EGG PRODUCTION ESTIMATES OF ANCHOVY BIOMASS IN THE SOUTHERN BENGUELA SYSTEM

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ABSTRACT

The spawning biomass of the southern Benguela anchovy (*Engraulis capensis*) stock has been estimated annually since 1984 by means of acoustics and the egg production method (EPM), both techniques being integrated into one survey. In 1985 and 1986 the survey area was stratified on the basis of expected fish distribution patterns, and the transects were randomized within limits to allow rigorous investigation of the survey variance of both the EPM and acoustic estimates. The acoustic estimates of relative fish density in the vicinity of trawl stations were incorporated to weight individual trawl parameters for the egg production method, and within-stratum variances were estimated from the weighted mean parameter values for each transect. In 1986 the acoustic and EPM estimates agreed within 15%, but in 1985 the acoustic estimate was about 30% greater than the EPM estimate. High coefficients of variation of 0.35 to 0.41 were associated with the EPM estimates, mainly reflecting imprecision in the estimation of egg mortality rate and female spawning fraction. This paper briefly presents the results of the surveys, and provides a complete description of the statistical methods appropriate to a randomized, stratified design for egg production surveys, incorporating the necessary weighting factors for trawl parameters.

RESUMEN

La biomasa de desove de la anchoveta del cabo, *Engraulis capensis*, ha sido estimada anualmente desde 1984 por medio de detección acústica y el método de producción de huevos (MPH); estas técnicas fueron usadas conjuntamente en nuestros cruceros. En 1985 y 1986, el área investigada fue estratificada en base a la distribución esperada de peces, y los transectos fueron distribuidos al azar dentro de ciertos límites, permitiendo estudiar rigurosamente la varianza de los valores estimados a través de detección acústica y por el método de producción de huevos. Las estimaciones de la densidad relativa de peces por medio de detección acústica en la vecindad de las estaciones de pesca fueron usadas para ponderar los parámetros de la red de arrastre necesarios para el método de producción de huevos. Dentro de cada estrato, las varianzas fueron estimadas a partir de los valores promedios ponderados para cada transecto. En 1986, las estimaciones acústicas y las por el método de producción de huevos coincidieron dentro de un 15%, pero en 1985 la estimación acústica fue alrededor de un 30% mayor que aquella obtenida por el método de producción de huevos. Coeficientes de variación entre 0.35 y 0.41 asociados con el método de producción de huevos, reflejan imprecisión en la estimación de la tasa de mortalidad de huevos y en la fracción de hembras que desova. Este trabajo presenta brevemente los resultados de los cruceros de investigación. Además, se provee una descripción completa de los métodos estadísticos apropiados para un diseño estratificado y aleatorio de cruceros específicamente programados para estimar la producción de huevos, incorporando los factores de ponderación necesarios para los parámetros de la red de arrastre.

INTRODUCTION

The estimation of population size by means of surveys plays an increasing role in fish stock assessments, either within some form of management plan in which recommended yields are a function of stock size (e.g., MacCall 1980) or to provide auxiliary information in catch-at-age analyses (e.g., Methot 1986). Pelagic fish surveys have employed vertical echo sounding (e.g., papers in Nakken and Venema 1983; Hampton 1987), mapping of schools by means of side-directed sonar (Hewitt et. al. 1976) or aircraft-borne remote sensors (Cram and Hampton 1976), and estimation of the abundance of eggs or larvae in the plankton. The latter method includes both the estimation of total annual egg or larval production by integrating over the results of repeated within-season surveys (Lockwood et al. 1981; Smith and Richardson 1977) and the more recently developed egg produc-

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tion method (EPM), in which egg production and specific fecundity are measured daily during a single survey (Parker 1980).

The utility of any survey method depends on its accuracy and precision. Sampling error may be minimized by appropriate survey design and sufficient sampling intensity, but some methods require parameters that are not estimated during each survey and therefore have unquantified variances (for example, the values of specific fecundity at different times during the spawning season in the integrated larval abundance method, or the proportion of schools detectable by aircraft-borne sensors). In the egg production method, all the parameters and their variances are estimated from a single survey, and the sampling intensity required to achieve a desired precision can be considered in the survey design (Picquelle 1985). Egg production surveys of engraulid biomass have been implemented in three of the major eastern boundary current systems: off California (e.g., Bindman 1986), off Peru (Alheit et al. 1984), and off southern Africa (this study).

The spawning population of the southern Benguela anchovy, *Engraulis capensis*, has been surveyed annually since 1983 by means of vertical echo integration (Hampton 1987), and egg samples have been collected during these cruises at regular stations along the acoustic survey grids for the estimation of daily egg production. From 1985, the proportion of the female population spawning each night (the spawning fraction) has been estimated by histological examination of ovaries (Hunter and Macewicz 1985), and in 1985 and 1986 the egg production method provided second biomass estimates in addition to the acoustic estimates. In 1984 the spawning fraction was estimated from the incidence of females with hydrated oocytes, but this was found to be an unacceptably biased method, and the spawning biomass in that year can only be roughly estimated from assumed values of spawning fraction. However, an approximate value can be obtained by comparing the incidence of hydrated females in 1984 with observations in other years when the histological method was also implemented.

Assuming the egg production biomass estimate to be less subject to bias than the acoustic estimate (a direct estimate of target strength has not yet been obtained for *E. capensis*), a method has been developed (Hampton et al., in press) in which the acoustic estimate in 1986 was adjusted by the ratio of egg production to acoustic biomass estimates in 1985 to allow the two 1986 estimates to be combined directly. The combined estimate was expected to be more accurate than either of the separate estimates. The results of the direct surveys of southern Benguela anchovy biomass initially allowed the identification of appropriate levels of yield for the resource (Armstrong and Butterworth 1986), and catches have subsequently been increased from 300,000 tons in 1986 to 600,000 tons in 1987, largely on the basis of the biomass estimates presented here.

In this paper we describe the methods and results of the egg production surveys of anchovy biomass in the southern Benguela Current system during 1984, 1985, and 1986, and provide a detailed account of the parameter and variance estimation procedures appropriate for a stratified random survey. Our method differs from that employed off California and Peru in that the fish densities estimated by means of vertical echo sounding are incorporated as weighting factors for the spawning parameters, and the survey transects, rather than the individual stations, are considered to be the basic sampling units for variance estimation.

METHODS

Biomass Model

The egg production method of estimating the spawning biomass of a fish population (Parker 1980) involves determining the average total number of eggs spawned per day by the population (the daily egg production) and the average number of eggs spawned daily per unit mass of the population (the daily specific fecundity). These estimates are obtained from simultaneous collections of fish and planktonic eggs across the spawning grounds. Biomass is calculated from the expression:

$$\hat{B} = \hat{P}_o A \frac{\hat{W}}{\hat{F}\hat{S}\hat{R}} \tag{1}$$

where

$\hat{B}$ = estimated spawning biomass,
$\hat{P}_o$ = estimated mean daily egg production per unit area,
A = area within which $\hat{P}_o$ is estimated,
$\hat{W}$ = estimated mean mass of individual females,
$\hat{F}$ = estimated mean batch fecundity (eggs per female),
$\hat{S}$ = estimated mean fraction (by number) of the female population spawning each night, and
$\hat{R}$ = estimated mean ratio of female to total spawning biomass.

Defining a further variable $\hat{Q}$ as the ratio $\hat{W}/\hat{F}$ ($\hat{F}$ is obtained from a linear relationship between batch fecundity and female mass in the surveys described here), the approximate normalized variance of $\hat{B}$ is given by:

$$\frac{V(\hat{B})}{\hat{B}^2} = \frac{V(\hat{P}_o)}{\hat{P}_o^2} + \frac{V(\hat{Q})}{\hat{Q}^2} + \frac{V(\hat{S})}{\hat{S}^2} + \frac{V(\hat{R})}{\hat{R}^2} + 2\left[\frac{\mathrm{COV}(\hat{P}_o\hat{Q})}{\hat{P}_o\hat{Q}} + \frac{\mathrm{COV}(\hat{R}\hat{S})}{\hat{R}\hat{S}} - \frac{\mathrm{COV}(\hat{P}_o\hat{R})}{\hat{P}_o\hat{R}} - \frac{\mathrm{COV}(\hat{P}_o\hat{S})}{\hat{P}_o\hat{S}} - \frac{\mathrm{COV}(\hat{Q}\hat{R})}{\hat{Q}\hat{R}} - \frac{\mathrm{COV}(\hat{Q}\hat{S})}{\hat{Q}\hat{S}}\right] \tag{2}$$

The ratio estimate of spawning biomass from equation 1 is subject to small-sample bias arising from the asymmetry in the distribution of products or quotients of variables which themselves have more or less symmetrical distributions. The larger the coefficients of variation, the larger will be the bias. The bias is given as:

$$E(\hat{B}) - B' = B'\left[\frac{V(\hat{R})}{\hat{R}^2} + \frac{V(\hat{S})}{\hat{S}^2} + \frac{\mathrm{COV}(\hat{P}_o\hat{Q})}{\hat{P}_o\hat{Q}} + \frac{\mathrm{COV}(\hat{R}\hat{S})}{\hat{R}\hat{S}} - \frac{\mathrm{COV}(\hat{P}_o\hat{R})}{\hat{P}_o\hat{R}} - \frac{\mathrm{COV}(\hat{P}_o\hat{S})}{\hat{P}_o\hat{S}} - \frac{\mathrm{COV}(\hat{Q}\hat{R})}{\hat{Q}\hat{R}} - \frac{\mathrm{COV}(\hat{Q}\hat{S})}{\hat{Q}\hat{S}}\right] \tag{3}$$

where $E(\hat{B})$ is the expected value of the estimate from equation 1 and B' is the true biomass. An approximate estimate of bias is obtained by substituting $\hat{B}$ for B' in the right-hand side of equation 3. The estimated spawning biomass from equation 1 can then be corrected by subtracting the bias value given by equation 3.

Survey Design

The parameters for the southern Benguela anchovy stock were estimated during surveys lasting between two and three weeks, timed to coincide with peak anchovy spawning, which occurs around November each year (Shelton 1986). The surveys were conducted on board the Sea Fisheries Research Institute research ship *Africana*, a 76-m stern trawler capable of aimed midwater trawling to a depth of about 500 m.

The survey design in 1984 was based on a systematic grid of transects running approximately perpendicular to the coastline and spaced 37 km (20 n.mi.) apart at the inshore stations (Figure 1). A total area of 125,700 km^2 was surveyed from November 5 to 23. In 1985 and 1986 the survey area was stratified according to consistent patterns of fish distribution observed in previous spawning surveys, and in 1986 the density of sample transects was increased in strata with expected high fish densities. Within each stratum, the spacing between transects was randomized within limits to allow variances to be estimated on the assumption of random sampling (Figures 2 and 3). Full randomization was avoided to reduce the risk of large areas being left unsampled. A two-stage randomization procedure was adopted to provide a compromise between unrestricted random and equally spaced transects, without invalidating the variance estimates (Jolly and Hampton, MS in prep.) The 1985 and 1986 surveys covered areas similar to those in the 1984 survey, from November 11 to 26 and November 12 to 28, respectively. The egg production survey area A in each year excluded an outer zone of zero egg density in order to minimize the variance estimate. The positive egg strata were terminated within the offshore or inshore boundaries of the survey grid after two successive zero egg stations beyond the last positive egg station on each transect. Embedded areas of zero egg density were not excluded.

A Simrad EK-S 38-kHz scientific echo sounder was run continuously between egg stations, and the echoes were integrated in 1-m depth strata by means of a custom-built digital data logger. In addition to providing a further estimate of biomass, the acoustic density estimates were used to weight the egg production survey trawl parameters, as described later. A full description of the acoustic system and data analysis is given by Hampton (1987).

Collection of Eggs

Anchovy eggs were sampled at stations spaced 9.3 km (5 n.mi.) apart by means of vertical hauls of a CalVET net (Smith et al. 1985) from 200 m or near the seabed, depending on the sounding. In areas of zero egg abundance, the distance between stations was frequently extended to 18.6 km (10 n.mi.) to save time. Temperature profiles were recorded from an electronic temperature/depth sensor suspended below the net. The number of CalVET stations occupied in the positive egg strata of the 1984–86 surveys were 281, 245, and 271, respectively.

Collection of Fish

Pelagic fish were caught, both for acoustic target identification and for estimation of spawning parameters, by means of an Engels-308 midwater trawl with an 8-mm cod-end liner, towed on 32-mm

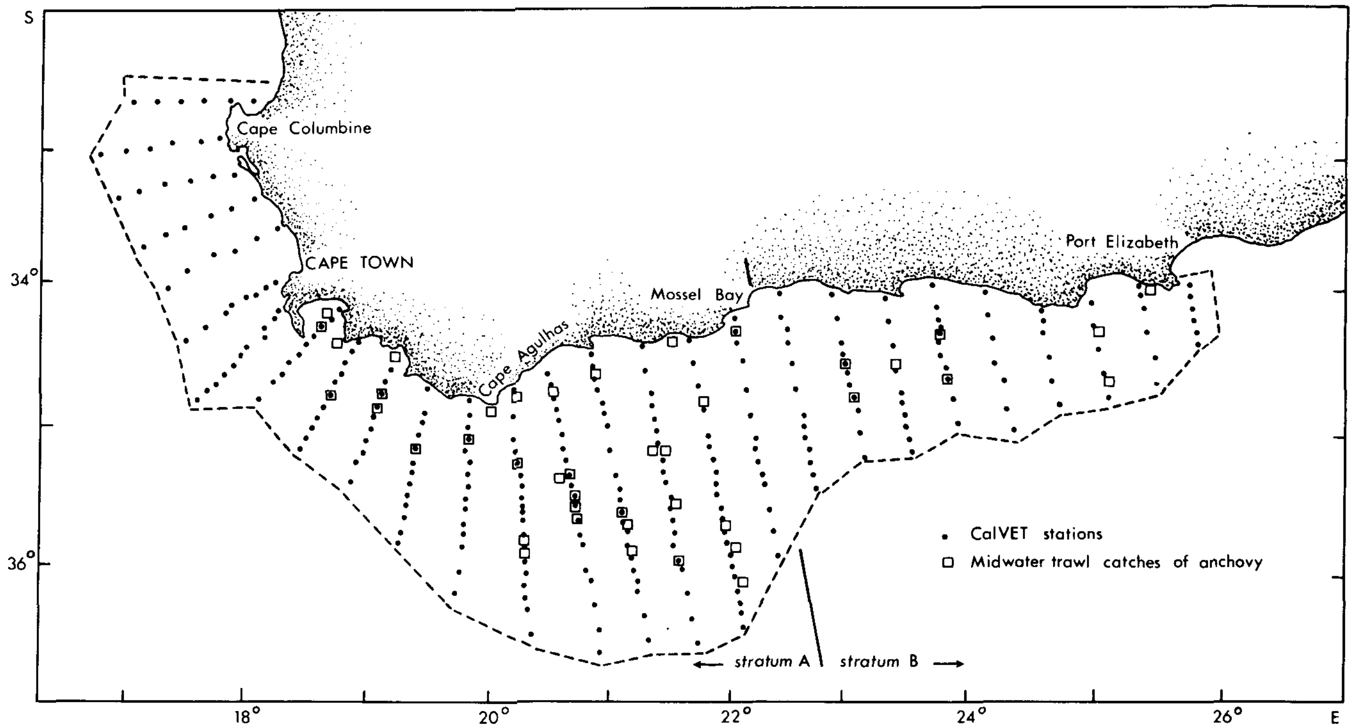

Figure 1. Position of egg stations and midwater trawl catches of anchovy in November 1984. The *post-hoc* delimitation of strata is indicated.

steel warps with 32-m sweeps and 6-m^2 steel doors. A mouth opening of approximately 15 m was recorded with this net at average towing speeds of 3–4 knots (depending on currents). Fishing operations were carried out during day and night when targets were sufficiently abundant to require identification or to provide usable information on spawning parameters. Nighttime trawling was facilitated by the dispersal of the anchovy into diffuse layers, usually just above the thermocline, which varied in depth from about 20 m in shallow water to over 50 m offshore.

The performance of the gear and the entry of fish into the net were monitored by means of a 49-kHz net-sonde mounted on the top panel of the net; the duration of the tows could therefore be varied according to the apparent catch rate. Nighttime tows generally consisted of a double oblique haul through the scattering layer, and all tows were completed in the shortest possible time in order to bring the fish to the surface alive. Catches of anchovy averaged 40–80 kg.

Parameter Estimation for Daily Egg Production

The CalVET net samples of anchovy eggs were sorted and staged according to the criteria given by Moser and Ahlstrom (1985). The average age of eggs in each stage was estimated from egg development-temperature relationships obtained by means of incubation experiments carried out on field-collected eggs during the 1984 survey, and described in Valdes et al. (1987). The relationship between the average age t_p of an egg in development stage p and the ambient temperature v°C was described by the exponential function:

$$t_p = \exp(A_p - B_p v) \qquad (4)$$

Values of A_p and B_p for egg stages 3 to 11 were obtained from the experiments carried out during the 1984 survey (Table 1). The parameters for stage 2 could not be determined from the field-sampled eggs, and the relationship for this stage was there-

TABLE 1
Parameters of the Relationship (Equation 4) Estimated from Incubation Experiments Carried Out on Field-Collected Eggs during the November 1984 Spawner Biomass Survey

Development stage p	Parameter Ap	Parameter Bp
2	3.755	0.1183
3	5.197	0.1576
4	5.559	0.1586
5	5.941	0.1600
6	5.875	0.1390
7	5.915	0.1286
8	5.914	0.1206
9	6.387	0.1428
10	6.215	0.1298

Development stages are after Moser and Ahlstrom (1985).

fore assumed to be similar to that of the California anchovy (Lo 1985).

Temperatures in the upper mixed layer were generally uniform, and values at 5 m were used to determine the ages of eggs at each station. (Previous studies of the vertical distribution of anchovy eggs in the survey area [Shelton 1986; Shelton et al., MS in prep.] showed that the eggs occurred at various depths from near the surface to just above the thermocline.)

Spawning was assumed to occur synchronously at 2200 h, based on the incidence of anchovies with both hydrated oocytes and new postovulatory follicles in trawl samples (Melo et al., MS in prep.). The eggs in each developmental stage could therefore be allocated to one of up to three previous nights' spawnings, according to the estimated ages of the eggs in the various stages. The earliest time of spawning each night was taken to be 1700 h; if the age estimated for a given egg stage from equation 4 indicated that spawning occurred before 1700 h, the eggs were assumed to have been derived from the preceeding night's spawning, but having developed more slowly than expected from the temperature at 5-m depth. Because this temperature represents the warmest that the eggs are likely to have encountered in the water column, there is a much higher probability that an egg would be underaged than overaged. The egg stages at each station were grouped by spawning night, and the number of eggs in each group was determined. The mean age of eggs in each group was then reestimated as the time elapsed between spawning at 2200 h and the time of sampling. Zero egg abundance was recorded if a batch of eggs from a previous night's spawning was expected, but not observed.

Egg numbers were assumed to decline at a constant exponential rate according to the model:

$$P_t = P_o \exp(-Z\,t) \qquad (5)$$

where

P_o is the mean total daily egg production and
P_t is the mean egg abundance at age t.

The mean hourly instantaneous rate of egg mortality, Z, was estimated by regressing the natural logarithms of the estimated total abundances of eggs in one-hour age classes against age with weighting values equivalent to the inverse of the variance of each abundance value (see Appendix 1).

The mean density of eggs in each age class (expressed as eggs m^{-2}) was first estimated for separate survey strata by averaging the station values for that age class within each stratum, giving 10-mile stations twice the weighting of stations spaced 5 miles apart to allow for the greater area represented by the 10-mile stations. These mean densities were then multiplied by the stratum areas and summed to give overall abundance of eggs of age t to $t+1$ h. None of the one-hour age classes had zero total abundance of eggs in the 1984–86 surveys, but in the event of this occurring, the age classes could be further amalgamated to eliminate the zeroes. Alternatively, an equivalent nonlinear regression package could be employed, provided the regression data could be weighted as described. Details of the linear regression procedure are given in Appendix 1. Only the abundances of eggs aged between 5 and 50 h were included in the regression to avoid biases caused by hatching or incomplete recruitment of the eggs to the plankton.

In the above procedure, the estimates of egg density in each age class were weighted by stratum area to estimate total egg abundance at each age. This procedure was adopted to reduce any bias that may have arisen if egg mortality varied between survey strata with different fish densities or environmental conditions, even though such variations are unlikely to be detectable at the present sampling rate. A slight reduction in the variance of the egg mortality estimate could have been obtained by abandoning stratum weighting on the basis that between-stratum variations could not be detected with acceptable levels of confidence.

Weighting Procedures and Variance Estimation for $\mathbf{P_o}$

The values of abundance of eggs at age 5 to 50 h at each CalVET station were divided by the estimated survival rate $\exp(-Zt)$ to provide up to three estimates of daily egg production (depending on the number of batches expected at the ambient temperature and time of sampling). These values were averaged to give a station value $\hat{P}_{o_{ijk}}$, and a weighted mean value of age was computed. (Parameters for strata, transects, and stations are suffixed i, j, and k respectively.) The station values were then averaged to give transect estimates $\hat{P}_{o_{ij}}$ and $\bar{t}_{ij}$, with any missing 5-mile station values being obtained by interpolation between adjacent 10-mile stations on the same transect. Stratum mean values $\hat{P}_{o_i}$ were calculated as weighted means of the transect values, with weights equal to the lengths L_{ij} of the transects (weighting expressions for transect and stratum values of spawning parameters are summarized in Table 2 for easy reference):

$$\hat{\hat{P}}_{o_i} = \frac{\Sigma_j L_{ij} \hat{\hat{P}}_{ij}}{\Sigma_j L_{ij}} \tag{6}$$

$V_o(\hat{\hat{P}}_{o_i})$, the approximate variance of $\hat{\hat{P}}_{o_i}$ ignoring at this stage the additional variance associated with the estimation of Z, was obtained from the following equation, which is derived from the formula for the variance of a ratio estimator for subsampling given in Cochran (1977):

$$V_o(\hat{\hat{P}}_{o_i}) = \frac{\frac{n_i}{n_i - 1} \sum_j L^2_{ij} (\hat{\hat{P}}_{o_{ij}} - \hat{\hat{P}}_{o_i})^2}{\left(\sum_j L_{ij}\right)^2} \tag{7}$$

where n_i is the number of sample transects in stratum i. Since each transect provides a random sample of the stratum mean, the sampling variance is fully expressed in the variance between transects, irrespective of the variation within the transects. This does not imply that the within-transect variation (and hence the station allocation) is immaterial, for the variation between transects will be affected by the within-transect variation.

The survey mean value $\hat{\hat{P}}_o$ was obtained by averaging over strata with weights equal to A_i, the areas of the strata:

$$\hat{\hat{P}}_o = \frac{\Sigma_i A_i \hat{\hat{P}}_{o_i}}{\Sigma_i A_i} \tag{8}$$

The component of variance in $\hat{\hat{P}}_o$ arising from sampling error in the estimation of egg abundance was given by:

$$V_o(\hat{\hat{P}}_o) = \frac{\Sigma_i A^2_i V_o(\hat{\hat{P}}_{o_i})}{(\Sigma_i A_i)^2} \tag{9}$$

The overall variance of $\hat{\hat{P}}_o$, $V(\hat{\hat{P}}_o)$, was obtained by including the error associated with the estimation of egg mortality:

$$\frac{V(\hat{\hat{P}}_o)}{\hat{\hat{P}}_o^2} = \frac{V_o(\hat{\hat{P}}_o)}{\hat{\hat{P}}_o^2} + (\hat{\bar{t}})^2 V(Z) \tag{10}$$

where $V(Z)$ is the variance of the hourly egg mortality estimate, and $\hat{\bar{t}}$ is the weighted mean age of eggs over the survey area. The component $(\hat{\bar{t}})^2 V(Z)$ expresses the uncertainty involved in back-calculating egg abundance at age zero from station values of egg abundance at age, where the average time elapsed from age zero in the samples is $\hat{\bar{t}}$ h.

Spawning Parameter Estimation

A random sample of 150 anchovies was taken from each midwater trawl catch where possible for estimation of sex ratio and mean female mass; an additional 25 females were taken at random and preserved in 10% Formalin for estimation of spawning fraction. The caudal lengths (Lc) of the 150 fish were recorded, and each fish was slit along the abdomen to allow the sex and maturity stage to be determined. The females were separated from the males and immature fish, and blast frozen in sealed plastic bags with as much air excluded as possible. Hydrated females were excluded, but were measured to the nearest millimeter. The samples were weighed ashore while still frozen, and the sex ratios ($\hat{R}_{ijk}$) and mean female masses ($\hat{\bar{W}}_{ijk}$) were determined. The masses of hydrated females were estimated from a length-mass relationship for females with active but nonhydrated ovaries (to adjust for the temporary gain in mass), and included in the estimation of $\hat{\bar{W}}_{ijk}$ and $\hat{\bar{R}}_{ijk}$. Because this procedure was necessary only for a small fraction of the sampled female fish, errors in this approximation were considered to have a negligible effect on the estimates of R and $\bar{W}$. Very few immature anchovies were recorded, even in 1986, when a relatively large component of late-recruiting fish of 8–10-cm Lc were present in the survey area. Thus the 1984–86 EPM estimates represent total biomasses at the times of the surveys.

The spawning fractions $\hat{S}_{ijk}$ were estimated from the incidence of females with day-1 postovulatory follicles in the random samples of 25 females, according to the methods given by Hunter and Macewicz (1985). Day-0 females were found to be oversampled by the midwater trawl to an extent similar to that observed off California (Picquelle and Stauffer 1985). Samples in which most females contained hydrated ovaries were regularly taken

TABLE 2
Weighting Expressions for Transect and Stratum Mean Values of Spawning Parameters

	Parameter P_o	W,S	R
Transects j	L_{ij}	$L_{ij} \hat{\bar{d}}_{ij} \frac{\hat{\bar{R}}_{ij}}{\hat{\bar{W}}_{ij}}$	$L_{ij} \hat{\bar{d}}_{ij}$
Strata i	A_i	$A_i \hat{\bar{d}}_i \frac{\hat{\bar{R}}_i}{\hat{\bar{W}}_i}$	$A_i \hat{\bar{d}}_i$

Where L_{ij} = length of transect j, stratum i
A_i = area of stratum i
$\hat{\bar{d}}_{ij}$ = mean density of fish along transect j, estimated by acoustics
$\hat{\bar{d}}_i$ = mean density of fish in stratum i, estimated by acoustics

during the evening spawning period, and these samples were often characterized by anomalous sex ratios. To correct for oversampling of day-0 females and the consequent undersampling of day-1 and day-2+ females, the method given by Picquelle and Stauffer (1985) was applied. In this method, it was assumed that the proportion of day-0 and day-1 spawners in the population should on average be equivalent. Hence the number of day-0 spawners in a sample was replaced by the number of day-1 spawners, and the overall sample size was adjusted accordingly. If the number of day-1 spawners in a sample was N^1_{ijk} and the number of day-2+ spawners was $N^{2^+}_{ijk}$, the spawning fraction $\hat{S}_{ijk}$ was calculated as:

$$\hat{S}_{ijk} = \frac{N^1_{ijk}}{2\,N^1_{ijk} + N^{2^+}_{ijk}} \qquad (11)$$

Batch fecundity could not be estimated for each trawl station because of the small proportion of trawls containing hydrated females. However, the batch fecundity was found to be a linear function of ovary-free female mass in each year, and a linear regression allowed the population mean batch fecundity $\hat{F}$ to be predicted from the mean female mass $\hat{W}$, with a suitable adjustment for the discrepancy between the mass of live and preserved specimens. The variance of this predicted value was then a function of the variance of the regression slope, the residual sums of squares of the regression data, the number of observations and the mean mass of the females in the regression, and the between-transect variation in $\hat{W}$. (Had a nonlinear relationship been obtained, $\hat{F}$ would of necessity have been estimated by computing an $\hat{F}_{ijk}$ for each trawl station.) Females that were hydrated but not yet ovulated were collected during each survey and preserved in 10% buffered Formalin. The batch fecundities were determined by means of the hydrated oocyte method described by Hunter et al. (1985), the sample sizes ranging from 53 to 81 in the three surveys.

Weighting Procedures and Variance Estimation for Spawning Parameters

The procedure described in Picquelle and Stauffer (1985) for averaging station values of spawning parameters of the northern anchovy is based on the assumption that the number of samples in a given area will be proportional to the abundance of fish in that area, providing self-weighted estimates of the parameters. Equal subsample sizes are attempted, but as this is not always attained in practice, the station parameter values are weighted by subsample size on the premise that departures from the target subsample size represent errors in judgment sampling. This argument depends on the method of trawling adopted in the surveys described by Picquelle and Stauffer (1985), in which a midwater trawl with a large mouth opening is towed at a constant depth for a fixed period at locations where anchovy are indicated by sonar targets or eggs in the plankton (P. E. Smith, Southwest Fisheries Center, pers. comm.)

This method of station weighting was considered inappropriate for the surveys described here because the trawling operation was varied on the basis of the net-sonde or vertical echo-sounder record to ensure an adequate sample size, and because the ratio of number of samples to the abundance of females (as estimated from acoustics and values of sex ratio and female mass from midwater trawl samples) was found to be up to four times greater in strata with low female abundance than in strata with high female abundance. This was partly a consequence of the requirement for regular identification of acoustic targets. Further, the adoption of transects as sampling units meant that the individual station values of spawning parameters were obtained as weighted means of the station values (as described below), and transect weighting factors that would allow unbiased estimation of stratum means and variances of the parameters were then derived.

The most appropriate weighting factors were the anchovy density estimates obtained from vertical echo integration. Surface schooling was rarely encountered during the spawning stock surveys to an extent sufficient to bias the density estimates, and tended to be more a feature of the eastern Agulhas Bank, where the fish and egg densities were both generally low. The thermocline was comparatively shallow in this region (Largier and Swart 1987), resulting in a greater proportion of the fish occupying the near-surface region of the upper mixed layer. This problem was partially corrected for by discarding acoustic density estimates from intervals during which schools were frequently detected on the side-directed sonar but not recorded by the vertical echo sounder. Errors in the target strength expression were considered to be unimportant in the derivation of weighting factors, because only relative values of fish density were required.

Transect values $\hat{W}_{ij}$, $\hat{R}_{ij}$, and $\hat{S}_{ij}$ were derived by linking each acoustic interval (the section of transect surveyed between egg stations) with the trawl samples that were considered to provide a reliable identification of the acoustic targets. Each trawl sample was therefore allocated to a segment of transect for which a "biomass" value was calculated as the sum of the products of the interval lengths and the mean fish densities for the intervals, as determined acoustically. These values were used as weighting factors w_{ijk} for the station values $\hat{R}_{ijk}$, but were multiplied by the ratio $\hat{R}_{ijk}/\hat{W}_{ijk}$ to give weighting factors in terms of female numbers for the parameters $\hat{W}_{ijk}$ and $\hat{S}_{ijk}$. The station parameters were averaged, incorporating these weighting factors, to give the transect values $\hat{\hat{W}}_{ij}$, $\hat{\hat{R}}_{ij}$, and $\hat{\hat{S}}_{ij}$.

Stratum values of the spawning parameters were obtained by averaging over transects with weights $w_{ij} = L_{ij}\,\hat{\bar{d}}_{ij}$ for sex ratio and $w_{ij} = L_{ij}\,\hat{\bar{d}}_{ij} \cdot \hat{\hat{R}}_{ij}/\hat{\hat{W}}_{ij}$ for the other parameters, L_{ij} and $\hat{\bar{d}}_{ij}$ being the length of transect j and the mean anchovy density (g m^{-2}) for transect j, respectively, as determined during the acoustic survey.

Thus for a given trawl parameter $\hat{\hat{\mu}}$:

$$\bar{\mu}_i = \frac{\Sigma_j\, w_{ij}\, \hat{\hat{\mu}}_{ij}}{\Sigma_j w_{ij}} \qquad (\hat{\hat{\mu}}_{ij} = \hat{\hat{W}}_{ij}, \hat{\hat{R}}_{ij}, \hat{\hat{S}}_{ij}) \tag{12}$$

where w_{ij} is the weighting factor for a transect parameter value $\hat{\hat{\mu}}_{ij}$.

Variances were estimated as:

$$V(\hat{\hat{\mu}}_i) = \frac{\frac{n_i}{n_i - 1} \Sigma_j\, w^2_{ij}\, (\hat{\hat{\mu}}_{ij} - \hat{\hat{\mu}}_i)^2}{(\Sigma_j\, w_{ij})^2} \tag{13}$$

where n_i = number of transects in stratum i.

Finally, the stratum values $\hat{\bar{R}}_i$ were averaged with weights w_i equal to the acoustically derived biomasses $A_i\,\bar{d}_i$ (where A_i is the stratum area and $\hat{\bar{d}}_i$ is the stratum mean density), and stratum values $\bar{W}_i$ and $\bar{S}_i$ were averaged with weights equivalent to female numbers ($A_i\,\hat{\bar{d}}_i\,\hat{\bar{R}}_i/\hat{\bar{W}}_i$). The variances were then computed as weighted means over strata:

$$\hat{\bar{\mu}} = \frac{\Sigma_i w_i\, \hat{\hat{\mu}}_i}{\Sigma_i w_i} \qquad (\hat{\hat{\mu}}_i = \hat{\hat{W}}_i, \hat{\hat{R}}_i, \hat{\hat{S}}_i) \tag{14}$$

$$V(\hat{\bar{\mu}}) = \frac{\Sigma_i\, w^2_i\, V(\hat{\hat{\mu}}_i)}{(\Sigma_i\, w_i)^2} \tag{15}$$

The relationship between batch fecundity and female mass was described by a linear regression, allowing the overall mean batch fecundity to be predicted at this stage from the value $\hat{\bar{W}}$. The independent variable in the regression was ovary-free preserved mass. The estimate of mean weight was divided by the factor 1.0224 to adjust for a predicted 2.7% increase in mass after 60 days in 10% Formalin (Hunter 1985) and for the removal of the ovaries, which prior to hydration were determined to weigh on average 5% of the ovary-free live mass in the most abundant size classes of females.

To facilitate variance computations in the present situation, in which batch fecundity was a linear function of female mass, a variable $\hat{Q}$ was defined as the ratio $\hat{\bar{W}}/\hat{F}$. The variance of $\hat{Q}$ arising from sampling error in the estimation of $\hat{\bar{W}}$ was estimated as:

$$V_o(\hat{Q}) = \left[\frac{1 - b\,\hat{Q}}{\hat{F}}\right]^2 V(\hat{\bar{W}}) \tag{16}$$

where b was the slope of the batch fecundity regression. Equation 16 is a shorthand method for obtaining the variance of the ratio $\hat{\bar{W}}/\hat{F}$ when $\hat{F}$ is a linear function of $\hat{\bar{W}}$. (Expansion of the bracketed term with $\hat{Q}$ replaced by $\hat{\bar{W}}/\hat{F}$, and multiplication through by $V(\hat{\bar{W}})$, retrieves the separate expressions for the variances and covariances of $\hat{\bar{W}}$ and $\hat{F}$.) The total variance of $\hat{Q}$ was estimated by including the component of variance arising from estimation error in the fecundity-mass relationship:

$$\frac{V(\hat{Q})}{\hat{Q}^2} = \frac{V_o(\hat{Q})}{\hat{Q}^2} + \frac{1}{\hat{F}^2}\left[\frac{S^2_{FW}}{n_{FW}} + S^2_b\,(\hat{\bar{W}} - \bar{W}')^2\right] \tag{17}$$

where S^2_{FW} = the residual sums of squares of the regression,
S^2_b = the variance of the slope b,
n_{FW} = the number of observations in the regression,
$\hat{\bar{W}}$ = the adjusted estimate of mean female mass in the population, and
$\bar{W}'$ = the mean ovary-free mass of preserved females in the regression.

Combination of Strata

If a stratum has fewer than about eight sampled transects, the estimates of variance for that stratum will tend to be unreliable. Since most sampling effort should be concentrated in the higher-density strata, small numbers of transects will usually occur in low-density strata, particularly when the absence of targets or rough sea conditions result in no trawl samples being taken to estimate spawning parameters on some transects. Rather than obtain estimates of parameters that are highly variable and have unreliable variance estimates, it is advisable to group these strata so as to have about ten or more transects in each group. Average parameters and variances are then estimated for each group. The advantage of stratification is retained in full, the variances of the estimated mean parameter values being based on within-stratum variation.

The principle is described in Cochran (1977), where the resulting estimates are called "combined" in contrast to "separate" estimates for each stratum. An adaptation of Cochran's method suitable for egg production survey parameters is described in Appendix 2. A number of low-density strata were combined in this manner during the 1985 and 1986 surveys, as indicated on Figures 2 and 3.

Covariance Estimation

An advantage of working with transect-based values of parameters is that the covariances between all parameters can be easily worked out. For two parameters $\hat{\mu}(1)_i$ and $\hat{\mu}(2)_i$ estimated for stratum i, in which the transect weighting factors are $w(1)_{ij}$ and $w(2)_{ij}$, the covariance for stratum i is given by:

$$\mathrm{COV}\,(\hat{\mu}(1)_i\, \hat{\mu}(2)_i) = \frac{\frac{n_i}{n_i - 1}\sum_j w(1)_{ij}\, w(2)_{ij}\, (\hat{\mu}(1)_{ij} - \hat{\mu}(1)_i)\,(\hat{\mu}(2)_{ij} - \hat{\mu}(2)_i)}{\Sigma_j w(1)_{ij}\, \Sigma_j w(2)_{ij}} \quad (18)$$

Covariances were determined for the parameters $\hat{P}_{oi}$, $\hat{W}_i$, $\hat{R}_i$, and $\hat{S}_i$ in each stratum.

Using the same notation as above, the overall covariance values are derived as weighted averages over strata:

$$\mathrm{COV}(\mu(1)\, \mu(2)) = \frac{\Sigma_i\, w(1)_i\, w(2)_i\, \mathrm{COV}\,(\hat{\mu}(1)_i\, \hat{\mu}(2)_i)}{\Sigma_i\, w(1)_i\, \Sigma_i\, w(2)_i} \quad (19)$$

Covariance estimates involving $\hat{W}$ were then adjusted to give the corresponding covariances involving $\hat{Q}$ (the ratio estimate $\hat{W}/\hat{F}$) by multiplying by the factor $(1 - b\hat{Q})/\hat{F}$. The final covariances were accordingly those involving the parameters $\hat{P}_o$, $\hat{R}$, $\hat{S}$, and $\hat{Q}$ (see equations 2 and 3).

RESULTS

Distribution Patterns

The egg distribution patterns were very similar during the three surveys, with the bulk of the

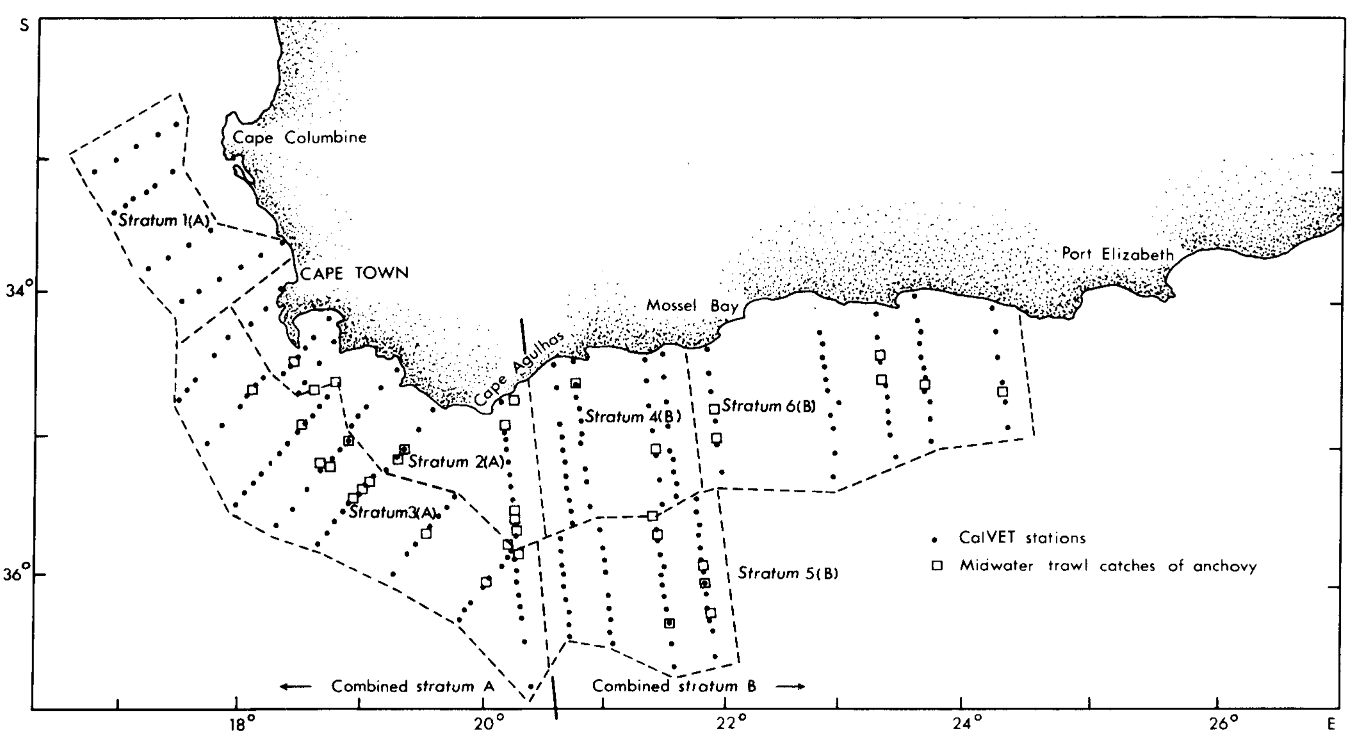

Figure 2. Position of egg stations and midwater trawl catches of anchovy in November 1985. The boundaries of six predefined strata are indicated; the original strata 1–3 and 4–6 were subsequently combined to form the redefined strata A and B for analysis.

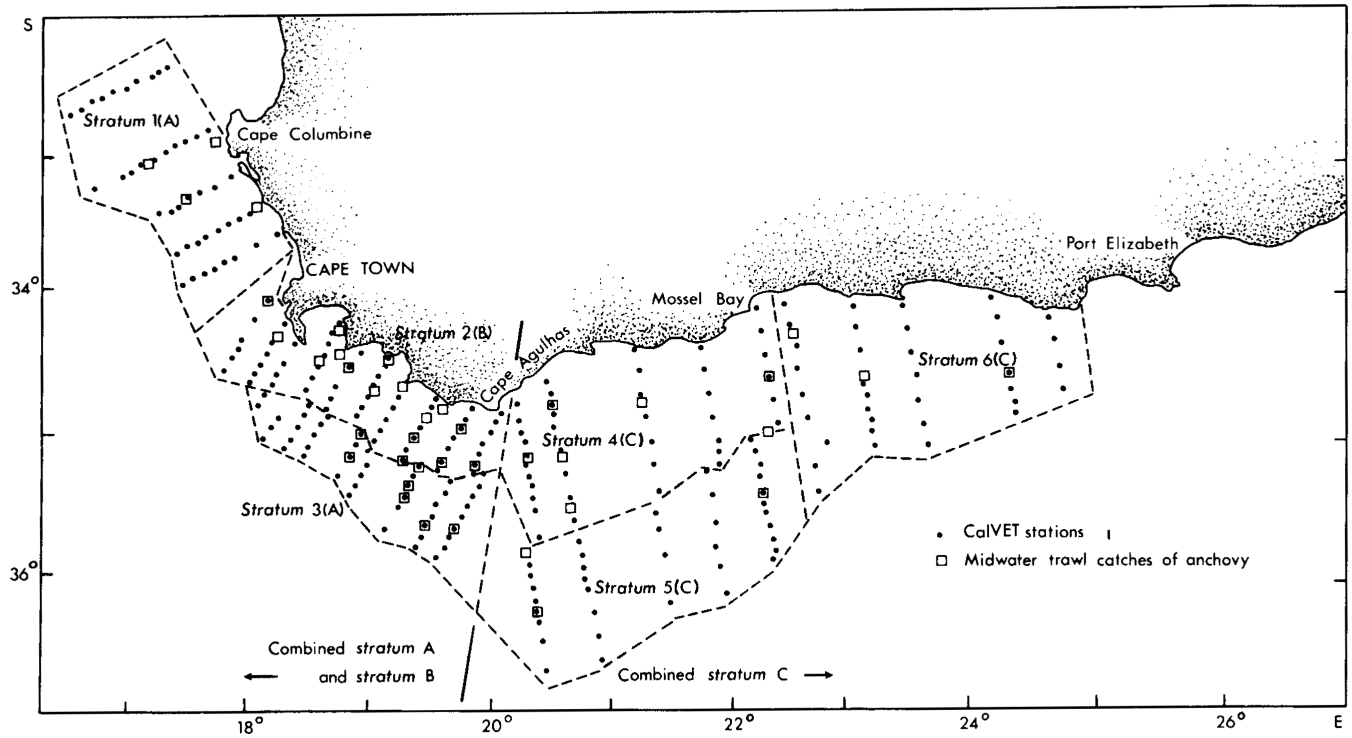

Figure 3. Position of egg stations and midwater trawl catches of anchovy in November 1986. The boundaries of six predefined strata are indicated; strata 1 and 3 and 4–6 were subsequently combined to form the redefined strata A and C for analysis.

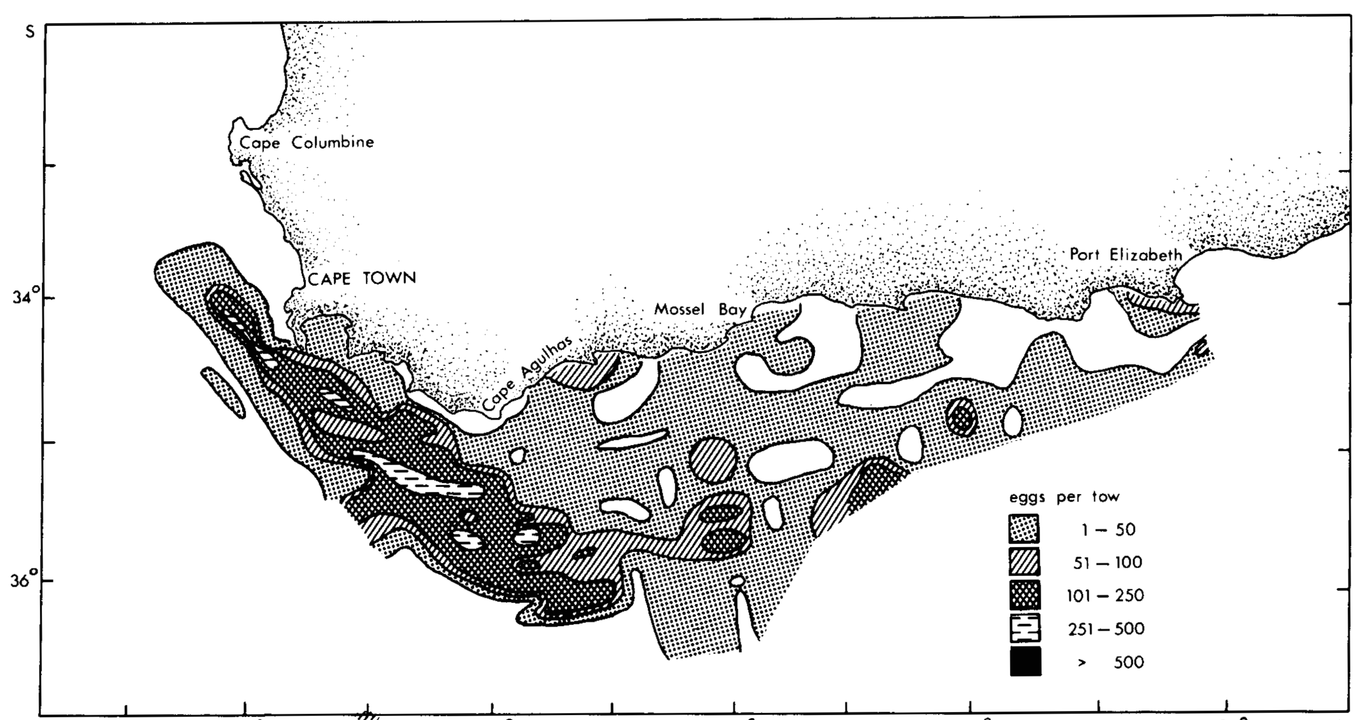

Figure 4. Anchovy egg distribution in 1984.

spawning occurring offshore over the western Agulhas Bank (Figures 4–6). There was evidence of advection of eggs around Cape Point and northwards along the west coast, supporting the hypothesis of Shelton and Hutchings (1982) that fast currents associated with the upwelling and shelf-

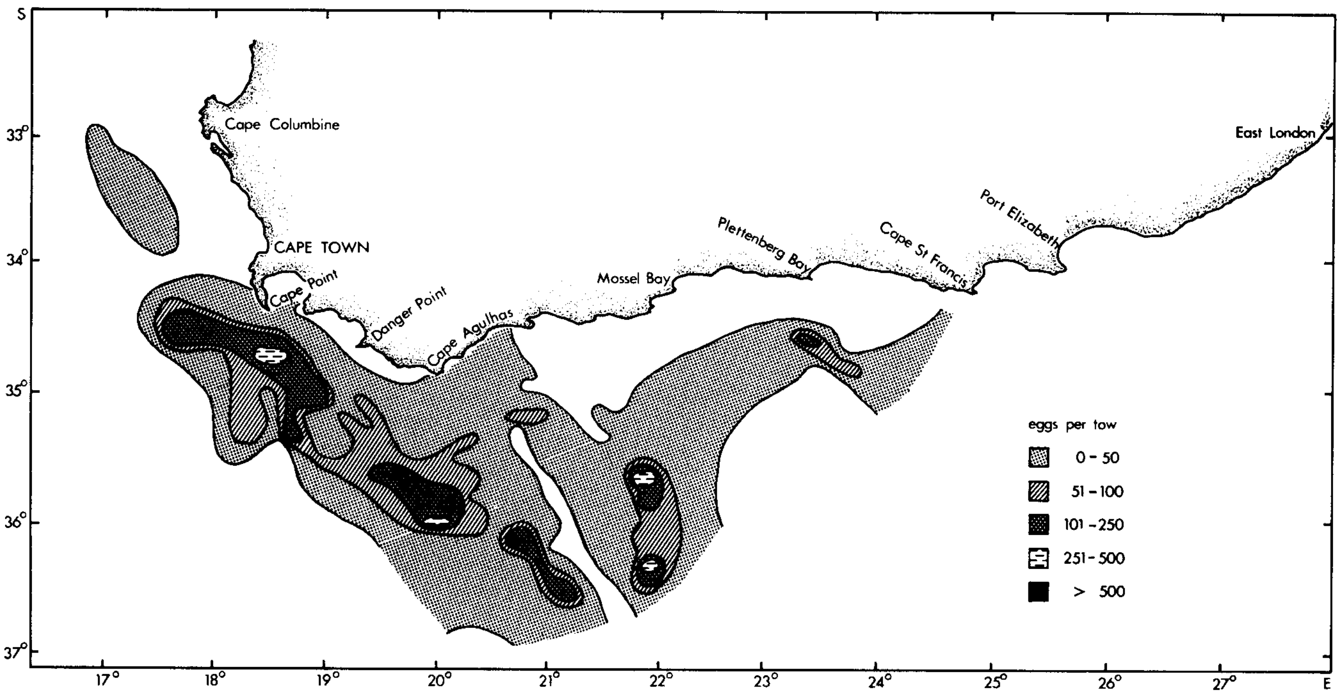

Figure 5. Anchovy egg distribution in 1985.

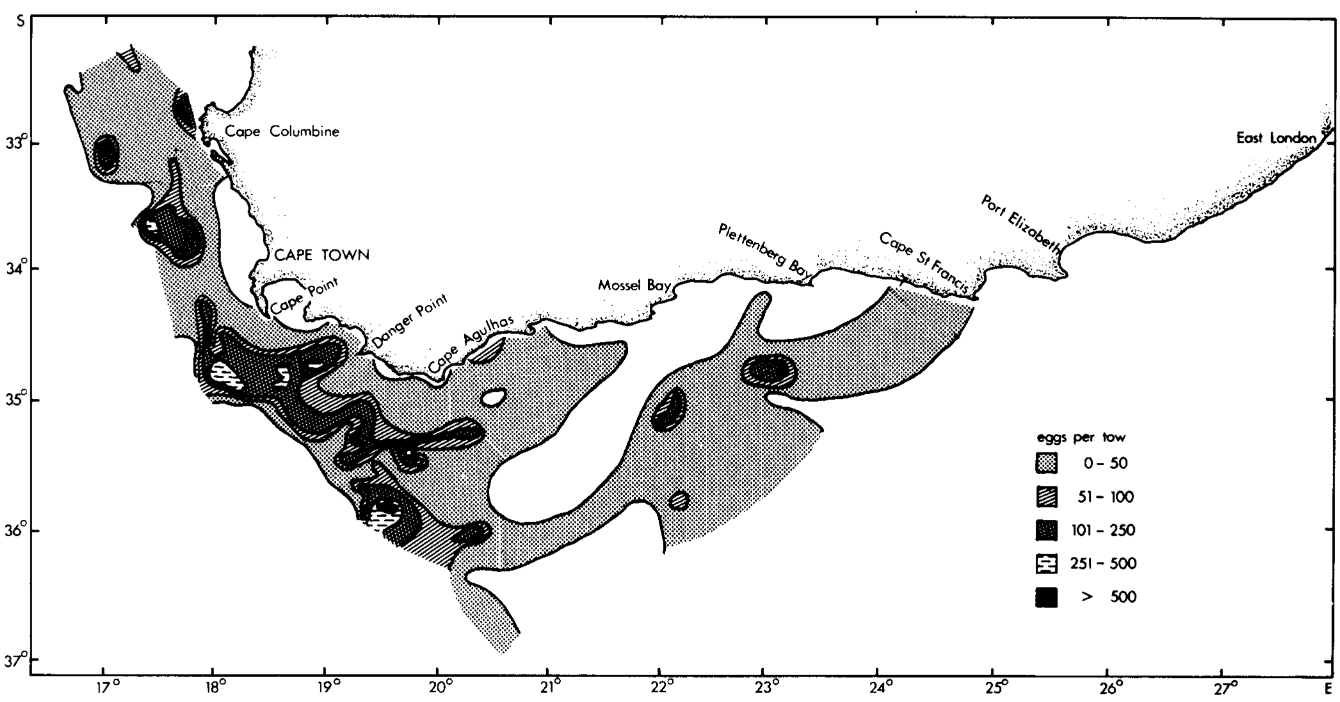

Figure 6. Anchovy egg distribution in 1986.

edge fronts are important for the rapid transport of eggs and larvae toward the west coast nursery areas. There was evidence, however, that spawning in 1986 was also taking place to the north of Cape Point. A remarkable feature of the three surveys was that the areas of the positive egg strata remained roughly constant at 106,000 to 110,000 km^2. Surface temperatures over the spawning area were fairly uniform at 17°–19°C (Figures 7–9), with the great majority of positive egg stations occurring within these temperature limits.

In 1984 and 1985, the fish distribution patterns

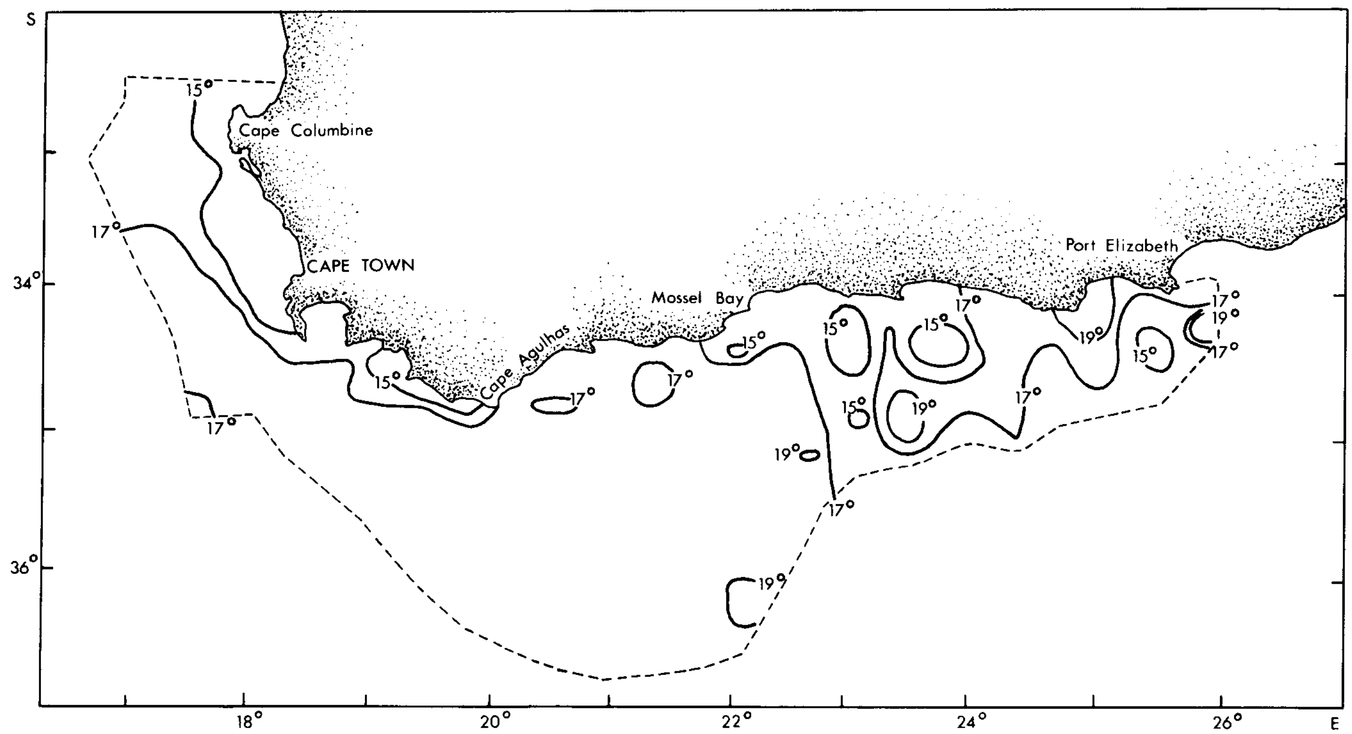

Figure 7. Temperature isotherms at 5-m depth, November 1984.

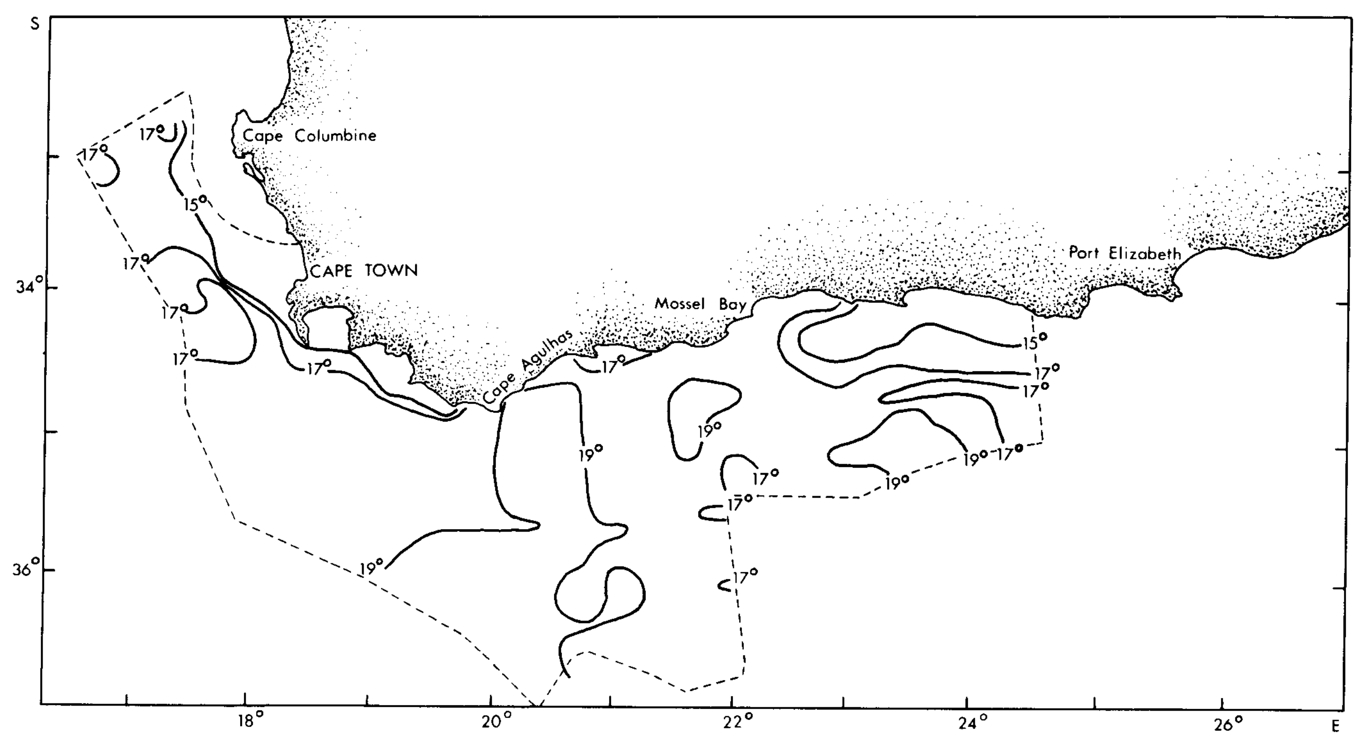

Figure 8. Temperature isotherms at 5-m depth, November 1985.

determined from the acoustic surveys were very similar to the egg distributions, although there was a tendency for the area of high egg density over the western Agulhas Bank to occur slightly offshore of the region of high fish density (Figures 10 and 11). The situation in 1986 was different in that high concentrations of young adult anchovy occurred close to the coastline along the south coast, with shoals

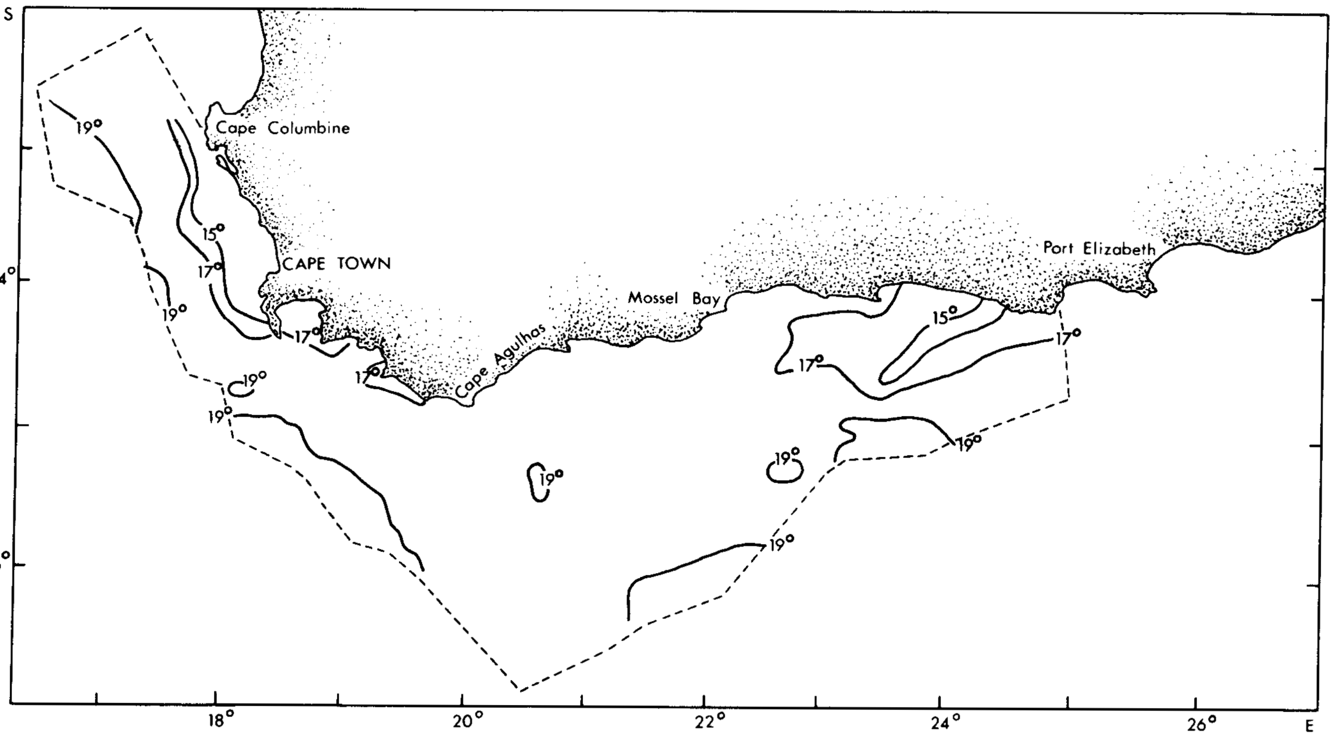

Figure 9. Temperature isotherms at 5-m depth, November 1986.

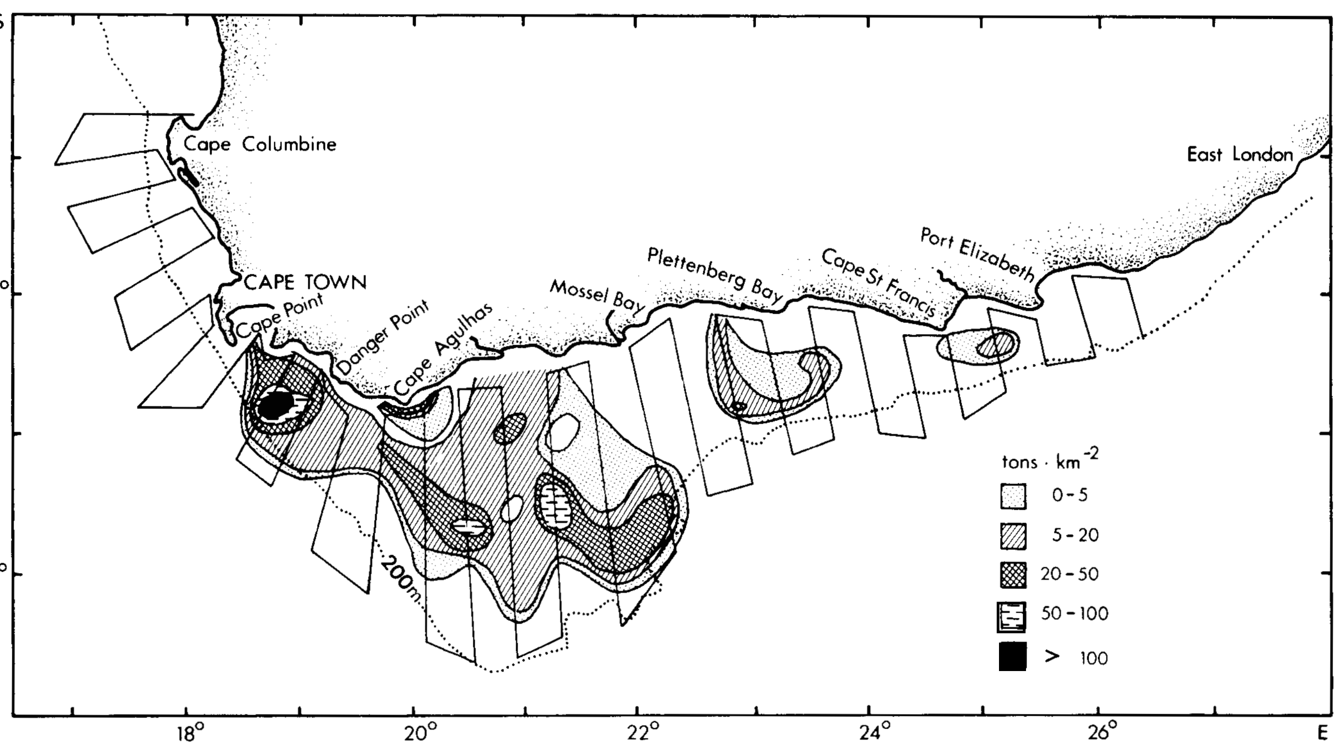

Figure 10. Anchovy density distribution in November 1984, as determined from acoustic data (after Hampton 1987).

also being distributed along the west coast between Cape Point and Cape Columbine (Figure 12). A comparison between the weighted length frequencies of anchovy in the three years (obtained by weighting the sample length frequencies by the same general procedure described for the spawn-

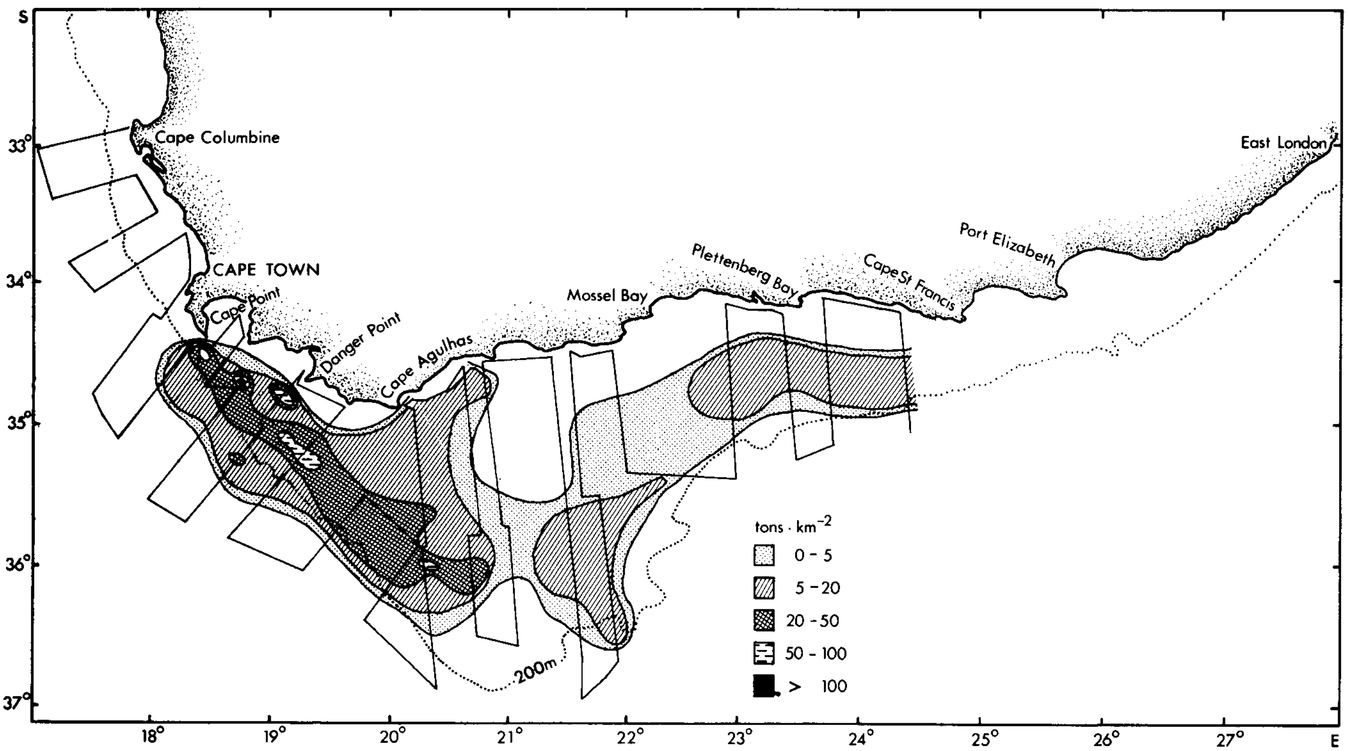

Figure 11. Anchovy density distribution in November 1985, as determined from acoustic data (after Hampton 1987).

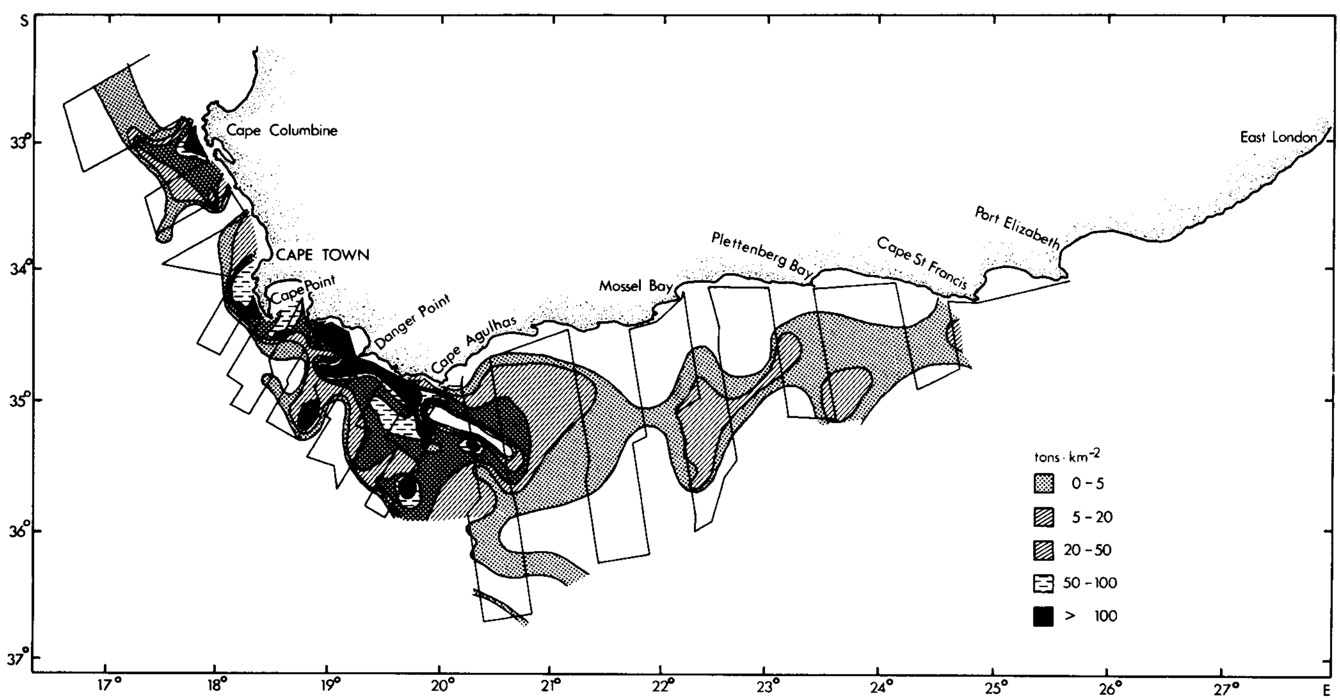

Figure 12. Anchovy density distribution in November 1986, as determined from acoustic data.

ing parameters) shows the presence of these smaller fish in much greater numbers in 1986 than in the previous years (Figure 13).

A consistent tendency for a zone of low egg and fish density to separate areas of spawning over the western and eastern regions of the Agulhas Bank, and for two-year-old and older anchovies to be found mainly in the eastern area provided a clear

TABLE 3
Estimates of Hourly Instantaneous Mortality Rate (Z) of Anchovy Eggs

Year	Z (h^{-1})	Variance	95% confidence limits	
1984	0.0010	8.39×10^{-5}	−0.0170	0.0190
1985	0.0093	3.00×10^{-5}	−0.0014	0.0200
1986	0.0115	6.96×10^{-5}	−0.0049	0.0279

basis for stratification of the survey grid. The systematic grid in 1984 was stratified *post hoc* on this basis, whereas in 1985 and 1986 the surveys were stratified at the design stage, as described earlier. It was subsequently found that some of the strata in 1985 and 1986 contained insufficient transects for reliable variance estimates to be obtained, and strata were combined as described in Appendix 2 (Figures 2 and 3).

Parameter and Variance Estimates

Estimates of hourly egg mortality rate Z and the variances of these estimates in each year are given in Table 3, and the regressions of *Ln* (abundance at age) against age are shown in Figure 14. The 95% confidence intervals were very wide, encompassing zero mortality in each year. The 1985 estimate exhibited the smallest variance, but it was clear that the intensity of sampling, or the method of estimating Z, was, in most years, inadequate for reliable estimation of the average hourly mortality rate.

The daily egg production for the various strata in each year is given in Table 4, and shows the greater amount of spawning over the western region of the Agulhas Bank. Weighted mean $\hat{P}_o$ values for each survey are given in Table 5. Total daily egg production was lowest in 1985, but also had the lowest variance of the values from the three surveys. The variances of $\hat{P}_o$ in 1984 and 1986 were inflated by imprecise estimates of Z, but a substantial decline in the between-transect normalised variance of $\hat{P}_o$ from 0.032 in 1984 to 0.012 in 1986 was evident. This may, to a large extent, reflect improvements in survey design and the increase in sampling effort in the high-density strata in 1986.

The spawning parameters of mean female mass, batch fecundity, sex ratio, and spawning fraction are given for separate strata in Table 4, and as weighted means for the entire survey areas in Table 5. Spawning fraction values based on histological examination of ovaries were not available for 1984. The mean female mass was 2–3 g lower in 1986 than in 1984 or 1985, because of the abundance of small fish of 8–10 cm Lc inshore in stratum B in 1986.

The spawning fraction in 1985 was estimated to be nearly 20% of the female population, nearly

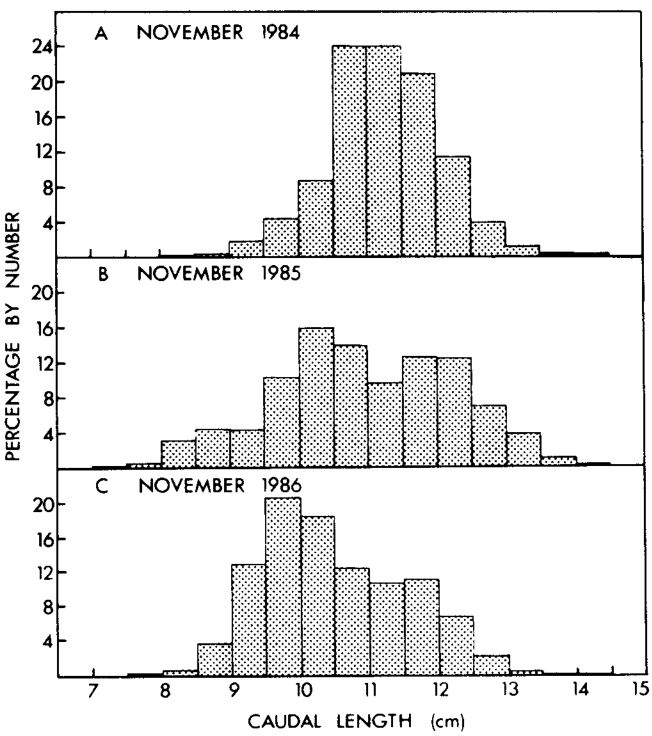

Figure 13. Weighted population length frequencies for the anchovy stocks surveyed in November 1984, 1985, and 1986.

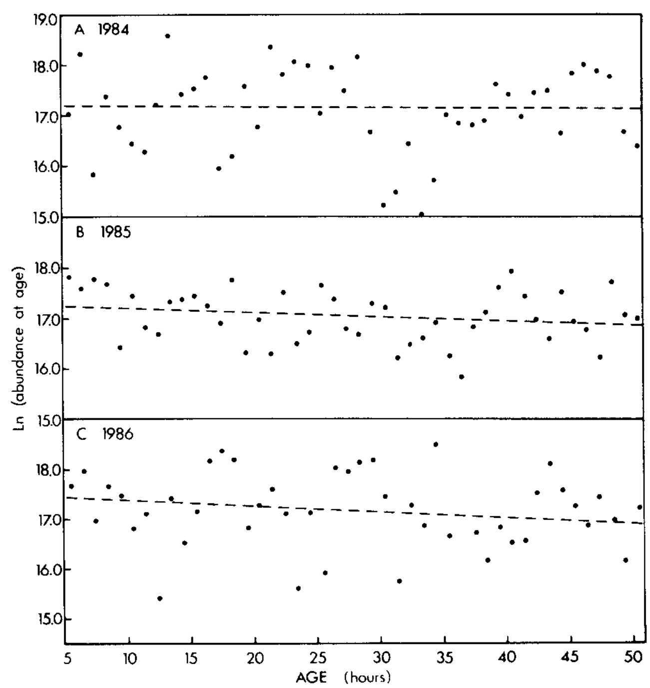

Figure 14. Egg mortality curves for anchovy in November 1984, 1985, and 1986. (See Table 3 for mortality parameters.)

TABLE 4
Estimates of Parameters and Coefficients of Variation for Separate Strata

	Stratum i					
	A		B		C	
Parameter $\hat{\mu}_i$	Mean	CV	Mean	CV	Mean	CV
November 1984*						
$\hat{P}_{o_i}$ (eggs $d^{-1}m^{-2}$)	511	0.20†	133	0.35†	—	—
$\hat{W}_i$ (g)	14.95	0.03	17.94	0.02	—	—
$\hat{F}_i$ (eggs $female^{-1}$)	7,820		10,032			
$\hat{R}_i$	0.509	0.05	0.493	0.35	—	—
Area (km^2)	72,223		34,103			
Biomass from acoustics (kt)	903		68			
November 1985						
$\hat{P}_{o_i}$ (eggs $d^{-1}m^{-2}$)	392	0.15†	256	0.30†	—	—
$\hat{W}_i$ (g)	13.68	0.06	15.89	0.13	—	—
$\hat{F}_i$ (eggs $female^{-1}$)	7,510		9,548			
$\hat{R}_i$	0.485	0.06	0.469	0.13	—	—
$\hat{S}_i$ (day^{-1})	0.181	0.40	0.205	0.30	—	—
Area (km^2)	55,133		51,575			
Biomass from acoustics (kt)	717		264			
November 1986						
$\hat{P}_{o_i}$ (eggs $d^{-1}m^{-2}$)	1,082	0.15†	884	0.17†	155	0.30†
$\hat{W}_i$ (g)	13.53	0.06	10.51	0.03	12.85	0.11
$\hat{F}_i$ (eggs $female^{-1}$)	7,026		4,714		6,506	
$\hat{R}_i$	0.573	0.03	0.528	0.04	0.583	0.03
$\hat{S}_i$ (day^{-1})	0.101	0.50	0.108	0.27	0.064	0.52
Area (km^2)	28,568		13,777		67,496	
Biomass from acoustics (kt)	369		842		425	

*No histologically derived estimate of $\hat{S}$ is available in this year.
†Between-transect variation only.

double the value obtained in 1986. The variance of the spawning fraction was, however, very high in 1985, and was the dominant source of uncertainty in the 1985 EPM biomass estimate (Table 5). The estimates of spawning fraction for the combined strata A and B in 1985 were very similar (Table 4).

TABLE 5
Estimates of Mean Spawning Parameter Values and Normalized Variances and Covariances

	Year					
	1984		1985		1986	
Parameter $\hat{\mu}$	Mean	Variance $\hat{\mu}^2 \times 10^{-3}$	Mean	Variance $\hat{\mu} \times 10^{-3}$	Mean	Variance $\hat{\mu} \times 10^{-3}$
$\hat{P}_o$ (eggs $d^{-1}m^{-2}$)	389.4	97.0	326.5	41.1	487.6	62.4
$\hat{W}$ (g)	15.12	—	14.20	—	11.70	—
$\hat{F}$ (eggs)	7,953	—	7,991	—	5,627	—
$\hat{Q}$ ($=\hat{W}/\hat{F}$)	—	1.5	—	2.8	—	3.0
$\hat{R}$	0.508	2.8	0.481	3.1	0.553	0.4
$\hat{S}$ (day^{-1})	—	—	0.186	95.9	0.095	45.9
2 Σ covariances	—	6.7		19.2		8.4
Area (km^2)	106,326	—	106,708	—	109,841	—
EPM biomass estimate (kt)[a]	—	—	614	162.1 (CV = 0.41)	2,006	120.0 (CV = 0.35)
Biomass from acoustics (kt)[b]	1,067	(CV = 0.23)	975	(CV = 0.16)	1,747	(CV = 0.14)

[a]Adjusted for small sample bias.
[b]Final estimates, adjusted for fish inshore of the survey grid (Hampton 1987).

TABLE 6
Estimated Parameters of Regressions of Batch Fecundity against Ovary-Free Preserved Fish Mass ($F = a W + b$)

Year	a	b	S^2_{FW}	S^2_b	$\bar{W}'(g)$	N_{FW}
1984	759.31	−3295.0	4.156×10^6	7581.7	15.909	53
1985	942.60	−5102.0	6.373×10^6	3722.7	16.686	80
1986	782.79	−3332.9	4.744×10^6	3973.3	13.684	81

Between-stratum variations were also relatively small in 1986, despite the increased occurrence of young adult fish in the inshore strata.

The relationships between batch fecundity and ovary-free mass of preserved females were very similar in the three years (Figure 15; Table 6). The variance components of the regressions and the between-transect variation in $\bar{W}$ made a relatively minor contribution to the final variance of the biomass estimate (Table 5).

The sex ratio $\hat{R}$ was close to 0.5 in each survey, and although the coefficient of variation of the estimates was relatively small, much of the variation was attributable to the anomalous values obtained in some catches taken during the evening spawning period.

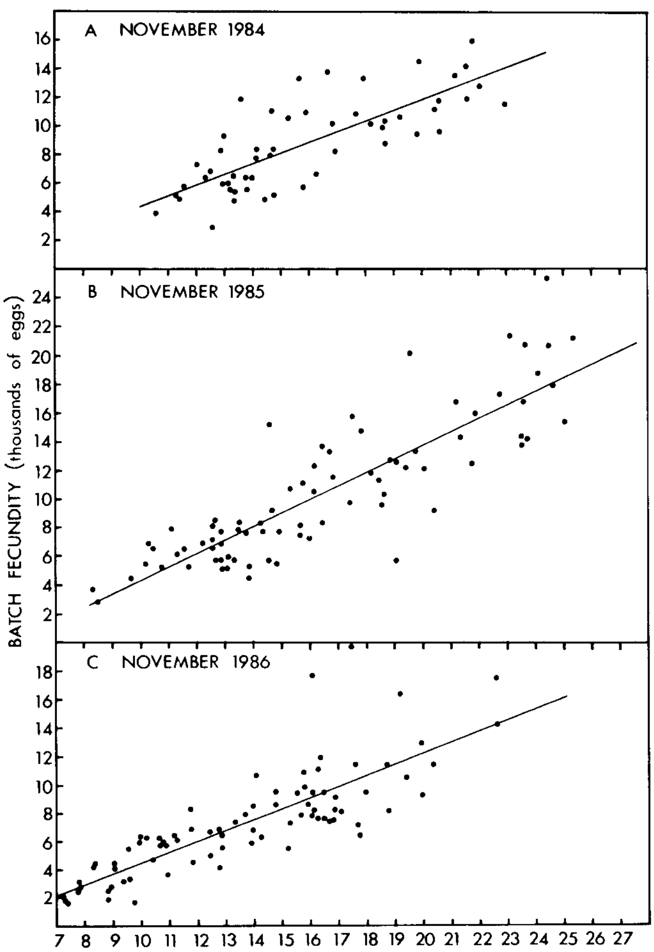

Figure 15. Regressions of batch fecundity against ovary-free mass of preserved female anchovy in November 1984, 1985, and 1986. (See Table 6 for regression parameters.)

The estimates of biomass and coefficient of variation (CV) in 1985 and 1986 are given in Table 5. A 50% increase in total daily egg production between 1985 and 1986, and a reduction in the estimated spawning fraction in 1986 compared to 1985, implied a trebling of the biomass from approximately 0.6 to 2.0 million tons. In comparison, the estimate from acoustics of 1.7 million tons in 1986 was only 80% greater than the corresponding estimate in 1985. The CV's of the EPM estimates were, however, relatively high at 0.35 to 0.41, and consequently the biomass estimates from the two methods are unlikely to differ significantly each year. Poor precision of the spawning fraction estimate in 1985 was largely responsible for the high CV in that year (Table 5).

The spawning biomass in 1984 can be only roughly estimated by assuming a range of possible spawning fraction values. A comparison of the occurrence of hydrated female anchovy (determined macroscopically) in the three surveys indicated that the incidence of such females in 1984 was intermediate between the incidences in trawl samples taken in 1985 and 1986. Thus by taking the 1985 and 1986 spawning fraction estimates as bounding the range of possible 1984 estimates, a range of 1984 biomass estimates of 0.8 to 1.5 million tons is obtained, with an average of 1.2 million tons. In comparison, the 1984 estimate from acoustics was 1.1 million tons. It should be noted that the relatively low CV estimates for the acoustic survey results reflect only the sampling error, and do not include the variance associated with the target strength expression (Hampton 1987).

The differences between the results obtained by adopting the transect rather than the individual trawl stations as the sampling unit, and by incorporating acoustic data to weight the sample means, are shown in Table 7. In both 1985 and 1986, the mean female mass was greater when the values from individual trawl stations were weighted only by sample size. This was caused by oversampling of the low-density strata on the eastern Agulhas Bank, where most of the two-year-old and older

TABLE 7
Estimates of Means and Coefficients of Variation of Spawning Parameters Obtained from (A) the Transect Method with Acoustic Weightings and (B) Averaging Individual Station Values with Weights Proportional to Subsample Size

	1985				1986			
	A		B		A		B	
Parameter	Mean	CV	Mean	CV	Mean	CV	Mean	CV
$\hat{\bar{W}}$ (g)	14.20	0.05	16.09	0.05	11.70	0.04	12.67	0.05
$\hat{\bar{R}}$	0.48	0.06	0.48	0.07	0.55	0.02	0.58	0.03
$\hat{\bar{S}}$ (day^{-1})	0.19	0.31	0.15	0.14	0.10	0.21	0.12	0.20

anchovy were encountered, and resulted in a 5% to 8% increase in the estimated batch fecundity per unit female mass. Sex ratio and spawning fraction were not significantly correlated with female mass, and were not consistently affected by the weighting procedure. The CV's of the mean female mass and sex ratio were very similar between the two methods, whereas the CV of the spawning fraction tended to increase when acoustic weightings were applied. Although the two methods did not produce substantially different results in 1985 and 1986, the acoustically weighted estimates are less likely to be biased in situations where the fish density and spawning parameters are correlated.

DISCUSSION

The egg production method has proved to be a valuable, if labor-intensive, method for obtaining biomass estimates each year for the southern Benguela anchovy stock, in addition to the estimates obtained from acoustic surveys. The major sources of uncertainty in the egg production biomass estimates have been associated with the estimation of egg mortality rate Z and spawning fraction $\bar{S}$, which together accounted for more than 80% of the sum of the squared CV's of the egg production survey parameters in 1985 and 1986. Improvements in the survey design involving stratification and intensification of survey effort in areas where high densities of fish were expected were implemented in order to minimize sampling error, but it is clear that the ±300 CalVET stations have been insufficient for acceptable precision in estimating egg mortality by the regression procedure adopted each year.

Although an increase in the number of egg stations through additional transects would be expected to reduce the estimate of variance, there may be more appropriate methods of estimating Z than by incorporating all values of egg abundance and age into a single regression. This is particularly the case if egg mortality varies nonrandomly between stations and transects. Recent studies of egg cannibalism in the southern Benguela anchovy stock have provided evidence of density-dependent cannibalism rates (Valdes et al. 1987), and such a mechanism could be expected to cause patchy variations in egg mortality rate related to the density-distribution of spawning adults, their daily specific fecundity, and the local abundance of other food items.

A bias in the estimation of daily egg production may occur if processes such as cannibalism on newly spawned eggs invalidate the assumption of constant egg mortality rate between spawning and hatching. The study of Valdes et al. (1987) showed that within an area of intense spawning where sampling took place, eggs were most frequently encountered in anchovy stomachs during the evening spawning period. Although these eggs could not be staged, the possibility remains that dense aggregates of newly spawned eggs may elicit a feeding response, particularly in the areas of intense spawning. The mortality on these eggs may therefore be higher than on the eggs of age 5 to 50 h, which are represented in the egg mortality regression, resulting in an underestimate of abundance at the time of spawning for certain batches of eggs sampled. It would be necessary to stage the eggs in the stomachs of predators to adequately address this problem.

Improved estimates of spawning fraction and daily egg production would primarily result from increased sampling effort in the high-density strata. In 1986 the sampling effort in terms of the density of transects was about twice as great in the high-density strata as in the low-density strata. However, to reduce the CV of the spawning biomass from 35% to 20% would require at least a further doubling of the overall survey effort by increasing the density of sample transects. Weighed against this reduction in estimated variance would be a substantial slowing down of the survey vessel across the spawning grounds, with a resultant danger of temporal trends in spawning intensity introducing a further component of variation into the final estimate. An additional consideration at present is that the biomass estimates are required for input into management procedures three months after completion of the survey in November. Any substantial increase in survey effort would therefore be limited by the time required to process the samples. Ultimately, the level of uncertainty in the biomass estimate that is acceptable in a stock assessment context will relate to how much the estimate influences future harvests, and how much the stock is being exploited. Such considerations may be explored through stochastic modeling exercises like those of Armstrong and Butterworth (1986) and Bergh and Butterworth (1987).

Hampton et al. (in press) demonstrate that using acoustic information to weight the spawning parameters imposes no additional covariance between the biomass estimates obtained from the two methods, and that the covariance between the egg and acoustic estimates in both 1985 and 1986 was low. The two estimates can therefore be treated as independent, and the similarity between them gives some confidence in the target-strength expression adopted for the acoustic survey. However, until the target strength of *Engraulis capensis* is determined by a reliable method, and its contribution to the error quantified, the acoustic estimates must be regarded as having a potentially large and unknown bias, precluding the direct combination of the acoustic and egg production estimates. However, a method has been developed (Hampton et al., in press) for combining the results of the two surveys, making use of the ratio of the egg production and acoustic biomass estimates in year i to adjust the acoustic estimate in year $i+1$, providing a less-biased estimate to combine with the egg production estimate of biomass in year $i+1$. An optimum combination is obtained of the acoustic method, which provides estimates with high relative precision but potentially low accuracy, and the egg production method, which is assumed to be accurate but has provided relatively imprecise biomass estimates. Hampton et al. discuss appropriate methods for minimizing the variance of the combined estimate.

ACKNOWLEDGMENTS

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APPENDIX 1
Estimation of *Z* by Linear Least Squares Regression

An efficient estimator of the mean hourly instantaneous egg mortality rate Z is required to allow the station values of egg abundance at age (P_t; equation 5) to be raised to the expected abundance at age zero. In the surveys described in this paper, the abundances of eggs in 1-hour age classes were estimated for separate survey strata and then summed over strata to give total estimated abundance at age. The natural logarithms of the abundance estimates $\hat{P}_t$ were then regressed against age for ages $t = 5$ to 50 h. The estimate of the slope, $\hat{Z}$; the variance around the regression line, S^2_{yt}; and the variance of $\hat{Z}$ were obtained from the following expressions:

$$\hat{Z} = \frac{\Sigma_t\, w_t\,(y_t - \bar{y})(t - \bar{t})}{\Sigma_t\, w_t\,(t - \bar{t})^2} \tag{20}$$

$$S^2_{yt} = \frac{N}{(N-2)\,\Sigma_t w_t}\left[\Sigma_t w_t\,(y_t - \bar{y})^2 - \frac{[\Sigma_t w_t\,(y_t - \bar{y})(t - \bar{t})]^2}{\Sigma_t w_t\,(t - \bar{t})^2}\right] \tag{21}$$

$$V(\hat{Z}) = \frac{S^2_{yt}}{\dfrac{N}{\Sigma_t w_t}\Sigma_t w_t (t - \bar{t})^2} \tag{22}$$

where t = mean age in each one-hour age class,
y_t = Ln ($\hat{P}_t$),
w_t = weighting factor for y_t, and
N = the number of age classes in the regression.

For each 1-hour age class, the natural logarithm of the abundance value was weighted by $n_t \exp(-Z\,t)$, where n_t is the number of egg batches contributing to age class t (including zeros), and t is the age in hours. It can be easily shown that, on the assumption that the abundances of eggs in the nightly batches sampled at each station approximately follow a Poisson distribution, the reciprocal of the variance of Ln(P_t) for a given t is approximately $n_t \exp(-Z\,t)$. The weighting values were iteratively adjusted using successive estimates of Z until convergence was attained, the initial estimate of Z being obtained with weighting by n_t only.

APPENDIX 2
Averaging over Strata with Few Sampled Transects

A method is required for combining strata in which there are too few transects to allow reliable estimates of variances. The method must retain the advantages for minimization of variance afforded by the original stratification. An adaptation of the method given in Cochran (1977, pp. 165–167), suitable for egg production surveys, is provided here.

Let $\hat{\mu}_{ij}$ be the mean value of parameter μ (= P_o,W,R,S) for transect j in stratum i, calculated with appropriate station weighting, and let w_{ij} be the weighting factor for $\hat{\mu}_{ij}$. A new variate is formed as:

$$y_{ij} = w_{ij}\hat{\mu}_{ij} \tag{23}$$

The principle is to replace the separate stratum means, $\hat{\mu}_i$, by an average μ formed by summing the y_{ij} values over transects and strata, with appropriate stratum weighting, and dividing by the corresponding sum of the w_{ij}. Applying this principle to the group of strata to be combined gives a $\hat{\mu}_c$ (c for "combined") identical to that derivable from equations 6 and 8 or 12 and 14.

To estimate the variance of $\hat{\mu}_c$, unweighted stratum means are formed of y_{ij} and w_{ij} as:

$$\bar{y}_i = \frac{1}{n_i}\Sigma_j w_{ij}\hat{\mu}_{ij} \tag{24}$$

$$\bar{G}_i = \frac{1}{n_i}\Sigma_j w_{ij} \tag{25}$$

where n_i is the number of transects in stratum i.

The stratum mean value of the parameter μ is simply the ratio y_i/G_i (equivalent to equations 6 and 12), and the mean value $\hat{\mu}_c$ over the strata to be combined is obtained, as before, from equations 8 and 14. The variance of $\hat{\mu}_c$ is given by:

$$V(\hat{\mu}_c) = \frac{\sum_i \left(\frac{w_i}{\bar{G}_i}\right)^2 \frac{S_i^2}{n_i}}{\left[\sum_i \left(\frac{w_i}{\bar{G}_i}\right)\bar{G}_i\right]^2} \tag{26}$$

$$= \frac{\sum_i \left(\frac{w_i}{\bar{G}_i}\right)^2 \frac{S_i^2}{n_i}}{\left(\sum_i w_i\right)^2}$$

where $S^2_i = S^2_{iy} - 2\hat{\mu}_c S_{iyw} + \hat{\mu}^2_c S^2_{iw}$,

and
$$S^2_{iy} = \frac{1}{n_i - 1}\Sigma_j(y_{ij} - \bar{y}_i)^2 \tag{28}$$

$$S_{iyw} = \frac{1}{n_i - 1}\Sigma_j(y_{ij} - \bar{y}_i)(w_{ij} - \bar{G}_i) \tag{29}$$

$$S^2_{iw} = \frac{1}{n_i - 1}\Sigma_j(w_{ij} - \bar{G}_i)^2 \tag{30}$$

The w_i are the stratum weighting factors for $\hat{\mu}_i$ as defined in Table 2.

The "combined" stratum is treated exactly as an independent single stratum in further computations of means and variances of the egg production parameters. The full benefit of stratification is retained because the variance represents only the variation within strata.