Assessing the abundance and distribution of eggs of sardine, *Sardinops sagax*, and round herring, *Etrumeus whiteheadi*, on the western Agulhas Bank, South Africa, using a continuous, underway fish egg sampler

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ABSTRACT

A continuous, underway fish egg sampler (CUFES) was employed to assess the abundance and distribution of eggs of both sardine, *Sardinops sagax*, and round herring, *Etrumeus whiteheadi*, on the Western Agulhas Bank, South Africa, during September 1996. Samples were collected while underway along six inshore/offshore transects, and at stations along the transects. Volumetric estimates of egg density (eggs m^{-3}) from on-station CUFES samples were highly correlated with both volumetric and areal (eggs m^{-2}) estimates of egg density from samples collected from CalVET net hauls at these stations, demonstrating the validity of this novel sampling technique. Sardine and round herring eggs were encountered in a band running parallel to the coast and extending from 10 to 30 nautical miles offshore to the shelf edge, and highest egg densities were associated with strong north-west-flowing currents in the region of the shelf edge. Collecting samples while underway increased the precision of the estimate of mean egg density for sardine eggs but not for round herring eggs. The use of CUFES in obtaining a fine-scale resolution of sardine egg distribution, and as a tool for stock assessment, are discussed.

Key words: pelagic fish eggs, sampling, CUFES, *Sardinops sagax*, *Etrumeus whiteheadi*.

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INTRODUCTION

The Agulhas Bank is a triangular extension of the continental shelf south of Africa, extending within the latitudes 34–37°S, from Cape Point in the west (18°E) to East London in the east (28°E). Divided at Cape Agulhas into western and eastern sectors, the Bank acts as a boundary area between the two major oceanic currents of this region: the warm Agulhas Current to the east and the cold Benguela Current to the west (Shannon, 1985; Boyd and Shillington, 1994; Hutchings, 1994). In addition to maintaining a high diversity of commercially exploited species (Augustyn *et al.*, 1994; Japp *et al.*, 1994; Roel *et al.*, 1994), the Agulhas Bank is the principal spawning area for several pelagic fish, including Cape anchovy, *Engraulis capensis*, sardine, *Sardinops sagax*, and round herring, *Etrumeus whiteheadi* (Roel and Armstrong, 1991; Shelton *et al.*, 1993; Roel *et al.*, 1994). Eggs spawned by these species on the Agulhas Bank are transported via a shelf-edge frontal-jet current to the productive west coast nursery area (Shelton and Hutchings, 1982; Fowler and Boyd, 1998), where they recruit to the fishery during autumn and winter (Crawford *et al.*, 1980).

The reproductive strategy of the Cape anchovy is well understood, with this species spawning from October to March (Shelton and Hutchings, 1990; Melo, 1994) primarily over the western Agulhas Bank (Hutchings, 1994; Roel *et al.*, 1994). That of sardine is less understood, but they appear to spawn throughout the year, principally from August to March (Armstrong *et al.*, 1989; Akkers and Melo, 1996; Fowler *et al.*, 1996; Huggett *et al.*, 1998). Sardine eggs and early larvae have been found along almost the entire South African coast, from the Natal Bight (32°E) in the east (Beckley and Hewitson, 1994; Connell, 1996) to St Helena Bay (17°E) in the west (Roel *et al.*, 1994; Fowler *et al.*, 1996). The reproductive strategy of round herring is also poorly understood, but spawning appears to occur throughout the year with a winter peak (Roel and Melo, 1990), mainly along the edge of the continental shelf (Roel and Armstrong, 1991; Roel *et al.*, 1994).

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The daily egg production method (DEPM, Lasker, 1985) was used in conjunction with the hydro-acoustic method to estimate the spawning biomass of Cape anchovy from 1984 to 1993 (Armstrong *et al.*, 1988; Shelton *et al.*, 1993; Hampton, 1987, 1992, 1996). Sardine biomass in South African waters has to date been estimated acoustically (Hampton, 1987, 1992), and the applicability of employing the DEPM for this species is currently under investigation. The biomass of several sardine stocks worldwide has been estimated using the DEPM (Cunha *et al.*, 1992; Garcia *et al.*, 1992; Alheit, 1993; Bentley *et al.*, 1996; Fletcher *et al.*, 1996; Lo *et al.*, 1996), this method being considered to provide unbiased estimates of spawner biomass, whereas acoustically derived estimates may be biased due to target strength and calibration errors (Armstrong *et al.*, 1988; Hampton, 1996; Barange and Hampton, 1997). However, the DEPM may give estimates that carry a high variance, resulting firstly from the contagious horizontal distribution of pelagic fish eggs (Smith *et al.*, 1985) and secondly from the imprecision associated with estimates of egg mortality (Shelton *et al.*, 1993). Such variance could be reduced by increasing the number of egg samples collected (Alheit, 1993; Shelton *et al.*, 1993), although logistical constraints often preclude this.

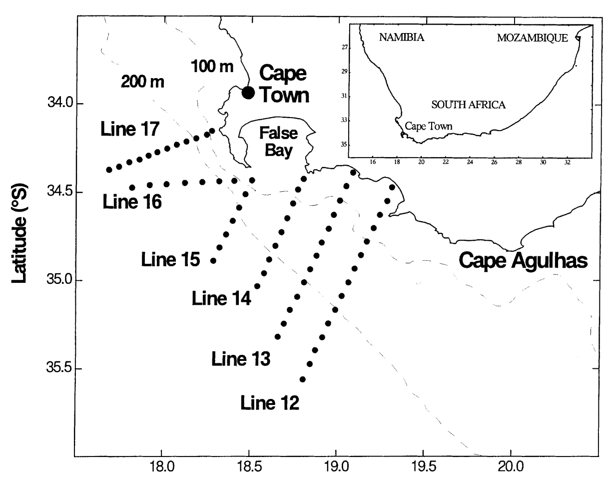
A novel survey technique for sampling the distribution of pelagic fish eggs, which has the potential to increase the precision of egg abundance estimates significantly, has recently been developed (Checkley *et al.*, 1997). A continuous, underway fish egg sampler (CUFES) has been used successfully to sample the eggs of menhaden, *Brevoortia tyrannus*, pinfish, *Lagodon rhomboides*, northern anchovy, *Engraulis mordax*, and Pacific sardine, *Sardinops sagax*, on both the east and west coasts of the United States. In this paper we describe the application of the CUFES in assessing the abundance and distribution of sardine and round herring eggs over the western Agulhas Bank. In addition, estimates of egg density from the CUFES are compared with those derived from conventional CalVET net samples, and the precision of the survey estimate derived using each sampling technique is compared using both standard sampling statistics and geostatistical analysis. Finally, the distribution of sardine and round herring eggs is compared with physical and biological parameters measured during the survey.

MATERIALS AND METHODS

Sampling was conducted aboard the FRS *Algoa* from 26 to 30 September 1996. Adverse weather kept the ship confined to False Bay for the first day-and-a-half of the cruise, during which time CUFES and CalVET net samples were collected. Thereafter a grid over the western Agulhas Bank was surveyed (Fig. 1), consisting of six inshore/offshore lines spaced ≈15 nautical miles apart, and extending to beyond the edge of the continental shelf (200 m). Stations were positioned 5 nautical miles apart along each line with the exception of Line 17, the SARP IV weekly monitoring line (Huggett *et al.*, 1998), where interstation distance was 3 nautical miles. Simultaneous CUFES and CalVET net samples were collected while the vessel was on station, and CUFES samples were also collected between stations while the vessel was underway.

A full description of the CUFES has been provided elsewhere (Checkley *et al.*, 1997). Essentially, the system consists of a high-volume, submersible pump fixed rigidly to the ship's hull, a sample concentrator, and a mechanical sample collector. Water is pumped from 3 m depth to the concentrator, where particles retained by a 500 μm mesh are concentrated in a reduced flow. This flow is then directed to the mechanical sample collector, which allows for sequential collection of samples. CUFES sample intervals during this survey were 5 min for on-station samples, and 5–12 min (mean = 8.4 ± 2.5 min corresponding to 1.4 ± 0.4 nautical miles) for underway samples. The start and end times of every interval, and the ship's position at these times, were recorded from the ship's GPS (global positioning system). The CUFES operated continuously throughout the survey, sampling from 3 m depth at a pump flow rate of 500 l min^{-1} (± 10%) and with a flow to the sample collector of 20 l min^{-1}. Prior to the concentrator, a small fraction

Figure 1. Site map, bathymetry and station positions from the CUFES cruise, 26–30 September 1996.



of the flow was diverted for measurement of temperature and salinity using Seabird Electronics temperature and conductivity sensors, and chlorophyll *a* fluorescence using a Turner Designs fluorometer, for which only relative fluorescence units (volts) are reported here.

At each station a vertical CalVET net haul (25 cm diameter) was made from 70 m depth or from within 5 m of the bottom, and the volume filtered by the net calculated using standard protocols (Smith *et al.*, 1985). The mean volume filtered for CalVET net samples was 3.13 ± 0.85 m^3. Vertical temperature profiles were recorded with an electronic temperature/depth sensor suspended below the net and having an accuracy of 0.5°C. At stations on Line 17, a Magnum rosette fitted with an Aquatracka fluorometer was deployed to 200 m depth or to within 10 m of the bottom to provide temperature and fluorescence profiles. Each CalVET net haul was made during the 5 min interval over which the on-station CUFES sample was collected to ensure simultaneous sampling. Immediately after collection, CUFES samples were examined under a light microscope and sardine eggs enumerated. Samples were then fixed and preserved in 5% buffered formalin for subsequent laboratory analysis, where eggs were identified and counted. At stations where >5 sardine eggs were counted in a CUFES sample, multiple CUFES and CalVET net samples were collected to allow for the assessment of between-sample variance. Currents at 30 m depth were measured at each station using a hull-mounted 150 kHz RDI narrowband acoustic Doppler current profiler (ADCP). Methods of current data collection and analysis are described by Boyd *et al.* (1992).

Contour plots depicting the horizontal distribution at 3 m depth of temperature, salinity, chlorophyll *a* fluorescence, and volumetric fish egg abundance, together with currents at 30 m depth, were generated using the kriging routine of the SURFER® for Windows program (Golden Software Inc.) with an anisotropy ratio of 0.5 perpendicular to the isobaths.

Two methods were used to compare the precision of the estimates of egg density from the two samplers. Firstly, precision was assessed using the inter-transect variability in mean egg density as described by Jolly and Hampton (1990). This approach uses the sampling transect as the basic unit, and assumes that samples are independent. Because the transects of this survey were not randomly positioned, this method could provide slightly biased variance estimates. However, because the aim was to compare sampler precision, this potential bias was considered to be of secondary importance. The second approach used geostatistical analysis, and computed experimental isotropic variograms of egg density using the estimator:

$$\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [Z(x_i + h_i) - Z(x_i)]^2, \qquad (1)$$

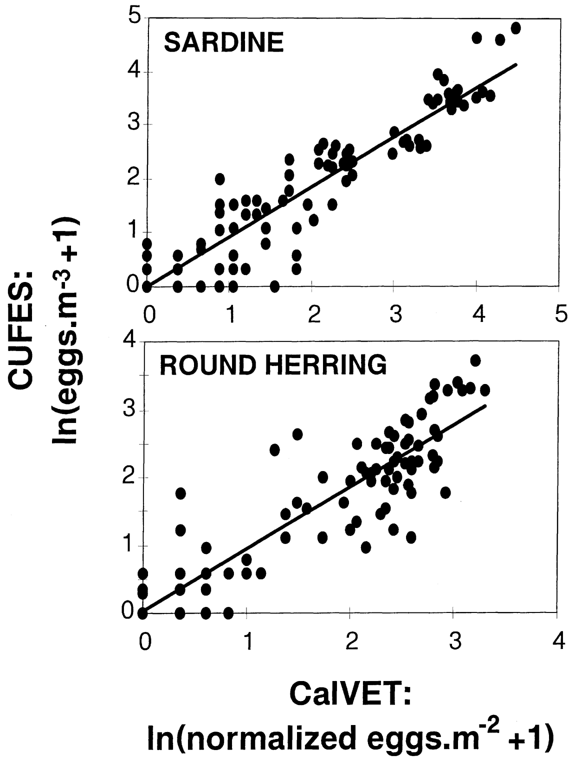
where $Z(x_i)$ is the density for the *i*-th data point, and $N(h)$ is the number of pairs of points which are a distance h apart. Variograms were fitted to exponential models (Cressie, 1993), using the EVA software (Petitgas and Prampart, 1993), and model parameters were used to compare the performance of the different sampling techniques and efforts. Variances were estimated using the variogram models fitted, according to procedures described in Petitgas (1993) and Petitgas and Prampart (1993). In the intrinsic interpretation such estimation does not require randomization of the samples (Petitgas, 1993), although it assumes a certain degree of stationarity of the spatial process, i.e. it must have some homogeneity and should be repeatable in space. The estimated precisions were used to quantify the statistical advantage provided by underway as opposed to on-station sampling.

RESULTS

Samplers

A total of 294 CUFES (153 on-station and 141 interval) and 153 CalVET net samples was collected during the survey. The eggs of sardine, round herring and lanternfish, *Maurolicus muelleri*, dominated samples. Sardine egg counts made at sea immediately after collection of the CUFES sample were highly correlated with laboratory egg counts from those samples ($r^2 = 0.97$; $n = 294$; $P < 0.0001$), demonstrating that sea counts are reliable indicators of egg abundance. High correlation coefficients were also observed between ln-transformed volumetric estimates of egg density (eggs m^{-3}) from the CUFES samples and ln-transformed volumetric estimates of egg density from the CalVET net ($r^2 = 0.92$ and 0.88 for sardine and round herring, respectively), and between ln-transformed volumetric estimates of egg density from the CUFES samples and ln-transformed normalized estimates of areal egg density (ln [eggs m^{-2} *0.02] + 1) from the CalVET net ($r^2 = 0.92$ and 0.88 for sardine and round herring, respectively; Fig. 2a,b). Areal egg densities were normalized by multiplying by 0.02 to ensure that the regression of CUFES volumetric egg density on CalVET areal egg density passed through, or close to, the origin. These high correlation coefficients indicate that these samplers provide

Figure 2. Comparison between volumetric egg densities (eggs m^{-3}) measured using CUFES (at 3 m depth) and areal egg densities (eggs m^{-2}) measured using CalVET net (from 70 m depth to the surface) for (a) sardine, *Sardinops sagax* ($y = 0.9276x + 0.0147$; $r^2 = 0.92$; $n = 153$; $P < 0.001$) and (b) round herring, *Etrumeus whiteheadi* ($y = 0.9109x + 0.0302$; $r^2 = 0.88$; $n = 153$; $P < 0.001$). Data are ln transformed (ln eggs + 1).



comparable estimates of fish egg abundance under the conditions encountered.

Varying numbers (3–7) of replicate CUFES and CalVET net samples were collected at 14 stations during the survey (Tables 1 and 2). The mean volume sampled by the CUFES at these stations was 2.5 ± 0.0 m^3 whilst that sampled by the CalVET net was 3.6 ± 0.1 m^3. Mean volumetric egg densities from each sampler were compared using Welch's *t*-test approximation, which allows for the comparison of means from populations with unequal variances (Zar, 1984). Significant ($P < 0.05$) differences between CUFES- and CalVET net-derived mean volumetric egg densities for sardine eggs were observed at six stations, with the CUFES samples having more eggs per cubic metre than the CalVET net samples in all of these cases. Stations where there was no significant difference between CUFES- and CalVET net-derived estimates, generally occurred towards the beginning of the survey (Table 1). The between-replicate variance for sardine eggs was higher for CUFES than for CalVET net samples; coefficients of variation (CVs) ranged from 6% to 129% and had a mean value of 37% for the CUFES samples, whereas CVs ranged from 0% to 52% and had a mean value of 29% for the CalVET net samples. High (>50%) CV values from the CUFES samples were, however, associated only with low mean volumetric egg densities.

For round herring eggs, significant differences between CUFES- and CalVET net-derived mean volumetric density were observed at only two stations. CUFES samples showed higher densities than CalVET

Table 1. Mean volumetric density of sardine, *Sardinops sagax*, eggs from CUFES and CalVET net samples at stations where multiple samples were collected. The coefficient of variation (%) is given in parentheses following each egg density value.

Station	Sampling date and time	Number of replicates	CUFES eggs m^{-3}	CalVET eggs m^{-3}	*t*-value[a]
12-07	27 Sept., 15:02	5	3.20 (37)	2.45 (41)	1.088
12-08	27 Sept., 16:34	3	3.73 (6)	2.40 (52)	1.814
12-09	27 Sept., 17:31	3	2.13 (85)	2.50 (39)	−0.307
12-10	27 Sept., 18:38	7	13.20 (14)	13.91 (16)	−0.638
12-11	27 Sept., 20:00	7	31.83 (13)	24.83 (15)	3.316*
13-08	28 Sept., 07:04	7	31.94 (8)	25.24 (30)	2.233
13-07	28 Sept., 08:21	7	9.60 (24)	5.66 (15)	4.230*
13-06	28 Sept., 09:28	3	0.40 (100)	0.00 (0)	1.732
14-06	28 Sept., 19:45	3	8.93 (7)	4.43 (35)	4.684*
14-07	28 Sept., 20:39	3	1.47 (129)	3.42 (42)	−1.424
15-04	29 Sept., 02:51	5	10.24 (24)	5.23 (21)	4.106*
15-03	29 Sept., 04:03	3	43.33 (17)	20.95 (9)	5.025*
16-02	29 Sept., 07:16	3	4.27 (44)	1.01 (33)	2.940
16-03	29 Sept., 08:07	3	106.80 (12)	41.23 (24)	7.145*

Table 2. Mean volumetric density of round herring, *Etrumeus whiteheadi*, eggs from CUFES and CalVET net samples at stations where multiple samples were collected. The coefficient of variation (%) is given in parentheses following each egg density value.

Station	Sampling date and time	Number of replicates	CUFES eggs m^{-3}	CalVET eggs m^{-3}	*t*-value[a]
12-07	27 Sept., 15:02	5	0.56 (80)	0.74 (51)	−0.674
12-08	27 Sept., 16:34	3	4.67 (41)	4.98 (21)	−0.253
12-09	27 Sept., 17:31	3	2.53 (40)	3.86 (34)	−1.387
12-10	27 Sept., 18:38	7	5.54 (39)	6.54 (12)	−1.150
12-11	27 Sept., 20:00	7	9.94 (26)	8.89 (17)	0.938
13-08	28 Sept., 07:04	7	14.00 (49)	8.56 (13)	2.087
13-07	28 Sept., 08:21	7	8.23 (31)	5.99 (20)	2.085
13-06	28 Sept., 09:28	3	0.40 (100)	0.56 (50)	−0.568
14-06	28 Sept., 19:45	3	8.40 (27)	6.17 (15)	1.605
14-07	28 Sept., 20:39	3	3.60 (59)	5.53 (39)	−1.110
15-04	29 Sept., 02:51	5	24.40 (6)	12.17 (24)	8.397*
15-03	29 Sept., 04:03	3	14.04 (20)	7.31 (22)	3.817*
16-02	29 Sept., 07:16	3	9.73 (33)	2.29 (31)	3.922
16-03	29 Sept., 08:07	3	31.60 (23)	14.20 (11)	4.010

net samples at these stations, which occurred at the end of the survey along Line 15 (Table 2). Between-replicate variance for round herring eggs was again higher for CUFES than for CalVET net samples, with CVs ranging from 6% to 100% and having a mean value of 41% for the CUFES samples, whereas CalVET net sample CVs ranged from 11% to 51% and had a mean value of 26%. As was the case for sardine eggs, high CV values from the CUFES samples were associated with low means.

Oceanography

Oceanographic conditions (Fig. 3) observed during the survey were relatively homogeneous as a result of storm-induced mixing prior to and during the initial stages of the cruise. Sea surface temperature increased gradually from 14°C inshore to 16°C offshore and, with the exception of Line 17, the upper water column (to 70 m depth) was predominantly isothermal (Fig. 4). Sea surface salinity also increased offshore, although a tongue of lower-salinity (35–35.2) water was evident at the offshore stations of Lines 14 and 15. Currents at 30 m depth indicated a predominantly westward flow, and the shelf-edge jet current off Cape Point was particularly evident with current speeds of up to 50 cm s^{-1} being recorded in this region. A strong, southerly counter-current was observed at the inshore stations of Line 17. Chlorophyll *a* fluorescence data were not collected along Lines 12 and 13, but decreased in an offshore direction over the rest of the survey area.

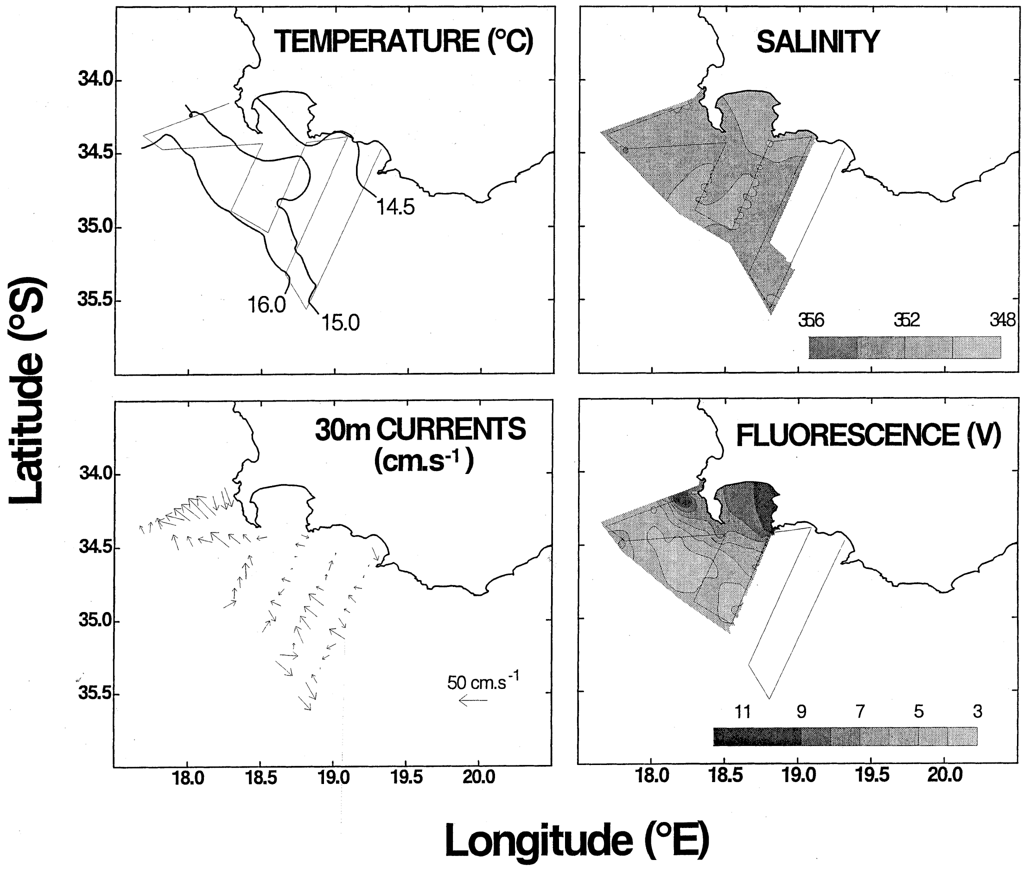
Egg distributions

Sardine and round herring eggs were confined to a band running parallel to the coast and extending from 10 to 30 nautical miles offshore to the shelf edge (Fig. 5). Sardine eggs were more abundant than those of round herring. The highest egg densities for both species were observed above the 200 m isobath along Lines 15 and 16. These peak densities were associated with the strong north-westerly flow of the jet current in this region. Profiles of volumetric egg density along each line for both species showed that round herring eggs were more broadly distributed across the shelf than were sardine eggs (Fig. 6), which showed pronounced peaks in density along all lines.

Statistical and spatial analysis

Mean weighted volumetric densities per line were higher for on-station CUFES samples than CalVET net samples for sardine eggs on all six lines, and for round herring eggs for three lines (Table 3). For underway CUFES samples, densities were higher for four lines for sardine and five lines for round herring eggs. Whilst the survey-weighted mean egg densities for on-station and underway CUFES samples were higher than those from CalVET net samples for the eggs of both species, these differences were not significant (*t*-test; $P > 0.05$). CalVET net samples provided the lowest survey CVs (20% and 11% for sardine and round herring eggs, respectively), and on-station CUFES samples the highest (37% and 28% for sardine

Figure 3. Sea surface temperature (°C), salinity and chlorophyll *a* fluorescence (volts) at 3 m depth together with currents at 30 m depth (cm s^{-1}) during the CUFES cruise.



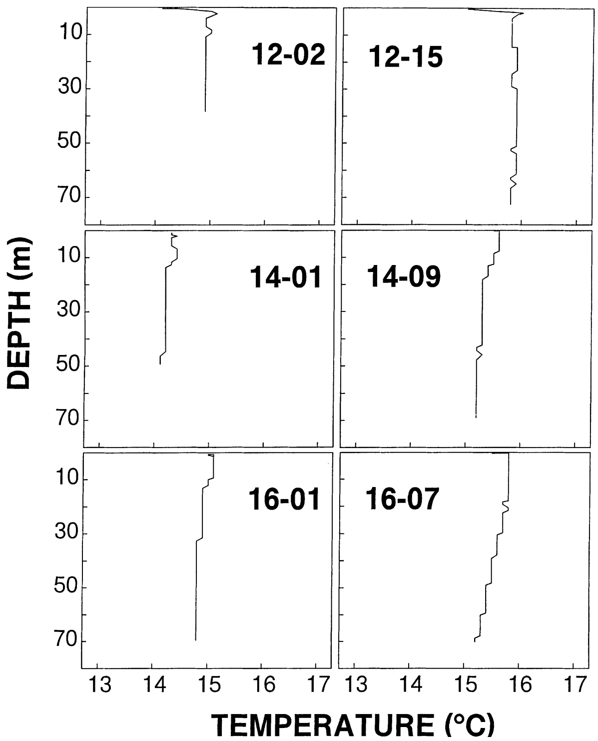
and round herring eggs, respectively). Underway CUFES samples reduced the survey CV by 40% compared with on-station CUFES for sardine eggs, but did not alter significantly the survey CV for round herring eggs (Table 3).

Experimental variograms for on-station and underway CUFES and CalVET net samples were normalized to the sampling variance for comparative purposes (Fig. 7). Statistics for the data and the models fitted are shown in Table 4. The variograms are characterized by a sharp increase at small ranges, which is indicative of spatial structure. The sill (or maximal variance) is reached at autocorrelation ranges of between 10 and 18 nautical miles for both sardine and round herring eggs. Volumetric egg densities were higher from on-station and underway CUFES samples than from CalVET net samples for both sardine and round herring eggs. Underway CUFES samples provided the lowest, and on-station CUFES samples the highest, geostatistical CV for sardine eggs (28.7% and 39.5%, respectively), whereas CalVET net samples had the lowest CV (20.8%) for round herring eggs (Table 4).

DISCUSSION

CUFES was employed to assess the abundance and distribution of pelagic fish eggs on the western Agulhas Bank, and its performance was tested by comparison with estimates of egg abundance derived from CalVET net samples. Under the oceanographic conditions encountered during this survey, which are typical for the region at this time of year (Boyd *et al.*, 1985), CUFES proved to be dependable, simple to operate, and provided reliable, real-time information on the abundance and distribution of sardine and round herring eggs. The assessment of between-replicate variance demonstrated the better replicability of CalVET net compared with on-station CUFES samples. This is not surprising, given that on-station CUFES samples were collected from a single depth at one position whereas CalVET net samples were vertically

Figure 4. Vertical temperature (°C) profiles from the inshore (left panel) and offshore (right panel) stations along Lines 12, 14 and 16.



integrated over 70 m. Small-scale variability in vertical egg distribution would therefore have a greater effect on on-station CUFES samples, and was most likely responsible for the higher variance observed. Additionally, the smaller volume sampled by the on-station CUFES (2.5 m^3) compared with the CalVET net (3.6 m^3) could also be responsible for the higher variance of the CUFES samples, because small sample size is usually related to higher variability. However, the high CVs observed from the CUFES samples were only associated with low mean values; at moderate to high egg densities (>10 eggs m^{-3}) the CVs for both sardine and round herring eggs collected with the CUFES were less than 50%, and were comparable to the CVs for eggs collected with the CalVET net. At moderate to high egg densities therefore, CUFES provides the same degree of replicability as does the CalVET net.

The highly significant correlations observed in this study between CUFES-derived volumetric density estimates and CalVET net-derived volumetric and areal density estimates for both sardine and round herring eggs demonstrate the suitability of CUFES as a sampler of fish eggs. Checkley *et al.* (1997) also found good agreement between estimates of egg density from these two samplers, and reported correlation coefficients (r^2 values) of 0.85 and 0.62 for ln-transformed volumetric estimates of egg density from CUFES samples and ln-transformed volumetric estimates of egg density from CalVET net samples for northern anchovy, *Engraulis mordax*, and Pacific sardine, *Sardinops sagax*, respectively. The slope of the linear regression relating CUFES- to CalVET net-derived volumetric densities of eggs was significantly greater than 1 for sardine in Checkley *et al.*'s (1997) study, and for both sardine and round herring in this study, indicating that the eggs of these species were concentrated in surface waters. This is consistent with previous observations. O'Toole (1977) found that 75% of the eggs of sardine collected from the upper 75 m of the water column off Namibia were concentrated above the thermocline in the top 20 m,

Figure 5. Spatial distribution of sardine, *Sardinops sagax*, and round herring, *Etrumeus whiteheadi*, eggs (eggs m^{-3}) sampled at 3 m depth using both underway and on-station CUFES sampling.

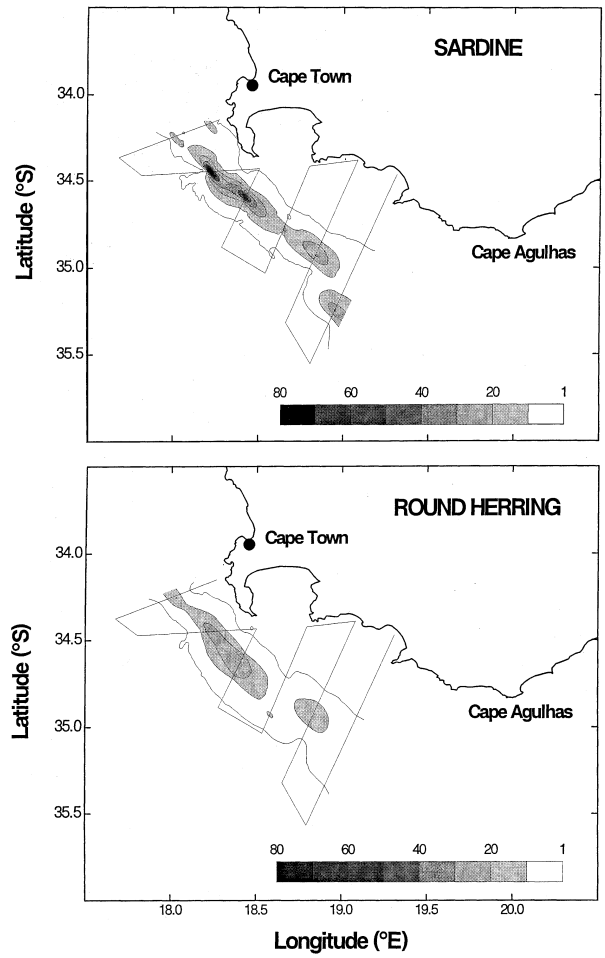


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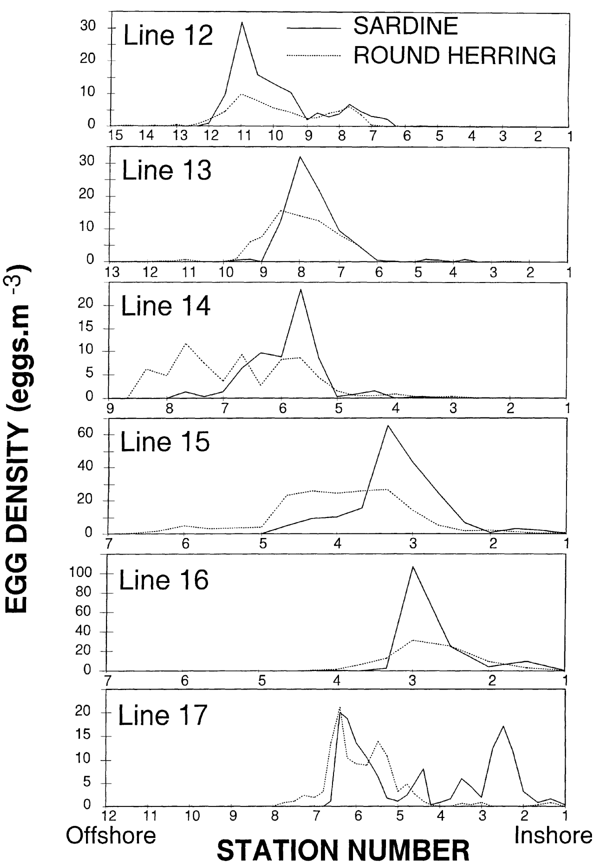
Figure 6. Cross-shelf distributions of sardine, *Sardinops sagax*, and round herring, *Etrumeus whiteheadi*, eggs (eggs m^{-3}) along Lines 12–17 as measured by on-station and underway CUFES sampling at 3 m depth. Note that the *x* and *y* axes are scaled differently.



and Konishi (1980) reported that the eggs of the Japanese sardine (formerly *S. melanosticta*; Parrish *et al.*, 1989) and round herring, *Etrumeus micropus*, were most abundant in the surface layers. Similarly, the eggs of another clupeoid, the pilchard, *Sardina pilchardus*, showed a tendency to be located in the upper water layers above the thermocline (Coombs *et al.*, 1985; Ferreiro and Labarta, 1988).

The concentration of sardine and round herring eggs in the surface waters was further indicated by significant differences observed between CUFES- and CalVET net-derived volumetric mean densities of eggs at stations where multiple paired samples were taken. Where such differences were observed, CUFES-derived estimates were always greater than those derived from CalVET net samples. These differences appeared to follow the same temporal trend for both sardine and round herring; CUFES and CalVET net samples taken at the beginning of the cruise were not significantly different from each other, whereas those taken towards the end of the cruise were. This trend may be indicative of stabilization of the upper mixed layer, following storm-induced mixing immediately prior to and during the initial stages of the cruise, which would have resulted in more homogeneous vertical egg distributions. Interspecific differences in this temporal trend, with only 2 of the last 4 multiple stations showing significant differences between samplers for round herring eggs, whereas 6 of the last 10 multiple stations were significantly different for sardine eggs, may indicate differences in ascension rates of the eggs and hence vertical egg distribution patterns of these two species. Some evidence for this has been provided by Olivar and Shelton (1993), who found that whilst

Table 3. Mean volumetric egg density (eggs m^{-3}) by sampling line and survey mean from on-station CUFES and CalVET net samples, and from underway CUFES samples.

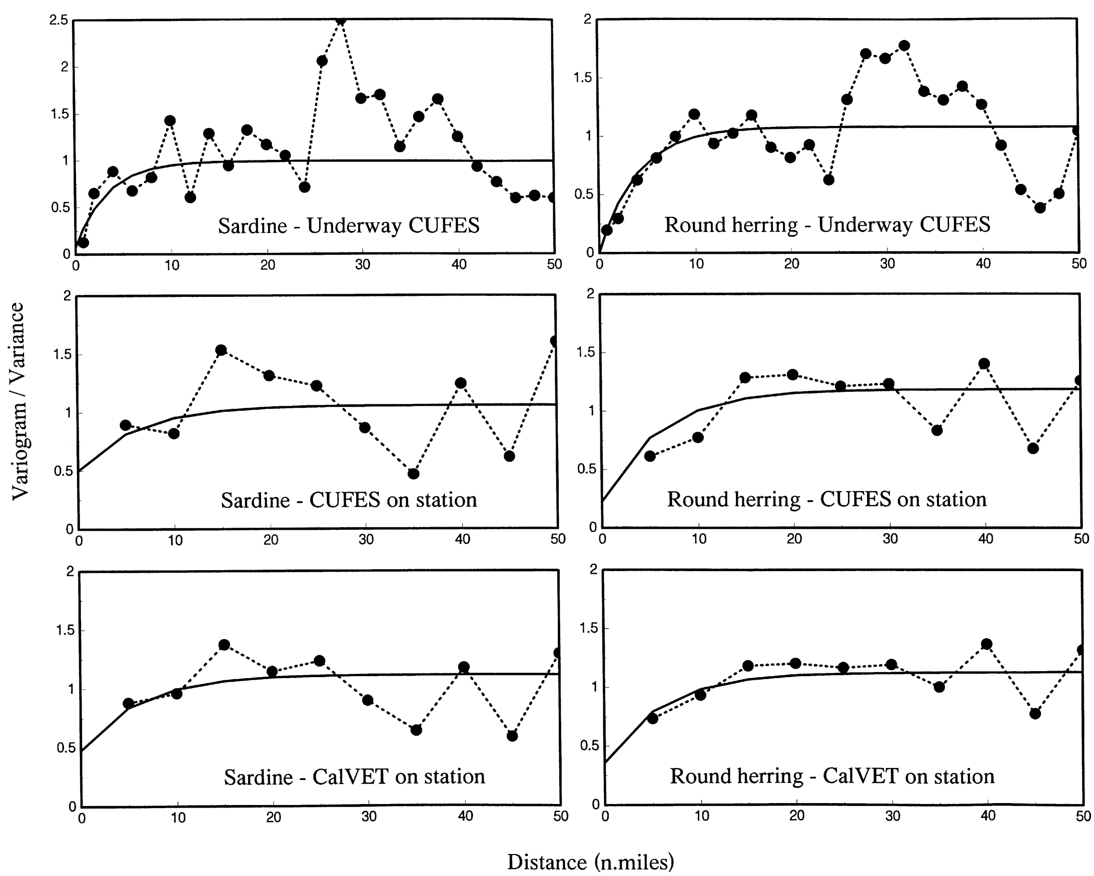
	On station				Underway			
	Sardine		Round herring		No. of stations	Sardine	Round herring	No. of intervals
Line	CalVET	CUFES	CalVET	CUFES		CUFES	CUFES	
12	3.09	3.66	1.81	1.71	15	2.88	1.7	21
13	2.48	3.23	1.69	2.39	13	2.53	2.4	17
14	1.12	1.20	2.63	2.18	9	3.84	4.03	13
15	3.82	7.82	3.21	7.26	7	10.29	9.99	12
16	6.24	15.98	2.52	6.25	7	4.99	5.37	8
17	1.60	1.77	1.42	1.27	12	3.99	3.09	32
Weighted mean	2.95	4.96	2.10	3.06		4.15	3.75	
CV (%)	20	37	11	27		22	28	

Table 4. Statistical values and exponential model parameters fitted to the experimental variograms computed for underway CUFES, on-station CUFES and on-station CalVET net volumetric egg density data.

	On station				Underway	
	Sardine		Round herring		Sardine	Round herring
	CalVET	CUFES	CalVET	CUFES	CUFES	CUFES
Statistics						
Mean (eggs m^{-3})	2.83	4.69	2.06	2.95	4.41	3.83
Sampling variance	54.6	236	12.4	33.7	75.6	41.7
Variogram fit						
Nugget	29	125	5	9	5	0
Range	18	18	18	18	10	12
Sill	61	250	14	40	75	45
Geostatistical CV (%)	32.2	39.5	20.8	24.1	28.7	26.1

over 80% of sardine eggs were found in the upper 25 m of the water column of the Benguela Current, only 50% of round herring eggs were found in the upper 50 m. Similarly, Konishi (1980) reported that whereas the eggs of both the Japanese sardine and round herring were concentrated in the surface waters, those

Figure 7. Variograms of sardine, *Sardinops sagax*, and round herring, *Etrumeus whiteheadi*, egg data from underway CUFES, on-station CUFES and CalVET net samples.

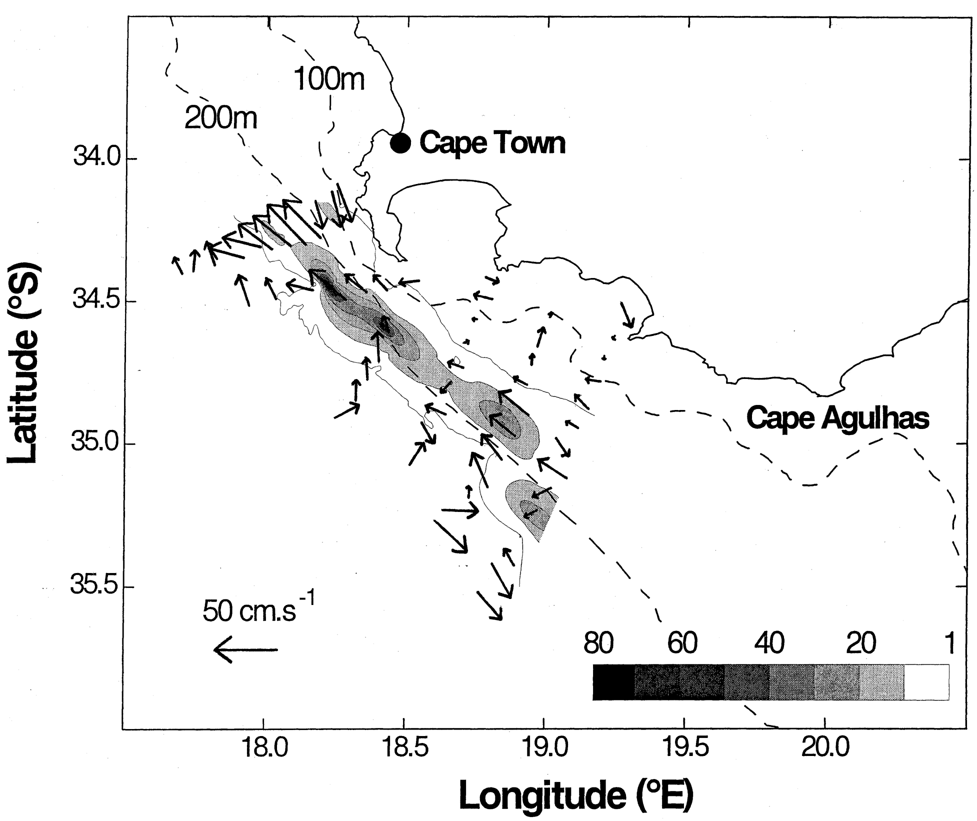


of round herring were found slightly deeper than those of sardine. Interspecific differences in egg buoyancy and ascension rates need to be tested through experiments such as those of Sundby (1997), because these differences are likely to be responsible for biases in the data provided by CUFES.

High-resolution distribution maps for both sardine and round herring eggs were obtained using CUFES data. Whereas CalVET net hauls provide a vertically integrated estimate of egg density at a single location on a survey grid, CUFES samples provide a horizontally integrated estimate of egg density from a single depth along a survey grid. This horizontal integration provides high-resolution information concerning egg spatial structure, and allows the identification of fine-scale features that may be affecting egg distributions. Sardine and round herring eggs were associated with the region of strong north-westerly flow above the 200 m isobath at the shelf edge (Fig. 8), and along Line 17 were concentrated on the inshore edge of the frontal zone. Anchovy eggs are closely associated with this frontal zone (Shelton and Hutchings, 1990), and they and other plankton are entrained in the equatorward jet current and transported to the nursery area on the west coast. Variations in the behaviour of this jet current are thought to have the potential for considerable loss from the system of pelagic fish eggs and larvae, which could occur if the jet is diverted offshore (Hutchings, 1992; Shannon *et al.*, 1996).

Statistical analysis using the method of Jolly and Hampton (1990) provided estimates of mean volumetric sardine egg density which had similar CVs from both underway CUFES and CalVET net samples. However, the geostatistical analysis indicated that underway CUFES samples provided the most precise estimate. Increased sampling effort therefore seems to be effective in increasing the precision of the estimate for sardine egg density. This suggests that the biggest problem in the estimation of mean density is the patchiness of distribution, which will be partially solved by increased effort. The geostatistical CVs are higher than those derived using the method of Jolly and Hampton (1990), perhaps because of the small-scale variability, which was overcome in the latter

Figure 8. Spatial distribution of sardine, *Sardinops sagax*, eggs (eggs m^{-3}) sampled by CUFES at 3 m depth in relation to the bathymetry and currents at 30 m depth.



method by using the transect as the basic sampling unit. However, the use of anisotropic models and tighter domain definitions in the geostatistical analysis should bring the CVs closer together.

For round herring eggs, both the statistical and geostatistical analyses indicated that the CalVET net samples provided the most precise estimate of mean volumetric density, and that underway and on-station CUFES samples provided estimates with higher CVs. These results suggest that the observed variability is not only due to patchiness, and that the factors causing this variability either are unaffected by the amount of effort applied, or balance each other out. For example, the advantages of the increased sampling effort may be invalidated by the problems posed by a method that is essentially two-dimensional when the variable in question is three-dimensional. Both the statistical and geostatistical analyses have highlighted the interspecific differences in egg distributions between sardine and round herring. Increased sampling effort via CUFES appears effective in negating problems posed by the highly patchy distribution of sardine eggs, whereas increased sampling does not affect the precision of estimates of round herring egg densities. For both species, however, the increased small-scale resolution will improve our understanding of fish spawning processes, and of the dispersion of spawning products after spawning takes place.

CUFES appears to be well suited for incorporation into the DEPM for estimating sardine spawning stock biomass. Aside from increasing precision, the higher horizontal resolution provided from underway sampling could enable a reduction in the number of CalVET net stations, and hence save time and improve survey efficiency. However, the positive bias of CUFES, resulting from the fact that it samples in the region of peak egg density, means that information obtained from vertically integrated egg samplers will be required to complement CUFES samples. Furthermore, the vertical distribution of eggs with respect to age category should be investigated, because the DEPM requires age-specific estimates of egg density and biased sampling with respect to age category could bias biomass estimates. In this regard, however, Checkley *et al.* (1997) found that all developmental stages except the first of Pacific sardine, *S. sagax*, eggs were sampled with equal efficiency by CUFES and CalVET nets.

As has been the case for anchovy (Hampton, 1996), the DEPM will be useful in scaling acoustic estimates of sardine biomass, which may be biased by the effects of fish behaviour such as near-surface shoaling, aggregations, and near-shore distributions (Coetzee, 1997). Because the distribution of sardine eggs, like that of sardine juveniles and adults, is highly patchy (Barange and Hampton, 1997), the continuous nature of the CUFES makes this survey technique very well suited to this species, and will allow better spatial resolution and more precise estimates of egg abundance, and hence of population biomass.

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