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Fisheries Research 86 (2007) 179–187
FISHERIES RESEARCH
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Early life-history strategy of Cape hake in the Benguela upwelling region

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Received 3 January 2007; received in revised form 29 May 2007; accepted 2 June 2007

Abstract

The spatial and temporal variability of the egg and larval abundance of *Merluccius* spp. in the Benguela Jet Current was analysed. The Cape hakes, occurring in waters off South Africa, are important for the commercial fisheries in the southern Benguela system, but information on their early life-history strategy is sparse. Data and samples, for this study, were collected during bimonthly cruises of the South African Sardine and Anchovy Recruitment Project (SARP) from August 1995 to July 2003. Samples were collected with a mini-bongo net (300 μm mesh) on a transect crossing the Benguela Current off the Cape Peninsula at 34.15°S, 18.29°E extending 58 nm offshore. Eggs and larvae were commonly found in currents with north-westerly flow, suggesting that the Benguela Jet Current transports eggs and larvae of *Merluccius* spp. to the northern nursery areas. Spawning grounds of *Merluccius* spp. appeared to be on the western Agulhas Bank during August 1996 to July 1998. Two possible spawning grounds in different water depths were identified, suggesting spawning by both Cape hake species, *M. capensis* and *M. paradoxus*. Peak abundances of eggs and larvae of *Merluccius* spp. were found from June to October, a time of reduced offshore transport. Abundances of eggs and larvae were low in austral summer and autumn. Spawning intensity was higher during times of reduced upwelling as shown by correlations of abundances of early life stages with the upwelling index. This leads to the assumption that the early life-history strategy of *Merluccius* spp. is well adapted to the variability in upwelling intensity.

Keywords: Cape hake; *Merluccius capensis*; *Merluccius paradoxus*; Early life-history strategy; Optimal environmental window; Upwelling; Benguela current; South Africa

1. Introduction

Fish species in highly dynamic systems show adaptations of their life-history strategies to the variability in the physical environment. In the southern Benguela system, the pronounced seasonal but also short-term variability is likely to influence the spawning strategies of many different fish species (Hutchings et al., 2002). Dominant fish species, in this system, are anchovy, sardine, mackerel, round herring, horse mackerel, and hake (Crawford, 1980). These species spawn a great number of small eggs, which are widely dispersed by ocean currents (Hutchings et al., 2002). In the southern Benguela upwelling system, eggs and larvae of clupeoid species, such as anchovy and sardine are transported to their northern nursery areas by the Benguela Jet Current (Huggett et al., 1998).

The demersal fishery on Cape hake, *Merluccius* spp. *Rafinesque, 1810* is the second largest sector in the South African fishing industry, and also the most valuable resource (FAO, 2001). For stock assessment, acoustic estimates and catch-at-age data from the fishery are used in models, in which recruitment, mortality and growth are assumed to be constant (Hutchings, 1992). For the hake fishery as well as for other commercial fisheries, an indicator of successful recruitment would be advantageous at the beginning of the year, before intensive fishing begins (Huggett et al., 1998). Therefore, it is important to understand the abiotic and biotic mechanisms, which influence variability in recruitment.

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doi:10.1016/j.fishres.2007.06.003

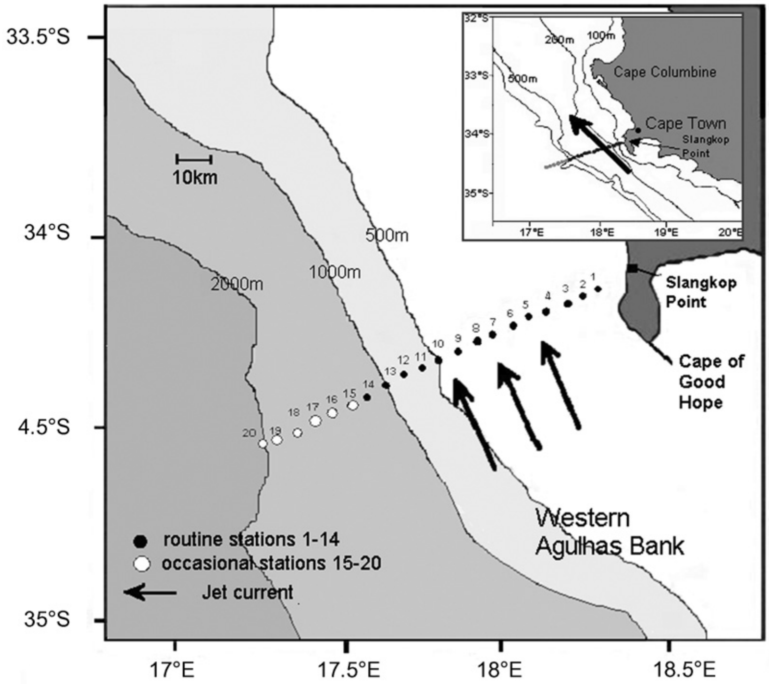


Fig. 1. Study area with 14 routine stations and 6 occasional stations on the transect, jet current flow indicated by arrows (adapted from Huggett, 2001).

Larval transport is a complex process and variability is high in dynamic upwelling areas (Hutchings, 1992; Cowen, 2002). Species living in such regions must have developed mechanisms to cope with the changeable environment, such as opportunistic strategies, alteration of their behaviour, or taking advantage of more predictable system attributes, such as seasonal cycles or spawning in locations of desirable environmental conditions (Shelton, 1986). Our knowledge about population dynamics of marine fish species during their early life stages indicates that different factors can interact to influence the extremely high egg and larval mortality (Cury and Roy, 1989; Roy et al., 1992; Huggett et al., 1998). Larvae can be transported by offshore filaments, originating from offshore Ekman transport during the upwelling season, into unfavourable regions like the oligotrophic open ocean, where food availability is low (Hutchings et al., 2002). For larvae, the time of first feeding is a critical life stage. The match–mismatch hypothesis (Cushing, 1975) describes the strategy whereby the spawning of fish matches the availability of prey for larvae. The stability hypothesis (Lasker, 1981) assumes that in a predominantly stable environment, food aggregates in layers, so that first feeding success for fish larvae is more likely. However, in a stable water column, nutrients can become limiting, so that a minimum of mixing is needed to provide sufficient food (Shelton and Hutchings, 1990; Largier et al., 1992). The two hypotheses mentioned before are combined with the “optimal environmental window” (OEW) hypothesis by Cury and Roy (1989). The OEW hypothesis suggests that there is a dome-shaped relationship between upwelling strength and recruitment: if upwelling is too strong, increased turbulence prevents first feeding of larvae, whereas weak upwelling limits primary production and consequently food availability. Therefore, both negative and positive correlations between upwelling and recruitment can exist (Cury and Roy, 1989; Roy et al., 1992; Waldron et al., 1997).

Larvae of the genus *Merluccius* are easily distinguishable from other larvae, but they show very little difference between *Merluccius* species (Olivar et al., 1988). There are two species of Cape hake off South Africa. The shallow-water Cape hake, *Merluccius capensis* Castelnau, 1861, lives in inshore waters over the shelf down to 380 m depth, whereas the deep-water Cape hake, *Merluccius paradoxus* Franca, 1960, lives in deeper waters from approximately 150 m down to 500 m depth (Payne, 1989). Catch data represent both species in unknown proportions, because it is difficult to distinguish between them (Botha, 1985). On the Agulhas Bank, around 70% are thought to be *M. capensis*, whereas on the rest of the South African west coast, 90% of Cape hake are *M. paradoxus* (Payne, 1989). The two species are thought to spawn at different depths, but little is known about their biology, especially of the spawning season and the early life stages (Botha, 1973, 1985).

In August 1995, the South African Sardine and Anchovy Recruitment Project (SARP) 3 was initiated as a monitoring program along a transect crossing the Benguela Jet Current off the Cape Peninsula. Bimonthly sampling along the line was thought to be useful in predicting recruitment, as the location of the transect is a critical gateway for the transport of eggs and larvae to the northern nursery area (Hutchings, 1992). Spatial and temporal variability in egg and larval abundance was investigated with emphasis on early life stages of the clupeoids *Sardinops sagax* Jenyns, 1842 and *Engraulis encrasicolus* Linnaeus, 1758. Results from this project supported the hypothesis of Shelton and Hutchings (1982) that the frontal jet current transports spawning products to the west coast nursery grounds. Sampling was designed primarily for collecting data on clupeoids, hence there may be limitation regarding the resolution of the data for *Merluccius* spp. However, the SARP cruises from 1995 onwards provide a unique dataset, which may shed more light on the early life history of *Merluccius* spp. in the Benguela Jet Current.

The objectives of this paper are to describe spatial and temporal variability of the abundance and transport of eggs and larvae of *Merluccius* spp. in the highly variable environment of the southern Benguela system. It was investigated whether there is a seasonal spawning pattern for *M. capensis* and *M. paradoxus*, and whether spawning products of both species are transported by the Benguela Jet Current. Furthermore, it was investigated whether the life-history strategies of *M. capensis* and *M. paradoxus* are adapted to the pronounced variability in this environment. The results of this study aim at providing details of the early life-history strategies of these commercially important fish species off South Africa with potential applications to fisheries management of hake.

2. Material and methods

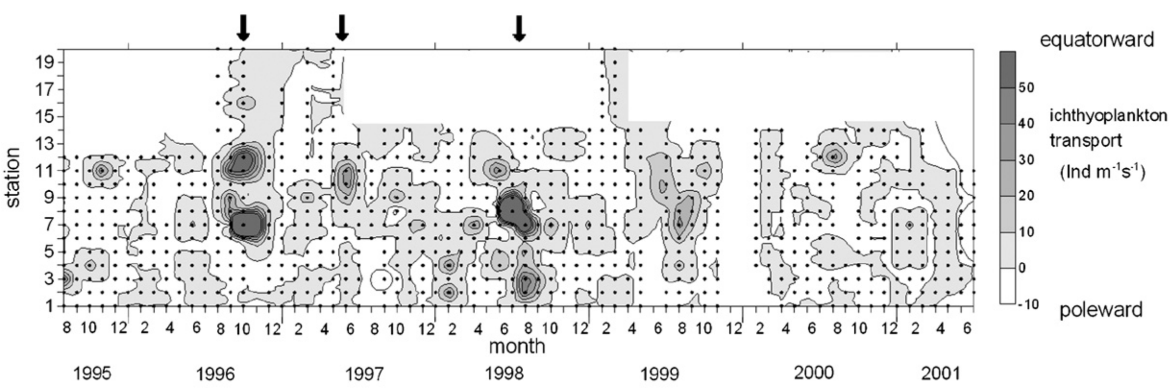
The SARP monitoring line is located along a 58 nm long transect running west to south-west off Slangkop Point and crossing the Benguela Jet Current off the Cape Peninsula at 34°09.0′S, 18°17.8′E to 34°33.8′S, 17°14.2′E (Fig. 1). Twenty stations, positioned 3 nm apart, are located on the transect situated next to the north-western edge of the western Agulhas Bank, which extends from Cape Point to Cape Agulhas.

Sampling on the monitoring line took place approximately bimonthly from August 1995 to July 2003. One sampling year is defined to extend from August to July of the following year. Samples were taken on a number of different vessels (*F.R.S. Africana*, *F.R.S. Algoa*, *R.S. Sardinops*, *M.F.V. Osprey*, *R.V. Ecklonia*, *R.V. Dr. Fridtjof Nansen*). Sampling at 7.4% of the 2232 stations had to be cancelled due to bad weather. At each station from 1995 to 2001, current data were collected. Currents were measured at 30 m depth with an acoustic doppler current profiler (ADCP). Vertical profiles of temperature at each station were measured with a portable CTD on the small vessels, and a CTD-rosette sampler on the large vessels.

Ichthyoplankton samples were collected mainly during daytime using mini-bongo nets of 300 μm mesh size, with a 0.025 m^2 mouth area. The net was lowered to the sampling depth and towed obliquely towards the surface at a rate of 1–2 ms^{-1}, while the vessel was doing 2 knots. At station 1 maximum sampling depth was 70 m, at the other stations about 90 m. A flowmeter was attached to the mini-bongo net to determine the volume of water filtered. Samples were preserved with 5% seawater buffered formaldehyde.

In the laboratory eggs and larvae were identified and counted. The body length of larvae of *Merluccius* spp. caught from August 1996 to July 1998 was measured from the tip of the upper jaw

(a) *Merluccius* spp. eggs



(b) *Merluccius* spp. larvae

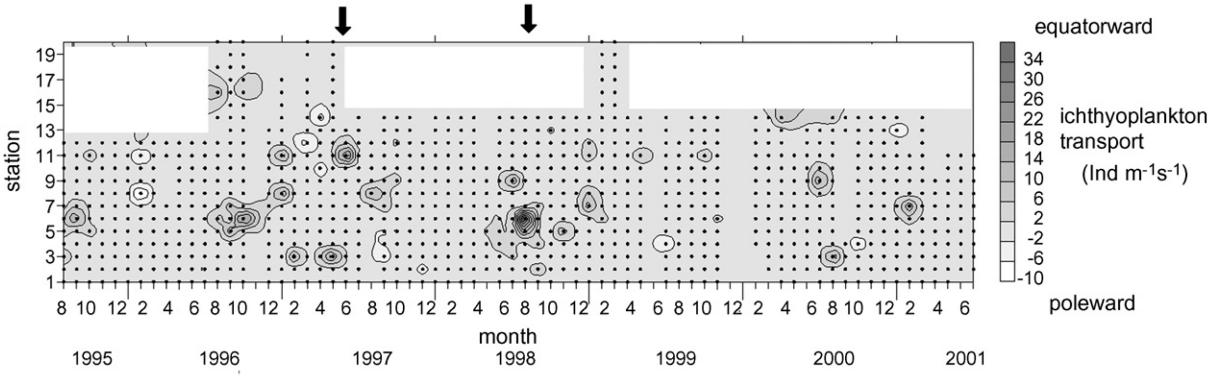


Fig. 2. Longshore transport of *Merluccius* spp. eggs (a) and *Merluccius* spp. larvae (b) [Ind m^{-1} s^{-1}] per month and station from August 1995 to July 2001. Arrows indicate high transport rates.

to the posterior end of the notochord, to the nearest 0.1 mm. Lengths of larvae from other years were in the same range.

Raw CTD-profile data were processed using the relevant instrument software (e.g. Aquasoft, Seasoft), which compensated for small time lags in measuring the different parameters. Only data from downcasts were used.

Onshore currents were defined as flow from SW to NE and are positive cross shelf currents. Offshore currents were defined as flow from NE to SW and are negative cross shelf currents. Positive longshore current flow is in a north-westerly (equatorward) direction, while negative flow is in a south-easterly (poleward) direction. Austral winter was defined as the months June to August, spring as September to November, summer as December to February and austral autumn as March to May.

Transport of *Merluccius* spp. eggs and larvae was calculated for the different stations and in the different sampling years. As longshore currents were measured at 30 m depth, and eggs and larvae were collected over greater water column depths of 70 and 90 m, respectively, the transport of eggs and larvae is an estimate for each station. Contour plots of plankton transport per station and SARP year were drawn with SURFER for Windows 8.01 (Golden Software Inc., USA) using linear interpolation (kriging).

For the calculations of age range and modal age of *M. capensis* larvae, an egg duration time of 60 h after fertilization and an average length of larvae after hatching of 2.35 to 2.60 mm was used (Matthews and de Jager, 1951; Olivar et al., 1988), together with the only reference of the average growth rate of Cape hake larvae of 0.45 mm per day at 17 °C (O’Toole, 1978). These data, together with the length frequencies, were used to estimate age ranges and modal age for larvae caught from August 1996 to July 1998.

Age ranges and modal age data were used together with vector-averaged current velocities to calculate the likely minimum and maximum spawning range and modal spawning range. Current velocities of 10–15 cm s^{-1} in a WNW direction were observed across the inner western Agulhas Bank (Boyd and Oberholster, 1994). These distances would change considerably, if spawning occurred near the 200 m isobath or farther offshore, where average current velocity is 20–30 cm s^{-1}. Length frequency plots were drawn with STATISTICA 6.1 (Stat. Soft Inc., USA) using median and minimum maximum whisker range. Plots of modal spawning distance per month of *M. capensis* and *M. paradoxus* during August 1996 to July 1998 were drawn with Ocean Data View 2.0 (Schlitzer, 2004) and Microsoft PAINT 5.1 (Microsoft Corporation, USA).

Mean abundance of eggs and larvae was standardized to numbers per m^2 of sea surface. Graphs of mean monthly abundance of eggs and larvae were drawn with STATISTICA 6.1 (Stat. Soft Inc., USA) using mean and standard deviation. For the statistical analysis, the non-parametric Kruskal–Wallis test was used to compare the distribution of eggs and larvae per month.

Table 1
Larval age range (days) and estimated spawning distance range (km) together with mean monthly temperature (°C), number of larvae measured and larval abundances (number per m^2) during each month of the South African Sardine and Anchovy Recruitment Project (SARP) from August 1996 to July 1998 for *Merluccius* spp.

SARP cruise no	Time	Mean monthly temperature (°C)	Number of larvae measured	Age range (d after birth)[a] and modal age	Spawning distance range (km)[b] and modal spawning distance	Abundance (number per m^2)
4	August 96	15.2	9	3.2–5.6 [3.5]	27.4–72.9 [38]	4.1
4	September 96	15.5	7	3.3–5.5 [5.1]	28.1–71.3 [55]	8.5
4	October 96	16.0	55	2.5–12.4 [8.3]	21.6–160.9 [90]	8.6
4	November 96	–	–	no larvae	–	–
4	December 96	19.3	9	2.5–8.6 [5.7]	21.6–111.8 [62]	2.8
4	January 97	18.0	7	4.4–15.9 [4.7]	38.2–206.8 [51]	3.2
4	February 97	19.3	2	2.5–2.9 [2.7]	21.6–38.4 [29]	2.2
4	March 97	17.8	9	2.5–10.8 [8.0]	21.6–140.4 [86]	3.4
4	April 97	18.3	8	2.5–10.8 [4.1]	21.6–140.4 [44]	3.6
4	May 97	16.2	2	3.5–15.9 [9.8]	30.2–206.8 [106]	1.4
4	June 97	15.9	13	2.5–5.9 [3.5]	21.6–77.24 [38]	6.2
4	July 97	13.3	1	2.5–2.6 [2.6]	21.6–34.1 [28]	0.6
5	August 97	17.3	1	3.6–4.1 [3.9]	30.9–54.0 [42]	6.0
5	September 97	15.3	24	2.5–8.6 [4.1]	21.6–111.9 [44]	7.5
5	October 97	16.6	22	2.5–13.8 [3.5]	21.6–178.2 [38]	4.3
5	November 97	–	–	no larvae	–	–
5	December 97	14.2	5	2.5–9.7 [5.0]	21.6–125.8 [54]	2.9
5	January 98	–	–	no larvae	–	–
5	February 98	17.1	1	4.3–4.8 [4.8]	37.1–62.6 [52]	0.8
5	March 98	–	–	no larvae	–	–
5	April 98	16.5	2	9.1–12.4 [11.8]	78.9–160.9 [127]	0.3
5	May 98	17.4	1	3.8–4.4 [4.1]	33.1–57.3 [44]	1.3
5	June 98	16.7	7	3.6–5.3 [3.9]	30.9–68.6 [42]	3.6
5	July 98	15.6	3	3.2–6.8 [6.6]	27.4–88.5 [71]	4.4

Modal age and corresponding distance are shown in parentheses.

[a] Assumes daily growth rates of 0.45 mm d^{-1} at 17 °C (O’Toole, 1978).

[b] Assumes vector-averaged current speed of 10–15 cms^{-1} in a west to north-westerly direction (Boyd and Oberholster, 1994).

The upwelling index was calculated from the difference between the sea surface temperatures (SST) at station 12 and 1. The difference between the SST at the most inshore station and the offshore station can be taken as an approximate estimate for the strength of the upwelling (Skogen, 2005). The upwelling strength is, therefore, categorized on a scale from 0 (=very low) to 13 (=very strong). To detect correlations between egg and larval abundances and the upwelling index, the non-parametric Spearman rank correlation R was used. Correlations were calculated with SPSS for Windows 10.0 (SPSS Inc., USA) and plots were drawn with STATISTICA 6.1 (Stat. Soft Inc., USA).

3. Results

3.1. Trends in transport of spawning products

Current speeds between 1.0 and 152.8 cm s^{-1} in a north to north-westerly direction were recorded on the transect. Longshore transport of *Merluccius* spp. eggs was most intense in October during 1996 and in June 1997, and from June to August during 1998 (Fig. 2a). Maximum transport occurred between stations 6 and 12. During 2000–2001 egg transport was lower than in the previous years.

For *Merluccius* spp. larvae, transport was highest during 1996 and 1998 (Fig. 2b). At the inner stations, larval transport was low throughout all sampling years, except for station 3 with a somewhat higher transport in May of 1997 and in August of 2000. Highest larval transport usually occurred between stations 5 and 11. During 2000–2001 longshore transport was less intense.

3.2. Length frequency distribution and drift tracks

Length frequency distributions of *Merluccius* spp. larvae reveal that during August 1996 to July 1998 mostly newly hatched larvae were caught (Fig. 3(a, b)). During all sampling years, 60 to 70% of larvae were between 2 and 4 mm long (Fig. 3(a, b)). Older larvae larger than 6 mm were rarely found during both years and no larvae larger than 8 mm were found.

Larval length was used for the back-calculation of modal age. Mean monthly temperatures in the spawning area ranged from 13.3 to 19.3 °C. For larvae captured during 1996/1997 age ranged between 2.6 and 9.8 days (Table 1). Adding 60 h for the development of the eggs, the spawning place may be roughly calculated at a location 28–106 km away from the station where the larvae were caught. During 1997/1998, the modal age of larvae ranged between 3.5 and 11.8 days. A similar approach for 1997/1998 revealed the distance of potential spawning areas to lie between 38 and 127 km away. Considering the drift direction it can be assumed that most spawning took place south to south-east of the transect (Fig. 4). Origins of larvae were concentrated on the shelf and upper slope. The farthest modal spawning distance occurred in October 1996 at stations 6 and 16 followed by July 1998 at station 3. In the latter month, spawning took place farther east than during other months.

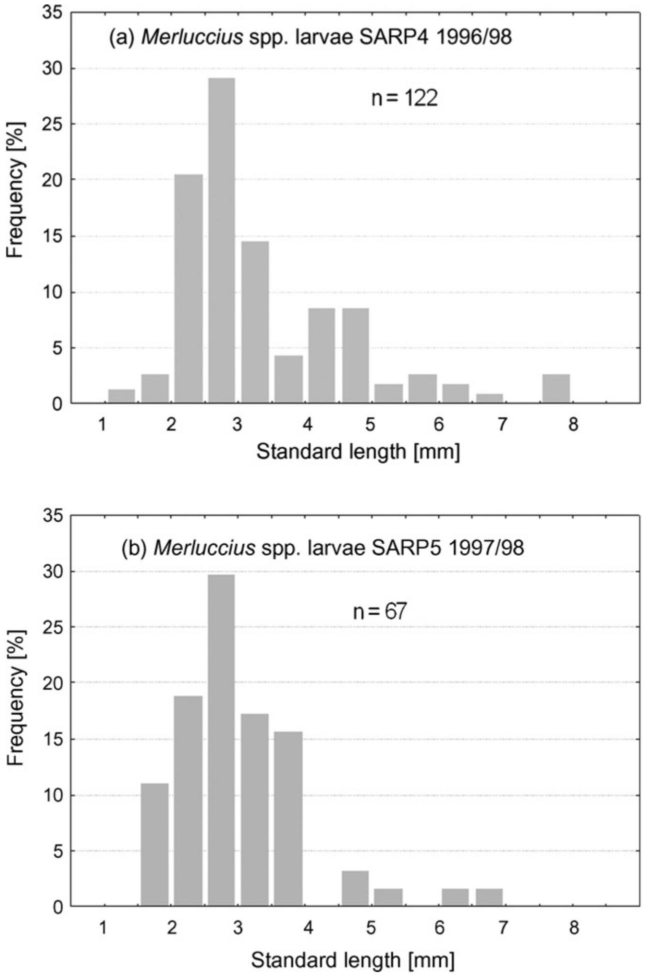


Fig. 3. Length frequency distribution of *Merluccius* spp. during 1996/1997 (a) and 1997/1998 (b). Total number of larvae measured is indicated. Larvae were grouped in 0.5 mm classes.

3.3. Seasonality

Merluccius spp. eggs were most abundant in austral winter and early spring, from June to October (Fig. 5a). In austral summer the abundance of hake eggs clearly declined. However, eggs were still found in low numbers from December to February. Larvae of *Merluccius* spp. were least abundant in November and December as well as in March and April (Fig. 5b). In general, numbers were low in late austral spring, summer and autumn, and the highest abundance occurred from June to October (Fig. 5b). *Merluccius* spp. larvae were less abundant than eggs. The mean abundance of larvae was highest in August and October, with approximately 4 larvae m^{-2}, whereas the highest average egg abundance was approximately 60 eggs m^{-2} in July (Fig. 5(a, b)).

The variations between the monthly abundances of eggs were significantly different with $p < 0.01$ in the Kruskal–Wallis test (results not shown). The Kruskal–Wallis test for larvae showed that differences between the monthly larval abundances were statistically significant with $p < 0.05$. The Kruskal–Wallis test provides a ranking of months, which indicates months of both greatest and least similarity. From June to September there seems

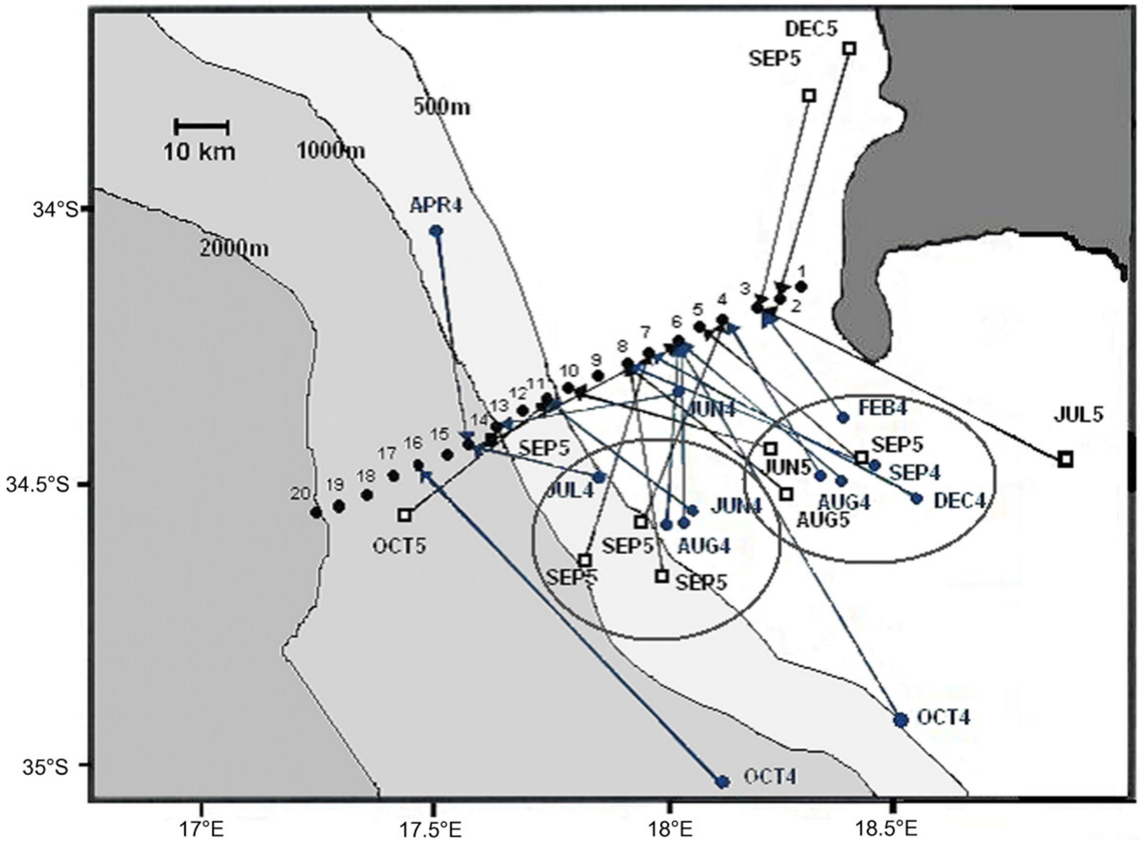


Fig. 4. *Merluccius* spp. modal spawning distance during months of high larval abundances in 1996/1997 (circle) and 1997/1998 (rectangle). Numbers on the transect indicate stations. Arrows indicate spawning distance and current direction.

to be a similar distribution of abundances of hake eggs. These months show a difference in the ranking compared to the other months from October to May. For larvae the months from June to October show a similar distribution compared to the other months (results not shown).

Mean egg abundances and variations of *Merluccius* spp. were highest at an upwelling index of 2–6 on a scale of 0–13 (Fig. 6a). At an upwelling index >6 abundances of eggs declined clearly. For *Merluccius* spp. larvae, abundances were highest at an upwelling index of 2–7 (Fig. 6b). An exception was the high abundances at the upwelling index of 0 and 1 with only one data point each. Larval abundances were low at an upwelling index of 8–10, but rose again at an upwelling index of 11 and 12. The highest average egg abundance was approximately 48 eggs m^{-2} at an upwelling index of 3, whereas the mean abundance of larvae was highest at an upwelling index of 2, with approximately 10 larvae m^{-2} (Fig. 6(a, b)).

4. Discussion

4.1. Transport and distribution of ichthyoplankton

Eggs and larvae of *Merluccius* spp. were commonly found along the transect, when the jet current moved in a north to north-westerly direction. This suggests that a substantial number of these early spawning products are transported via the jet current to the nursery area off Cape Columbine. The jet current was previously identified as a transport vector for early life stages of anchovy and sardine (Hutchings, 1992; Fowler and Boyd, 1998; Huggett et al., 1998). Transport of *Merluccius* spp. eggs and larvae occurs during a time of weak to moderate jet current flow in a north to north-westerly direction. An individual based model (IBM) showed that particles of medium density (such as most pelagic fish eggs) are transported in large amounts in strong to medium currents, whereas transport of lighter and heavier particles is reduced (Mullon et al., 2003; Parada et al., 2003). In a strong current flow a great proportion of these can be advected offshore (Parada et al., 2003). In contrast, a weak to moderate jet current transports fewer eggs and larvae towards the nursery areas, but most of these early life stages are carried inshore (Parada et al., 2003). Hence, the concentration of *Merluccius* spp. eggs in moderate currents could be a result of buoyancy-dependent transport and a spawning strategy to prevent offshore losses. Larval density is different from egg density in most fish species due to the loss of the chorion, and in the IBM no impact of density on transport of larvae was detected (Parada et al., 2003).

The horizontal distribution of *Merluccius* spp. eggs along the transect shows that the highest mean ichthyoplankton transport for all years was between stations 6 and 11, where the bottom depth ranges between 200 and 500 m. In another study, *M. capensis* eggs were found over 60–300 m depth, with the majority of

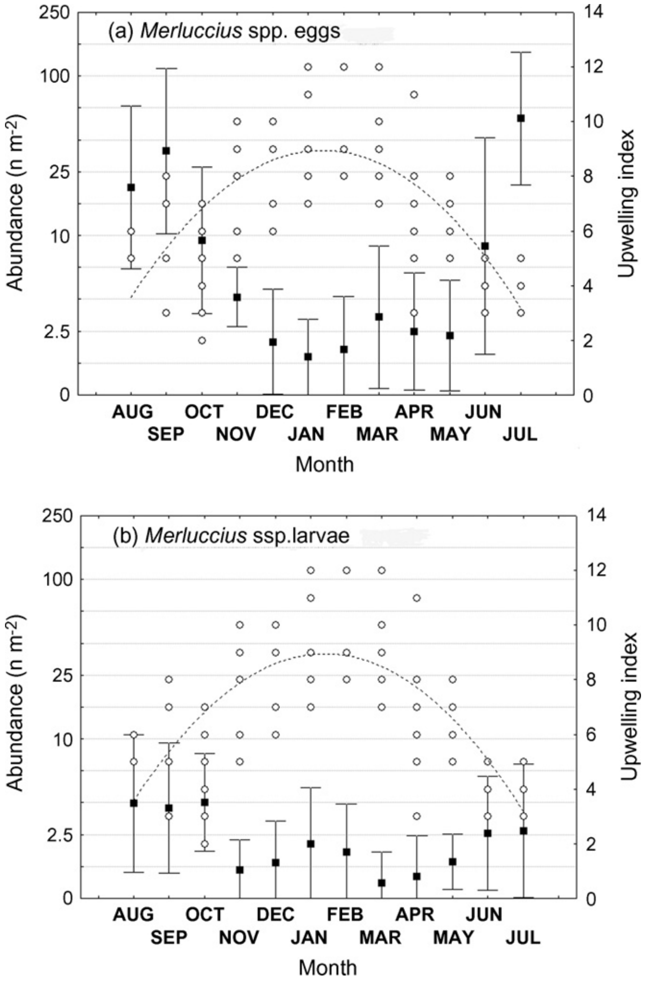


Fig. 5. Averaged values (± S.D.) of egg (a) and larval (b) abundances of *Merluccius* spp. ($n\,m^{-2}$) per month and upwelling index per month (line with dots).

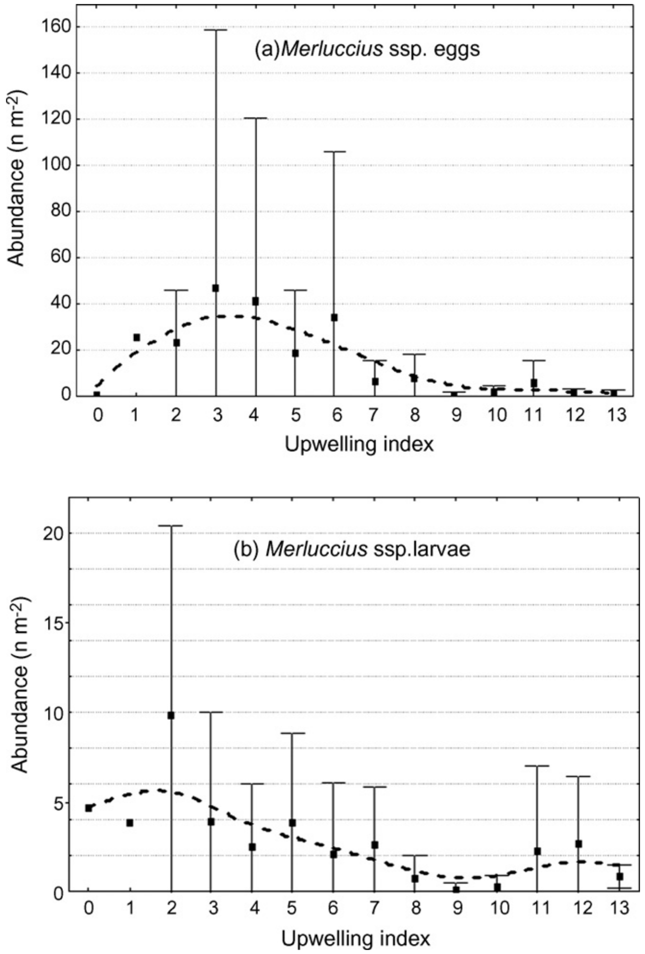


Fig. 6. Averaged values (± S.D.) of egg (a) and larval (b) abundances of *Merluccius* spp. ($n\,m^{-2}$) in correlation with the upwelling index (line).

eggs over bottom depths of 150–200 m (Olivar et al., 1988). In a drift pattern-model of anchovy larvae on the west coast in the southern Benguela, it was concluded that particles outside the 500 m isobath are likely to be advected offshore (Skogen et al., 2003). This indicates that *M. capensis* and *M. paradoxus* have developed a spawning strategy to avoid offshore losses of early life stages.

4.2. Possible spawning grounds of M. capensis and M. paradoxus

Larger larvae were scarce in the SARP catches due to the small nets used. Recently, hatched *Merluccius* spp. larvae of less than 8 mm body length predominated in the samples analysed by O'Toole (1978) and larvae larger than 10 mm were only caught during night time hauls. Small larvae of *M. productus*, the Pacific hake, were caught in the upper 50–100 m during daytime sampling by Bailey (1982), whereas larger larvae were caught deeper. During night time, however, large *M. productus* larvae were also caught in 25–50 m depth (Bailey, 1982), which indicates diurnal migration or avoidance of plankton sampling nets in the daytime. Therefore, it is likely that only larvae, which were spawned close to the transect over the western Agulhas Bank (WAB) and transported directly by the shelf edge jet current were caught.

Estimated spawning distances during 1996/1997 and 1997/1998 based on current directions at the relevant stations also suggest that the early life stages found during these 2 years were spawned over the western Agulhas Bank. According to our study the *Merluccius* spp. larvae have two potential spawning grounds on the western Agulhas Bank. One is closer inshore in the vicinity of the Cape of Good Hope, at approximately 100–300 m depth. The other spawning ground is farther offshore above a bottom depth of 400–1000 m. Olivar et al. (1988) found that *M. capensis* moves onshore to spawn at bottom depths of 100–200 m. Both spawning grounds lie approximately 20–40 km linearly to the southeast of the transect. In previous studies, it was found that *M. capensis* and *M. paradoxus* spawn at different depths (Assorov and Berenbeim, 1983; Botha, 1985, 1986). The two spawning grounds indicate spawning of both *Merluccius* species over the western Agulhas Bank, although, current velocities resulting from averaged data may be underestimated. Nevertheless, spawning in the shallow waters of the western Agulhas Bank may be beneficial for larval survival, as these larvae are more likely to be transported via the jet current towards the nursery areas.

4.3. Seasonal abundance of eggs and larvae of Merluccius spp.

Eggs and larvae of *M. capensis* and *M. paradoxus* were predominantly found in the Benguela Jet Current from June to October. In contrast, negligible quantities of eggs and larvae were collected during austral summer and autumn. This indicates that maximum spawning activities on the western Agulhas Bank occur in winter and early spring. Other studies showed that hake spawn throughout the year, but with distinct peaks during particular seasons (O'Toole, 1978; Shelton, 1986; Payne, 1986). Highest larval abundances off the west coast of South Africa in 1977 and 1978 were found in August to September and May to August, respectively (Shelton, 1986). Off the coast of Namibia, peaks in egg and larval abundance occurred from September to December (O'Toole, 1978; Botha, 1986). For the Mediterranean hake *M. merluccius* peak spawning seasons varied with geographic region (Papaconstantinou and Stergiou, 1995). This seems to be also true for *M. capensis* and *M. paradoxus*, as all available data suggest that spawning takes place all year round with different peaks in different geographic locations.

Differences between spawning seasons off Namibia and off South Africa may be explained by the different timing of strongest upwelling in the northern (autumn and winter) and the southern (summer) Benguela system (Parrish et al., 1983; Duncombe Rae, 2005). In an earlier study, it was suggested that *M. capensis*, *Trachurus capensis* Castelnau 1861 (maasbanker) and *Etremeus whiteheadi* Wongratana, 1983 (round herring), spawn in late winter and early spring in the southern Benguela system, because Ekman offshore transport is weaker during this period of reduced upwelling (Hutchings et al., 2002). Intense upwelling occurs during months of strong equatorward wind stress (Shelton et al., 1985). This coast-parallel wind causes offshore Ekman transport of surface water masses (Schumann et al., 1982), in which larvae are advected offshore into waters with unfavourable environmental conditions (Roy et al., 1992). Abundances of early life stages in the upper 90 m of the water column were low during periods of minimal and maximal upwelling, which indicates that *M. capensis* and *M. paradoxus* avoid spawning during these periods. The "optimal environmental window" (OEW) hypothesis by Cury and Roy (1989) assumes that species have an optimum for an environmental parameter, such as wind intensity. Moderate winds induce moderate upwelling, which can be seen as the OEW for spawning and larval survival (Roy et al., 1992). The negative relationship between intense upwelling in the southern Benguela system and spawning of *M. capensis* and *M. paradoxus* is thus consistent with the OEW hypothesis.

In winter, high water column stability at the spawning grounds off the west coast of South Africa can lead to low food supply for adult spawners and larvae (Shelton and Hutchings, 1990; Largier et al., 1992). For the Pacific hake, first feeding is not as crucial as for other fish species in upwelling systems, since Pacific hake have a lower growth rate and a bigger mouth for larger prey compared to other fish species in the same system (Bailey, 1982). Furthermore, starvation effects in hake larvae occur up to three times later after complete yolk utilization as compared to anchovy (Lasker et al., 1970). If this applies to the Cape hakes, *M. capensis* and *M. paradoxus*, it may explain why it is possible for these species to spawn mainly during a time of reduced upwelling and food supply.

5. Conclusions

The hydrographical and biological aspects of the early life history of Cape hake discussed above are important factors that influence their reproduction patterns. However, the reproductive strategy of each species is a consequence of compromises between many different parameters on the basis of the environmental capacity of the species (Roy et al., 1992). Therefore, it is possible that other factors, which could not be resolved, in this study, may also influence the spawning strategies and reproduction success of the investigated species.

Three main conclusions emerge from our study: first, the Benguela Jet Current off the Cape Peninsula was identified as an important vector in the transport of *M. capensis* and *M. paradoxus* eggs and larvae derived from the western Agulhas Bank to their northern nursery grounds. Second, backtracking the origin of larvae from current vectors shows that *M. capensis* and *M. paradoxus* larvae caught during this study were spawned on the western Agulhas Bank, which is, therefore, identified as an important spawning ground for both species. Third, the early life-history strategy of *Merluccius capensis* and *M. paradoxus* is adapted to the variability in upwelling intensity, i.e., the spawning season of these species is tuned to reduced offshore transport to increase larval survival.

Acknowledgements

The data, in this study, were obtained from Marine and Coastal Management, Department of Environmental Affairs and Tourism, Cape Town, South Africa collected by Dr. Jenny Huggett.

We would like to thank the MCM, Cape Town, for providing workplace and laboratory facilities. Special thanks are due to the working group biological oceanography, especially Mrs. S. M. Jones and Mr. C. J. Giddey.

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