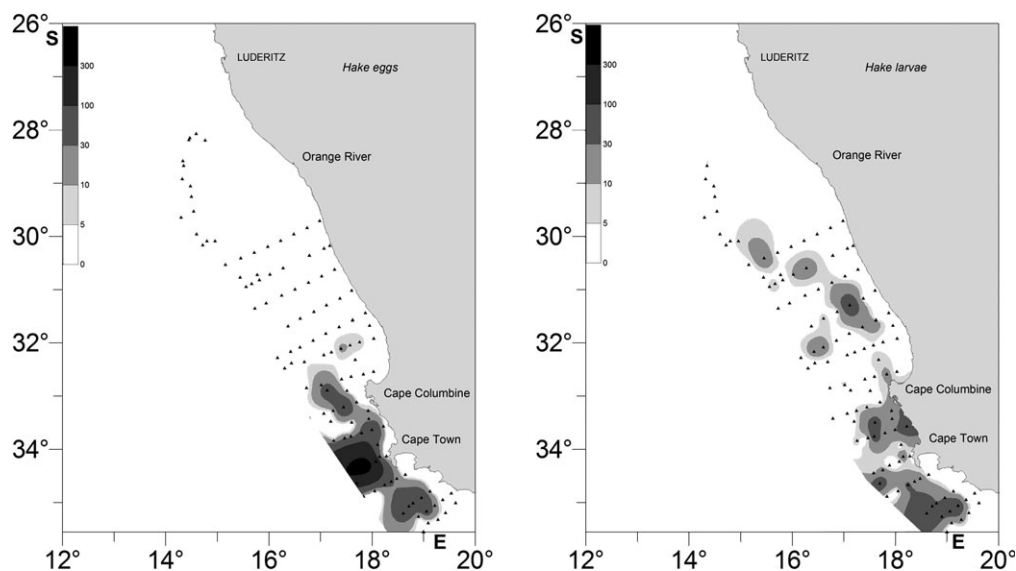
Fig. 3. Station map showing the distribution of eggs (left) and larvae (right) of Cape hakes (both species combined). Numbers per 10 m².

Heyden et al. (von der Heyden et al., 2007b). A total of 156 hake eggs and 41 hake larvae were successfully identified to species.

RESULTS

Circulation and drift routes

The horizontal distribution of the mean current averaged over the 20–80 m depth layer is shown in Fig. 1. For clarity, only survey transects perpendicular to the coast are shown. The two transects across the western Agulhas Bank (L01 and L02) display a weak flow that is variable but generally aligned with the bathymetry. Flow accelerates as it passes the Cape Peninsula where it forms a well-defined structure of the shelf edge jet current (L03 and L04). At Cape Columbine, the core of the current swings inshore and accelerates (L06).

North of Cape Columbine, the jet current diverges into an offshore branch, which flows along the shelf edge, and an inshore branch, which is aligned with the indentation of the shelf topography (Shannon, 1985; Boyd et al., 1992). This is only partly resolved in our data, because the transects in this region (L07 and L08) did not cover the most inshore region. As a result, flow into the offshore branch is well resolved, but the inshore branch is only partially covered. The signature of the inshore branch appears clearly on transect L09. It was also strong during the transit between transects L08 and L09 (not shown).

Along the west coast, the dual core structure of the jet current is clear (L10 to L12). The shelf bathymetry in this region exhibits a dual shelf break structure located at 200–380 m and 500 m, respectively. Both current branches match the shelf break locations. The offshore branch follows the outer shelf break, departing from the survey area just south of Child's Banks (L12). The inshore branch aligns well with the inner shelf break, approaching the coast where the shelf narrows (L11) and departing offshore as it broadens along the Namaqua Coast (L14).

A southward flowing current separates the inshore current branch from the coast. The region affected by this flow is broad in the north (L14) but vanishes on transect L10. However, our observations did not extend to the inshore region shallower than 90 m bottom depth where southward inshore flow has previously been observed along the entire west coast (Holden, 1985; Boyd et al., 1992).

In order to summarize the observed flow patterns, we derived a gridded distribution of currents based on all ADCP data using ordinary kriging (Chilés and Delfiner, 1999), which is shown in Fig. 2.

Wind data from the survey have been analyzed but are not shown because of relatively little significance in the context of the paper. The wind conditions were typical for the early upwelling season: wind from predominantly south-easterly directions, speed reaching 7 m s⁻¹. Two wind reversals were experienced, the first when the ship was surveying Lines 01 and 02 and the second across Lines 11 and 12 (See Fig. 1). The wind reversals were short lived and apparently had no effect

on the flow structure, as the jet remained strongly equatorward during both these reversals.

We have not considered tides in this paper. Along open coasts in a wind-driven coastal upwelling system, the tides produce typically a second-order effect to the processes on the time scales characterizing geostrophically balanced baroclinic jets and wind events (e.g. Huthnance and Baines, 1982). Given the complexity of de-tiding procedures, this is a widely adopted approach for describing ADCP-derived currents in the regions where the observed tidal effects are small (e.g. Kosro, 2002). Along the open coasts of Benguela tidal amplitudes are in a range 1 m (Frank Shillington, personal communication, See also http://www.mobilegeographics.com:81/).

Horizontal distribution of eggs and larvae

Hake eggs were only observed in the southernmost part of the survey area, mostly between Cape Columbine and Cape Agulhas over bottom depths ranging from 150 to 1500 m, and no eggs were found north of about 32°S (Fig. 3). Highest concentrations of eggs were observed on the transect (L03) running southwestward off the Cape Peninsula, reaching peak egg densities of $341-411$ eggs $10 \, \mathrm{m}^{-2}$ at the three outermost stations. In addition, there was a relatively high-density patch of eggs $(25-95$ eggs $10 \, \mathrm{m}^{-2})$ mid-shelf off Cape Columbine and another one in the southernmost part of the survey area, on the western Agulhas Bank $(20-100$ eggs $10 \, \mathrm{m}^{-2})$. A relatively small, low-density patch (15 eggs $10 \, \mathrm{m}^{-2}$) was observed to the north of Cape Columbine.

Hake larvae were observed throughout the survey area (Fig. 3). A peak concentration of 72 larvae $10 \, \mathrm{m}^{-2}$ was recorded on the western Agulhas Bank. From here, a band of hake larvae stretched northward to about 30°S. The shelf was not surveyed further north, so it is not possible to establish the northern boundary of the larval distribution.

A total of 156 hake eggs and 41 hake larvae were successfully identified to species and the genetic data suggested that there were clear differences in cross-shelf distribution of eggs and larvae between the two hake species (Figs 4 and 5). Eggs of *M. paradoxus* were clearly distributed over greater bottom depths than those of *M. capensis* (Fig. 5). About 60% of the *M. capensis* eggs were found between 120 and 300 m bottom depth, whereas 90% of the *M. paradoxus* eggs were found further offshore, between 340 and 1500 m bottom depth. The average bottom depth over which *M. paradoxus* and *M. capensis* eggs were found was 855 and 228 m, respectively. Larval *M. paradoxus* were distributed over greater bottom depths than larval *M. capensis*, on average 250 and 181 m, respectively (Fig. 5).

There were also differences in latitudinal distribution of eggs and larvae between the two species (Fig. 6). *Merluccius capensis* eggs and larvae tended to be very closely distributed latitudinally. In contrast, *M. paradoxus* eggs tended to be found south of *M. capensis* eggs and larvae, whereas *M. paradoxus* larvae were clearly distributed north of the *M. capensis* area of concentration. *Merluccius paradoxus* thus shows a greater disparity between egg and larval distributions in comparison with *M. capensis*.

Larval size and age distribution

The hake larvae collected during the survey were relatively small, overall varying between 2 and 15 mm total length. The length frequency distribution shows that total length of most individuals ranged between 3 and 6 mm (Fig. 7). Assuming a growth rate of 0.45 mm day^{-1} (Grote, 2005) for both species, we estimated that most of these larvae were between 1 and 2 weeks old at the time of collection. It should be noted that, since body size was measured onboard, i.e. before the results from the genetic analysis were available, the data in Fig. 7 are presented for the two species combined.

Vertical distribution

Hake eggs and larvae were found throughout the water column between the surface and 200 m depth. The vertical distribution of eggs of the two species was similar (Fig. 8) with highest concentrations in the $50-100 \, \mathrm{m}$ depth interval. The concentration of *M. paradoxus* eggs was, however, much higher (with a maximum mean density of ca. 20 eggs $100 \, \mathrm{m}^{-3}$) compared to *M. capensis* eggs (maximum mean density: ca. 2 eggs $100 \, \mathrm{m}^{-3}$).

The larval vertical distribution differed between the two species even though maximum mean concentrations were of the same order of magnitude. Whereas *M. paradoxus* larvae had a maximum concentration in the $50-100 \, \mathrm{m}$ interval (on average 3 larvae $100 \, \mathrm{m}^{-3}$), highest concentrations (on average 2 larvae $100 \, \mathrm{m}^{-3}$) of *M. capensis* larvae were found in the upper 50 m. It should be noted, however, that the number of eggs and larvae used in these analyses were relatively low (18 *M. capensis* eggs from 7 stations, 12 *M. capensis* larvae from 7 stations, 57 *M. paradoxus* eggs from 4 stations and 28 *M. paradoxus* larvae from 13 stations). The reason for this is that some of the stations had to be excluded because eggs/larvae from different depth strata were preserved together and these results should therefore be interpreted with caution.
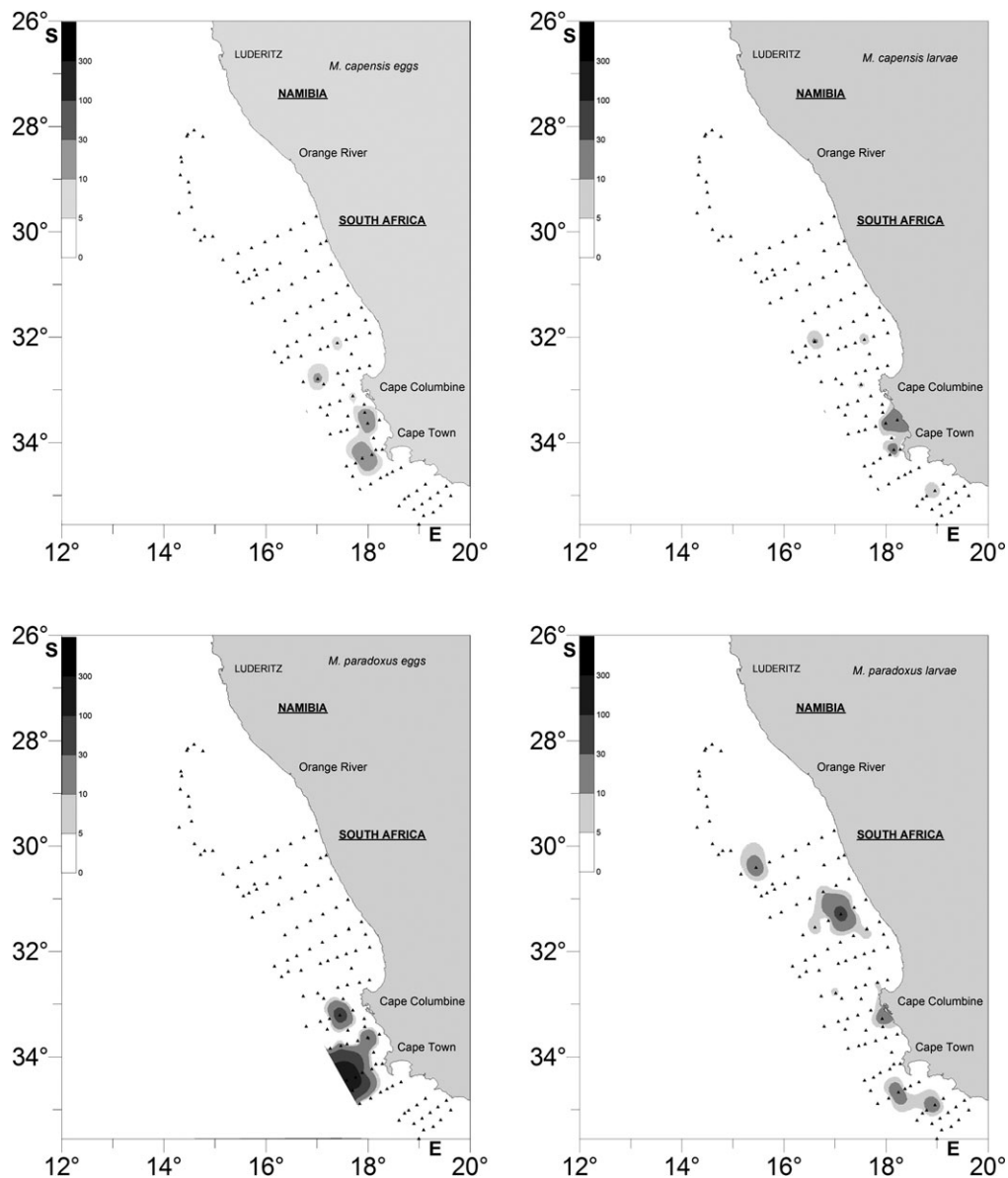
Fig. 4. Distribution of eggs (left) and larvae (right) of *M. capensis* (upper) and *M. paradoxus* (lower). Numbers per 10 m².
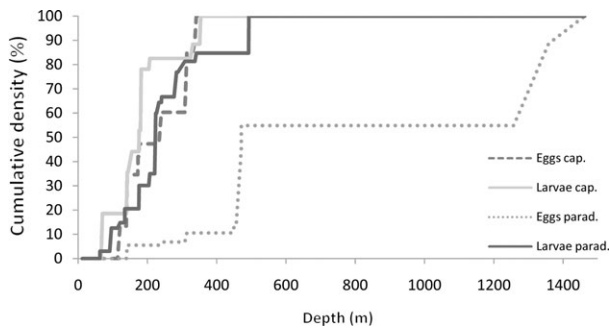

Fig. 5. Cumulative density plots of eggs and larvae of *M. capensis* and *M. paradoxus* sorted by increasing depth.
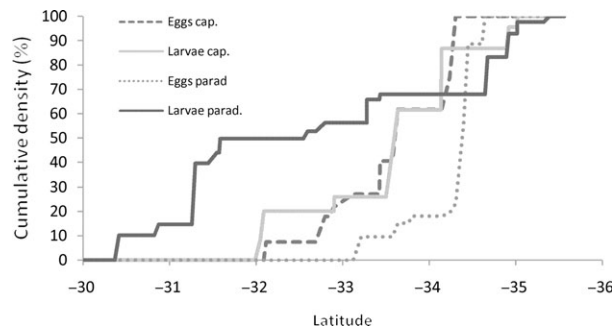

Fig. 6. Cumulative density plots of eggs and larvae of *M. capensis* and *M. paradoxus* sorted by increasing latitude (degrees south).

DISCUSSION

During the survey, no hake eggs were found to the north of 32°S. This indicates that, based on our knowledge of the circulation in the region, the main spawning grounds of hake are south of that area. The distribution of hake larvae, however, was well aligned with the two branches of the northward-flowing coastal current on the west coast. The geographical separation of eggs and larvae along the drift paths of the coastal current imply that hake use the coastal jet as a principal transport
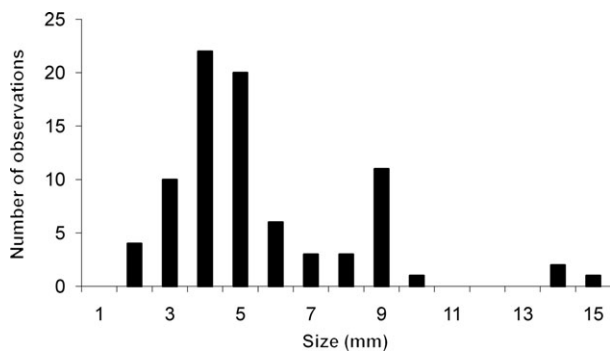

Fig. 7. Size frequency distribution of hake larvae caught in the Multinet (both species combined).

mechanism to carry their spawning products from the upstream spawning areas on the western Agulhas Bank and southwestern Cape coast to the nursery grounds on the west coast. This pattern manifests essentially the same reproduction strategy that characterizes many dominant fish species around South Africa such as anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) (Crawford *et al.*, 1987; Hutchings *et al.*, 2002). The hake eggs and larvae are, however, found deeper than eggs and larvae of pelagic species, making them less vulnerable to offshore advective losses due to Ekman transport (Sundby *et al.*, 2001; Hutchings *et al.*, 2002).

North of Cape Columbine, the coastal jet divides into an offshore and an inshore branch. The offshore drift route follows the outer shelf to exit the survey area south of Child's Bank (transect L13). Transport along this route may cause advective loss of eggs and larvae away from the coast into the deep ocean. However, the data presented here indicate that it is mainly the inshore drift route that transports larvae along the west coast northward toward the Orange Banks.

Botha (Botha, 1980) found 50% hake maturity (both sexes) off the Western Cape coasts in size classes 36–48 cm in *M. capensis* and 38–47 cm in *M. paradoxus* (corresponding to ages of 4 years in males and 5 in females for both species). Spawning for both species was found
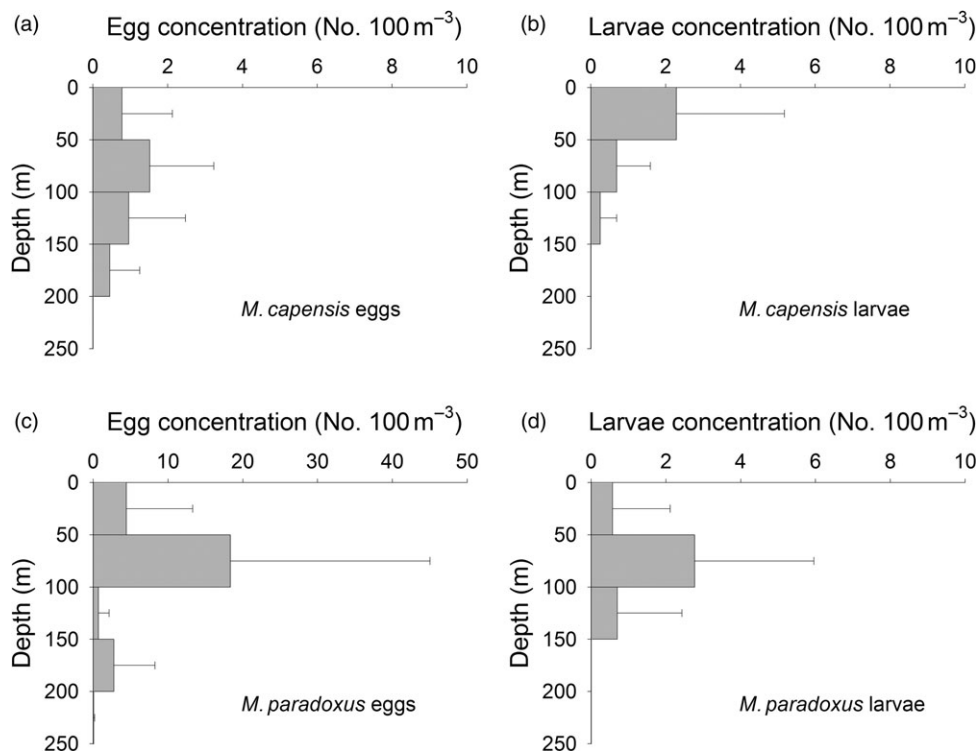

Fig. 8. Mean vertical distribution of eggs (left) and larvae (right) of *M. capensis* (upper) and *M. paradoxus* (lower). Error bars indicate standard deviation of mean concentrations.

to occur mainly from spring to early autumn, reaching a maximum between November and December, with a secondary peak in February–March for *M. paradoxus* (O'Toole, 1978; Botha, 1980; Assorov and Berenbeim, 1983). Spawning on Agulhas Bank may occur throughout the year (Kono, 1980). Spawning is believed to be heaviest over the shelf-break near St Helena Bay (33°S), along the western and southern edge of the Agulhas Bank, and off Namibia in the vicinity of Walvis Bay (Crawford *et al.*, 1987). Little details were available however as to the specific differences between species. It is believed that nursery areas of *M. paradoxus* are located northwest of Cape Columbine, up to Hondeklip Bay (Payne *et al.*, 1986) and juvenile *M. capensis* were plentiful off the Orange River (Macpherson *et al.*, 1985). No large-scale alongshore migrations have been reported for hakes, but it has been found that there are size-dependent inshore–offshore migrations of both species (Crawford *et al.*, 1987). Data accumulated during surveys conducted with R/V "Dr Fridtjof Nansen" annually since 2001 under the BENEFIT-BCLME hake project have shown that the two hake species have differential nursery areas (T. Strømme *et al.*, unpublished data).

The main nursery area of *M. capensis* is located immediately shoreward of the eastern drift route (Hutchings *et al.*, 2002), whereas that of *M. paradoxus* seems to be located further north, over the Orange Banks shelf at around 100 m bottom depth (T. Strømme *et al.*, unpublished data). This may be explained by differences in cross-shelf distribution between the two species. The latitudinal difference in egg and larval distribution showed clearly that *M. paradoxus* larvae had drifted farther away from the spawning grounds than *M. capensis* larvae. The observed difference between the two species in terms of bottom depth, over which their eggs were found, may result in differential drift routes of eggs and larvae (Olivar and Shelton, 1993). In the present study, *M. paradoxus* eggs were found farther offshore (over an average bottom depth of 855 m) than *M. capensis* eggs (on average over a bottom depth of 228 m). Likewise, differences, albeit smaller, were also observed among the depth distributions of the larvae. Therefore, the eggs and larvae of *M. capensis* are likely to be transported inshore of the main jet current, having a slower transport towards the west coast nursery areas compared to eggs and larvae of *M. paradoxus*. On the other hand, *M. paradoxus* eggs and larvae seem to be transported within the eastern branch of the jet current, which follows the inner shelf break northward toward the Orange Banks nursery grounds. Such differential transport routes match the current-closure system proposed by Nelson and Hutching (Nelson and Hutching,

1987), which explains for instance how planktonic organisms with limited swimming abilities such as fish larvae, copepods (Verheye *et al.*, 1991) and euphausiids (Pillar *et al.*, 1989) can maintain their populations within the system.

Von der Heyden *et al.* (Von der Heyden et al. 2007a), using preliminary results from the present survey, noted that the average bottom depth where hake eggs were caught varied significantly between the two species. *Merluccius capensis* eggs were reportedly found over an average depth of 231 m, whereas *M. paradoxux* eggs were found over 613 m (348 m when the two deepest stations were excluded). In contrast, there appeared to be no marked difference in the average bottom depth where the larvae were found, being 215 for *M. paradoxus* and 201 m for *M. capensis*. It must be stressed that these reported values are incorrect because Von der Heyden *et al.* (Von der Heyden *et al.*, 2007a) based their calculations solely on the number of specimens without adjusting for differences in filtered volume among net hauls, which were at times considerable. Thus, the correct average bottom depth over which hake eggs were found was 228 m for *M. capensis* and 855 m for *M. paradoxus*, and that of larvae was 181 m for *M. capensis* and 250 m for *M. paradoxus*. We therefore conclude that, contrary to Von der Heyden *et al.* (Von der Heyden *et al.*, 2007a), both the eggs and the larvae of *M. paradoxus* were distributed in deeper waters than *M. capensis*.

The hake eggs and larval concentrations found during September–October 2005 appear to be relatively low (maximum 411 eggs 10 m^{-2} and 72 larvae 10 m^{-2}) compared with, for instance, pelagic species such as sardine and anchovy for which eggs and larvae are often found in concentrations in excess of 5000 eggs/larvae 10 m^{-2} (van der Lingen and Huggett, 2002). These early-spring concentrations are, nevertheless, higher than subsequent observations in the same area at different times of year (E.K. Stenevik and H.M. Verheye, unpublished data). Early spring has previously been found to be the most important spawning time for hakes in this region (Crawford *et al.*, 1987; Grote *et al.*, 2007) even though some spawning activity may take place throughout the year (Shelton, 1986).

The results on larval distribution and abundance presented here concern larvae up to 15 mm SL, because larger larvae, if present at the time of sampling, avoid the 0.25 m^2 Multinet used in this study. This represents a gap in our knowledge of the distribution of hake larvae/juveniles between 15 and 40–50 mm, and as a result, we are currently unable to present the complete drift pattern of the early life-history stages of the Cape hakes. Juveniles (>40 mm) have been caught in bottom trawl samples in the nursery areas in January, and we

recommend that further surveys focus on the period following the main spawning in September using larger nets, such as the Methot net. The additional information thus obtained will enable us not only to cover this important window in the life-cycle of Cape hakes in the southern Benguela, but it will also shed more light on the mechanisms underlying the apparent difference in nursery areas between the two species.

ACKNOWLEDGEMENTS

REFERENCES

Alheit, J. and Pitcher, T. J. (1995) *Hake: Biology, Fisheries and Markets*. Chapman & Hall, London, UK.

Assorov, V. V. and Berenbeim, D. Y. (1983) Spawning grounds and cycles of Cape hakes in the Southeast Atlantic. *Colln. scient. Pap. Int. Commn. SE. Atl. Fish.*, **10**, 27–30.

Botha, L. (1980) The biology of Cape hakes *Merluccius capensis* Cast. and *M. paradoxus* Franca in the Cape of Good Hope area. PhD Thesis. University of Stellenbosch, South Africa.

Boyd, A. J., Taunton-Clarke, J. and Oberholster, G. P. J. (1992) Spatial features of the near-surface and midwater circulation patterns of western and southern South Africa and their role in the life histories of various commercially fished species. *S. Afr. J. Mar. Sci.*, **12**, 189–206.

Chilés, J. -P. and Delfiner, P. (1999) *Geostatistics. Modeling Spatial Uncertainty.* John Wiley & Sons, New York.

Crawford, R. J. M., Shannon, L. V. and Pollock, D. E. (1987) The Benguela System part IV. The major fish and invertebrate resources. *Oceanogr. Mar. Biol. Ann. Rev.*, **25**, 355–505.

Gordoa, A., Macpherson, E. and Olivar, M. P. (1995) Biology and fisheries of Namibian hakes (*M. paradoxus* and *M. capensis*). In Alheit, J. and Pitcher, T. J. (eds), *Hake Fisheries, Ecology and Markets*. Chapman & Hall, London, pp. 49–88.

Grote, B. (2005) Temporal variability of the transport of larvae of non-clupeoid fish species in the Benguela jet cuttent off South Africa. Diploma Thesis. University of Bremen, Germany.

Grote, B., Ekau, W., Hagen, W. *et al.* (2007) Early life-history strategy of Cape hake in the Benguela upwelling region. *Fish. Res.*, **86**, 179–187.

Holden, C. J. (1987) Observations of low-frequency currents and continental-shelf waves along the west coast of South Africa. *S. Afr. J. Mar. Sci.*, **5**, 197–208.

Hutchings, L., Beckley, L. E., Griffiths, M. H. *et al.* (2002) Spawning on the edge: spawning grounds and nursery areas around the southern African coastline. *Mar. Freshwater Res.*, **53**, 307–318.

Huthnance, J. M. and Baines, P. G. (1982) Tidal currents in Northwest African upwelling regions. *Deep-Sea Res. Part A*, **29**, 285–306.

Japp, D. W., Sims, P. and Smale, M. J. (1994) A review of fish resources of the Agulhas Bank. *S. Afr. J. Sci.*, **90**, 123–134.

Kono, H. (1980) Age and growth of the Cape hakes, *Merluccius capensis* and *Merluccius paradoxus*, on the Agulhas Bank and adjacent slopes. *Colln. scient. Pap. Int. Commn. SE. Atl. Fish*, **7**, 175–209.

Kosro, P. M. (2002) A poleward jet and an equatorward undercurrent observed off Oregon and northern California, during the 1997–98 El Nino. *Prog. Oceanogr.*, **54**, 343–360.

Macpherson, E., Roel, B. A. and Morales, B. Y. O. (1985) Reclutamiento de la merluza y abundancia y distribucion de diferentes especies comerciales en las divisions 1.4 y 1.5 durante 1983–1984. *Colln. scient. Pap. Int. Commn. SE. Atl. Fish*, **12**, 1–61.

Martos, A. R. and Peralta, L. F. (1995) Biology and fisheries of northwest African hakes (*M. merluccius, M. senegalensis* and *M. polli*). In Alheit, J. and Pitcher, T. J. (eds), *Hake Fisheries, Ecology and Markets*. Chapman & Hall, London, pp. 89–124.

Nelson, G. and Hutching, L. (1987) Passive transportation of pelagic system components in the southern Benguela area. *S. Afr. J. Mar. Sci.*, **5**, 223–234.

Olivar, M. P. and Fortuño, J. M. (1991) Guide to Icthyoplankton of the Southeast Atlantic (Benguela Current Region). *Sci. Mar.*, **55**, 383.

Olivar, M. P. and Shelton, P. A. (1993) Larval fish assemblages of the Benguela current. *Bull. Mar. Sci.*, **53**, 450–474.

O'Toole, M. J. (1978) Aspects of the early life history of the hake *Merluccius capensis* Castelnau off South West Africa. *Fish. Bull. S. Afr.*, **10**, 20–36.

Payne, A. I. L. and Punt, A. E. (1985) Biology and fisheries of South African Cape hakes (M. capensis and M. paradoxus). In Hake Fisheries, ecology and markets. In Alheit, J. and Pitcher, T. J. (eds), *Hake Fisheries, Ecology and Markets*. Chapman & Hall, London, pp. 15–47.

Payne, A. I. L., Augustyn, C. J. and Leslie, R. W. (1986) Results of the South African hake biomass cruises in division 1.6 in 1985. *Colln. scient. Pap. Int. Commn. S.E. Atl. Fish.*, **13**, 181–196.

Pillar, S. C., Armstrong, D. A. and Hutchings, L. (1989) Vertical migration, dispersal and transport of *Euphausia lucens* in the southern Benguela current. *Mar. Ecol. Prog. Ser.*, **53**, 179–190.

Shannon, L. V. (1985) The Benguela ecosystem 1. Evolution of the Benguela physical features and processes. *Oceanogr. Mar. Biol. Ann. Rev.*, **23**, 105–182.

Shelton, P. A. (1986) Fish spawning strategies in the variable southern Benguela current region. PhD Thesis. University of Cape Town, Cape Town, South Africa.

Sundby, S., Boyd, A. J., Hutchings, L. *et al.* (2001) Interaction between Cape hake spawning and the circulation in the Northern Benguela upwelling ecosystem. In Payne, A. I. L., Pillar, S. C. and Crawford, R. J. M. (eds). *A Decade of Namibian Fisheries Science. S. Afr. J. Mar. Sci.* **23**, 317–336.

van der Lingen, C. D. and Hugget, J. A. (2002) The role of ichthyoplankton surveys in recruitment research and management of South African anchovy and sardine. In Browman, H. I. and Skiftesvik, A. B. (eds), *The Big Fish Bang: Proceedings of the 26th annual larval fish conference*. Institute of Marine Research, Bergen, Norway, pp. 303–343.

Verheye, H. M., Hutchings, L. and Peterson, W. T. (1991) Life history and population maintenance strategies of *Calanoides carinatus* (Copepoda: Calanoida) in the southern Benguela ecosystem. *S. Afr. J. Mar. Sci.*, **11**, 179–191.

1156

von der Heyden, S., Lipinski, M. R. and Matthee, C. A. (2007a) Species-specific genetic markers for identification of early life-history stages of Cape hakes, *Merluccius capensis* and *Merluccius paradoxus* in the southern Benguela Current. *J. Fish. Biol*, **70**(Suppl. B), 262–268.

von der Heyden, S., Lipinski, M. R. and Matthee, C. A. (2007b) Mitochondrial DNA analyses of the Cape hakes reveal an expanding, panmitic population for *Merluccius capensis* and population structuring for mature fish in. *Merluccius paradoxus. Mol. Phyl. Evol.*, **42**, 517–527.