EGG CANNIBALISM BY ANCHOVY IN THE SOUTHERN BENGUELA CURRENT REGION

by

Edy Sylvia Valdes Rodriguez

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Department of Zoology

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TO MY PARENTS MEMORY AND TO DAVID, MY HUSBAND

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ACKNOWLEDGEMENTS

the word processor program.

DECLARATION

This is to declare that this dissertation has not been previously submitted for any degree at any other University. The collection of samples analysed in this thesis were obtained on Sea Fisheries Research Institute (SFRI) R.S. Africana 1984-1985 anchovy spawning cruises by SFRI personnel. Anchovy eggs were sorted from plankton samples, staged and aged by myself in the laboratory. Samples of adult fish were measured, weighed and de-stomached by myself in the laboratory, and I counted the number of anchovy eggs in the stomachs of fish. Additional information from the Cape Egg and Larva Program (CELP), such as supplementary data on eggs sampled on the West Coast and data from incubation experiments carried out on board of R.S. Africana vessel were provided by Mr. P. A. Shelton. The Monte Carlo simulation and the first model for calculating the egg survival-egg production relationship were developed with the help of Dr. M.J. Armstrong. The subsequent models and general quantification of the thesis was made with the help of Dr. M. O. Bergh.

Edy Sylvia Valdes Rodriguez

ABSTRACT

Samples of adult anchovy and plankton were collected on Sea Fisheries Research Institute R.S. Africana 1984-1985 anchovy spawner biomass estimation cruises. A total of 40 sets of anchovy samples of 30 fish each and 40 plankton samples were taken roughly at the same time within an area of intensive spawning over the Agulhas Bank, using an Engels 308 midwater trawl and a CalVET net respectively. Fish samples were frozen in a deep freeze at - 20° C shortly after capture. Plankton samples were stored in formaldehyde solution. Fish were measured (total length), weighed (total and ovary mass) and de-stomached. Weight of the stomach contents were determined and anchovy eggs in the stomach were counted. Anchovy eggs in CalVET net samples were counted and staged. Frequency distributions of densities of eggs in the plankton on the Agulhas Bank and off the West Coast were plotted to compare egg density in the two areas. Approximately 53% of the eggs caught over Agulhas Bank occurred in only 25% of samples, indicating a patchy distribution. A frequency distribution was plotted of abundance of eggs in the stomachs of fish.

Egg patchiness caused a skewed frequency distribution of egg abundance in anchovy stomachs. Feeding time was estimated from an examination of the relationship between weight of stomach contents versus time of day, taking into account time for gut evacuation.

Based upon a developmental stage/temperature/age key, mortality rates of eggs in the sea were calculated, and it was estimated that 44% of anchovy eggs were lost daily. Taking into account estimated rates of egg mortality, egg production, gastric evacuation rate, number of eggs eaten and feeding time, cannibalism was estimated to account for about 62%-70% of the egg mortality. The rate of cannibalism was shown to be consistent with a density-dependent functional response.

1.INTRODUCTION

Anchovy _Engraulis capensis_ (Fig. 1) is currently the main contributor to the South African pelagic fishery. The success of this fishery largely depends on stable recruitment, which in turn is dependent on the consistent production of eggs and the survival of the early reproductive stages. However, clupeoid populations world-wide are notoriously variable Murphy 1977, Blaxter and Hunter 1982, Lasker and MacCall 1983).

The main cause of variability in clupeoid populations is thought to be the effect of environment on the survival of the early stages (Csirke 1979,1980a, MacCall 1980, Parrish 1983, Smith 1985). The environment may also affect the reproductive capacity of adults (Stander and Decker 1969).

In the Californian anchovy, _E. mordax_, density dependence is thought to account for only 10 % of the variability in the survival of the early stages (MacCall 1980). Crawford et al. (1983) have emphasized the predominance of environmental factors in the population variability of _E. capensis_.

Shelton et al. (1985) reported on the effects of short and long period environmental variability on the anchovy population in the Benguela Current system and found that, while short period
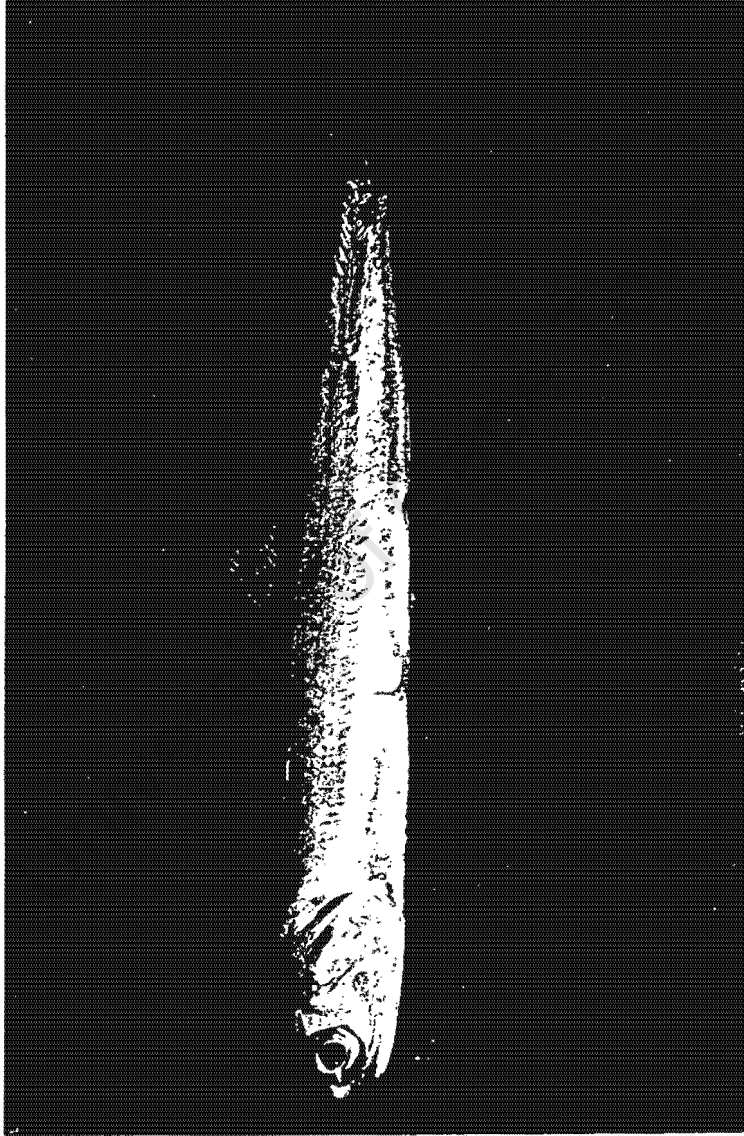
FIG. 1   Anchovy _Engraulis capensis_ (Gilchrist)..

variability was filtered out by the population, it fluctuated in phase with longer period environmental variability. Although density dependence resulting from such processes as cannibalism or competition may be small relative to the effect of the environment, density dependence is the underlying functional response determining optimal yield (Shelton and Armstrong 1983).

Egg cannibalism in clupeoid populations has been noted to occur in various parts of the world by a number of workers: Argentine anchovy, _Engraulis anchoita_ (Ciechomski 1967); Japanese anchovy, _E. japonicus_ (Hayasi 1967) ; Californian anchovy, _E. mordax_ (Loukashkin 1970); Peruvian anchovy, _E. ringens_ (Rojas de Mendiola 1980, Rojas de Mendiola and Ochoa 1973, Rojas de Mendiola et al. 1969). Recently the importance of cannibalism in the mortality of the eggs of _E. mordax_ and _E. ringens_ has been demonstrated by quantitative comparison of daily egg production with estimated rates of egg consumption (Hunter and Kimbrell 1980, MacCall 1980, Santander et al. 1983).

MacCall (1980) considered two mechanisms by which mortality is likely to be dependent on stock density: cannibalism by the parents on their own progeny, and food limitation. Anchovy eggs and yolk sac larvae would only be subject to cannibalism (MacCall 1980) or predation (Brownell 1983, Lasker 1985) by other components of the biota. However, after yolk sac absorption, competition for food and predation may play an important role. Hjort's (1926)

original hypothesis that the mortality of first-feeding larvae might be strongly influenced by the amount and kind of food available, has been supported by a number of scientists (Lasker 1975, Parrish et al. 1983). The Benguela system appears to exceed food requirements of the adult anchovy population during "normal" periods (Shannon and Field 1985). However, the temporal and spatial scale at which food becomes available to fish, and particularly to larvae, may be limiting (Shannon and Field 1985).

Hunter 1982 (in Lasker 1985) found a smooth monotonic exponential decrease in number of eggs and larvae and he suggested that this "lays to rest the Hjort hypothesis of a high larval mortality resulting from starvation beginning at yolk absorption" at least for Californian anchovy. Kawai and Isibasi (1983) doubted whether lack of food or predatory loss to other fish would be the major causes of larval mortality. They hypothesized that cannibalism on larvae and predation would be the major causes of larval mortality. Cushing and Harris (1973) and Jones (1973) suggest models in which larval mortality is the result of density-dependent competition for food-organisms.

Cannibalism on eggs in E. mordax has been shown to account on 28 % of the total egg mortality (Hunter & Kimbrell 1980, Mac Call 1980). In Peru egg cannibalism in E. ringens accounted on 10 % of the total egg mortality (Santander et al. 1983).

Ricker (1954, 1958) was the first to explicitly consider cannibalism as a density dependent cause of recruitment. In his model, Ricker differentiates between two causes of mortality : independent of the population size, and dependent on the population size. The result of increased density dependent mortality is to cause a more steeply declining right-hand limb of the stock-recruit curve, ie., the more domed the curve becomes. The Ricker model is based on a predator-prey interaction, where any increase in the abundance of eggs or larvae is simultaneously followed by an increase in the abundance of the predators (Ricker 1958, Csirke 1980b). The most obvious case of predation is cannibalism by adults on their own eggs.

The purpose of this thesis is to assess the impact of egg cannibalism on total egg mortality in South African anchovy, and to study the relationship between cannibalism and density of eggs in Cape anchovy in order to evaluate whether this conforms to a density-dependent or density-independent response.

2. SAMPLING METHODS

2.1 Sampling strategy

Anchovy stomach samples and plankton samples were collected on Sea Fisheries Research Institute R.S. Africana cruises of 5-30 November 1984 and 11 November to 2 December 1985 over the Agulhas Bank region (Fig. 2). These cruises were arranged so as to coincide with the peak of the anchovy spawning season (P. Shelton, 1986), as the main aim was to determine anchovy spawner stock biomass (Hampton et al. 1985).

2.2 Egg sampling and processing

Anchovy eggs were collected in 31 vertical hauls with the CalVET (Calcofi Vertical Egg Tow) net (Smith et al. 1985) from a depth of 200 m (or 10 m of the bottom if shallower) to the surface over a period of 4 days at stations positioned within high densities of both eggs and spawning fish during the November 1984 cruise (Fig. 2). An additional 9 hauls were made during the November 1985 cruise in roughly the same area of the Agulhas Bank. The CalVET net has been specifically designed to sample eggs for the estimation of daily egg production. The net consists of two principal parts: the mouth of $0.05m^2$ area and the mesh of 0.150mm, selected to retain anchovy eggs (Smith et al. 1985).
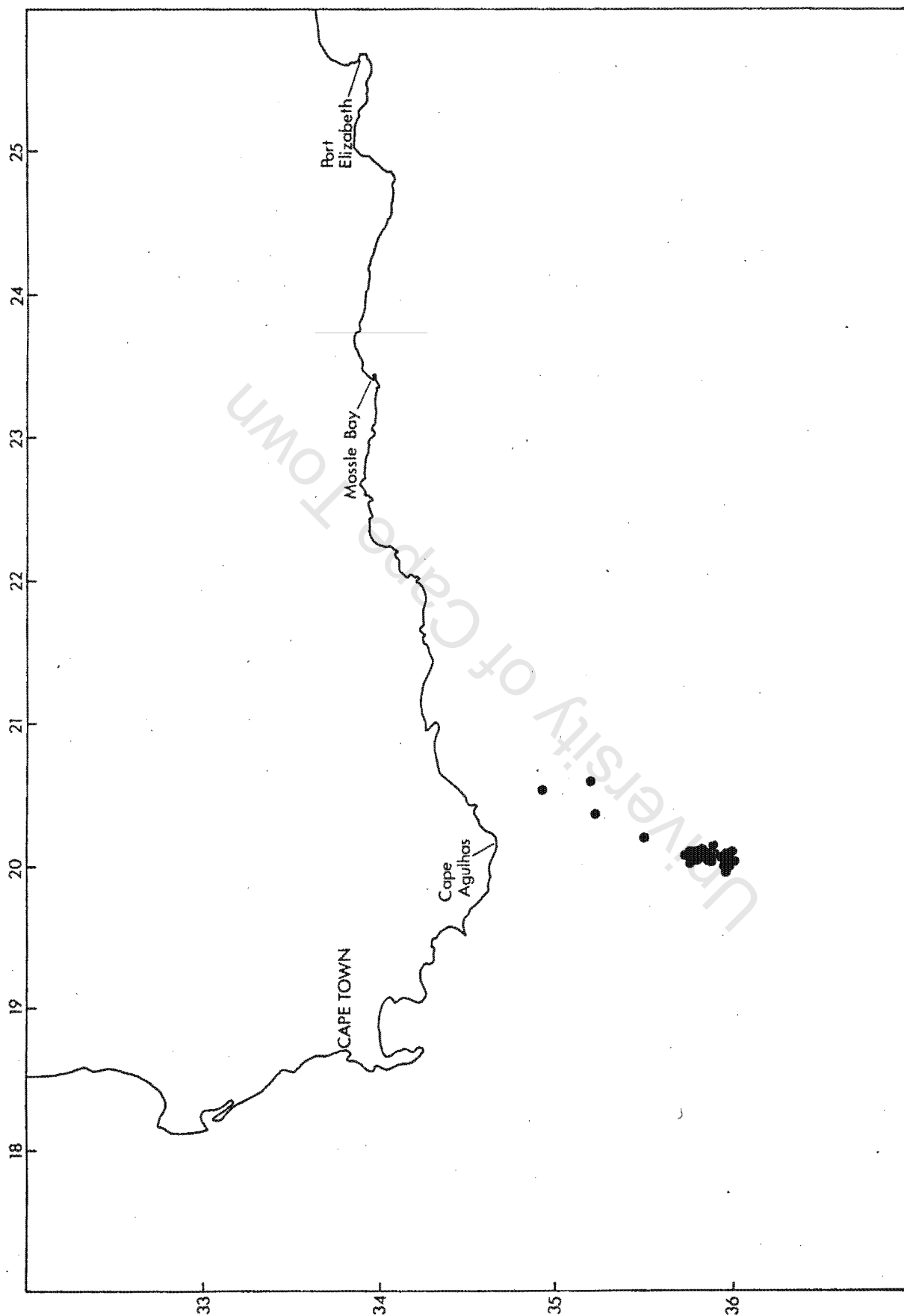
FIG. 2   Map showing the location of the study area on the Agulhas Bank, and the west and south coastline of South Africa. Dots show the position of the stations where samples were taken during 1984-1985 anchovy spawning cruises.

The total length of the net is less than 1.5m (Fig. 3). During each tow the net was retrieved rapidly at 1 m.sec^{-1} to avoid uneven trajectories due to ship's drift and undersea currents. An Universal Underwater Unit designed by Sea Fisheries Research Institute was attached below the CalVET net. The unit contained a temperature probe and depth sensor connected to an HP 87 microprocessor on board the vessel, which recorded and plotted the temperature/depth profile for the tow.

After the completion of a CalVET tow the net was washed down with a fine water spray and the plankton sample was immediately preserved in a 300ml jar filled with 4% buffered formaldehyde/sea water solution. In the laboratory anchovy eggs were removed from the plankton samples under a binocular dissecting microscope with a 20 x magnification. Eggs were assigned to 11 stages based on the degree of embryonic development following the method of Moser and Alhstrom (1985) (Fig. 4). The abundance of each stage in the samples was standarized to the number under 1m^2 of sea surface area. The time of peak spawning was determined from the time of day that newly fertilized eggs appeared in the egg collection and from observations on the spawning behaviour or condition of the adults sampled (M. Armstrong, SFRI, pers. comm.). Data from incubation experiments carried out using the thermal gradient incubator method of King (1977) on board the R.S. Africana during the November, 1984 cruise (Fig. 5) were used, together with in situ measurements of surface temperature
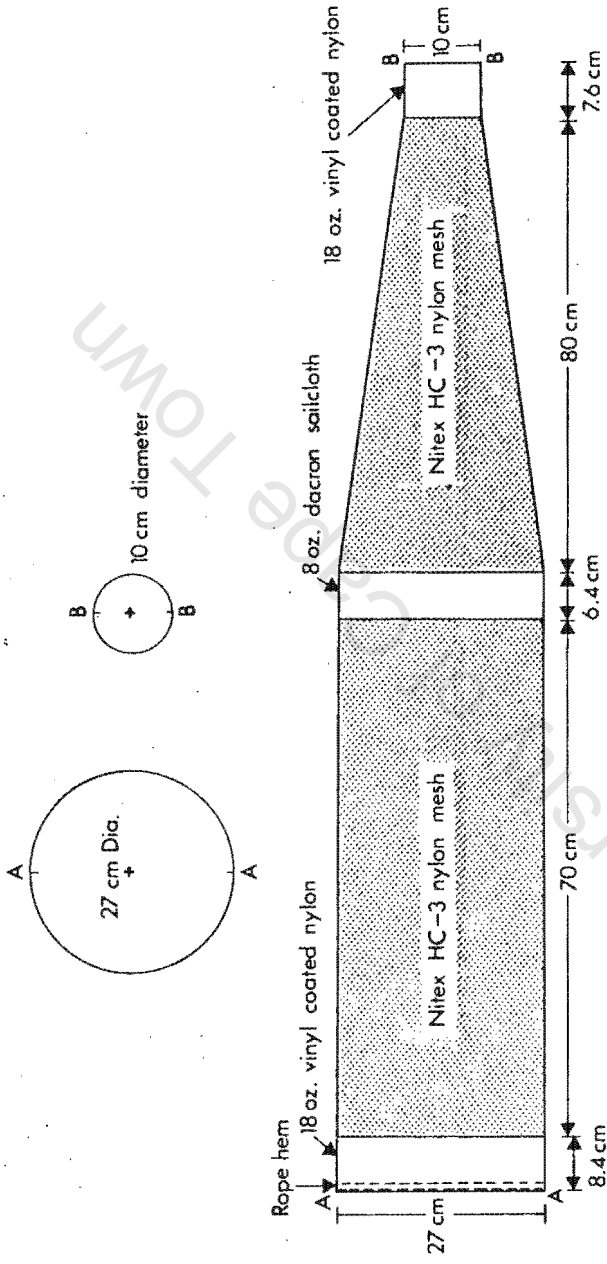
FIG. 3   Schematic drawing of the CalVET net sampler (from Smith et al. 1985).
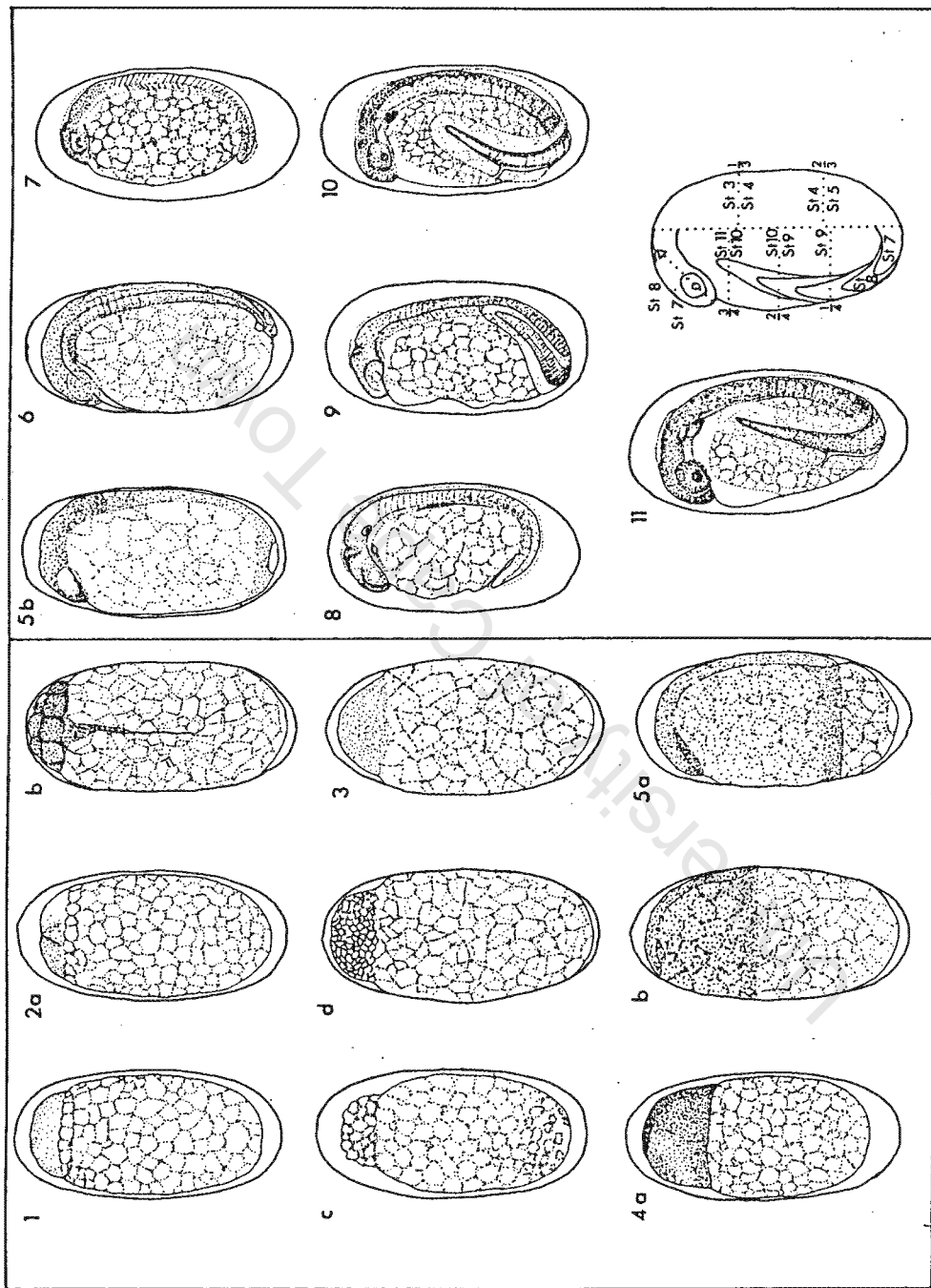
FIG. 4   Eleven developmental stages of anchovy eggs and diagrammatic egg showing relationship of epiboly and tail length to stage (from Moser and Ahlstrom 1985).
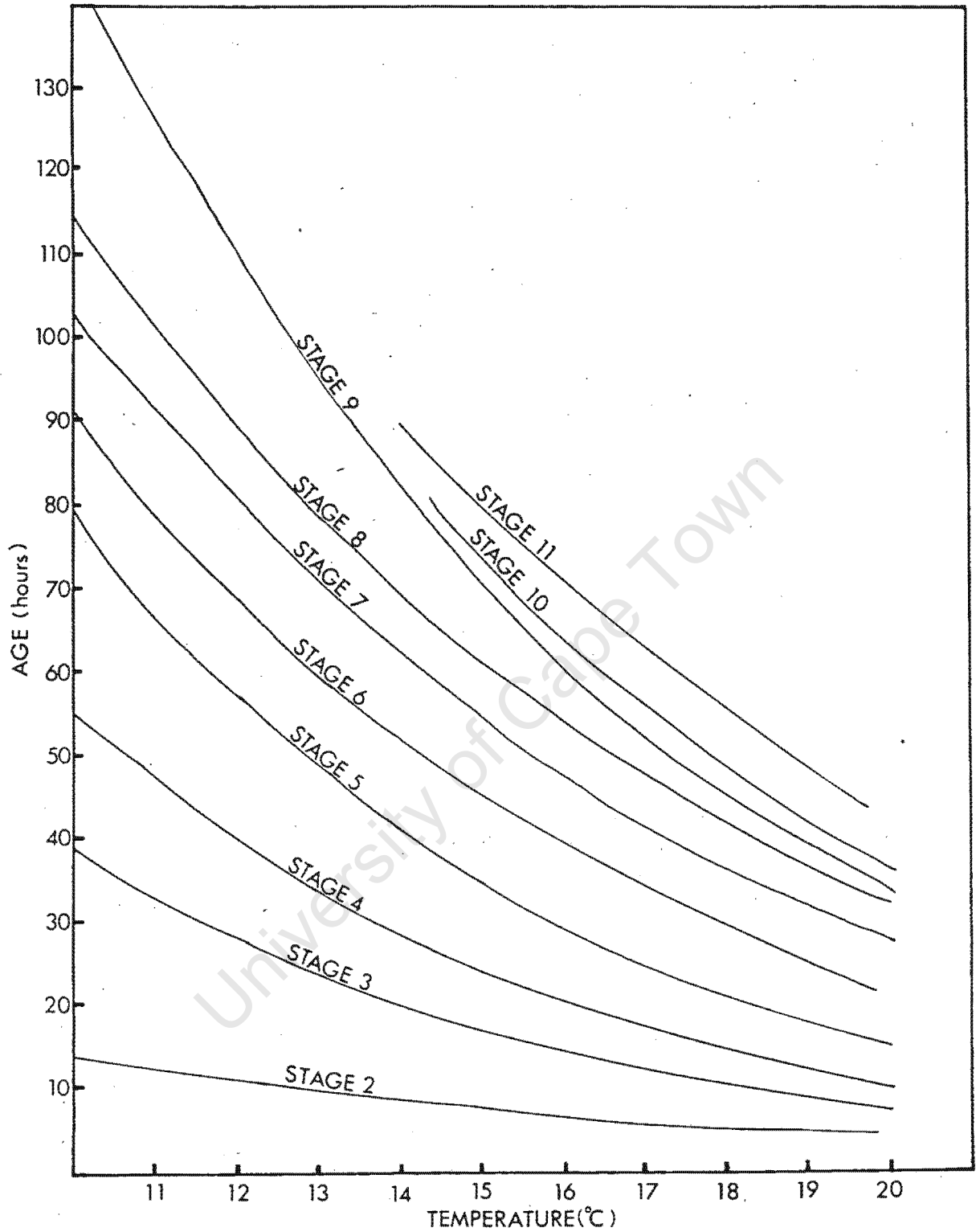
FIG. 5   Anchovy egg development curves showing the predicted mean age of 11 developmental stages at temperature between 11°C and 20°C (from Armstrong and Shelton, in prep.)

to estimate the age of each stage in hours. The surface temperature represents the maximum incubation temperature that eggs would be likely to encounter in the upper mixed layer. Data from age and abundance of eggs were used to estimate hourly egg mortality rates.

2.3 Stomach sampling and processing

A total of 40 sets of anchovy samples of 30 adult fish each were collected by means of the Engels 308 midwater trawl in roughly the same area and at the same time as the CalVET samples. The trawl is rectangular with extended lower wings and a mesh size of 800mm at the headline and at a towing speed of ca. 3 knots a mouth opening of 15-18m is mantained (H. Crous, SFRI, pers. comm.). The cod-end was fitted with a cod-end liner (length 5m) of 12mm mesh size. Samples were preserved by blast freezing at -20°C immediately after capture.

In the laboratory fish were measured (total length), weighed (total and ovary mass) and de-stomached. The weights of the stomach contents were determined and anchovy eggs in the stomach counted.

3. DATA ANALYSIS AND RESULTS

3.1 Estimation of egg mortality rate

Fig. 6 shows the anchovy egg distribution map during November 1984 survey and all the grid stations. Frequency distributions of the densities of eggs in the plankton over the Agulhas Bank (Fig. 2) and off the West Coast (Fig. 6) were plotted for comparison (Fig. 7). The density of eggs over the Agulhas Bank was higher than the density off the West Coast, confirming that the Agulhas Bank is the major spawning area for Cape anchovy. Approximately 55% of the eggs collected occurred in only 25% of the samples, and the largest number collected in one haul, 12 360 (per m^2), represented about 8% of the total number collected, which is an indication of the degree of patchiness found in egg distributions at sea. The mean density was 3755.6 eggs per m^2.

The mortality of anchovy eggs was assumed to conform to an exponential decay model (Lasker and Smith 1976) of the form:

$$E_t = E_o * \exp(-Z * t) \qquad (1)$$

where E_t = number of eggs at age t

E_o = number of eggs at age 0

Z = hourly instantaneous rate of mortality

t = age of eggs (hours)
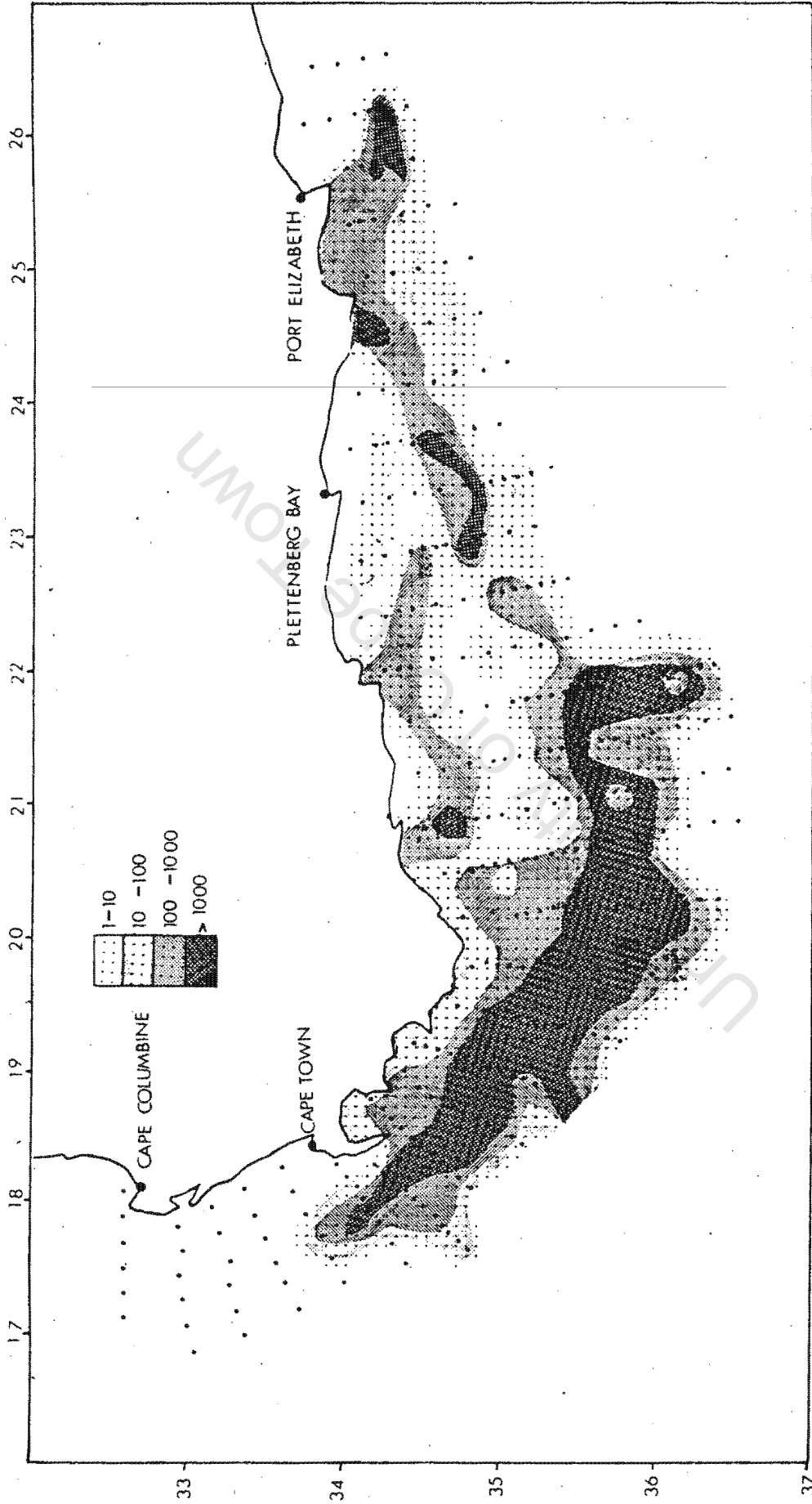
FIG. 6   Map showing the anchovy egg distribution during November 1984 survey and all the grid stations (from Shelton 1986).
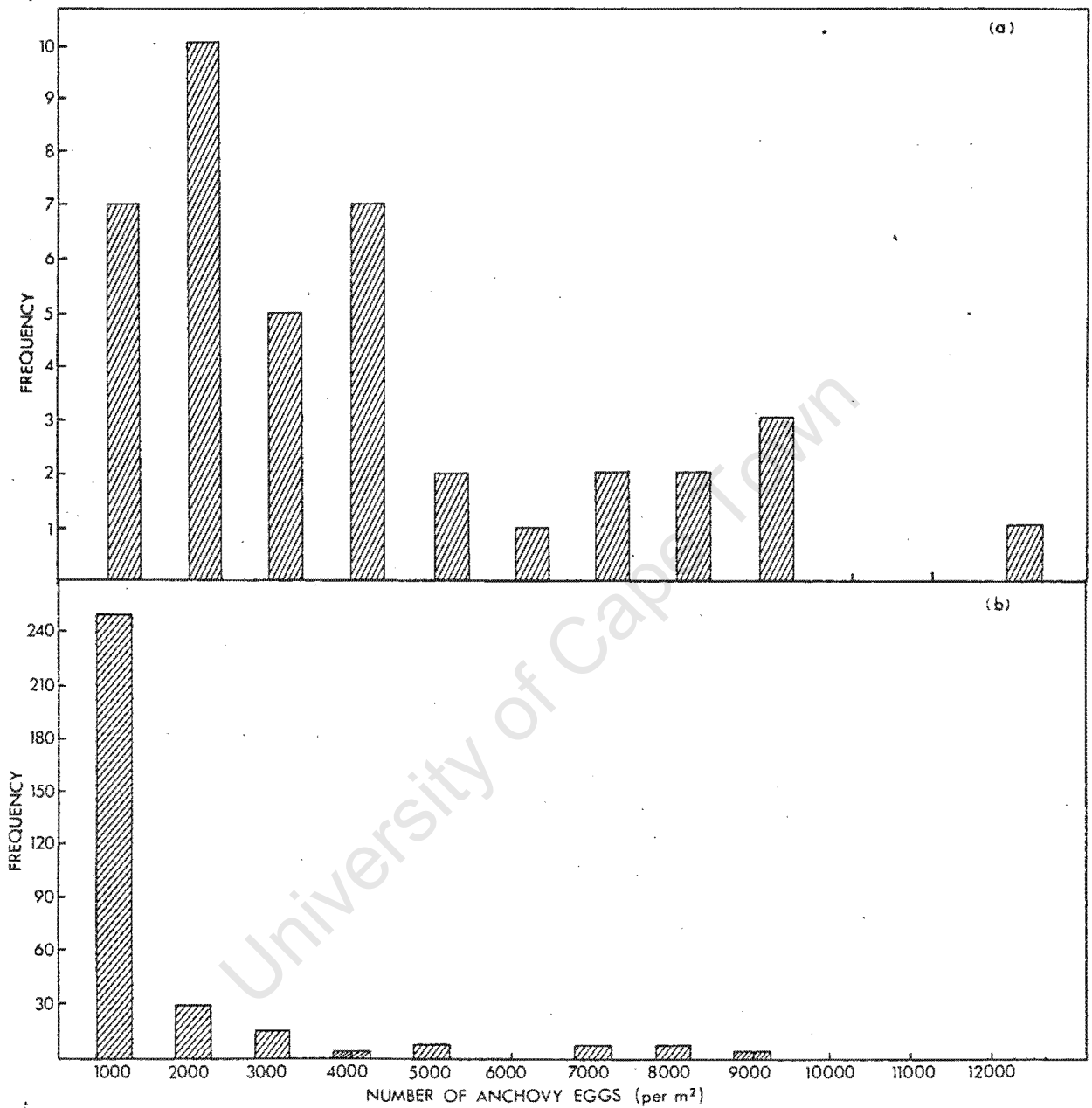
FIG. 7   a) Frequency distribution of egg densities in the plankton on Agulhas Bank area. b) Frequency distribution of egg densities in the plankton off the West Coast.

Estimates of Eo and Z were obtained by non-linear least squares regression of egg density versus age (Gauss Newton method; SAS Inst. Inc. 1982) (Fig. 8), where the age of eggs in CalVET net samples was determined initially using the egg development stage/temperature/ age-key (Fig. 5) and subsequently modified according to the time of sampling relative to the 21h00 spawning peak (M. Armstrong, SFRI, pers. comm.). Only egg stages fully recruited to the plankton but not yet hatched were used in the regression, so that the earliest and latest developmental stages were omitted from the calculations. The parameter estimates were:

Parameter	mean	asymptotic SE	95% asymtotic confidence interval
Eo	1908.8	509.16	896.92 - 2920.62
Z	0.024	0.01	0.0026 - 0.0459

Coefficient of determination (r^2) 0.58

Number of observations 90

3.2 Estimation of egg consumption rate and cannibalism mortality

The frequency distribution of numbers of eggs per stomach was plotted (Fig. 9). Eggs were found in the stomachs of 60% of the adult anchovy sampled (Fig. 10 and 11). There was a mean of 19.9 (SE = 7.1) anchovy eggs per stomach. The maximum number of eggs

$E_t = 1908.82e^{(-0.024t)}$
$r^2 = 0.53$
$n = 90$

AGE OF EGGS (hours) - t

NUMBER OF EGGS ('000) PER m² AT AGE t - Et
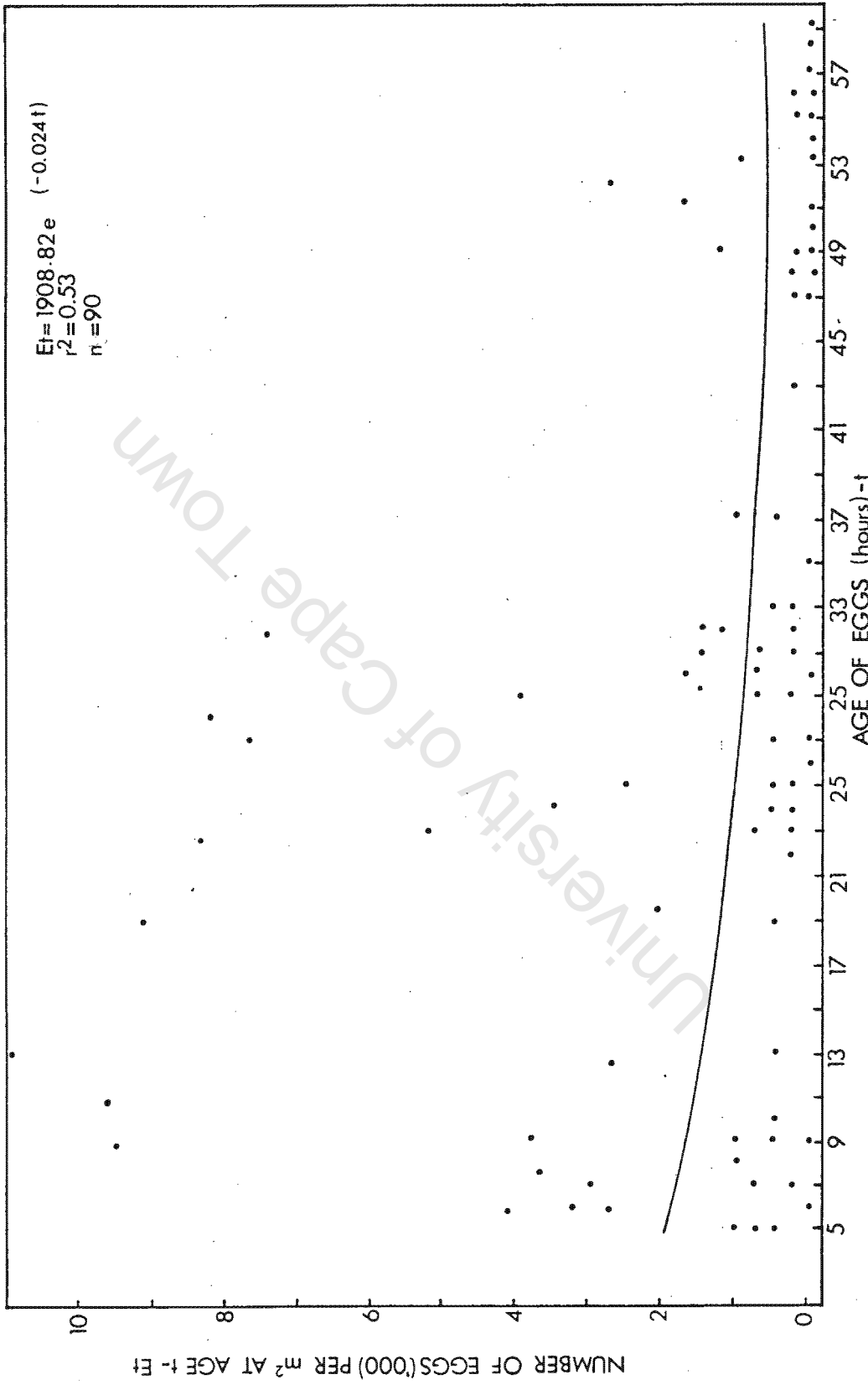
FIG. 8   Mortality curve for egg anchovy.
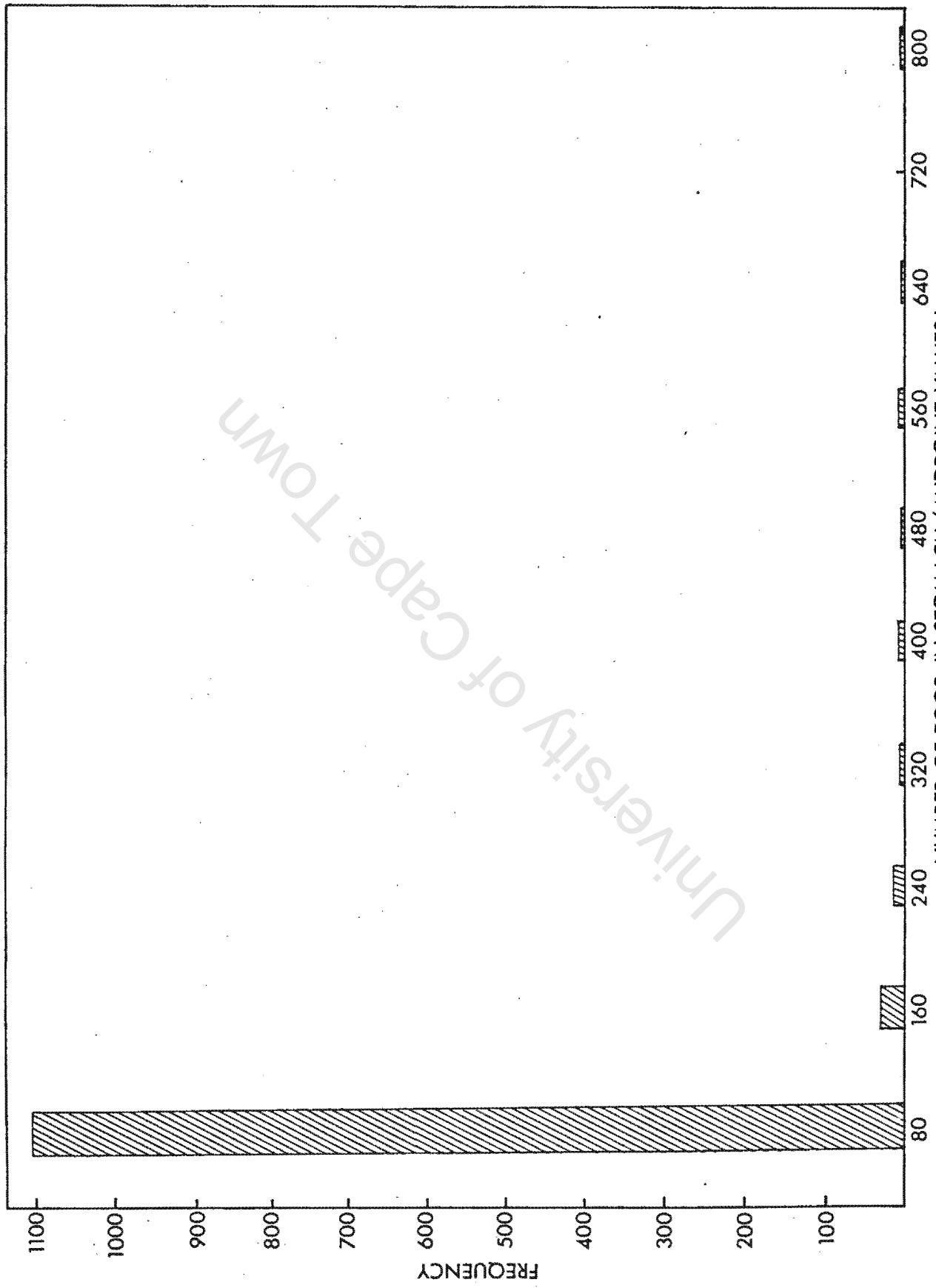
FIG. 9   Frequency distribution for eggs in the stomach of anchovy.

FIG. 10   Anchovy eggs in the stomachs of adults. a) 10 x magnifi-
cation. b) 20 x magnification.

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FIG. 11   Anchovy eggs in the stomachs of adults(40 x magnifica-
            tion).

found in a single stomach was 815 eggs, which formed 3.5% of the total number in the stomachs of all fish sampled.

A direct relationship was found between the weight of the stomach and number of eggs observed per stomach (Fig. 12), suggesting that eggs were an important item in the diet of adult anchovy sampled during the present study. To estimate the duration of feeding, the weight of food in the stomach, the number of eggs in the stomach, the percentage of fish without eggs in the stomach and the number of eggs in the stomach per unit weight of stomach contents were plotted against time of day (Fig. 13) (Keast and Welsh 1968, Noble 1972). A third order polynomial regression was fitted to the data using a linear least squares method (SAS Inst. Inc. 1982). The data suggest that a reduction or cessation in feeding occurred from ca. sunset (20h-21h) to ca. sunrise (05h-06h).

The mean number of eggs observed per stomach during the feeding time (from 05h00 to 20h00) was 36.74 (SE = 12.72) (see Appendix 1). If the mean number of eggs per stomach during the feeding period and the duration of feeding are considered, the impact of cannibalism on egg mortality can be assessed using the equation of Darnell and Meierotto 1962, Tyler 1970, Noble 1972).

The average daily consumption of eggs by anchovy was estimated from 630 fish samples collected during feeding time, using the
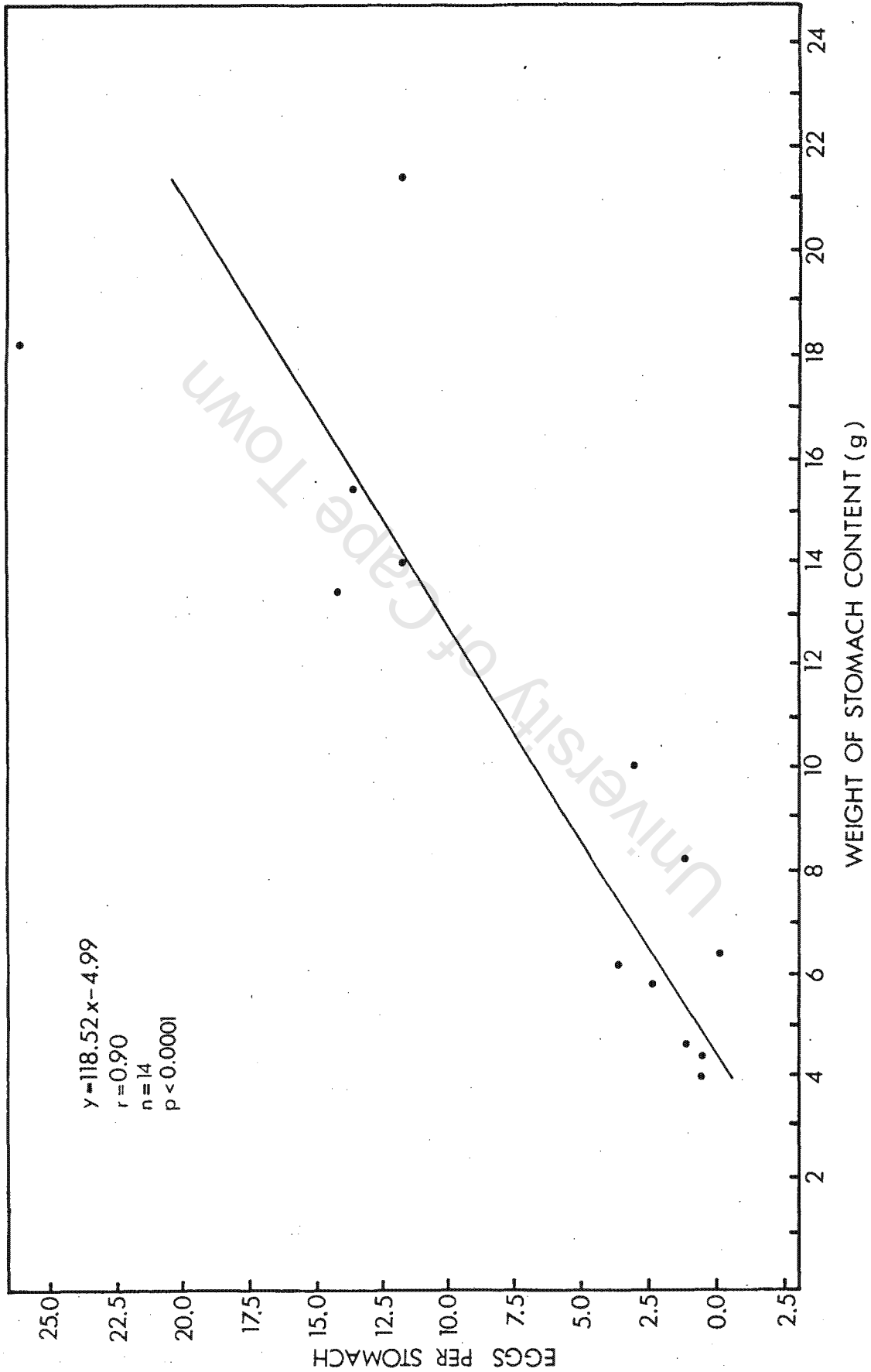
FIG. 12 Linear relationship between egg observed per stomach and weight of stomach content. Points are means for 30 fish and means of 2-4 trawls.
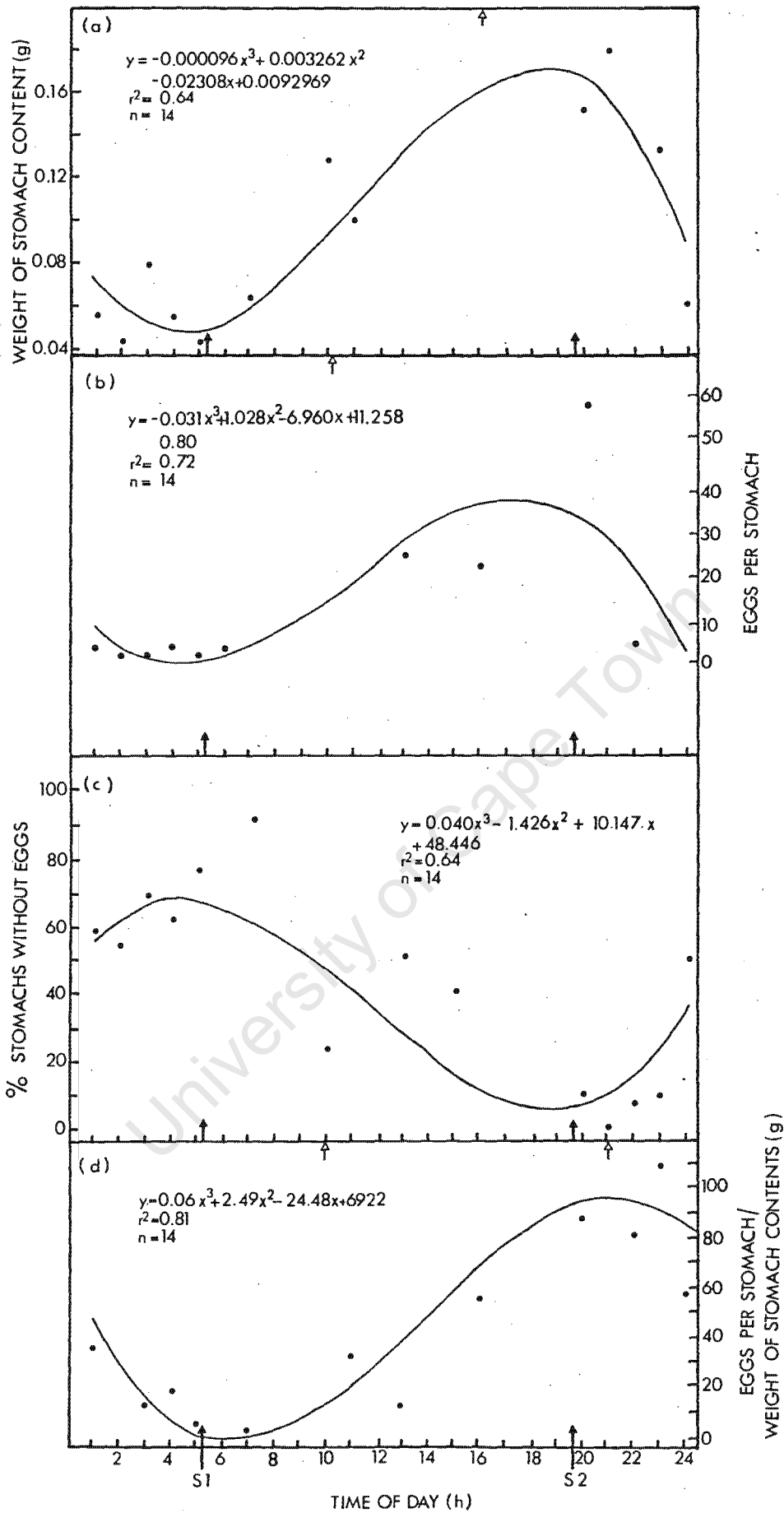
FIG. 13   Third order polinomial model for a) weight of stomach
contents versus time of day; b) number of eggs in fish
stomachs versus time of day; c) percentage of fish
without eggs in the stomach versus time of day; d)
number of eggs in the stomach per unit weight of
stomach contents versus time of day. Points are means
for 30 fish and means of 2-4 trawls. Full arrows (S1
and S2) indicate sunrise and the sunset respectively.
Open arrows indicate points out of range of scale.

following equation (Darnell and Meierotto 1962, Tyler 1970, Noble 1972) :

$$C = EE * g * t \qquad (2)$$

where C = number of eggs eaten per fish during time t

EE = mean number of eggs observed per stomach

g = hourly instantaneous rate of gastric evacuation

t = duration of feeding (hours)

For values of EE = 36.74, g = 0.701 (Hunter and Kimbrell 1980) and t = 15, the mean daily consumption per fish, C, was calculated as:

$$C = 36.74 * 0.701 * 15$$

$$= 386.32 \ eggs.d^{-1}$$

Given a mean weight per fish of 14.5 g calculated from 630 fish, this would be equivalent to 26.64 $eggs.g^{-1}.d^{-1}$.

Under steady-state conditions, equation (2) results from the balance for eggs per stomach (or per fish), EE(t), as follows (M.O. Bergh, University of Cape Town, UCT, pers. comm.):

rate of change   = rate of egg ingestion - rate of egg evacuation
of eggs per stomach

$$\frac{dEE(t)}{dt} = R(t) * w/(pF) - g * EE(t) \ (eggs.fish^{-1}.h^{-1}) \ (3)$$

Where EE(t) = total number of eggs per fish stomachs

R(t) = rate of egg ingestion $(eggs.fish^{-1}.h^{-1}.m^{-2})$

w = weight of fish (g)

ρF = density of fish $(g.m^{-2})$

and g has been defined in equation (2).

Therefore,

$$C(t) = \int_0^t R(t) * w/\rho F * dt \qquad (4)$$

where C(t) is the total number of eggs consumed per fish after time t.

$$C(t) = \int_0^t \left(\frac{dEE(t)}{dt} + g * EE(t) \right) * dt \qquad (5)$$

$$= EE(t) - EE(0) + \int_0^t g * EE(t) * dt \qquad (6)$$

Thus it can be seen that equation (2) results from assuming that:

1) EE(t) = EE(0)

2) EE(t) is independent of t; EE(t) = EE, so that

$$C(24) = \int_0^{24} g * EE(t) * dt = g * EE * t \qquad (7)$$

Because of the cubic equation describing the feeding rhythm shown in Fig. 13(b), i.e. $EE(t) = a*t^3 + b*t^2 + c*t + d$, the integral to obtain C(24), the total number of eggs eaten in a 24 hour period per fish, is as follows:

$$C(24) = EE(24) - EE(0) + \int_0^{24} g * (at^3 + bt^2 + ct + d)dt \; (eggs.fish^{-1}) \qquad (8)$$

$$= 299 \; eggs.fish^{-1}.d^{-1}$$

For a mean weight per fish = 14.5 g, $C(24) = 20.6 \; eggs.g^{-1}.d^{-1}$

Thus, using equation (8) the total number of eggs eaten daily per fish was calculated as $20.6 \; eggs.g^{-1}.d^{-1}$, whereas using equation (2)

the mean daily egg consumption per fish was calculated as 26.64 eggs.$g^{-1}.d^{-1}$.

The proportion of egg production consumed by cannibalism was calculated by assuming that a single day's consumption of eggs from the daily cohorts produced during the preceding 2-3 days was equivalent to the consumption of eggs from a single cohort during the 2.5 days between fertilization and hatching (at 15 C). Thus:

$$Zc = C/F \qquad (9)$$

where Zc = proportion of egg production consumed due to cannibalism

C = number of eggs eaten per gram of fish per day

F = egg production per gram of fish body weight per night

F was calculated as:

$$F = f * d * s \qquad (10)$$

where f = eggs produced per gram of females (batch fecundity)

d = proportion of females spawning each night (spawning fraction)

s = ratio of mass of females to the combined mass of males and females (sex ratio)

During the November 1984 survey, batch fecundity and spawning fraction of anchovy were estimated to be 536 eggs.g   and 0.15

respectively (M.Armstrong,SFRI, pers.comm.). The sex ratio was 0.54 from the 630 fish sampled. Therefore, eggs produced per gram of all fish per night was calculated as:

$$F = 536 * 0.15 * 0.54$$
$$= 43.4 \text{ eggs.g}^{-1}.\text{night}^{-1}$$

The proportion of egg production consumed by cannibalism was calculated from equation (2) as :

$$Zc = 26.64/43.41$$
$$= 0.61$$

Alternatively, considering equation (8):

$$Zc = 20.6/43.41$$
$$= 0.47$$

The proportion of egg mortality caused by cannibalism (Pc) during the 60 hour period prior to hatching was calculated as the proportion of egg production consumed due to cannibalism divided by the proportion of egg production lost due to all causes of mortality. Using data from equation (2):

$$Pc = ((EE * g * t)/F))/(1 - \exp(- 60 * Z)) \tag{11}$$

where EE,g and t were defined in equation (2), F was defined in equation (10) and Z was defined in equation (1). The mean and variance of Pc were estimated empirically by Monte Carlo simulation

(see Appendix 2), using the standard error of EE (page 23) and the standard error of Z (page 18). 3000 values of EE and Z were generated and the mean and standard deviation of Pc was calculated. Only positive values of EE and Z were accepted, and only values of Pc between 0 and 1.0 were included in the calculation.

The mean value of Pc obtained (to one decimal place) was 0.7 irrespectively of using the arithmetic or geometric mean despite truncation of the distribution of Pc estimates at 1.0 (Fig.14). The standard error of Pc was 0.2. Therefore, cannibalism may account for 30% to 100% (mean ± 2 SE) of the total egg mortality, with a best estimate value of 70%.
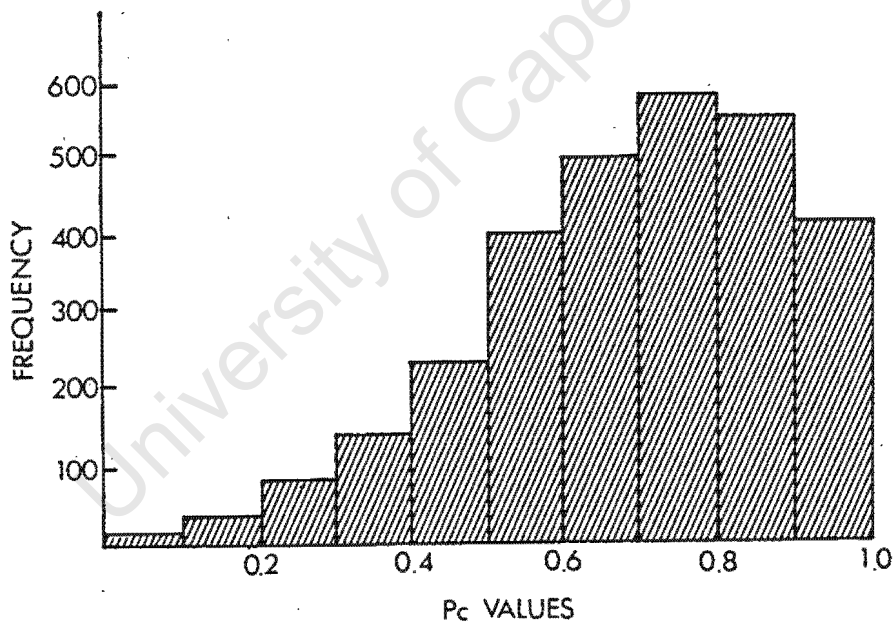
FIG. 14 Frequency distribution output of Pc from the Monte Carlo simulation.

Alternatively, using data from equation (8), Pc was calculated as:

$$Pc = Zc/(1-\exp(-60 * z) \qquad (12)$$

where Zc and Z were defined in equations (9) and (1) respectively.

$$Pc = 0.47/(1-\exp(-60 * 0.024))$$

$$= 0.62$$

Therefore, when the evaluation of the relevant integral is carried out (equation (8)) cannibalism may account for 62% of the total egg mortality.

The rate of egg cannibalism was estimated as follows (MacCall 1980, Santander et al. 1983):

$$Rc = Pc * Z \qquad\qquad (13)$$

where Rc = hourly instantaneous rate of egg cannibalism and Pc and Z have been defined in equations (11) and (1) respectively.

Considering the two calculated values of Pc = 0.70 and Pc = 0.62 (equations (2) and (8) respectively), the instantaneous rates of egg cannibalism were calculated as $0.0168 \ h^{-1}$ and $0.01488 \ h^{-1}$.

3.3 Evaluation of the functional response of cannibalism

Mean eggs per stomach of single fish versus egg density at sea shown a non-linear relationship. To test for non-linearity, a quadratic equation was fitted to the data:

$$EE = m * ED^2 + n * ED + s \qquad (14)$$

where EE = number of eggs observed per stomach

ED = no. of eggs in sea per m^2 (egg density)

m,n,s = parameters of quadratic equation

If the relationship is linear, the parameter a would not be significally different from zero. The following parameter values were obtained:

parameter	mean	SE	95% confidence interval
m	0.000003	0.0000003	0.0000024 - 0.0000036
n	- 0.021095	0.0039345	0.013226 - 0.028960
s	36.051570	10.0523245	15.95 - 56.15

The t value for testing the nul hypothesis (Ho) that m = 0 is 9.60. Thus, for n-2 degrees of freedom Ho is rejected (p<0.0001).

Coefficient of determination (r^2) 0.95

Number of observations 21

Despite the good fit of the quadratic equation, it was consi-dered inappropiate for modelling egg cannibalism because the

curve has a minimum at relatively high positive egg density of 3516.6 m^{-2}. For modelling egg cannibalism, an exponential relationship was chosen as an empirical representation of the relationship between eggs observed per stomach and egg density over the range of egg densities observed at sea.

The relationship between mean number of eggs observed in anchovy stomachs in a trawl sample versus egg density per m^2 at the nearest CalVET station was then plotted for 21 trawl samples of 30 fish each taken during the fish feeding period of 05h00 to 20h00 and an exponential relationship was fitted using linear least squares regression (SAS Inst. Inc. 1982, Fig. 15a). The exponential curve obtained (Fig. 15b) can be described by the equation:

$$EE = \gamma * \exp(\theta * ED) \tag{15}$$

where EE = number of eggs observed per stomach

ED = no. of eggs in sea per m^2 (egg density)

γ, θ = parameters of exponential curve

Estimates of parameters were as follows :

parameter	mean	SE	95% confidence interval
ln γ	- 0.24	0.34	- 0.92 , 0.44
θ	0.0005	0.00006	0.00038 , 0.00062

Coefficient of determination (r^2) 0.81

Number of observations 21
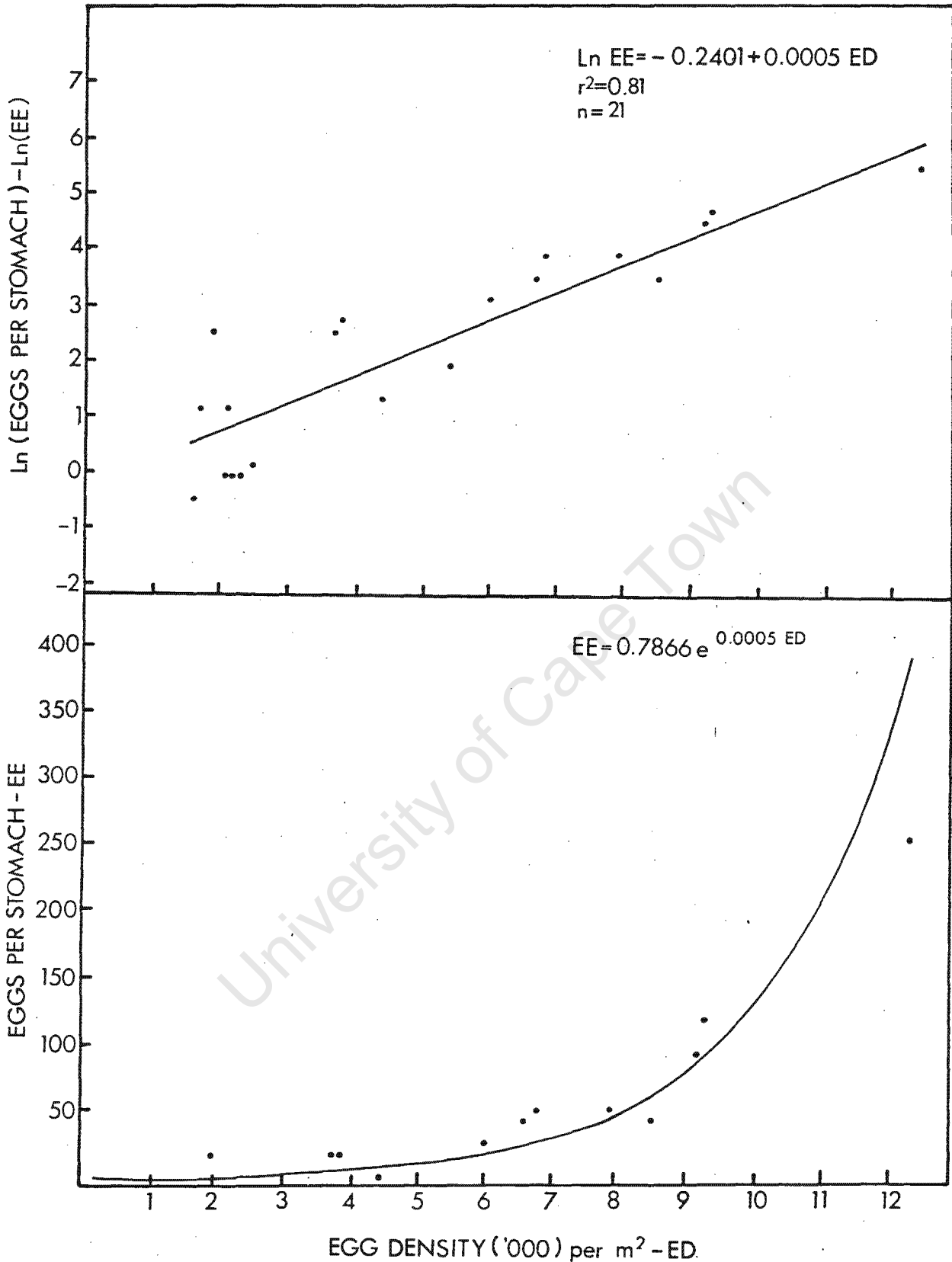
FIG. 15   Mean number of eggs observed in anchovy stomachs versus
egg density at the nearest CalVET station. Points are
means for 30 fish. a) Log fitted curve. b) Exponential
plotting.

Thus, eggs per stomach (EE) is given by (Fig. 15) as:

$$EE = 0.787 * \exp (0.0005 * ED)$$

The good experimental fit to the data ($r^2 = 0.81$), suggests that cannibalism may be a mechanism regulating egg survival. However, it is possible that the apparently non-linear fit is due to statistical effects such as might result from the very skew distribution of eggs per stomach, coupled with a variance proportional to the mean, but nevertheless with an underlying linear relationship between median values of EE(t) and ED(t). Furthermore, a non-linearity in the EE to ED relationship is not essential for a density-dependent cannibalistic effect, as discussed below. Essentially, all that is required for density dependence is that the value of the density-dependent parameter of the Ricker function (β) be significantly positive.

The Ricker curve (Ricker 1975) describes a stock-recruitment relationship in which the initial production of offspring is proportional to stock size, but their subsequent mortality rate is also proportional to adult stock size. The Ricker curve can be used to relate eggs hatching to eggs produced:

$$EH = \alpha * EP * \exp(- \beta * EP) \tag{16}$$

where EH = eggs hatched

α = density-independent coefficient

EP = egg production

β = density-dependent coefficient

If the time of day is ignored, assuming a steady state situation, the balance for eggs in stomachs in terms of eggs.m^{-2}, $\overset{\bullet}{EE}(t)$, in the sea is (M.O. Bergh, UCT, pers. comm.):

$$\frac{d\overset{\bullet}{EE}(t)}{dt} = \beta * (S/V) * ED(t) - g * \overset{\bullet}{EE}(t) \qquad (eggs.m^{-2}.h^{-1}) \qquad (17)$$

where $\overset{\bullet}{EE}(t)$ = eggs per m^2 in fish stomachs

$\beta * (S/V) * ED(t)$ = rate of egg ingestion

$ED(t)$ and g have been defined in equations (14) and (2) respectively. Note: $S/V = \rho F$ and β is the density-dependent parameter of the Ricker curve. (Note: this model assumes the eggs are ingested by filtration, since the rate of ingestion is proportional to fish density or egg density).

Making the steady state assumption amounts to setting this to zero, so that:

$$\overset{\bullet}{EE}(t) = \beta * (S/V) * ED(t)/g \qquad (eggs.m^{-2}) \qquad (18)$$

To convert to eggs per stomach, both sides of this relationship need to be divided by (S/V)/w, resulting in a <u>linear</u> relationship between EE(t) (eggs per stomach) and ED(t):

$$EE(t) = w * \beta * ED(t)/g \qquad (eggs.stomach^{-1}) \qquad (19)$$

3.4 Evaluation of the relationship between eggs hatching and egg production

Taking into account the linear relationship between egg density and egg production (Csirke 1980a), the rate of egg survival (equations (1)), gut evacuation rate (from Californian anchovy) and eggs eaten by a single predator (equations (2),(8) and (15)), a simulation model was built (Fig. 16) to quantify the relationship between the number of eggs hatching and numbers of eggs produced under a unit surface area for the following conditions : a) egg production varies because number of spawning fish per m^2 varies, with constant specific fecundity, and b) egg production varies because specific fecundity varies, with fish density constant (ie. spawning fraction may decrease at the beginning and end of the spawning season, (Hunter and Leong 1981)).

In the first approach, the nightly egg production per fish per m^2, the time and period of feeding, the density independent mortality rate and the parameters of the functional relationship between egg density and eggs eaten per fish were held constant. A steady state between eggs produced and eggs hatching could therefore be attained by running the model over a sufficient length of time for eggs hatching to stabilize (Fig. 17).

The model was age-structured in that nightly cohorts of eggs

FIG. 16   Diagrammatic representation of the model.
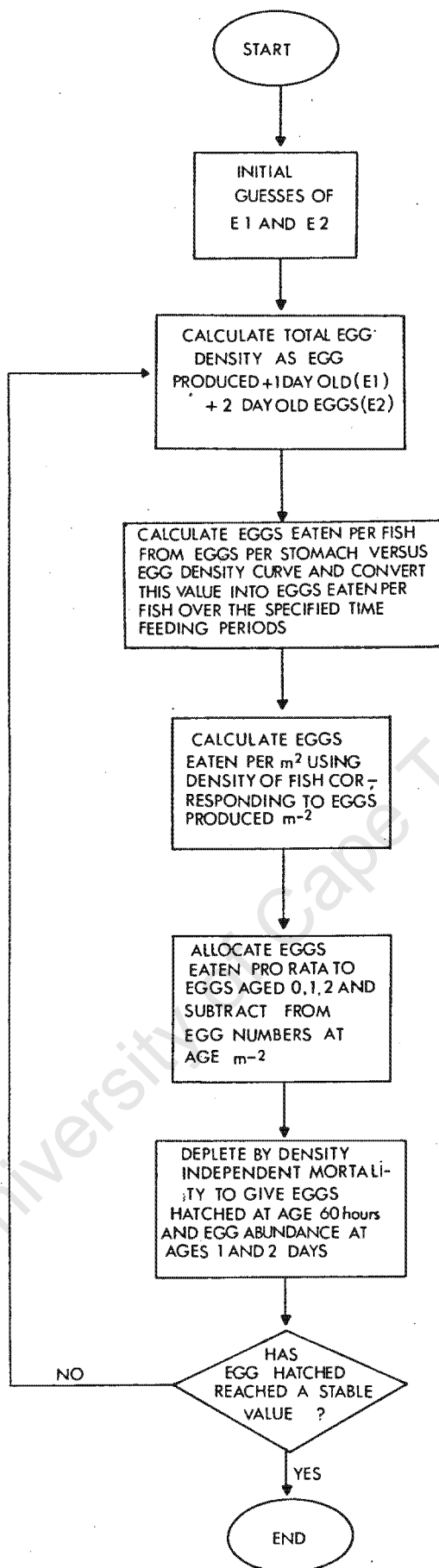
FIG. 17   Flowchart of the model.

were assumed to be generated as an pulse at 21h00 and decayed by density independent and density dependent mortality until hatching. Feeding by anchovy on eggs was partitioned into two periods : a 6 hour period centred around peak egg production at 21h00 (18h00 - 24h00) and a 9 hour period centred around 13h30 (09h00 - 18h00). This simulated the observed feeding period (Fig. 13). For simplicity, consumption was assumed to occur instantaneously at 13h30 and 21h00. The number of eggs consumed during each period was calculated using equation (15), which was used to estimate the number of eggs in each stomach according to the density of eggs in the plankton, and equation (2), in order to convert this value into number of eggs consumed over the specified time periods. Total egg density was measured at the median time of each feeding period. The exponential function was truncated at the maximum observed number of eggs per stomach, ie. 815, to avoid extrapolation beyond the observed data (see Appendix 3).

An estimate of density-independent mortality (M) of 0.0072 h^{-1} was calculated at a spawning fraction of 0.15, by substracting the estimate of mean cannibalism mortality rate (equation (13) based on equation (2)) from the value of total mortality rate (equation (1)). Estimates of density-independent mortality (M) of 0.0168.h^{-1} and 0.0000.h^{-1} were also calculated in the same manner, corresponding to the lower and upper 95% confidence limits of the mean value of proportion of eggs lost by cannibalism (equation

(11)). Eggs hatched were related to eggs produced for a series
of values of egg production and for the three estimates of
density-independent (M), and for a spawning fraction estimate of
0.15. The results are also expressed as eggs hatched versus fish
density (Fig. 18).

Eggs hatched were related to eggs produced for a series of
values of egg production and for spawning fraction estimates of
0.05, 0.10, 0.15, 0.20 and 0.30 using the value of density-
independent mortality of $0.0072.h^{-1}$ (Fig. 19a). The results are
also expressed as eggs hatched versus fish density (Fig. 19b).

The curves (Fig. 18 and 19) represent the recruitment of eggs
to larvae for the area of the Agulhas Bank studied. The shape of
the curves differs from the typical Ricker curve because the
number of eggs hatched falls to zero beyond a certain egg densi-
ty. This is a result of using instantaneous feeding as opposed to
continuous feeding in the simulation model. The curves (Fig. 19)
show that when egg production increases because of an increase in
either the number of spawning fish per unit area or the specific
fecundity, the density-dependent mortality caused by egg canniba-
lism also increases. This results in a domed curve with maximum
numbers of eggs hatching at an egg production of $3000.m^{-2}$ or 4.76
$fish.m^{-2}$ at a spawning fraction of 0.15 (Fig. 19). Smaller spawning
fractions resulted in poorer survival to hatching because of the
larger densities of fish required for a given egg production.
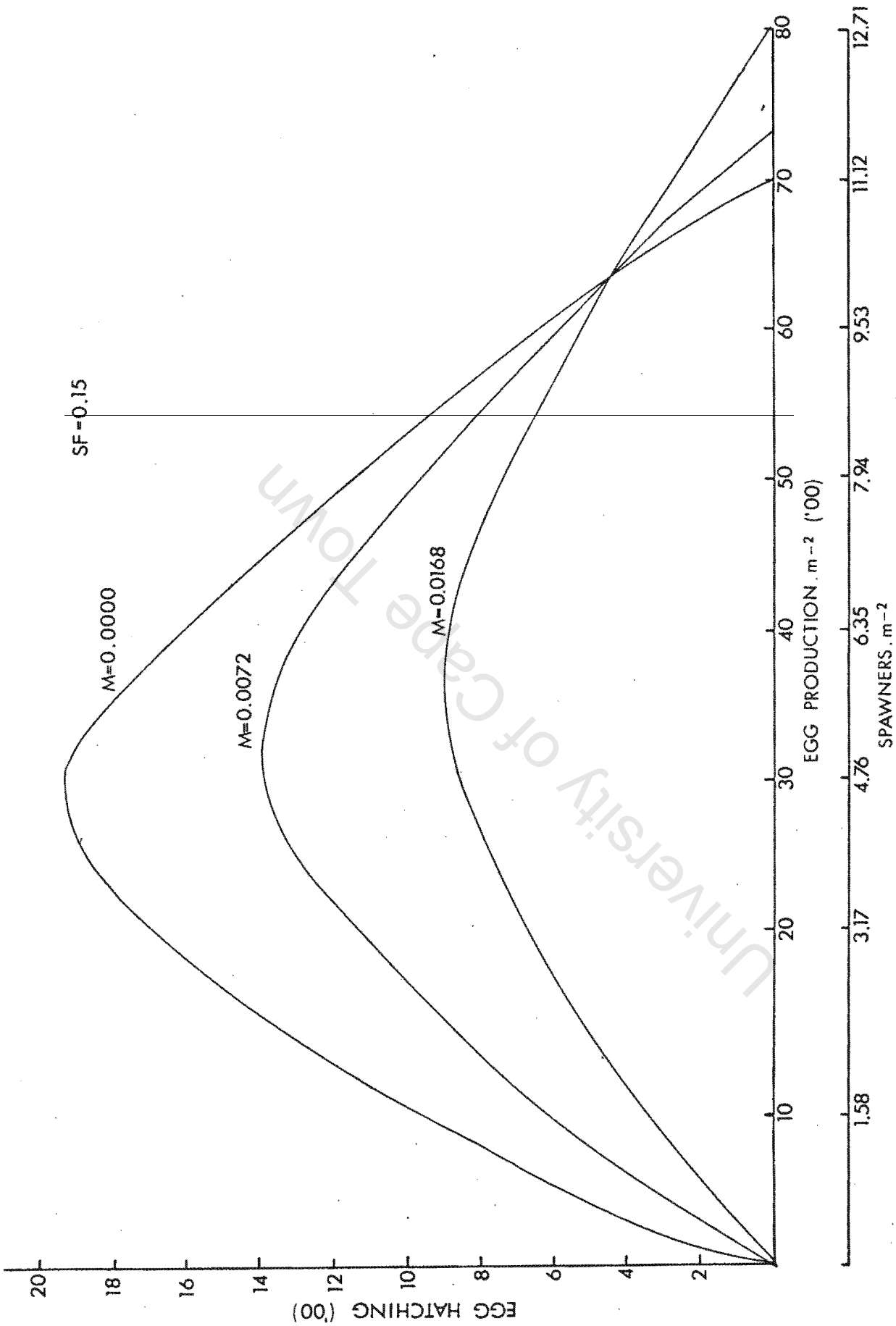
FIG. 18 Egg hatching-egg production curves and egg hatching-spawners curves for a spawning fraction (SF) = 0.15 and at density independent mortality (M) = 0.0072.h^{-1}, 0.0168.h^{-1} and 0.0000.h^{-1}.

42
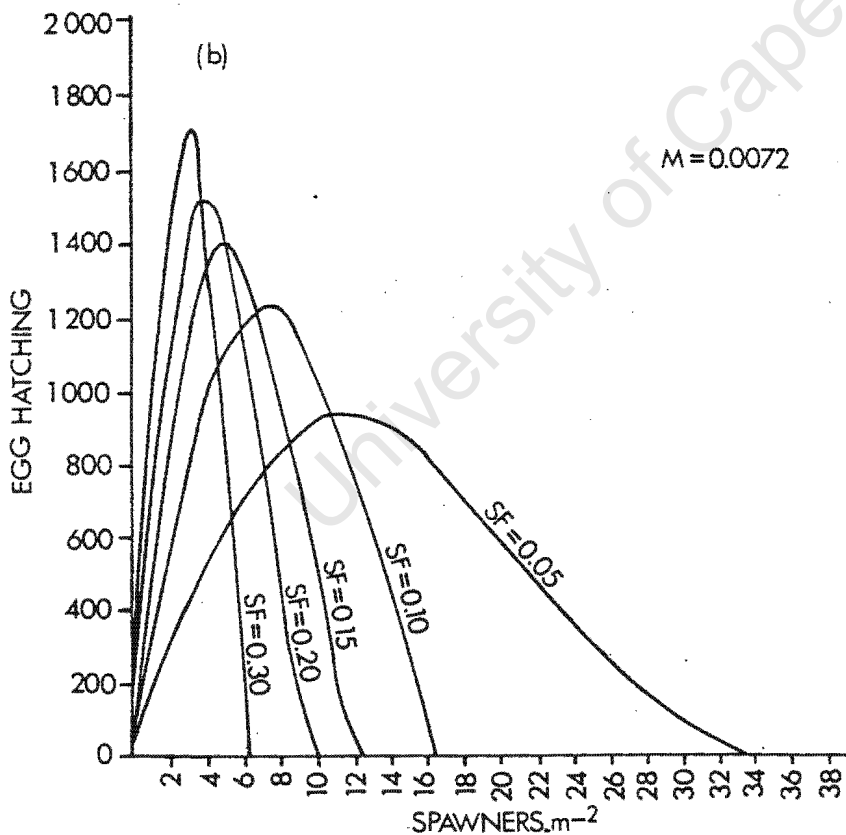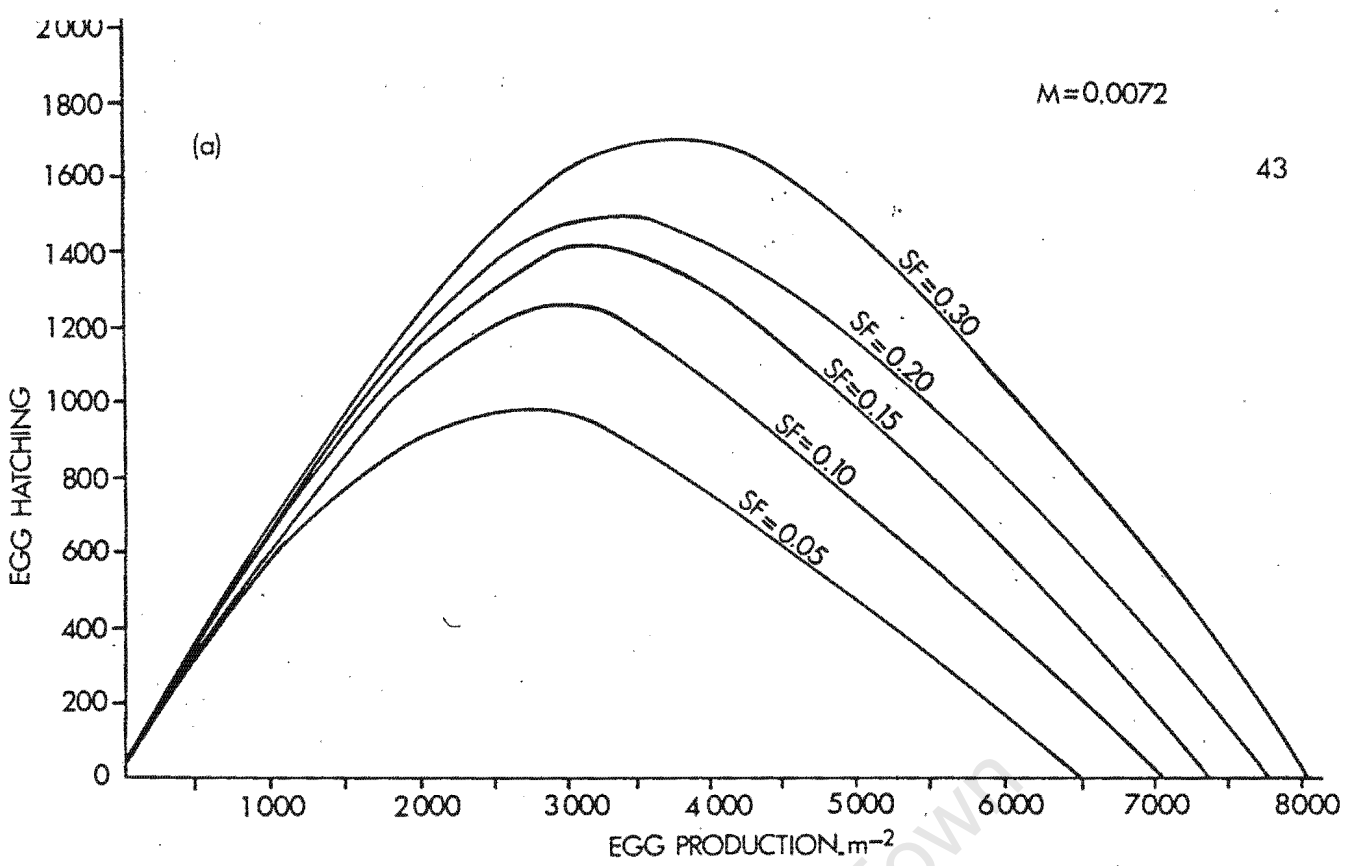
FIG. 19   a) Model output of egg hatching-egg production curves and
b) model output of egg hatching-spawners curves for
different spawning fractions (SF) and at density
independent hourly mortality (M) = 0.0072.

The above mentioned "first approach" model used equation (2) to estimate the total consumption of eggs assuming a pulse of egg production at 21h00. Strictly speaking, because of the strong dependence of EE(t) on time, dynamic effects need to be considered. An alternative approach was developed by fixing certain aspects of the dynamic behaviour of the idealised 1 m^2 ensemble of fish, eggs in stomachs, and eggs per m^2 sea water (inclusive of fish volume) and analytically evaluating the relationship between egg hatching and egg production.

An estimate of density-independent mortality (M) of 0.0091 h^{-1} was calculated at a spawning fraction of 0.15, by substracting the estimate of cannibalism mortality rate (equation (13) based on equation (8)) from the value of total mortality rate (equation (1)). An estimate of fish density was calculated using a very simple analogy of the egg production method, considering the spawning biomass necessary per m^2 to give a density of age 0 eggs from Fig. 8 and knowing batch fecundity, sex ratio and spawning fraction.

Because of the good fit for the EE(t) versus t relationship and for the EE(t) versus ED(t) relationship, it is theoretically posible to calculate β as a function of time as follows (M.O. Bergh, UCT, pers. comm.):

$$EE(t) = at^3 + bt^2 + ct + d \quad \text{(from Fig. 13b)}$$

and

EE(t) = γ * exp(θ * ED) (from equation (15))

therefore

$$ED(t) = 1/\theta \ \ln(1/\gamma(a*t^3 + b*t^2 + ct + d) \tag{20}$$

The balance equation for ED(t) is:

$$\frac{dED(t)}{dt} = - M * ED(t) - \beta(t) * (S/V) * ED(t) \quad (eggs.m^{-2}.h^{-1}) \tag{21}$$

where M is the density—independent mortality coefficient estimated above.

Therefore, since ED(t) is function of t, $\beta(t)$ is given by the relationship:

$$\beta(t) = (\frac{dED(t)}{dt} + M * ED(t)/\rho F/ED(t) \quad (m^2.g^{-1}.h^{-1}) \tag{22}$$

Therefore, knowing M, $\beta(t)$, ρF and the boundary condition ED(0) (estimated by extrapolating Fig. 8 backwards exponentially to age 0), a procedure can be devised which solves equation (21) to give numerically estimates of ED(60) at various fish densities and various values of ED(0). Note however, that ρF and ED(0) are related by the relationship: $E*\rho F = ED(0)$.

However, it is scarcely worth proceeding beyond this stage, since there is a fundamental conflict between the model, and reality. Note that over the period 05h00 to 20h00, the eggs per stomach, EE(t), increases in time. Therefore, ED(t) will also increase over that period according to equation (15). In terms of the assumption of a pulse of spawning at 21h00, this model predicted increase in ED(t) between 05h00 and 20h00 is therefore impossible. One result of this is that the calculated B(t) function will be negative over the period of increasing ED(t).

One is forced therefore to dispense with the $EE = \gamma * \exp(\theta * ED)$ relationship, in developing a suitable model of the dynamic behaviour of $\beta(t)$ and thus of EE(t) and ED(t) (Appendix 4).

Using the estimates of M,a,b,c,d,g,ED(0) and ρF, the 24 hour period values of $\beta(t)$ were calculated at 1/2 hourly intervals using the model described in Appendix 4. As with the previous model, $\beta(t)$ values were negative over a large portion of the daily cycle. This suggests again that the given cubic EE(t) function is incompatible with the model and a requirement that $\beta(t) \geq 0$.

An overall problem with the basic methodology employed here has therefore arisen in attempting to unify the findings into a single model of egg mortality incorporating egg cannibalism. The method used so far has been typified by a series of separate

regressions leading to equations which are then used in a deter-
ministic and fully constrained fashion in the final modelling
stage. The resulting incompatibilities required first that the
exponential EE(t)-ED(t) relationship be discarded. A subsequent
model however points to problems with the cubic form of EE(t).
Rather than discard information, a different approach could be
used in future work, which nevertheless takes account of the
basic observations which are recorded in this thesis. The main
feature of such a more statistical approach would be to do an
overall regression at the final modelling stage. Thus although
the basic functional form of EE(t) and EE(ED) could be pre-defined,
the function parameters would be fitted in terms of the overall
model and forcing $\beta(t) \geq 0$.

The consideration of egg cannibalism as a density-dependent mechanism allows the evaluation of the significance of cannibalism to the stock-recruitment relationship of anchovy to be examined.

The Ricker curve has a maximum when EP $= 1/\beta$ (Ricker 1973). At this stock size the density-dependent term is exp (-1), and the survival rate from density-dependent sources of mortality is therefore 36.8% ($e^{-1} = 0.368$). If cannibalism is the only source of density-dependent mortality, recruitment is maximal when the integration of the cannibalism mortality rate (Rc) over the time from spawning (To) to hatching (Th) is equal to unity (MacCall 1980):

$$\int_{To}^{Th} Rc\ (t)\ dt = 1 \tag{23}$$

where Rc was defined in equation (13).

Based on equations (2) and (8) Rc $= 0.0168\ h^{-1}$ and $0.01488\ h^{-1}$ respectively. By integrating the above integral over the egg stage duration (60 h), values of 1.00 and 0.89 were obtained respectively. Thus, if no further density dependent mortality occurs until recruitment, and if egg cannibalism is the sole density-dependent factor, recruitment for the year studied is close to its maximum level (MacCall 1980).

4. GENERAL DISCUSSION

The convexity of the South African coastline splits the habitat occupied by anchovy into a warm water Southern region and a cold water Western region. Anchovy egg production coincides in time with maximum upwelling but is highest in the warm Southern region where upwelling has minimal influence and egg development is rapid (Shelton and Armstrong 1983). The spawning habitat may be selected on the basis of food abundance and water temperature (Ciechomski and Booman 1982, MacCall 1980). Anchovy may therefore have selected the Agulhas Bank for spawning because water near the surface is generally warmer than 14 C, the lower thermal limit for normal egg development in E. capensis (King et al. 1978). Movement of the larvae from the warm-water southern spawning ground on the Agulhas Bank to the recruitment ground (and juvenile feeding region) on the West Coast is thought to be facilitated by a frontal jet current (Shelton and Hutchings 1981, 1982).

The survival rate during the pre-recruit stage largely determines recruitment variability (Smith 1985). Pre-recruit mortality operates on eggs, larvae and juveniles, the former two being planktonic and the latter nektonic. Mortality occurs from predation, starvation and disease (Lasker 1985). Starvation and predation are believed to be dominant sources of natural pelagic fish mortality (Smith and Lasker 1978). In addition, physical

transport of pre-recruits out of a given spawning/nursery area is also considered a major source of mortality since surrounding waters are typically unfavourable for survival, although actual mortality may be due to predation or starvation (Smith and Lasker 1978). The off-shore Ekman transport in the Benguela region during the peak of upwelling season (coincident with the spawning time for anchovy) may carry eggs and larvae out of the system, and strong winds might dilute food patches through turbulent mixing within the water column as found off California (Lasker 1975), causing great mortality in pre-recruits.

The current conflict over whether starvation or predation is more important in determining fish survival may be largely semantic. Implicit in the starvation hypothesis (Hjort 1926, Lasker 1975, Cushing 1975) is that starvation may not be the actual cause of death but simply that reduced food levels cause increased mortality. This can happen in four fundamental ways : 1) actual starvation, 2) reduced predator-avoidance, 3) reduced growth rate which prolongs the larval stage, thus increasing the period exposed to predation, and 4) increase of predation (and cannibalism as a form of predation). The effect of food concentration on growth and survival of fish larvae has been examined in a number of field and laboratory experiments (Lasker et al. 1970, Lasker 1978, Brownell 1985). High larval survival in artificial conditions at food concentrations equal to average concentrations found in the field suggest that starvation _per se_ is not the dominant

source of mortality (Methot 1981 in Smith 1985).

Starvation mortality is thought to be relatively more important during the first 1-2 weeks of feeding (Hunter 1984), whereas predation seems to be the dominant source of mortality throughout of the first year of life.

Predation as modified by food availability is clearly a very important source of egg and larval mortality (aside from physical advection). The Benguela system seems to exceed food requirements for adult anchovy during "normal" periods. Howver, the temporal and spatial scale at which food becomes available to fish and to larvae particularly, may be limiting (Shannon and Field 1985). Rates of cannibalism are likely to depend on the size, abundance, and distribution of adult food. Eggs patches probably elicit a feeding response by adults in the spawning area (MacCall 1980).

The amount of time spent on feeding will decrease as food abundance increases (O'Connell 1972). Although filter-feeders can continue feeding in darkness, as shown by Hettler (1976) and Holanov and Tash (1978), Cape anchovy possibly become satiated following the increase of food organisms at sea (eggs) during the spawning time (spawning activity indicated by the presence of fish with hydrated oocytes was observed to be concentrated between 18h00 and 24h00 with a pronounced peak at 21h00, M. Armstrong, SFRI, pers. comm.), because eggs were shown to be an important item in the diet of adult anchovy (Fig. 12) and a marked increase

in the incidence of anchovy eggs in anchovy stomachs per unit stomach weight centred at about 21h00 (Fig. 13d). Feeding therefore appears to be reduced or absent after 20h-21h (between 20h-21h and 05h-06h (Fig.13).

High field mortality rates of yolk sac larvae relative to eggs and older larvae have often been reported for anchovy. Egg mortality for Peruvian anchovy has been reported to amount to 60% daily (Santander et al. 1983). In California, the daily mortality of anchovy eggs was estimated to be 53% (Smith and Lasker 1978). In this study it was calculated that 44% of South African anchovy eggs are lost daily (Fig. 8).

Cannibalism has been shown to be an important cause of egg mortality. In this thesis cannibalism on anchovy eggs over the Agulhas Bank area may account for 62%-70% of egg mortality, with a range of values of 30% to 100% resulting from the variance of the estimates of mean number of eggs observed per stomach and rate of egg mortality (equation (5)). It has been reported by Santander et al. (1983) that in Peru egg cannibalism account for 10% of the total anchovy egg mortality. Hunter and Kimbrell (1980) and MacCall (1980) reported that in California the impact of cannibalism on total egg mortality was 28%. In Peru, the rate of anchovy cannibalism on eggs may be lower than in California or in South African anchovy, because the high density of food off Peru may result in less time being spent feeding or less feeding

on their own eggs (MacCall 1980).

The plot showing a decreasing rate of egg survival after cannibalism with increasing egg density (Fig. 15) suggests quantitatively that cannibalism in the South African anchovy is potentially an important compensatory regulatory mechanism of the size of the adult population.

There are at least three major types of density-relationships for predation (Solomon 1949). In (1) (Fig. 20), the number of prey killed increases linearly with prey density, and this means that is a "density-independent" relationship. In (2) the number of prey killed falls as density rises, or remain the same, or increase, so long as the percentage killed is less when density is high; this is an "inverse" density-relationship. In (3) the number of prey killed increases with rising prey density, and there is a proportional increase; this is a "density-dependent" relationship. Only type (3) is a regulatory relationship (Solomon 1976), but when predator and prey are part of the same life cycle like in adult anchovy predating on their own progeny, the non-linearity is not an essential condition for density dependence.
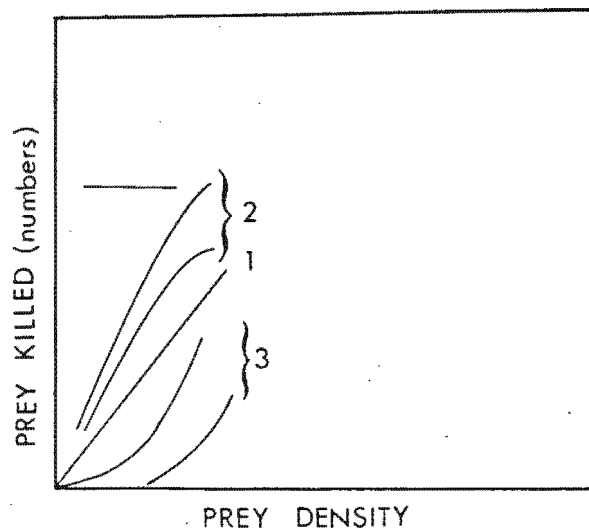
FIG. 20   Three basic density relationship in terms of number of prey killed against population density (from Solomon 1976).

The exponential relationship fitted by equation (15) represents a density-dependent mechanism regulating egg survival as a function of egg density. This relationship could be part of an S-shaped curve (Type III Holling's curve, Holling 1959),(Fig.21), because the food consumption rate must eventually become limited by handling time and stomach evacuation rate (Peterman 1977). All responses level off at high prey densities because the predator becomes satiated and/or runs out of time in which to eat more prey (Murdoch and Oaten 1975).

Since density dependence is assumed by even a linear EE/ED plot (i.e. β significative positive), the exponential shape of the EE/ED curve is suggestive of a further, viz. perhaps a greater proportion of eggs being consumed at increasing egg densities in the sea. This sort of effect, if manifest in other fish preying on anchovy eggs, would lead to a density-dependent response even in the absence of egg cannibalism.
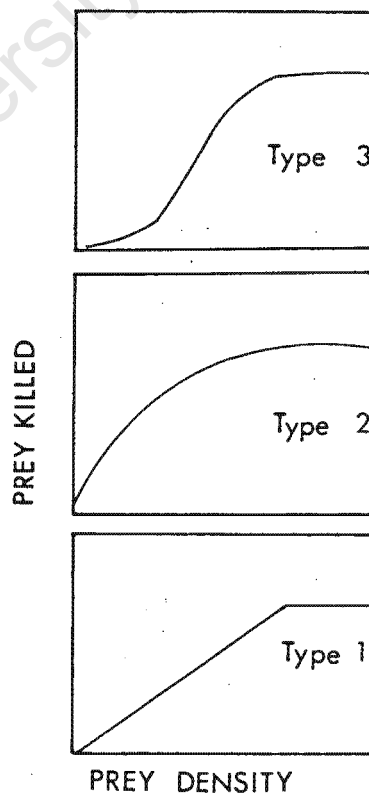
FIG. 21   Holling's three types of functional responses. For each type the number of prey killed by a single predator is graphed against prey density. Only type 3 yields density-dependent mortality (from Holling 1959).

Egg mortality, which becomes relatively heavier as egg density increases, thereby tends to stabilize the prevailing adult population level. Density-dependent mortality of this or other types has long been recognized as being the basis on which the maintenance of intensive long-term fisheries depends (Neave 1953).

The egg production-recruitment relationship in the Ricker model is regulated by a set of mechanisms acting upon the population during the different stages of life. From egg production to recruitment there might be several regulatory mechanisms which can operate to stabilize the size of the adult stock. As an example: cannibalism on eggs, larval competition, cannibalism on larvae, predation on all the different stages of life, change of age at maturity, change of fecundity, behaviour of adults i.e. breakdown of schools. While cannibalism and change in fecundity will provoke a compensatory regulation influencing the domed shape of the Ricker curve, larval competition will flatten the dome as it is related to the net egg production rather than parent stock (Csirke 1980b). Predation and breakdown of schools may provoke a depensatory (or non-compensatory) mortality causing a very reduced stock size, although change in age at maturity may keep the stock out of the depensation area (Armstrong et al. 1983, Shelton and Armstrong 1983).

Because an increase in the abundance of fish is followed by an increase in the abundance of eggs, the most important potential

regulatory mechanism is probably cannibalism by adults on their own eggs. Egg cannibalism has been shown in this study to be a potentially important underlying mechanism which confers structure to the scattered distribution of stock-recruitment points in Cape anchovy although its effect may be masked by a factor of 10:1 by environmental variability (MacCall 1980).

When warm events occur ("El Nino"), the rate of egg cannibalism might increase because density of adults increases in a local area independent of abundance. Not only may the density of spawners be high due to crowding into certain areas, but if food abundance is reduced, the fish will spend more than a usual proportion of their time feeding, which may result in greatly reduced recruitment due to intense egg cannibalism (MacCall 1980).

The output of the first model (Fig. 18 and 19) built to correlate egg hatching with egg production shows that for a given egg production, the cannibalism rate increases with decreasing spawning fraction. Because it was calculated that cannibalism may account for 62%-70% of the total egg mortality (equations (11) and (12)) and the curves of Fig. 19 were generated based on this assumption, egg production must be greater than 3000 eggs.m^{-2} (or fish denser than 4,76 fish.m^{-2}) at a spawning fraction of 15% for density dependent effects to become marked. Acoustic data from the November 1984 survey indicated that the average density of anchovy in the study area was 75g.m^{-2} (SE = 17.49). Assuming the

spawning fraction of 0.15 to be known precisely, the mean value of fish density corresponds to an egg production rate of 3265 eggs.m^{-2}.d^{-1} with 95% confidence interval of 1754-4776. This mean value is significantly greater (0.20<p<0.10) than the egg production obtained from the intercept of the egg mortality curve in Fig. 8. This discrepancy may reflect the consumption of newly spawned eggs by adult anchovy feeding intensively during the spawning period, and may indicate that cannibalism mortality is exerted mainly on newly spawned eggs. The intercept of the egg mortality curve may therefore be underestimated if a large cannibalism mortality of newly spawned eggs has occurred, because the regression only includes egg stages which are fully recruited to the plankton, which only occurs several hours after peak feeding. In an extreme case where cannibalism was entirely on newly spawned eggs because of dispersal of older eggs, the slope of the mortality curve would reflect only density-independent mortality, and the intercept would be underestimated by the number of eggs consumed per night per unit area.

The results of this model must be viewed as being of a qualitative nature, in view of the dynamic effects which are ignored. However, as is demonstrated by the two dynamic models which are presented, a fully dynamic description would require a separate research project, because the preliminary analyses are complicated by various conflicts in the basic equations. Thus the model results set out in Fig. 18 and 19 are the best that can be

attempted at this level, and are anticipated to produce results not too different to what might be produced by a more complete analysis.

5. CONCLUSIONS

By assessing the impact of egg cannibalism on egg mortality of South African anchovy over the Agulhas Bank area it was estimated that cannibalism can account for from 30% to 100% of the total egg mortality with estimates of 62%-70% for the area of intensive spawning which was investigated.

This cannibalistic behaviour was shown to be a potentially important density-dependent compensatory mechanism of the size of the adult stock by regulating egg survival as a function of egg density. The recruitment from spawning to hatching is therefore maximal for the 62%-70% estimates for egg cannibalism because the integration of the cannibalism mortality rate over the stage duration (60h) gives values of about 1.00. A justification for using the Ricker curve in Cape anchovy stock-recruitment relationships has been given.

Although the evaluation of density-independent and density-dependent coefficients show values of about 10 and 1 respectively, and the preponderance of the density-independent influence tends to mask the relative weak regulation of stock abundance (MacCall 1980), cannibalism on eggs is a potentially important underlying functional response determining optimal yield.

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TIME OF DAY	COLLECTION NUMBER	NUMBER OF FISH PER COLLECTION	NUMBER OF EGGS IN CalVET NET SAMPLES	MEAN EGGS PER FISH STOMACH
0800	0209	30	1680	3.06
1000	0210	30	5400	7.36
1000	0105	30	12360	249.27
1000	AA02	30	2080	1.00
1300	AA07	30	6000	24.71
1600	0106	30	3660	13.50
1600	0401	30	7644	36.09
1600	AA08	30	1940	13.76
1800	AA09	30	8500	38.40
2000	AA03	30	6800	52.16
2000	AA10	30	7880	54.00
2000	0301	30	9200	93.00
2000	0201	30	9340	119.63
2000	0402	30	3780	16.65
2000	0101	30	6640	37.82
2200	0203	30	3480	5.80
2200	AA0	30	861	0.65
2400	024	30	180	1.78
2400	003	30	3660	5.90
2400	102	30	60	0.13

APPENDIX 1

Incidence of anchovy eggs in the Agulhas Bank region and in
stomachs of Cape anchovy collected during 1984,1985 anchovy
spawning cruises:

TIME OF DAY	COLLECTION NUMBER	NUMBER OF FISH PER COLLECTION	NUMBER OF EGGS IN CalVET NET SAMPLES	MEAN EGGS PER FISH STOMACH
0100	0406	30	1280	0.6
0100	0205	30	4360	1.93
0100	0304	30	4820	2.20
0202	0407	30	1780	1.16
0202	0305	30	2740	0.16
0202	AA05	30	1520	0.62
0300	0206	30	1840	0.10
0300	0408	30	3680	0.23
0300	0306	30	680	0.53
0300	0103	30	1420	0.13
0400	0207	30	700	1.96
0400	0307	30	2720	0.56
0400	0409	30	3840	1.96
0400	0410	30	2560	1.33
0500	0308	30	4400	4.00
0500	0208	30	1580	0.73
0600	0104	30	2340	1.00
0700	AA06	30	2200	1.00
0700	0411	30	2079	3.20
0700	0309	30	2540	1.13

APPENDIX 2

Monte Carlo simulation program

```
&LIST

10  REM   MEANS AND STANDARD DEVIA
        TIONS OF VARIABLES
20 E = 36.74:SE = 12.72
30 Z = 0.024:SZ = 0.0109
35 J = 3000
40  REM   INITIALIZE COUNTERS
50 I = 0:SP = 0:PS = 0
55 H1 = 0:H2 = 0:H3 = 0:H4 = 0:H5
        = 0
56 H6 = 0:H7 = 0:H8 = 0:H9 = 0:Q =
        0
60 I = I + 1
65  PRINT I
70  GOSUB 1000
80 EE = (ZR * SE) + E
90  IF EE < 0 THEN  GOTO 70
100  GOSUB 1000
110 ZZ = (ZR * SZ) + Z
120  IF ZZ < 0 THEN  GOTO 100
130 P = (EE * 0.0167) / (1 -  EXP
        ( - 60 * ZZ))
140  IF P < 0 THEN  GOTO 70
150  IF P > 1.0 THEN  GOTO 70
160 SP = SP + P
170 PS = PS + P ^ 2
180  IF P >  = 0 THEN  IF P < 0.1
        THEN  LET H1 = H1 + 1
181  IF P >  = 0.1 THEN  IF P < 0
        .2 THEN  LET H2 = H2 + 1
182  IF P >  = 0.2 THEN  IF P < 0
        .3 THEN  LET H3 = H3 + 1
183  IF P >  = 0.3 THEN  IF P < 0
        .4 THEN  LET H4 = H4 + 1
184  IF P >  = 0.4 THEN  IF P < 0
        .5 THEN  LET H5 = H5 + 1
185  IF P >  = 0.5 THEN  IF P < 0
        .6 THEN  LET H6 = H6 + 1
186  IF P >  = 0.6 THEN  IF P < 0
        .7 THEN  LET H7 = H7 + 1
187  IF P >  = 0.7 THEN  IF P < 0
        .8 THEN  LET H8 = H8 + 1
188  IF P >  = 0.8 THEN  IF P < 0
        .9 THEN  LET H9 = H9 + 1
189  IF P >  = 0.9 THEN  LET Q =
        Q + 1
230  IF I = J THEN  GOTO 250
240  GOTO 60
250 PM = SP / I
260 VP = (PS - (SP ^ 2) / I) / (I
        - 1)
270  PRINT "MEAN P = ";PM
280  PRINT "VAR  P = ";VP
290  PRINT
300  PRINT H1,H2,H3,H4,H5,H6,H7,H
        8,H9,Q
400  GOTO 1200
1000 ZR = 2 *  RND (15) - 1:ZR =
        LOG ((1 + ZR) / (1 - ZR)) /
        1.82
1100  RETURN
1200  END
```

APPENDIX 3

Program of the model for calculating the egg survival-egg production relationship

```
]LIST

10   DIM E(3),EH(3)
15   REM   DENSITY INDEPENDENT MORT
     ALITY
20   M = .0072
25   MM =  EXP ( - M * 24)
26   REM   PARAMETERS OF EGGS EATEN
        PER FISH VERSUS EGG DENSITY

30   AL = 0.7866:EX = 0.0005
40   PRINT "EGG PRODUCTION PER M^2
     ?"
41   INPUT EP
45   REM   SPAWNING FRACTION/BATCH
        FECUNDITY/SEX RATIO
50   SF = 0.15
51   BF = 7772
52   SR = 0.54
53   GE = 0.701
55   REM   INITIAL GUESSES OF 1 AND
        2 DAY OLD EGGS
60   E(1) = 0
65   E(2) = 0
66   REM   NUMBER OF FISH TO PRODUC
        E OBSERVED EGG PRODUCTION EP

71   NF = EP / (SF * BF * SR)
90   REM
105  REM   TOTAL EGG DENSITY
120  EG = EP + E(1) + E(2)
125  REM   EGGS EATEN PER FISH
130  EE = AL * EXP (EX * EG)
131  IF EE > 815 THEN  LET EE = 8
     15
132  REM   CANT EAT MORE THAN IS T
     HERE
133  EE = EE * GE * 6 * NF
135  IF EE > EG THEN  LET EE = EG

136  REM   CALCULATE EGGS HATCHED
        AND EGG DENSITY AT 13H.50 FE
        EDING
140  EH = (E(2) - E(2) * EE / EG) *
      EXP ( - M * 12)
141  E(2) = (E(1) - E(1) * EE / EG
     ) *  EXP ( - M * 16.5)
142  E(1) = (EP - EP * EE / EG) *
      EXP ( - M * 16.5)
143  REM   EGG DENSITY
144  EG = E(1) + E(2): IF EG < 0.1
        THEN  LET EG = 0.1
145  EE = AL * EXP (EX * EG)
146  IF EE > 815 THEN  LET EE = 8
     15
147  EE = EE * GE * 9 * NF
148  IF EE > EG THEN  LET EE = EG

149  E(2) = (E(2) - E(2) * EE / EG
     ) *  EXP ( - M * 7.5)
150  E(1) = (E(1) - E(1) * EE / EG
     ) *  EXP ( - M * 7.5)
160  PRINT EH
200  GOTO 90
250  END
```

The following coupled differential equations must be solved to develop a model of the dynamic behaviour of $\beta(t)$, $EE(t)$ and $ED(t)$:

$$\frac{d\overset{\bullet}{EE}(t)}{dt} = \beta(t) * \rho F * ED(t) \; - \; g * \overset{\bullet}{EE}(t) \tag{1}$$

and

$$\frac{dED(t)}{dt} = -M * ED(t) \; - \; \beta(t) * \rho F * ED(t) \tag{2}$$

where $\overset{\bullet}{EE}(t)$ is in units of eggs.m^{-2} in fish stomachs, i.e. $\overset{\bullet}{EE}(t) = EE(t) * \rho F/w$. Equation 2 is readily solved to give:

$$ED(t) = \overset{\bullet}{ED}(0) * \exp \left(-M * t - \rho F * \int_0^t \beta(\psi) * d\psi \right) \tag{3}$$

Substituting this into equation (1) gives:

$$\frac{d\overset{\bullet}{EE}(t)}{dt} + g*\overset{\bullet}{EE}(t) = \beta(t)*\rho F*\overset{\bullet}{ED}(0)*\exp(-M*t-\rho F*\int_0^t \beta(\psi)*d\psi) \tag{4}$$

The left hand-side of equation (4) is a given function of t. On integrating both sides with respect to t, the result is (transfering $\rho F*ED(0)*\exp(-M*t)$:

$$\frac{1}{\rho F*\overset{\bullet}{ED}(0)} * \int_0^t \exp(M*t)*(d\overset{\bullet}{EE}(t)/dt + g*\overset{\bullet}{EE}(t))*dt \tag{5}$$

$$= \int_0^t \beta(t)*\exp(-\rho F*\int_0^t \beta(\psi)*d\psi) = \frac{1}{-\rho F}*\exp(-\rho F*\int_0^t \beta(\psi)\,d\psi) \Big|_0^t \tag{6}$$

$$= \frac{1}{-\rho F} * \left(\exp\left(-\rho F * \int_0^t \beta(\psi) * d\psi\right) - \exp\left(-\rho F * \int_0^0 * \beta(\psi) * d\psi\right) \right) \tag{7}$$

$$= -\frac{1}{\rho F} * \left(\exp\left(-\rho F * \int_0^t \beta(\psi) * d\psi\right) - 1 \right) \tag{8}$$

$$\therefore \exp\left(-\rho F * \int_0^t \beta(\psi) * d\psi\right) = 1 - \frac{\int_0^t \exp(M*t) * (d\dot{EE}(t)/dt + g*\dot{EE}(t)) * dt}{\dot{ED}(0)} \tag{9}$$

$$\therefore \int_0^t \beta(\psi) * d\psi = -\frac{1}{\rho F} \log\left(1 - \frac{\int_0^t \exp(M*t) * (d\dot{EE}(t)/dt + g*\dot{EE}(t) * dt}{\dot{ED}(0)}\right) \tag{10}$$

$$\therefore \beta(t) =$$

$$\frac{1}{\rho F} * \left(\frac{1}{1 - \int_0^t \exp(M*t) * \left(\dfrac{\dfrac{d\dot{EE}(t)}{dt} + g*\dot{EE}(t)}{\dot{ED}(0)} \right) * dt} \right) * \exp(M*t) * \left(\frac{\dfrac{d\dot{EE}(t)}{dt} + g*\dot{EE}(t)}{\dot{ED}(0)} \right) \tag{11}$$

$\dot{ED}(0)$ is the mean density of eggs in the sea at 21h00, which can be calculated from the results set out in Fig.8. If the fitted curve in Fig.8 is ED(t), the $\dot{ED}(0)$ is given by the following sum for $n \longrightarrow \infty$:

$$\dot{ED}(0) = ED'(0) + ED'(24) + ED'(48) + \ldots\ldots\ldots ED'(n*24) \tag{12}$$

$$= ED'(0) * (1 + \exp(-24*Z) + \exp(-48*Z) \ldots\ldots\ldots \exp(-n*24*Z)$$

In other words, for Z constant, the egg population at time 0 is

the sum of the numbers in each cohort, assuming breeding occurs once a day

Now, $\overset{\bullet}{EE}(t)$ is given:

$$EE(t) = a*t^3 + b*t^2 + c*t + d$$

where a,b,c,d, are taken from Fig. 13(b) and converted by the factor $\rho F/w$. Thus:

$$\beta(t) = \frac{1}{\rho F * \overset{\bullet}{ED}(0)} * \left(\frac{\exp(M*t)*(g*a*t^3 + (g*b+3*a)*t^2 + (g*c+2*b)*t + g*d+c)}{1 - (x)} \right) \quad (13)$$

where

$$x = ((\exp(M*t)*t^3/M - 3*t^2*\exp(M*t)/M^2 + 6*\exp(M*t)*t/M^3 - 6*\exp(M*t)/M^4$$

$$+6/M^4)*g*a + (\exp(M*t)*t^2/M - 2*t*\exp(M*t)/M^2 + 2*\exp(M*t)/M^3 - 2/M^3)*$$

$$(g*b+3*a) + (\exp(M*t)*t/M - \exp(M*t)/M^2 + 1/M^2)*(g*c+2*b) + (\exp(M*t)/$$

$$M - 1/M)*(g*d+c))/\overset{\bullet}{ED}(0)$$

APENDIX 5

Description of units

E_t	:	Eggs at age t	(eggs)
E_0	:	Eggs at age 0	(eggs)
Z	:	Instantaneous rate of egg mortality	(h^{-1})
t	:	time of day	(h)
C	:	Mean daily consumption of eggs per fish	(eggs.d^{-1}.$fish^{-1}$)
EE	:	Mean number of eggs per fish stomachs	(eggs. $fish^{-1}$)
g	:	Instantaneous rate of gastric evacuation for anchovy eggs	(h^{-1})
$EE(t)$	:	Total number of eggs per fish stomachs	(eggs.$fish^{-1}$)
$R(t)$	:	Rate of egg ingestion	(eggs.$fish^{-1}$.h^{-1}.m^{-2})
w	:	weight of fish	(g)
ρF	:	density of fish	(g.m^{-2})
$C(t)$	:	Total eggs eaten per fish t hours since peak spawning (assuming pulse at 21h00)	(eggs.$fish^{-1}$)
F	:	Egg production per gram of fish body weight per night	(eggs.g^{-1}.$night^{-1}$)
f	:	Eggs produced per gram of females (batch fecundity)	(eggs.g^{-1})
R_c	:	Instantaneous rate of egg cannibalism	(h)
ED and $ED(t)$	:	Eggs in sea per m from most recent nights spawning	(eggs.m^{-2})

EE$^{\bullet}$(t) : Eggs.m in fish stomachs
(=EE(t)w/pF)   (eggs.m^{-2})

β : Density-dependent coefficient
of egg mortality   (m^2.g^{-1}.h^{-1})

S   : Total spawning biomass   (g)

V   : Total spawning habitat volume   (m^2)

M   : Density-independent egg
mortality rate   (h^{-1})

EE$^{\bullet}$(t) : Eggs.m in fish stomachs
(=EE(t)w/pF)   (eggs.m^{-2})