EGG CANNIBALISM BY ANCHOVY IN THE SOUTHERN BENGUELA CURRENT REGION

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## Edy Sylvia Valdes Rodriguez

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submitted for the Degree of Master of<br>
Department of Zoology<br>
University of Cape Town<br>
Cape Town A thesis submitted for the Degree of Master of Science<br>Department of Zoology

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University of Cape Town

Cape Town Town

1986

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# WY PARENTS MEMORY AND TO DAVID, MY HUSI TO MY PARENTS MEMORY AND TO DAVID, MY HUSBAND MY PARENTS MEMORY AND TO DAVID,

### TABLE OF CONTENTS



#### I wish to express my thanks and appreciation to

My supervisors at the Zoology Department of the University of Cape Town (UCT), Cape Town, Dr. C. L. Griffiths and Professor J. G. Field, for their this study. interest and constructive criticism of I wish to express my thanks and appreciation to :<br>My supervisors at the Zoology Department of the University of<br>Cape Town (UCT), Cape Town, Dr. C.L.Griffiths and Professor<br>J. G. Field, for their interest and constructive c

I especially express my thanks to Drs. J. Alheit of the Alfred-Wegener-Institut for Polar and Marine Research, Bremerhaven, Germany, and M.0. Bergh of the University of Cape Town (UCT), Cape Town, for their constructive criticism and I am indebted to Dr. M.O. Bergh for his help in the quantification of the thesis. express my thanks to Drs. J. Alheit of the Alfred-Wegener-Institut for Polar and Marine Research, Bremerhaven,<br>Germany, and M.O. Bergh of the University of Cape Town (UCT),<br>Cape Town, for their constructive criticism and I am indebted to<br>Dr. M.O. Bergh for his help in the

chanks to Mr. P. A. Shelton, Sea Fishe<br>FFRI), Cape Town, for his able guidance<br>ion leading to the development and<br>n project; as well as I thank him his<br>glish writing.<br>to Dr. M.J.Armstrong, SFRI, for his<br>stions regarding th My sincere thanks to Mr. P. A. Shelton, Sea Fisheries Research Institute (SFRI), Cape Town, for his able guidance and invaluable discussion leading to the development and conclusion of this research project; as well as I thank him his patience with<br>my Spanish-English writing.<br>Many thanks to Dr. M.J.Armstrong,SFRI, for his criticism and my Spanish-English writing.

Many thanks to Dr. M. J. Armstrong, SFRI, for his criticism and helpful suggestions regarding the conclusion of this thesis.

Dr. R.J,M. Crawford, SFRI, for encouragement and able discussion.

Dr. D.C. Duffy, UCT, for his sincere advice and encouragement in the first steps towards the M.Sc. thesis. helpful suggestions regarding the conclusion of this t<br>Dr. R.J.M. Crawford, SFRI, for encouragement and able<br>Dr. D.C. Duffy, UCT, for his sincere advice and encourthe first steps towards the M.Sc. thesis.

the early work towards the thesis, and for his comments regarding work towards its development.

Dr. C.L. Brownell, SFRI, for his confidence and support in<br>the early work towards the thesis, and for his comments regarding<br>its development.<br>Mr. A. Berrutti and R. Prosch, scientific staff of the Pelagic<br>Section, SFRI, fo Mr. A. Berrutti and R. Prosch, scientific staff of the Pelagic Section, SFRI, for their steadfast support, co-operation and comments on the research work.

Mr. T. van Dalsen and their staff, SFRI, as well as Miss S. Wright, SFRI, for their efficiency in the drawing of the figures and SFRI, for photographing. I. van Dalsen and their staff, SFRI, as well as Miss S. Wright,<br>, for their efficiency in the drawing of the figures and<br>ographing.<br>D. Horstmann, SFRI, for his assistance in photographing ths<br>ach contents of anchovy.<br>B. We

Mr. D. Horstmann, SFRI, for his assistance ·in photographing ths stomach contents of anchovy.

Mr. B. Wessels and Mrs. A. Meltzer, SFRI, for their help in the search for references.

To all the staff of the Computer Section (SFRI) in general and specially to H. Coetzee for his aid and helpful co-operation in running the computer programs and to J.Roberts for his help with references.<br>staff of the Computer Section (SFRI) in general and<br>o H. Coetzee for his aid and helpful co-operation in<br>computer programs and to J.Roberts for his help with verthe word processor program.

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To Mr. J.P. Matthews, SFRI, for his kind advice and support in the administrative matters inherent to my research work, as well as for his sincere and sympathetic help in improving the English. To Mr. J.P. Matthews, SFRI, for his kind advice and support<br>in the administrative matters inherent to my research work, as<br>well as for his sincere and sympathetic help in improving the<br>English.

To all the Sea Fisheries Research Institute staff in general,<br>scientists, technical people and personnel of the R.S. Africana scientists, technical people and personnel of the R.S. Africana vessel, who have contribute in one or other manner to make this<br>thesis possible. To Sea Fisheries Research Institute for the thesis possible. To Sea Fisheries Research Institute for the logistical support given. Thanks to the people of the Benguela Ecology Program (BEP) for logistical Thanks to the people of the

the encouragement and the possibility of expressing in a lunch-time talk the scope of the research work done. Thanks to the people of the Benguela Ecology Program (BEP) for<br>the encouragement and the possibility of expressing in a lunch-time<br>talk the scope of the research work done.

I am indebted to Profesor R.D. Cherry, former Dean of the Faculty of Science of the University of Cape Town, for support and encouragement in my first steps of this research work and the opportunity to develop this M.Sc. thesis. I am indebted to Profesor R.D. Cherry, former Dean of the Faculty<br>of Science of the University of Cape Town, for support and<br>encouragement in my first steps of this research work and the<br>opportunity to develop this M.Sc. t

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to develop this M.Sc. thesis.<br>
express my thanks to Mr. G.H. Stand<br>
ries Research Institute, for his constant<br>
interest in my research work and f I wisht to express my thanks to Mr. G.H. Stander, Director of Sea Fisheries Research Institute, for his constant encouragement and helpful interest in my research work and for permission to use the results of this project for an M.Sc degree. and helpful interest in my research work and for permission to<br>use the results of this project for an M.Sc degree.<br>Finally, to my husband, D. Szeinfeld, for his support, gratifying

confidence in times of stress and constant encouragement towards<br>the M.Sc degree. the M.Sc degree.

#### DECLARATION

This is to declare that this dissertation has not been previously This is to declare that this dissertation has not been previously<br>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 of samples analysed in this thesis were obtained on Sea Fisheries<br>Research Institute (SFRI) R.S. Africana 1984-1985 anchovy spawning<br>cruises by SFRI personnel. Anchovy eggs were sorted from plankton<br>samples, staged and age 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. Larva Program (CELP), such as supplementary data on eggs sampled<br>on the West Coast and data from incubation experiments carried<br>out on board of R.S. Africana vessel were provided by Mr. P. A.<br>Shelton. The Monte Carlo simul calculating the egg survival-egg production relationship were<br>developed with the help of Dr. M.J. Armstrong. The subsequent<br>models and general quantification of the thesis was made with the<br>help of Dr. M. O. Bergh. 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. 0. Bergh.

Fith the help of Dr. M.J. Armstrong, 1<br>eneral quantification of the thesis was<br>1. 0. Bergh.<br>Cape Towns of Cape Towns and Transfer of Cape Towns and Edy Sylvia Valdes Rodriguez

ABSTRACT

the same time within an area of inte<br>ulhas Bank, using an Engels 308 midwat<br>respectively. Fish samples were fro<br>20°C shortly after capture. Plankto<br>formaldehyde solution. Fish were me<br>ghed (total and ovary mass) and de-sto 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 adult anchovy and plankton were collected on Sea<br>Fisheries Research Institute R.S. Africana 1984-1985 anchovy<br>spawner biomass estimation cruises. A total of 40 sets of anchovy<br>samples of 30 fish each and 40 plan 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 roughly at the same time within an area of intensive spawning<br>over the Agulhas Bank, using an Engels 308 midwater trawl and a<br>CalVET net respectively. Fish samples were frozen in a deep<br>freeze at - 20°C shortly after captu Weight of the stomach contents were determined and anchovy eggs<br>in the stomach were counted. Anchovy eggs in CalVET net samples<br>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. eggs in the plankton on the Agulhas Bank and off the West Coast<br>were plotted to compare egg density in the two areas. Approximately<br>53% of the eggs caught over Agulhas Bank occurred in only 25% of

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. was plotted of abundance of eggs in the stomachs of fish.<br>Egg patchiness caused a skewed frequency distribution of egg<br>abundance in anchovy stomachs. Feeding time was estimated from an<br>examination of the relationship betwe

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 densitydependent functional response. 2<br>2 Based upon a developmental stage/temperature/age key, mortality<br>rates of eggs in the sea were calculated, and it was estimated<br>that 44% of anchovy eggs were lost daily. Taking into account<br>estimated rates of egg mortal was estimated to account for about 62%-70% of the egg mortality.<br>The rate of cannibalism was shown to be consistent with a density<br>dependent functional response.

2

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#### l.INTRODUCTION 1.INTRODUCTION

Anchovy <u>Engraulis capensis</u> (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<br>is dependent on the consistent production of eggs and the survival<br>of the early reproductive stages. However, clupeoid populations is dependent on the consistent production of eggs and the survival of the early reproductive stages. However, clupeoid populations world-wide are notoriously variable Hunter 1982, Lasker and MacCall 1983). Murphy 1977, Blaxter and

Iasker and MacCall 1983).<br>
Cause of variability in clupeoid po<br>
e the effect of environment on the su<br>
(Csirke 1979, 1980a, MacCall 1980, Parri<br>
nvironment may also affect the reproduct<br>
cander and Decker 1969).<br>
1ifornian The main cause of variability in clupeoid populations is thought to be the effect of environment on the survival of the world-wide are notoriously variable Murphy 1977, Blaxter and<br>
Hunter 1982, Lasker and MacCall 1983).<br>
The main cause of variability in clupeoid populations is<br>
thought to be the effect of environment on the survival of the 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. of adults (Stander and Decker 1969).<br>
In the Californian anchovy, <u>E. mordax</u>, density dependence is<br>
thought to account for only 10 % of the variability in the<br>
survival of the early stages (MacCall 1980). Crawford et al.

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 in the population variability of <u>E. capensis</u>.<br>
Shelton et al. (1985) reported on the effects of short and<br>
long period environmental variability on the anchovy population<br>
in the Benguela Current system and found that, w



Anchovy Engraulis capensis (Gilchrist). FIG. 1

5<br>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<br>or competition may be small relative to the effect of the environ-<br>ment, density dependence is the underlying functional response 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). ermining optimal yield (Shelton and Armstrong 1983).<br>Egg cannibalism in clupeoid populations has been noted to

rious parts of the world by a numbe<br>
chovy, <u>Engraulis anchoita</u> (Ciechomski 19<br>
<u>japonicus</u> (Hayasi 1967) ; Californ<br>
oukashkin 1970); Peruvian anchovy, <u>E. 1</u><br>
1980, Rojas de Mendiola and Ochoa 1<br>
al. 1969). Recently the occur in various parts of the world by a number of workers:<br>Argentine anchovy, <u>Engraulis anchoita</u> (Ciechomski 1967); Japanese Argentine anchovy, Engraulis anchoita (Ciechomski 1967); Japanese anchovy, <u>E. japonicus</u> (Hayasi 1967) ; Californian anchovy, <u>E. mordax</u> (Loukashkin 1970); Peruvian anchovy, <u>E. ringens</u> (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<br>with estimated rates of egg consumption (Hunter and Kimbrell 1980,<br>MacCall 1980, Santander et al. 1983). with estimated rates of egg consumption (Hunter and Kimbrell 1980, MacCall 1980, Santander et al. 1983). Mendiola 1980, Rojas de Mendiola and Ochoa 1973, Rojas de<br>diola et al. 1969). Recently the importance of-cannibalism in<br>mortality of the eggs of <u>E. mordax</u> and <u>E. ringens</u> has been

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<br>and yolk sac larvae would only be subject to cannibalism (MacCall and yolk sac larvae would only be subject to cannibalism (MacCall 1980) or predation (Brownell 1983, Lasker 1985) by other components<br>of the biota. However, after yolk sac absorption, competition for<br>food and predation may play an important role. Hjort's (1926) 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 might be strongly influenced by the amount and kind of food<br>available, has been supported by a number of scientists (Lasker 1975, Parrish et al. 1983). The Benguela system appears to exceed<br>food requirements of the adult anchovy population during "normal"<br>periods (Shannon and Field 1985). However, the temporal and 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<br>particularly to larvae, may be limiting (Shannon and Field 1985). particularly to larvae, may be limiting (Shannon and Field 1985).

32 (in Lasker 1985) found a smooth mond<br>se in number of eggs and larvae and he s<br>rest the Hjort hypothesis of a high lan<br>om starvation beginning at yolk absorpt<br>nian anchovy. Kawai and Isibasi (1<br>of food or predatory loss Hunter 1982 (in Lasker 1985) found a smooth monotonic expone-<br>ntial decrease in number of eggs and larvae and he suggested that ntial 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 resulting from starvation beginning at yolk absorption" at least<br>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. whether lack of food or predatory loss to other fish would be the major causes of larval mortality. They hypothesized that canniba-<br>lism on larvae and predation would be the major causes of larval<br>mortality. Cushing and Ha

Cannibalism on eggs in E. mordax has been shown to account on 28 % of the total egg mortality (Hunter & Kimbrell 1980,<br>Mac Call 1980). In Peru egg cannibalism in <u>E. ringens</u> accounted<br>on 10 % of the total egg mortality (Santander et al. 1983). 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<br>population size. The result of increased density dependent<br>mortality is to cause a more steeply declining right-hand limb of 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. 7<br>Ricker (1954, 1958) was the first to explicitly consider<br>mibalism as a density dependent cause of recruitment. In<br>model, Ricker differentiates between two causes of mortal-The Ricker model is based on a predator-prey interaction, where<br>any increase in the abundance of eggs or larvae is simultaneously<br>followed by an increase in the abundance of the predators (Ricker

in the abundance of eggs or larvae is s<br>in increase in the abundance of the pred<br>? 1980b). The most obvious case of<br>by adults on their own eggs.<br>Discussed this thesis is to assess the<br>portality in South African<br>relationshi The purpose of this thesis is to assess the impact of egg cannibalism by adults on their own eggs.<br>The purpose of this thesis is to assess the impact of egg<br>cannibalism on total egg mortality in South African anchovy, and to study the relationship between cannibalism and density of eggs<br>in Cape anchovy in order to evaluate whether this conforms to a<br>density-dependent or density-independent response. 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<br>so as to coincide with the peak of the anchovy spawning season 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).<br>2.2 <u>Egg sampling and processing</u> 2.1 <u>Sampling strategy</u><br>Anchovy stomach samples and plankton samples were collected<br>on Sea Fisheries Research Institute R.S. Africana cruises of<br>5-30 November 1984 and 11 November to 2 December 1985 over

#### 2.2 Egg sampling and processing

Janux Legion (11g. 2). Incse cruises<br>
1986), as the main aim was to dete<br>
thiomass (Hampton et al. 1985).<br>
11ing and processing<br>
eggs were collected in 31 vertical h<br>
cofi Vertical Egg Tow) net (Smith et a<br>
200 m (or 10 m Anchovy eggs were collected in 31 vertical hauls with the Anchovy eggs were collected in 31 vertical hauls with the<br>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<br>surface over a period of 4 days at stations positioned within<br>high densities of both eggs and spawning fish during the November<br>1984 cruise (Fig. 2). An addition 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  $0.05 \text{m}^2$  area and the mesh of 0.150mm, selected to retain anchovy eggs (Smith et al. 1985). eggs for the estimation of daily egg production. The net consists<br>of two principal parts: the mouth of 0.05m<sup>2</sup> area and the mesh of<br>0.150mm, selected to retain anchovy eggs (Smith et al. 1985).



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The total length of the net is less than l.5m (Fig. 3). During The total length of the net is less than  $1.5$ m (Fig. 3). During<br>each tow the net was retrieved rapidly at  $1 \text{ m.s} e^{-1}$  to avoid uneven trajectories due to ship's drift and undersea currents. An Universal Underwater Unit designed by Sea Fisheries Research Universal Underwater 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. ies due to ship's drift and undersea currents. An<br>Underwater Unit designed by Sea Fisheries Research<br>was attached below the CalVET net. The unit contained

e completion of a CalVET tow the net<br>fine water spray and the plankton sample<br>ed in a 300ml jar filled with 4% buffet<br>er solution. In the laboratory anch<br>m the plankton samples under a binocul<br>with a 20 x magnification. Eg 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 microscope with a 20 x magnification. Eggs were assigned to 11<br>stages based on the degree of embryonic development following the<br>method of Moser and Alhstrom (1985) (Fig. 4). The abundance of<br>each stage in the samples was 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 microprocessor on board the vessel, which recorded and plotted<br>the temperature/depth profile for the tow.<br>After the completion of a GalVET tow the net was washed<br>down with a fine water spray and the plankton sample was imm from the time of day that newly fertilized eggs appeared in the<br>egg collection and from observations on the spawning behaviour or<br>condition of the adults sampled (M. Armstrong, SFRI, pers.<br>comm.). Data from incubation expe

thermal gradient incubator method of King (1977) on board the R.S. Africana during the November, 1984 cruise (Fig. 5) were used, together with <u>in situ</u> measurements of surface temperature



 $\overline{11}$ ...... ......



Eleven ma tic matic egg showing relationship of epiboly and tail<br>length to stage (from Moser and Ahlstrom 1985). developmental-stages of anchovy eggs and egg showing relationship of epiboly to stage (from Moser and Ahlstrom 1985) diagramand tail matic egg showing relationship of epiboly and tail Moser and Ahlstrom 1985).

FIG. 4



FIG. 5

Anchovy egg development curves showing the predicted mean age of 11 developmental stages at temperature 11 12 13 14 15 16 17 18 19 20<br>
TEMPERATURE(°C)<br>
Anchovy egg development curves showing the predicted<br>
mean age of 11 developmental stages at temperature<br>
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. represents the maximum incubation temperature that eggs would be<br>likely to encounter in the upper mixed layer. Data from age and<br>abundance of eggs were used to estimate hourly egg mortality rates.<br>2.3 <u>Stomach sampling and</u>

#### 2.3 Stomach sampling and processing

East by means of the Engels 500 minuw<br>same area and at the same time as the C.<br>is rectangular with extended lower win<br>n at the headline and at a towing speed<br>ing of 15-18m is mantained (H. Crous, S.<br>cod-end was fitted with 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. were collected by means of the Engels 308 midwater trawl in<br>roughly the same area and at the same time as the CalVET samples.<br>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 Sm) of 12mm mesh size. Samples were preserved by blast freezing at -20°C immediately after capture. size of 800mm at the headline and at a towing speed of ca. 3 knots<br>a mouth opening of 15-18m is mantained (H. Crous, SFRI, pers.<br>comm.). The cod-end was fitted with a cod-end liner (length 5m)<br>of 12mm mesh size. Samples we

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

#### 3. DATA ANALYSIS AND RESULTS

# 3.1 Estimation of egg mortality rate 15<br>3. DATA ANALYSIS AND RESULTS<br>3.1 Estimation of egg mortality rate

the density off the West Coast, confirming the major spawning area for Cape and<br>of the eggs collected occurred in only<br>it the largest number collected in one<br>epresented about 8% of the total numb<br>indication of the degree o Fig. 6 shows the anchovy egg distribution map during November distribution during November 1984 survey and all the grid stations. Frequency distributions of<br>the densities of eggs in the plankton over the Agulhas Bank 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,<br>which is an indication of the degree of patchiness found in egg which is an indication of the degree of patchiness found in egg distributions at sea. The mean density was 3755.6 eggs per  $\overline{\tt m}^2$  . (Fig. 2) and off the West Coast (Fig. 6) were plotted for compa-<br>rison (Fig. 7). The density of eggs over the Agulhas Bank was<br>higher than the density off the West Coast, confirming that the<br>Agulhas Bank is the major spawn

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

$$
Et = Eo * exp (-Z * t)
$$
 (1)

where  $Et = number of eggs at age t$ Eo = number of eggs at age  $0$ Et = number of eggs at age t<br>Eo = number of eggs at age 0<br>Z = hourly instantaneous rate of mortality t age of eggs (hours) age eggs (hours)



*°'* 





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; a) Frequency distribution of egg densities in the<br>plankton on Agulhas Bank area. b) Frequency distribution<br>of egg densities in the plankton off the West Coast.

the plankton but not yet hatched were<br>so that the earliest and latest develop<br>from the calculations. The parameter ex-<br>ean asymptotic SE 95% asymtotic confi<br>08.8 509.16 896.92 - 2<br>0.024 0.01 0.0026 -<br>of determination  $(r^2)$ Estimates of Eo and Z were obtained by non-linear least squares regression of egg density versus age (Gauss Newton method; squares regression of egg density versus age (Gauss Newton method;<br>SAS Inst. Inc. 1982) (Fig. 8), where the age of eggs in CalVET net samples was determined initially using the egg development net samples was determined initially using the egg development<br>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<br>were omitted from the calculations. The parameter estimates were: were omitted from the calculations. The parameter estimates were:





Coefficient of determination  $(r^2)$  .......... 0.58 Number of observations Number of observations ..................... 90 0.58 . . . . . . . . . . . . . . . . . 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<br>adult anchovy sampled (Fig. 10 and 11). There was a mean of 19.9<br>(SE = 7.1) anchovy eggs per stomach. The maximum number of eggs 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



l.O





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



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

found in a single stomach was 815 eggs, which formed 3.5% of the found in a single stomach was 81S eggs, which formed 3.S% of the total number in the stomachs of all fish sampled. total number in the stomachs of all fish sampled.

on, one percentage of from wrencast<br>he number of eggs in the stomach per u<br>ents were plotted against time of d<br>elsh 1968, Noble 1972). A third ord<br>as fitted to the data using a linear<br>Inst. Inc. 1982). The data suggest tha A direct relationship was found between the weight of the A direct relationship was found between the weight of the stomach and number of eggs observed per stomach (Fig. 12), stomach and number of eggs observed per stomach (Fig. 12), suggesting that eggs were an important item in the diet of adult suggesting that eggs were an important item in the diet of adult anchovy sampled during the present study. To estimate the duration 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 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) stomach contents were plotted against time of day (Fig. 13) Keast and Welsh 1968, Noble 1972). A third order polynomial<br>regression was fitted to the data using a linear least squares regression was fitted to the data using a linear least squares method (SAS Inst. Inc. 1982). The data suggest that a reduction method (SAS Inc. The data suggest that a reduction or cessation in feeding occurred from ca. sunset (20h-2lh) to or cessation in feeding occurred from ca. sunset (20h-2lh) to ca. sunrise (05h-06h). ca. sunrise (OSh-06h).

The mean number of eggs observed per stomach during the The mean number of eggs observed per stomach during the feeding time (from 05h00 to 20h00) was 36. 74 (SE = 12. 72) (see feeding time (from OShOO to 20hOO) was 36.74 (SE = 12.72) (see Appendix 1). If the mean number of eggs per stomach during the Appendix 1), If the mean number of eggs per stomach during the feeding period and the duration of feeding are considered, the feeding period and the duration of feeding are considered, the impact of cannibalism on egg mortality can be assessed using the impact of cannibalism on egg mortality can be assessed using the equation of Darnell and Meierotto 1962, Tyler 1970, Noble 1972). equation of Darnell and Meierotto 1962, Tyler 1970, Noble 1972).

The average daily consumption of eggs by anchovy was estimated The average daily consumption of eggs by anchovy was estimated from 630 fish samples collected during feeding time, using the from 630 fish samples collected during feeding time, using the





FIG. 13 FIG. 13

Third order polinomial model for a) weight of stomach Third order po1inomial model for a) weight of stomach contents versus time of day; b) number of eggs in fish contents versus time of day; b) number of eggs in fish stomachs versus time of day; c) percentage of fish stomachs versus time of day; c) percentage of fish without eggs in the stomach versus time of day; d) without eggs in the stomach versus time of day; d) number of eggs in the stomach per unit weight of number of eggs in the stomach per unit weight of number of oggs in die eerste day. Points are means for 30 fish and means of 2-4 trawls. Full arrows (Sl for 30 fish and means of 2-4 trawls. Full arrows (Sl and S2) indicate sunrise and the sunset respectively. and S2) indicate sunrise and the sunset respectively. Open arrows indicate points out of range of scale. Open arrows indicate points out of range of scale.

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

$$
C = EE * g * t \tag{2}
$$

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

EE mean number of eggs observed per stomach EE mean number of eggs observed per stomach

g hourly instantaneous rate of gastric evacuation <sup>g</sup>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:

 $C = 36.74 * 0.701 * 15$ 

$$
= 386.32 \text{ eggs.} d^{2}
$$

Given a mean weight per fish of  $14.5$  g calculated from  $630$  fish, this would be equivalent to 26.64 eggs.g<sup>-1</sup>.d<sup>-1</sup>.

an daily consumption per fish, C, was  $C = 36.74 * 0.701 * 15$ <br>=  $386.32$  eggs.d<sup>-1</sup><br>weight per fish of 14.5 g calculated f<br>equivalent to 26.64 eggs.g<sup>-1</sup>.d<sup>-1</sup>.<br>Ny-state conditions, equation (2) res<br>eggs per stomach (or per Under steady-state conditions, equation (2) results from the Under steady-state conditions, equation (2) results from the balance for eggs per stomach (or per fish), EE(t), as follows balance for eggs per stomach (or per fish), EE(t), as follows (M.0. Bergh, University of Cape Town, UCT, pers. comm.): (M.O. Bergh, University of Cape Town, UCT, pers. comm.):

rate of change  $\triangledown$  = rate of egg ingestion - rate of egg evacuation of eggs per stomach of eggs per stomach

 $dEE(t)$ dt = R(t) \* w/(pF) - g \* EE(t)(eggs.fish<sup>1</sup>.h<sup>-1</sup>)(3) dt dt

Where  $EE(t) = total number of eggs per fish stomachs$  $R(t)$  = rate of egg ingestion (eggs.fish<sup>-1</sup>.h<sup>-1</sup>.m<sup>-2</sup>)  $w = weight of fish (g)$ 

$$
\rho F = density of fish (g.m-2)
$$

and g has been defined in equation (2). and g has been defined in equation (2).

Therefore, Therefore,

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

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

$$
C(t) = \int_{0}^{t} \frac{dEE(t)}{dt} + g * EE(t)) * dt
$$
 (5)

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

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

$$
C(24) = \int_{0}^{24} g * EE(t) * dt = g * EE * t
$$
 (7)

Jo dt<br>
= EE(t) - EE(0) +  $\int_0^t g * EE(t)$ <br>
seen that equation (2) results from a<br>
1)<br>
D)<br>
dependent of t; EE(t) = EE, so that<br>  $\int_0^{24} g * EE(t) * dt = g * EE * t$ <br>
cubic equation describing the feeding<br>  $\frac{3}{2}$ <br>
i.e. EE(t) = a\*t + b\*t Because of the cubic equation describing the feeding' rhythm shown Because of the cubic equation describing the feeding' rhythm shown 3 2 in Fig. 13(b), i.e.  $EE(t) = a*t + b*t + c*t + d$ , the integral to obtain C(24), the total number of eggs eaten in a 24 hour period obtain G(24), the total number of eggs eaten in a 24 hour period per fish, is as follows: per fish, is as follows: 3 2

$$
C(24) = EE(24) - EE(0) + \int_{0}^{24} g * (at + bt + ct + d)dt(eggs, fish)(8)
$$
  
= 299 eggs.fish<sup>-1</sup>.d<sup>-1</sup>

For a mean weight per fish =  $14.5$  g,  $C(24)$  = 20.6 eggs.g<sup>1</sup>.d<sup>-1</sup> Thus, using equation (8) the total number of eggs eaten daily per Thus, using equation (8) the total number of eggs eaten daily per fish was calculated as 20.6 eggs.g<sup>d</sup>.d, whereas using equation (2)

the mean daily egg consumption per fish was calculated as 26.64 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 The proportion of egg production consumed by cannibalism was calculated by assuming that a single day's consumption of was calculated by assuming that a single day's consumption of eggs from the daily cohorts produced during the preceding 2-3 eggs from the daily cohorts produced during the preceding 2-3 days was equivalent to the consumption of eggs from a single days was equivalent to the consumption of eggs from a single cohort during the 2.5 days between fertilization and hatching (at cohort during the 2.5 days between fertilization and hatching (at 15 C). Thus: 15 e). Thus:

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

 $Zc = C/F$ <br>
portion of egg production consumed due<br>
shown the consequence of Cape Town of Fish body weight<br>
ced as:<br>  $F = f * d * s$ <br>
sproduced per gram of females (batch 1 where Zc = proportion of egg production consumed due to cannibalism 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<br>F was calculated as:

F was calculated as:

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

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

- <sup>d</sup>= proportion of females spawning each night (spawning <sup>d</sup>= proportion of females spawning each night (spawning fraction) fraction)
- s = ratio of mass of females to the combined mass of males and females (sex ratio) and females (sex ratio)

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

 $\mathbf{v}$ 28

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

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

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

 $Zc = 26.64/43.41$ 0.61 0.61 Alternatively, considering equation (8): Alternatively, considering equation (8):  $Zc = 20.6/43.41$  $= 0.47$ 

Om equation (2) as:<br>  $Zc = 26.64/43.41$ <br>  $= 0.61$ <br>  $Zc = 20.6/43.41$ <br>  $= 0.47$ <br>
ontion of egg mortality caused by cannot control of egg mortality caused by cannot<br>  $\therefore$  the period prior to hatching was call<br>  $\therefore$  egg prod The proportion of egg mortality caused by cannibalism (Pc) The proportion of egg mortality caused by cannibalism (Pc) during the 60 hour period prior to hatching was calculated as the during the 60 hour period to hatching was calculated as the proportion of egg production consumed due to cannibalism divided proportion of egg production consumed due to cannibalism divided by the proportion of egg production lost due to all causes of by the proportion of egg production lost due to all causes of mortality. Using data from equation (2): mortality. Using data from equation (2):

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

where EE,g and t were defined in equation (2), F was defined in 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 variance of Pc were estimated empirically by Monte Carlo simulation
30<br>(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  $\pm$  2 SE) of the total egg mortality, with a best estimate value of 70%. best estimate value of 70%. the standard error of 2 (page 18). 3000 values of EE and 2 were<br>generated and the mean and standard deviation of Pc was calcula-<br>ted. Only positive values of EE and 2 were accepted, and only<br>values of Pc between 0 and 1.0



FIG. 14 simulation.

Frequency distribution output of Pc from the Monte Carlo<br>
simulation.<br>
natively, using data from equation (8), Pc was calculated<br>  $Pc = 2c/(1-\exp(-60 \times z)$  (12) Alternatively, using data from equation (8), Pc was calculated as:

$$
Pc = 2c/(1-exp(-60 * z))
$$
 (12)

where Zc and Z were defined in equations (9) and (1) respectively.<br>  $Pc = 0.47/(1-\exp(-60 \times 0.024))$ 

$$
Pc = 0.47/(1-\exp(-60 * 0.024))
$$
  
= 0.62

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

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

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

where Re = hourly instantaneous rate of egg cannibalism and Pc and Z have been defined in equations (11) and (1) respectively. 1980, Santander et al. 1983):<br>  $RC = Pc * Z$  (13)<br>
where  $RC = hourly$  instantaneous rate of egg cannibalism and Pc<br>
and Z have been defined in equations (11) and (1) respectively.

or ogg cannibution and codimated at the end of extending the relation of  $Rc = Pc * Z$ <br>hourly instantaneous rate of egg canni<br>een defined in equations (11) and (1) re<br>ng the two calculated values of  $Pc =$ <br>ons (2) and (8) respec Considering the two calculated values of  $Pc = 0.70$  and  $Pc =$ 0.62 (equations (2) and (8) respectively), the instantaneous rates 0.62 (equations (2) and (8) respectively), the instantaneous ra<br>of egg cannibalism were calculated as 0.0168 h and 0.01488 h

3.3 Evaluation of the functional response of cannibalism 3.3

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:

where EE number of eggs observed per stomach where EE ED no. of eggs in sea perm (egg density) no. of eggs in sea per m (egg density) m, n, s = parameters of quadratic equation 2  $EE = m * ED + n * ED + s$ 2 (14) 2 EE = m \* ED + n \* ED + s<br>: eggs observed per stomach 2

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



Coefficient of determination  $(r^2)$  ........ 0.95 Number of observations . . . . . . . . . . . . . . . . . . . 21 Number ................... 21

Despite the good fit of the quadratic equation, it was considered inappropiate for modelling egg cannibalism because the curve has a minimum at relatively high positive egg density of curve has a minimum at relatively<sub>-</sub>high positive egg density of<br>3516.6 m<sup>-2</sup>. For modelling egg cannibalism, an exponential relationship was chosen as an empirical representation of the relationship between eggs observed per stomach and egg density<br>over the range of egg densities observed at sea. over the range of egg densities observed at sea.

ET station was then plotted for 21 trawl<br>
caken during the fish feeding period<br>
exponential relationship was fitted usin<br>
ession (SAS Inst. Inc. 1982, Fig. 15a). T<br>
ed (Fig. 15b) can be described by the et<br>  $EE = \gamma * exp(\theta * ED)$ <br> 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<br>curve obtained (Fig. 15b) can be described by the equation: curve obtained (Fig. l5b) can be described by the equation: stomachs in a trawl sample versus egg density per m<sup>2</sup> at the<br>nearest CalVET station was then plotted for 21 trawl samples of 30<br>fish each taken during the fish feeding period of 05h00 to<br>20h00 and an exponential relations

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

where EE = number of eggs observed per stomach

EE = number of eggs observed per stomach<br>ED = no. of eggs in sea per m<sup>2</sup> (egg density)

 $\gamma_{\theta}$  = parameters of exponential curve

Estimates of parameters were as follows

*e* 0.0005 0.00006



Coefficient of determination  $(r^2)$  ......... 0.81<br>Number of observations .................... 21 Number of observations. 0.81 21

 $\frac{33}{2}$ 33



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

Thus, eggs per stomach (EE) is given by (Fig. 15) as:<br> $EE = 0.787 * exp (0.0005 * ED)$ 

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

of eggs per stomach, coupled with a va<br>he mean, but nevertheless with an unde<br>between median values of EE(t) and ED(t)<br>ity in the EE to ED relationship is not<br>pendent cannibalistic effect, as discus<br>all that is required fo The good experimental fit to the data ( $\rm r^2 =$  0.81), suggests that cannibalism may be a mechanism regulating egg survival. However, it is possible that the apparently non-linear fit is due that cannibalism may be a mechanism regulating egg survival.<br>However, it is possible that the apparently non-linear fit is due<br>to statistical effects such as m<sup>'</sup>ight 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  $(\beta)$  be significantly positive. distribution of eggs per stomach, coupled with a variance propor-<br>tional to the mean, but nevertheless with an underlying linear<br>relationship between median values of  $EE(t)$  and  $ED(t)$ . Furthermore,<br>a non-linearity in the E the value of the density-dependent parameter of the Ricker function<br>
(8) be significantly positive.<br>
The Ricker curve (Ricker 1975) describes a stock-recruitment<br>
relationship in which the initial production of offspring i

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<br>rate is also proportional to adult stock size. The Ricker curve rate is also proportional to adult stock size. The Ricker curve can be used to relate eggs hatching to eggs produced:<br>  $EH = \alpha \quad * EP \quad * \exp(-\beta \quad * EP)$ <br>
where EH = eggs hatched<br>  $\alpha = \text{density-independent coefficient}$ <br>  $EP = \text{egg production}$ 

$$
EH = \alpha \quad * EP \quad * exp(- \beta \quad * EP)
$$
 (16)  
eggs hatched  
density-independent coefficient

where EH eggs hatched

 $\alpha$  = density-independent coefficient

EP egg production

# $\mathfrak{g}$  = density-dependent coefficient  $\mathfrak{g}$

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

 $=$   $\beta$  \* (S/V) \* ED(t) - g \* EE(t) (eggs.m<sup>-2</sup>.h<sup>-1</sup>) (17)  $\texttt{dEE}^\bullet(\texttt{t})$  $= \beta * (S/V) * ED(t) - g * EE(t)$  (eggs.m<sup>-2</sup>.h<sup>-1</sup>) (17) dt<br>where  $EE<sup>0</sup>(t)$  = eggs per m<sup>2</sup> in fish stomachs dt ED(t) = rate of egg ingestion<br>
have been defined in equations (14) and<br>  $S/V = \rho F$  and  $\beta$  is the density-dependent<br>
urve. (Note: this model assumes the egg<br>
on, since the rate of ingestion is pr<br>
or egg density).<br>
e stead  $\beta$  \* (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  $\beta$  is the density-dependent parameter of the Ricker curve. (Note: this model assumes the eggs are ingested by filtration, since th vely. Note:  $S/V = \rho F$  and  $\beta$  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 so that: zero, so that:

$$
EE2(t) = \vartheta * (S/V) * ED(t)/g \qquad (eggs.m-2) \qquad (18)
$$

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

 $EE(t) = w * 0 * ED(t)/g$  $(19)$  $\beta$  \* ED(t)/g (eggs.stomach<sup>-1</sup>)

## 3.4 Evaluation of the relationship between eggs hatching and egg

### production

number of eggs hatching and numbers of<br>
surface area for the following condit<br>
aries because number of spawning fish<br>
nt specific fecundity, and b) egg pro<br>
cific fecundity varies, with fish de<br>
g fraction may decrease at Taking into account the linear relationship between egg<br>ity and egg production (Csirke 1980a), the rate of egg survival density and egg production (Csirke 1980a), the rate of egg survival  $(e$ quations  $(1))$ , 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)). (equations (1)), gut evacuation rate (from Californian anchovy)<br>and eggs eaten by a single predator (equations (2),(8) and (15)),<br>a simulation model was built (Fig. 16) to quantify the relationship<br>between the number of e with constant specific fecundity, and b) egg production varies<br>because specific fecundity varies, with fish density constant<br>(ie. spawning fraction may decrease at the beginning and end of<br>the spawning season, (Hunter and

In the first approach, the nightly egg production per fish per  ${\tt m}^2$  , 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). 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<br>steady state between eggs produced and eggs hatching could<br>therefore be attained by running the model over a sufficient<br>length of time for eggs hatching to

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



\

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





period was carculated using equation (<br>
mate the number of eggs in each stomacl<br>
of eggs in the plankton, and equation<br>
this value into number of eggs cons<br>
ime periods. Total egg density was me<br>
of each feeding period. Th were assumed to be generated as an pulse at 2lh00 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<br>21h00 (18h00 - 24h00) and a 9 hour period centred around 13h30<br>(09h00 - 18h00). This simulated the observed feeding period<br>(Fig. 13). For simplicity, consumpt 2lh00 (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 2lh00. 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 n 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). ie. 815, to avoid extrapolation beyond the observed data (see<br>Appendix 3).<br>An estimate of density-independent mortality (M) of 0.0072 h<sup>-1</sup> 40<br>to be generated as an pulse at 21h00 and decayed<br>dependent and density dependent mortality until

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  $0.0168 \cdot h^{-1}$  and  $0.0000 \cdot h^{-1}$  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 was calculated at a spawning fraction of 0.15, by substracting<br>the estimate of mean cannibalism mortality rate (equation (13)<br>based on equation (2)) from the value of total mortality rate<br>(equation (1)). Estimates of densi 0.0168.h<sup>-1</sup> and 0.0000.h<sup>-1</sup> were also calculated in the same manne<br>corresponding to the lower and upper 95% confidence limits of<br>mean value of proportion of eggs lost by cannibalism (equat

41<br>(11)). Eggs hatched were related to eggs produced for a series of values of egg production and for the three estimates of<br>density-independent (M), and for a spawning fraction estimate of density-independent (M), and for a spawning fraction estimate of 0.15. The results are also expressed as eggs hatched versus fish<br>density (Fig. 18).<br>Eggs hatched were related to eggs produced for a series of 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-*0.05,* 0.10, 0.20 *0.30* independent mortality of  $0.0072.h^3$  (Fig. 19a). The results are also expressed as eggs hatched versus fish density (Fig. 19b).<br>The curves (Fig. 18 and 19) represent the recruitment of eggs

).15, 0.20 and 0.30 using the value of  $\dot{\rm c}$ <br>mortality of 0.0072.h<sup>-1</sup> (Fig. 19a). Th<br>ed as eggs hatched versus fish density (<br>s (Fig. 18 and 19) represent the recrui<br>r the area of the Agulhas Bank studied.<br>differs fro 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 density. This is a result of using instantaneous feeding as opposed to continuous feeding in the simulation model. The curves (Fig. 19) ty. This is a result of using instantaneous feeding as opposed to<br>continuous feeding in the simulation model. The curves (Fig. 19)<br>show that when egg production increases because of an increase in either the number of spawning fish per unit area or the specific<br>fecundity, the density-dependent mortality caused by egg cannibafecundity, the density-dependent mortality caused by egg cannibalism also increases. This results in a domed curve with maximum numbers of eggs hatching at an egg production of 3000. $\mathrm{m}^{\tt -2}$  or 4.76 fish. ${\tt m}^2$  at a spawning fraction of 0.15 (Fig. 19). Smaller spawning fractions resulted in poorer survival to hatching because of the<br>larger densities of fish required for a given egg production. larger densities of fish required for a given egg production.



0.0168.h-' and 0.0000.h-1 •





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  $\texttt{EE}(\texttt{t})$  on time, dynamic effects need to be considered. An alternative approach was developed by fixing certain<sup>'</sup> aspects of the dynamic behaviour of the idealised  $1 \text{ m}^2$  ensemble aspects of the dynamic behaviour of the idealised 1 m<sup>2</sup> ensemble<br>of fish, eggs in stomachs, and eggs per m<sup>2</sup> sea water (inclusive of fish volume) and analytically evaluating the relationship<br>between egg hatching and egg production. between egg hatching and egg production. 44<br>mentioned "first approach" model used equation (2) to<br>total consumption of eggs assuming a pulse of egg

hatching and egg production.<br>
te of density-independent mortality (M<br>
ted at a spawning fraction of 0.15, by<br>
of cannibalism mortality rate (equati<br>
(8)) from the value of total mortality<br>
timate of fish density was calcu An estimate of density-independent mortality (M) of 0.0091  $\overline{h}^1$ 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<sup>2</sup> to give a density of age 0 eggs<br>from Fig. 8 and knowing batch fecundity, sex ratio and spawning from Fig. 8 and knowing batch fecundity, sex ratio and spawning fraction. the estimate of cannibalism mortality rate (equation (13) based<br>on equation (8)) from the value of total mortality rate (equation<br>(1)). An estimate of fish density was calculated using a very<br>simple analogy of the egg prod

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

Bergh, UCT, pers. comm.):<br>  $\frac{3}{2}$ <br>  $\frac{2}{2}$ <br>
EE(t) = at + bt + ct + d (from Fig. 13b) and

 $EE(t) = \gamma * exp(\theta * ED)$  (from equation (15))

therefore

 $E D(t) = 1/\theta \ln(1/\gamma (a*t + b*t + ct + d))$  (20)

The balance equation for  $ED(t)$  is:

University of Cape Town  $dED(t)$ - M \* ED(t) -  $\beta$ (t) \* (S/V) \* ED(t) (eggs.m<sup>-2</sup>.h<sup>-1</sup>) (21) dt where *M* is the density-independent mortality coefficient estimated<br>above.<br>Therefore, since ED(t) is function of t,  $\beta(t)$  is given by the

above.

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

$$
\beta(t) = (\text{---} + M * ED(t)/\rho F/ED(t) \qquad (\text{m}^2 \cdot \text{g}^{-1} \cdot \text{h}^{-1})
$$
 (22)  
dt (12)  
Therefore, knowing M,  $\beta(t)$ ,  $\rho F$  and the boundary condition

ED(O) (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  $\rho$ F and ED(0) are related by the relationship:  $F_{\text{NP}} = ED(0)$ . Therefore, knowing M,  $\beta(t)$ ,  $\rho$ F and the boundary condition<br>ED(0) (estimated by extrapolating Fig. 8 backwards exponentially<br>to age 0), a procedure can be devised which solves equation (21)<br>to give numerically estimate

However, it is scarcely worth proceeding beyond this stage,<br>since there is a fundamental conflict between the model, and 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 OShOO 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). stomach,  $EE(t)$ , increases in time. Therefore,  $ED(t)$  will also<br>increase over that period according to equation (15). In terms of<br>the assumption of a pulse of spawning at 21h00, this model<br>predicted increase in ED(t) betwee

One is forced therefore to dispense with the EE =  $\gamma *$  exp( $\theta *$ ED) relationship, in developing a suitable model of the dynamic<br>behaviour of  $\beta(t)$  and thus of  $EE(t)$  and  $ED(t)$  (Appendix 4).<br>Using the estimates of  $M, a, b, c, d, g, ED(0)$  and  $\rho F$ , the 24 hour behaviour of  $\beta(t)$  and thus of EE(t) and ED(t) (Appendix 4).

L be negative over the period of increases<br>
rced therefore to dispense with the EE .<br>
p, in developing a suitable model of<br>  $\beta(t)$  and thus of EE(t) and ED(t) (Appen<br>
estimates of M,a,b,c,d,g,ED(0) and pF<br>
es of  $\beta(t)$  we Using the estimates of  $M$ , a, b, c, d, g, ED(0) and  $\rho$ F, the 24 hour period values of  $\beta(t)$  were calculated at 1/2 hourly intervals period values of  $\beta(t)$  were calculated at  $1/2$  hourly intervals<br>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)  $\geq 0$ . 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 An overall problem with the basic methodology employed here<br>has therefore arisen in attempting to unify the findings into a<br>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 deterregressions leading to equations which are then used in a deter-<br>ministic and fully constrained fashion in the final modelling stage. The resulting incompatibilities required first that the stage. The resulting incompatibilities required first that the<br>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 feature of such a more statistical approach would be to do an<br>overall regression at the final modelling stage. Thus although the basic functional form of EE(t) and EE(ED) could be pre-defined,<br>the function parameters would be fitted in terms of the overall the function parameters would be fitted in terms of the overall model and forcing  $\beta(t) \geq 0$ . model however points to problems with the cubic form of EE(t).<br>Rather than discard information, a different approach could be<br>used in future work, which nevertheless takes account of the<br>basic observations which are record

47

intersity of

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.<br>The Ricker curve has a maximum when  $EP = 1/\beta$  (Ricker 1973). At 48<br>The consideration of egg cannibalism as a density-dependent<br>mechanism allows the evaluation of the significance of cannibalism

of the cannibalism mortality rate (Rc)<br>
ug (To) to hatching (Th) is equal to u<br>  $\int_{T_0}^{T_0} \text{Re}(t) dt = 1$ <br>
defined in equation (13).<br>
equations (2) and (8) Rc = 0.0168 h<sup>1</sup> a<br>
y. By integrating the above integral 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 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<br>integration of the cannibalism mortality rate (Rc) over the time<br>from spawning (To) to hatching (Th) is equal to unity (MacCall integration of the cannibalism mortality rate (Re) over the time from spawning (To) to hatching (Th) is equal to unity (MacCall 1980): 1980) :

$$
\int_{T_0}^{T_1} \text{Rc (t) } dt = 1 \tag{23}
$$

 $J_{\text{To}}$ <br>where Rc was defined in equation (13).

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

#### 4. GENERAL DISCUSSION

on the basis of food abundance and wate<br>and Booman 1982, MacCall 1980). Anchovy<br>ed the Agulhas Bank for spawning becau<br>is generally warmer than 14 C, the<br>rmal egg development in <u>E. capensis</u> (Kir<br>ement of the larvae from 4. GENERAL DISCUSSION<br>The convexity of the South African coastline splits the habitat occupied by anchovy into a warm water Southern region and<br>a cold water Western region. Anchovy egg production coincides in<br>time with maximum upwelling but is highest in the warm Southern 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 is rapid (Shelton and Armstrong 1983). The spawning habitat may<br>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). 1981, 1982).<br>The survival rate during the pre-recruit stage largely deterhave selected the Agulhas Bank for spawning because water near<br>the surface is generally warmer than 14 C, the lower thermal<br>limit for normal egg development in <u>E, capensis</u> (King et al.<br>1978). Movement of the larvae from

mines 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 planktonic and the latter nektonic. Mortality occurs from preda-<br>tion, starvation and disease (Lasker 1985). Starvation and<br>predation are believed to be dominant sources of natural pelagic

transport of pre-recruits out of a given spawning/nursery area is<br>also considered a major source of mortality since surrounding<br>waters are typically unfavourable for survival, although actual<br>mortality may be due to predat 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 during the peak of upwelling season (coincident with the spawning<br>time for anchovy) may carry eggs and larvae out of the system, and<br>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.

water column as found off California (<br>
t mortality in pre-recruits.<br>
Int conflict over whether starvation or<br>
it in the starvation hypothesis (Hjort<br>
ing 1975) is that starvation may not<br>
th but simply that reduced food l 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<br>the field suggest that starvation <u>per se</u> is not the dominant the field suggest that starvation per se is not the dominant within the water column as found off California (Lasker 1975),<br>causing great mortality in pre-recruits.<br>The current conflict over whether starvation or predation is<br>more important in determining fish survival may be largel which prolongs the larval stage, thus increasing the period<br>exposed to predation, and 4) increase of predation (and cannibalism<br>as a form of predation). The effect of food concentration on growth<br>and survival of fish larva

*so*  50

source of mortality (Methot 1981 in Smith 1985).

source of mortality (Methot 1981 in Smith 1985).<br>Starvation mortality is thought to be relatively more important during the first 1-2 weeks of feeding (Hunter 1984), whereas<br>predation seems to be the dominant source of mortality throughout<br>of the first year of life.<br>Predation as modified by food availability is clearly a very<br>importa predation seems to be the dominant source of mortality throughout of the first year of life.

The benguela system seems to exceed 1000<br>chovy during "normal" periods. However,<br>scale at which food becomes available t<br>cularly, may be limiting (Shannon and Fi<br>nibalism are likely to depend on the siz<br>ution of adult food 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. However, 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). Rates of cannibalism are likely to depend on the size, abundance,<br>and distribution of adult food. Eggs patches probably elicit a<br>feeding response by adults in the spawning area (MacCall 1980).<br>The amount of time spent on f advection). The Benguela system seems to exceed food requirements<br>for adult anchovy during "normal" periods. However, the temporal<br>and spatial scale at which food becomes available to fish and to

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 2lh00, 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 abundance increases (O'Connell 1972). Although filter-feeders can<br>continue feeding in darkness, as shown by Hettler (1976) and<br>Holanov and Tash (1978), Cape anchovy possibly become satiated<br>following the increase of food o 18hOO and 24hOO with a pronounced peak at 21hOO, M. Armstrong,<br>SFRI, pers. comm.), because eggs were shown to be an important<br>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 2lh00 (Fig. 13d). Feeding therefore appears to be reduced or absent after 20h-21h (between 20h-21h<br>and 05h-06h (Fig.13). and 05h-06h (Fig.13). 52<br>in the incidence of anchovy eggs in anchovy stomachs per unit<br>stomach weight centred at about 21h00 (Fig. 13d). Feeding therefore

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

der et al. 1983). In California, the da<br>gs was estimated to be 53% (Smith and Las<br>t was calculated that 44% of South Afi<br>daily (Fig. 8).<br>Sm has been shown to be an important<br>n this thesis cannibalism on anchovy e<br>area may 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<br>Peru may result in less time being spent feeding or less feeding Peru may result in less time being spent feeding or less feeding eggs are lost daily (Fig. 8).<br>Cannibalism has been shown to be an important cause of egg<br>mortality. In this thesis cannibalism on anchovy eggs over the<br>Agulhas Bank area may account for 628-708 of egg mortality, with<br>a ran

on their own eggs (MacCall 1980).

their own eggs (MacCall 1980).<br>The plot showing a decreasing rate of egg survival after cannibalism with increasing egg density (Fig. 15) suggests cannibalism with increasing egg density quantitatively that cannibalism in the South African anchovy is quantitatively that cannibalism in the South African anchovy is<br>potentially an important compensatory regulatory mechanism of the size of the adult population. e of the adult population.<br>There are at least three major types of density-relationships

on (Solomon 1949). In (1) (Fig. 20), increases linearly with prey density, a<br>iensity-independent" relationship. In (2<br>led falls as density rises, or remain<br>long as the percentage killed is less<br>is is an "inverse" density-r 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, *oi*  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. that is a "density-independent" relationship. In (2) the number<br>of prey killed falls as density rises, or remain the same, or<br>increase, so long as the percentage killed is less when density<br>is high; this is an "inverse" de



PREY DENSITY

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). 54 54 exponential relationship fitted by equation (15) represents<br>
a density-dependent mechanism regulating egg survival as a<br>
function of egg density. This relationship could be part of an<br>
S-shaped curve (Type III Hollin

Significative positive), the exponent<br>3 significative positive), the exponent<br>urve is suggestive of a further, vi<br>portion of eggs being consumed at in<br>the sea. This sort of effect, if manif<br>on anchovy eggs, would lead to a Since density dependence is assumed by even a linear EE/ED plot (i.e.  $\beta$  significative positive), the exponential shape of plot (i.e.  $\beta$  significative positive), the exponential shape of<br>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 manifiest in other fish preying on anchovy eggs, would lead to a density-dependent response even in the absence of egg cannibalism. greater proportion of eggs being consumed at increasing egg<br>densities in the sea. This sort of effect, if manifiest in other<br>fish preying on anchovy eggs, would lead to a density-dependent<br>response even in the absence of e



FIG. 21 Holling's three types of functional responses. For each type the number of prey killed by a single predator is<br>graphed against prey density. Only type 3 yields<br>density-dependent mortality (from Holling 1959). 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 increases, thereby tends to stabilize the prevailing adult<br>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 different stages of life. From egg<br>there might be several regulatory mechan<br>tabilize the size of the adult stock. A:<br>on eggs, larval competition, cannibali<br>all the different stages of life, cha<br>ange of fecundity, behav 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 of schools. While cannibalism and change in fecundity will<br>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). types has long been recognized as being the basis on which the<br>maintenance of intensive long-term fisheries depends (Neave 1953).<br>The egg production-recruitment relationship in the Ricker<br>model is regulated by a set of mec the Ricker curve, larval competition will flatten the dome as it<br>is related to the net egg production rather than parent stock<br>(Csirke 1980b). Predation and breakdown of schools may provoke a<br>depensatory (or non-compensato

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 bonfers 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). own eggs. Egg cannibalism has been shown in this study to be a<br>potentially important underlying mechanism which confers structure<br>to the scattered distribution of stock-recruitment points in Cape<br>anchovy although its effec

ndent of abundance. Not only may th<br>ndent of abundance. Not only may th<br>high due to crowding into certain areas<br>s reduced, the fish will spend more<br>of their time feeding, which may resu<br>uitment due to intense egg cannibali 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 proportion of their in 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. $m<sup>-2</sup>$  (or fish denser than 4,76 fish.m<sup>-2</sup>) at a spawning fraction of 15% for<br>density dependent effects to become marked. Acoustic data from<br>the November 1984 survey indicated that the average density of<br>anchovy in the study area w 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  $75g.m<sup>-2</sup>$  (SE = 17.49). Assuming the The output of the first model (Fig. 18 and 19) built to<br>correlate egg hatching with egg production shows that for a given<br>egg production, the cannibalism rate increases with decreasing<br>spawning fraction. Because it was cal

Inty on newly spawned eggs. Ine Interce<br>
urve may therefore be underestimate<br>
mortality of newly spawned eggs has occu<br>
on only includes egg stages which are function<br>
that includes egg stages which are function<br>
an extrem 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<sup>-2</sup>.d<sup>-1</sup> with 95% confidence interval of 1754-4776. This mean<br>value is significantly greater (0.20<p<0.10) than the egg produc-<br>tion obtained from the intercept of the egg mortality curve in 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<br>spawning period, and may indicate that cannibalism mortality is spawning period, and may indicate that cannibalism mortality is exerted mainly on newly spawned eggs. The intercept of the egg exerted mainly on newly spawned eggs. The intercept of the egg<br>mortality curve may therefore be underestimated if a large cannibalism mortality of newly spawned eggs has occurred, because cannibalism mortality of newly spawned eggs has occurred, because<br>the regression only includes egg stages which are fully recruited to the plankton, which only occurs several hours after peak<br>feeding. In an extreme case where cannibalism was entirely on 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. of the mortality curve would reflect only density-independer<br>mortality, and the intercept would be underestimated by the<br>number of eggs consumed per night per unit area.<br>The results of this. model must be viewed as being o

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 tative nature, in view of the dynamic effects which are ignored.<br>However, as is demonstrated by the two dynamic models which are<br>presented, a fully dynamic description would require a separate<br>research project, because the

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#### 5. CONCLUSIONS

**I**<br>I

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. 59<br>States of egg cannibalism on egg mortality of<br>African anchovy over the Agulhas Bank area it was estimated<br>annibalism can account for from 30% to 100% of the total egg<br>ity with estimates of 62%-70% for the area of intens

on was investigated.<br>
mibalistic behaviour was shown to be<br>
msity-dependent compensatory mechanism<br>
tock by regulating egg survival as a fu<br>
recruitment from spawning to hatching<br>
the 62%-70% estimates for egg cannibalis<br> 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 survival 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 density. The recruitment from spawning to hatching is therefore<br>maximal for the 62%-70% estimates for egg cannibalism because the<br>integration of the cannibalism mortality rate over the stage<br>duration (60h) gives values of using the Ricker curve in Cape anchovy stock-recruitment relationships has been given. nships has been given.<br>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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## APPENDIX 1



#### **APPENDIX 2**  APPENDIX 2

# **Monte Carlo simulation program**  Monte Carlo simulation program

University of Cape Town 10 REM MEANS AND STANDARD DEVIA TIONS OF VARIABLES<br>20 E = 36,74:8E = 12,72  $\Sigma_{\rm Z} = 0.024$ :Sz = 0.0109 30 E <sup>1</sup> 54,7<br>39 J = 0.02<br>35 J = 3000 40 REM INITIALIZE COUNTERS 50 I = O:SP = O:PS = 0  $55$   $\overline{H1} = \overline{Q}$ : $\overline{H2} = \overline{O}$ : $\overline{H3} = \overline{O}$ : $\overline{H4} = \overline{O}$ : $\overline{H5}$ = **(:1**  56 H6 = O:H7 = O:HB = O:H9 - O:Q - () 56 H6 = 0:H7 = 0:H8 = 0:H9 - O:Q - **()**   $69$   $I = I + I$ <br> $65$   $F RINT$   $I$ 7ŏ GOŠUB looo<br>80 EE = (ZR \* SE) + E<br>90 IE\_EE\_< 0 THEN GOTO 70 **9(>**  90  $100<sub>1</sub>$ 110 110  $\overline{60}\overline{5}\overline{U} \overline{B}$  1000 $\overline{0}$ 110 ZZ = (ZR \* SZ) + Z<br>120 IF ZZ < 0 THEN GOTO 100  $\overline{130}$  P =  $\overline{C}$   $\overline{E}$   $\overline{x}$  0.0167)  $\overline{x}$  (1 - EXP 140 IF P < 140 IF P < 0 THEN GOTO 70<br>150 IF P > 1.0 THEN GOTO 7  $i$ . $\circ$  Then Goto 70 . **2**  I F ה"<br>TF:<br>P  $\frac{1}{1 + \frac{1}{1}}$ 184 **IF**<br>185 **IF** . *l ..* **;...,1**   $\overline{\text{I}}$   $\overline{\text{F}}$ *0* **·7**   $I_{\rm B}^2$ THEN **r·•. 1-·** .. · THEN<br>P -><br>THEN<br>P -> THEN<br>P > THEN<br>P ·rt--!E:.t·~J <u>if P > = 0.7 THEN IF</u><br><u>.8 THEN LET HB = HB +</u>  $+$   $+$   $-2$  $\equiv$  0 Then If P  $LET[H1 = H1 + 1]$  $= 0.1$  THEN IF LET H2 = H2 +<br>= 0.2 THEN IF<br>LET H3 = H3 +<br>= 0.3 THEN IF  $\begin{array}{rcl} \begin{array}{rcl} \text{LET} & \text{H4} & = & \text{H4} & + \\ \text{O} & 4 & \text{THEN} & \text{IF} \end{array} \end{array}$  $\frac{\text{LET H5 = H5 +}}{\text{O.5} \cdot \text{THEN} \cdot \text{IF}}$  $LET H6 = H6 +$ <br>= 0.6 THEN IF 188 IF  $E \geq \frac{151.87}{2.8}$  THEN IF  $\frac{1}{2}$  Then  $\frac{1}{2}$  Let  $\frac{1}{2}$  H9  $\pm$  H9  $\pm$ 189 IF P > = 0.9 THEN LET  $\overline{0}$  + 1 230 JF I = J THEN GOTO 250 CO-; +- 1 ~~u IF I = J THEN GOTO 250 ..:~Ll·l..) [~o'r[j *t::.1()*   $\frac{250}{260}$  PM =  $\frac{55}{1}$  / I<br>260 VP = (PS - (SP  $\sim$  2) / I) / (I  $\langle 0, 1 \rangle$  $F'$ p P  $\frac{1}{\mathsf{P}}$ **J.**  J. p P 1 **F'**  l j **F' FI**  l **1:::1**  l p 1 - 0  $\begin{array}{c} \leftarrow \circ \\ \leftarrow \circ \end{array}$  $\langle \cdot \rangle$  **(j)**  $\langle \cdot \rangle$  ()  $\langle \cdot \rangle$  ()  $\cdot$   $\bullet$   $\bullet$  $\langle \;\; \circ \;\; \circ$ .. ·: ·. *(.}*  Cl ··~· **271:) :28() :·::'.9()**  ::::;oo **Li-()() 1 ()(i()**   $P$ RINT "MEAN  $P = "$  ; FM F'RINT "VP:F: F' - ";VP 27C' F:-P I I\!T II r'1EPJ---j !=' --- ":; pr'i 280 F'Fn: NT "\.!P:R P - !!; !,)P i='FI!\!T **:'29 () j:' I:;: I !\} T**  ~~~~~QH1,H2,H3,H4,H5,H6,H7,H (3CTO 1200)<br>| ZR = 2 \* RND (15) - 1:ZR =<br>| LOG ((1 + ZR) / (1 - ZR)) *|* 1.82<br>RETURN<br>END  $\frac{1100}{1200}$  $SLIST$ 10 REM MEANS AND STANDARD DEVIA TIONS OF VARIABLES<br>20 E = 36,74:SE = 12,72<br>30 Z = 0.024:SZ = 0.0109<br>35 J = 3000 40 REM INITIALIZE COUNTERS<br>50 I = 0:SP = 0:PS = 0<br>50 I = 0:SP = 0:PS = 0  $\vec{55}$   $\vec{H1}$  = 0. $\vec{H2}$  = 0: $\vec{H3}$  = 0:H4 = 0:H5  $60$  I = I + 1 PRIhlT I C3ClSUB lOOO EE = (ZR \* SE) +- <sup>E</sup> IF EE < 0 THEN GOTO 70  $\overline{\mathsf{GOGUB}}$   $\overline{\mathsf{1000}}$  $ZZ = (ZR * SZ) + Z$ 120 IF 22 < 0 THEN GOTO 100<br>130 P = (EE \* 0.0167) / (1 - EXP<br>... (\_- 60 \* 2Z)) 140 IF P < 0 THEN GOTO 70  $150$   $\left[\text{IF} \right] \geq 1.0$  THEN  $\text{GUT}$   $\text{O}$   $\text{O}$ :!. ~}() ~}F: **::;: + F:**  170 PS = +- P A 2  $180$  IF P  $>$  = 0 THEN IF P<br>THEN LET H1 = H1 + 1<br>181 IF P  $\geq$  = 0.1 THEN IF  $\frac{1}{2}$  THEN  $\left[ \begin{array}{cc} \text{LET} & \text{H2} \end{array} \right]$  H2  $\left[ \begin{array}{cc} \text{H2} & \text{L2} \end{array} \right]$  $182$  IF  $P(\Sigma) = 0.2$  THEN IF  $\frac{1}{2}$   $\frac{1}{2}$  Hen  $\frac{1}{2}$   $\frac{1}{2}$   $\frac{1}{2}$   $\frac{1}{2}$   $\frac{1}{2}$   $\frac{1}{2}$   $\frac{1}{2}$   $\frac{1}{2}$  $183$  IF  $E[\geq]$  = 0.3 THEN IF  $10$  T4 THEN LET H4 = H4 +<br>184  $1$  P  $_2$  = 0.4 THEN IF  $\frac{1}{2}$  Then Let  $\frac{1}{2}$ H5 = H5  $\frac{1}{2}$  $185$  IF  $P(\Sigma) = 0.5$  THEN IF  $\frac{1}{2}$  THEN LET H6 = H6  $\pm$ 186 IF  $E[\Sigma] = 0.6$  THEN IF  $\frac{1}{2}$  THEN LET HZ  $=$  H7  $\pm$  $187$   $\left[\frac{1}{2}\right] = \left[\frac{1}{2}\right]$   $\left[\frac{1}{2}\right]$   $\left[\frac{1}{2}\right]$   $\left[\frac{1}{2}\right]$   $\left[\frac{1}{2}\right]$  $\frac{1}{2}$ e Then Let He $\frac{1}{2}$ H8  $\frac{1}{2}$  $188$  IF  $P_{\rm max} = 0.8$  THEN IF  $\frac{1}{2}$  Then let  $\frac{1}{2}$   $\frac{1}{2}$   $\frac{1}{2}$   $\frac{1}{2}$ Ib~ IF P > = 0.9 THEN LET  $250 \text{ PN} = 35 \text{ P}$ <br>260 VP = (PS - (SP  $\sim$  2) / I) / (I<br>- 1) 1 **FI**  1<br> **1**<br>
1<br>
0<br>
1 ---  $\langle \cdot \rangle$  **()**  $\le$   $\circ$  $<$   $\circ$  $\mathbf{m}$ 360 PRINT H1,H2,H3,H4,H5,H6,H7,H<br>B.H9.Q (30TO^1200)<br>ZR = 2 \* (RND (15) - 1;ZR =<br>^ LOG ((1 + ZR) / (1 - ZR))

#### **APPENDIX 3**  APPENDIX 3

### **Program of the model for calculating the egg survivalegg production relationship**

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 $^{10}_{15}$ 10 DIM EC3),EH(3) 10 DIM E(3).EH(3)<br>15 REM DENSITY INDEPENDENT MORT ALITY<sup>:</sup> 20 M =::0072<br>25 MM = EXP<br>26 REM PAR 25 MM = EXP ( - M \* 24) 26 REM PARAMETERS OF EGGS EATEN 4)<br>|EGGS EATEN<br>EGG DENSITY PER FISH VERSUS EGG DENSITY 30 AL = 0.7866:EX = 0.0005<br>40 PRINT "EGG PRODUCTION PER M^2<br>41 INPUT EP<br>52 REM SPAWNING FRACTION/BATCH<br>55 REM SPAWNING TRACTION/BATCH<br>55 REM INITIAL GUESSES OF 1 AND<br>55 GE = 0.701<br>55 GE TO 701<br>55 REM INITIAL GUESSES OF 1 A 30 AL = 0.7866:EX = 0.0005  $:EX = 0.0005$ 40 p1:;: I l\iT "EGG PRODUCT I 01\1 PEI:;: w· 2 *r.:•* **If**  PRODUCTION PER MA2 INFUT EP 41<br>45 45 REM SPAWNING FRACTION/BATCH REM SPAWNING FRACTION/BATCH FECUNDITY/SEX FECUNDITY/SEX RATIO **5()** ~}F ,,. .. **(; .. 15**   $50$  SF = 0.15<br>51 BF = 7772<br>52 SR = 0.54 51 BF =<br>52 SR = **53 GE** ::: () .. **7'C•l**  55 REM INITIAL GUESSES OF 1 AND GUESSES OF 1 AND 2 DAY OLD EGGS  $60 E(1) = 0$ **65 E**(2) = 0<br>66 REM \_NUMBER OF FISH TO PRODUC  $65 E(2) = 0$ 66 REM NUMBER OF FISH TO PRODUC E OBSERVED EGG FRODUCTION EP E OBSERVED EGG PRODUCTION EP 71 NF = EP / (SF \* BF \* SR)<br>90 FREM  $NF = EF$ HEr'! 105 REM TOTAL EGG DENSITY 120 EG = EP + ECll + EC2) REM TOTAL EGG DENSITY<br>EG = EP + E(1) + E(2)<br>REM EGGS EATEN PER FISH<br>EE = AL \* EXP (EX \* EG)<br>IE EE > 815 THEN LET EE = 8 125 REM EGGS EATEN PER FISH<br>130 EE = AL \* EXP (EX \* EG)<br>131 IF EE > 815 THEN LET EE = 8<br>15 132 REM CANT EAT MORE THAN IS T 133 FE = EE \* GE \* 6 \* NF :<br>135 FE = EE \* GE \* 6 \* NF :<br>136 TF EE > EG THEN LET EE = EG 136 REM CALCULATE EGGS HATCHED 136 REM CALCULATE EGGS HATCHED AND EGG DENSITY AT 13H.50 FE DENSITY AT 13H.50 FE EDING 140 EH = (E(2) - E(2) \* EE / EG) \*<br>EXP ( - M \* 12)<br>141 E(2) = (E(1) - E(1) \* EE / EG<br>) \* EXP ( - M \* 16.5)<br>142 E(1) = (EP - EP \* EE / EG) \* 140 EH = (E(2) - E(2) \* EE / EG) \*<br>
EXP ( - M \* 12)<br>
141 E(2) = (E(1) - E(1) \* EE / EG<br>
... ... ... EXP ( - M \* 16.5) 142 E(1) = CKP ( - M \* 16.5)<br>142 E(1) = CEP - EP \* EE / EG) \* 142 E(1) = (EP - EP \* EI<br>EXP ( - M \* 16.5)<br>143 REM EGG DENSITY  $($  -  $\mathbb{M}$  $\frac{1}{1}$ . 144 EG = ECl> + EC2): IF EG < 0.1 • :I. 145 EE = AL \* LET EG = 0.1<br>145 EE = AL \* EXP (EX \* EG) 145 EE = AL \* EF EG = 0.1<br>145 EE = AL \* EXP (EX \* EG) 146 IF EE > 815 THEN LET EE = 8 146 TE EE > 815 THEN, LET EE = 8 15 147 EE = EE \* GE \* 9 \* NF<br>148 IF EE > EG THEN LET EE = EG 149 E (2) = (E (2) - E (2) \* EE / EG<br>
) \* EXP ( - M \* 7.5)<br>150 E (1) = (E (1) - E (1) \* EE / EG<br>
) \* EXP ( - M \* 7.5)<br>160 PRINT EH 149 EC2) = CEC2l - EC2> \* EE <sup>I</sup>~b <sup>&</sup>gt;\* EXP ( - M \* 7 .. 5) END

### APPENDIX 4 75

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F. Equation 2 is readily solved to give:<br>
(a)  $x \exp(-M * t - \rho F * \int_0^t \beta(\psi) * d\psi)$ <br>
(b)  $y \exp(-M * t - \rho F * \int_0^t \beta(\psi))$ <br>
(c)  $\mathbb{E}(\mathbf{t}) = \beta(\mathbf{t}) * \rho F * \mathbb{E}(\mathbf{0}) * \exp(-M * t - \rho F * \int_0^t \beta(\psi))$ <br>
(e)  $\mathbb{E}(\mathbf{t}) = \beta(\mathbf{t}) * \rho F * \mathbb{E}(\mathbf{0})$ The following coupled differential equations must be solved to develop a model of the dynamic behaviour of  $\beta(t)$ ,  $EE(t)$  and  $ED(t)$ :  $dEE^{\bullet}(t)$  $dEE$ <sup> $\bullet$ </sup> $(t)$ dEE (t)<br>------ =  $\beta(t) * \rho F * ED(t) - g * EE^{\bullet}(t)$ dt dt and  $dED(t)$ ----- - M \* ED(t) - β(t) \* *p*F \* ED(t) dt where  $\mathbb{E}(\mathsf{t})$  is in units of eggs.m<sup>-2</sup> in fish stomachs, i.e.  $\mathbb{E}(\mathsf{t})$ EE(t) \*  $\rho$ F/w. Equation 2 is readily solved to give: ED(t) = ED(0) \* exp ( -M \* t - $\rho F$  \*  $\int_{0}^{t} \beta(\psi)$  \* d $\psi$ Substituting this into equation  $(1)$  gives:  $(1)$  $(2)$ ( 3)  $dEE(t)$ <br>----- + dt dEE(t)<br>----- + g\*EE(t) =  $\beta(t)$ \*pF\*ED(0)\*exp(-M\*t- $\rho F*$  $\int_0^t \beta(\psi) * d\psi$ ) (4)<br>dt The left hand-side of equation (4) is a given function of t. On<br>integrating both sides with respect to t, the result is (transfeintegrating both sides with respect to t, the result is (transferring  $\rho$ F\*ED(0)\*exp(-M\*t): 1  $\int_{\rho F^*ED(0)}^{t} \exp(M^*t) * (dEE(t))/dt + g*EE(t)) *dt$  $(5)$ ----- <sup>+</sup> \* d $\psi$  (3)<br> $-\rho F^*$  ( $\frac{1}{\beta}$  ( $\psi$ ) \* d $\psi$ ) (4)

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

$$
= \frac{1}{\rho F} \cdot \frac{1}{\rho F} \cdot \dot{\phi} \cdot (\exp(-\rho F \cdot \int_{0}^{t} \beta(\psi) \cdot d\psi) - \exp(-\rho F \cdot \int_{0}^{0} \dot{\phi} \beta(\psi) \cdot d\psi) \tag{7}
$$

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

exp(-PF\*J: ~(¥)\*d<I= 1 - J: exp{M\*t)\*(dEE~t)/dt + g\*EE~t))\*dt ED~O) ( 9) 1 **f:** exp(M\*t)\*(dEE~t)/dt <sup>+</sup>g\*E t»\*dt (

$$
\int_{0}^{t} \exp(M*t)*(dEE(t))/dt+g*EE(t)*dt
$$
  
.
$$
\int_{0}^{t} \rho(\psi)*d\psi=-1 \log(1 - \cdots)(10)
$$
  
ED(0)

$$
\int_{0}^{t} \beta(\psi) * d\psi = -\frac{1}{\rho^{F}} \log(1 - \frac{1}{\rho^{F}} \exp(M*t) * (dEE(t)) / dt + g * EE(t) * dt)
$$
\n
$$
= D(0)
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 $ED(0)$  is the mean density of eggs in the sea at 21h00, which can<br>be calculated from the results set out in Fig.8. If the fitted be calculated from .the results set out in Fig.8. If the fitted curve in Fig.8 is ED(t), the ED (0) is given by the following sum<br>for n—s∞: for  $n \rightarrow \infty$ :

$$
ED(0) = ED'(0) + ED'(24) + ED'(48) + \dots + CD'(n*24)
$$
\n
$$
= ED'(0) * (1 + exp(-24*2) + exp(-48*2) + \dots + exp(-n*24*2)
$$
\nIn other words, for Z constant, the egg population at time 0 is

y /M-3\*t<sup>2</sup> \*exp(M\*t)/M<sup>2</sup> +6\*exp(M\*t)\*t /M<sup>2</sup> 6\*e<br>
exp(M\*t)\*t<sup>2</sup> /M-2\*t\*exp(M\*t)/M<sup>2</sup> +2\*exp(M\*t)<br>
xp(M\*t)\*t/M-exp(M\*t)/M<sup>2</sup> +1/M<sup>2</sup>)\*(g\*c+2\*b)+<br>
c))/ED(0) the sum of the numbers in each cohort, assuming breeding occurs<br>once a day<br>Now, EE(t) is given: once a day Now,  $EF(t)$  is given: 3 2  $EE(t) = a*t + b*t + c*t + d$  $E E(t) = a*t + b*t + c*t + d$ <br>where a,b,c,d, are taken from Fig. 13(b) and converted by the factor  $\rho F/w$ . Thus: 1 exp(M\*t)\*(g\*a\*t<sup>3</sup> + (g\*b+3\*a)\*t<sup>2</sup> +(g\*c+2\*b)\*t+g\*d+c) *(3* Ct) = - - - - -.- - - \* c - -- -- ----- ----- -- ---------- - - -- - -- - -- - - -- -------) (U} exp(M\*t)\*( a\*2 ( +3\*a)\* +( +2\*b)\*t+ d+c) (J(t) --------\* ( -- --- ------------------ - ------ -- - --- - -----) **(lJJ**  *pF\*ED(O)* 1 (x) pF\*EDe(O) 1 (x) where  $x =$ ((exp(M\*t)\*t3 /M-3\*t<sup>2</sup> \*exp(M\*t)/M<sup>2</sup> +6\*exp(M\*t)\*t /M<sup>2</sup> 6\*exp(M\*t)/M<sup>4</sup>  $+6/M^4$ )\*g\*a+(exp(M\*t)\* $t^2$ /M-2\*t\*exp(M\*t)/M<sup>2</sup>+2\*exp(M\*t)/M<sup>3</sup>-2/M<sup>3</sup>)\*  $(g*b+3*a)+(\exp(M*t)*t/M-exp(M*t)/M^2+1/M^2)*(g*c+2*b)+(\exp(M*t)/M^2)$  $M-1/M$   $*(g*d+c)$   $/ED^{\bullet}(0)$ factor  $\rho F/w$ . Thus:<br>  $\begin{array}{l} 1 \qquad \exp(M*t)*(g* a * t^3 + (g * b + 3 * a) * t^2 + (g * c + 2 * b) * t + g * d + c) \\ \rho F * ED(0) \qquad \qquad 1 \qquad \qquad (x) \end{array}$ <br>
where<br>  $\begin{array}{l} x = \\ ((\exp(M*t)*t^3/M-3 * t^2 * \exp(M*t)/M^2 +6 * \exp(M*t)*t - /M^3 6 * \exp(M*t)/M^4 \end{array}$ 

#### APENDIX 5

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### Description of units

APENDIX<br>Description of<br>at age t Et Eggs at age  $t$  (eggs)  $\ddot{\cdot}$ Eggs at age to the ggs)<br>
Eggs at age 0 (eggs)<br>
Instantaneous rate of egg mortality ( $h^{-1}$ )<br>
time of day ( $h$ )<br>
Mean daily consumption of eggs per the<br>
fish (eggs.d<sup>-1</sup><br>
fish (eggs.d<sup>-1</sup><br>
stomachs (eggs.fi<br>
Instantaneous Eggs at age  $0$  (eggs) E o ( eggs ) Instantaneous rate of egg mortality( h<sup>-1</sup> )<br>time of day ( h ) z z time of day (h ) t t *c*  C Mean daily consumption of eggs per ean daily consumption of eggs per<br>
ish<br>
(eggs.<br>
ean number of eggs per fish<br>
tomachs<br>
matantaneous rate of gastric<br>
vacuation for anchovy eggs<br>
(h<sup>-1</sup><br>
otal number of eggs per fish<br>
tomachs<br>
ate of egg ingestion<br>
eight of Mean daily consumption of eggs per<br>fish<br>Mean number of eggs per fish<br>stomachs<br>Instantaneous rate of gastric<br>evacuation for anchovy eggs<br>Total number of eggs per fish<br>stomachs<br>Rate of egg ingestion<br>weight of fish<br>density of  $\bullet$ fish  $(eggs.d^{-1}.fish)$ fish Mean number of eggs per fish fish EE EE  $\overline{\phantom{a}}$  $(\texttt{eggs.} \texttt{fish})$ stomachs stomachs Instantaneous rate of gastric g g  $\int$   $\ln^{-1}$ evacuation for anchovy eggs<br>Total number of eggs per fish<br>stomachs<br>Rate of egg ingestion evacuation for anchovy eggs  $\lambda$ Total number of eggs per fish  $EE(t)$ :  $(\texttt{eggs}. \texttt{fish}^{-1})$ stomachs Rate of egg ingestion  $(\text{eggs}. \text{fish}^{-1}. \text{h}^{-1}. \text{m}^{-2})$  $R(t)$  $\ddot{\cdot}$ weight of fish of fish w ( g ) ( g (  $g.m^{-2}$  )  $( g.m<sup>-2</sup> )$ <br>(eggs.fish<sup>-1</sup>) density of fish  $\rho$  F  $C(t)$  $\bullet$ Total eggs eaten per fish t hours since peak spawning (assuming since peak spawning (<br>pulse at 21h00)<br>Egg production per gr<br>body weight per night pulse at 2lh00) Egg production per gram of fish F F  $\ddot{\bullet}$  $(eggs . g<sup>-1</sup> .night<sup>-1</sup>)$ body weight per night Eggs produced per gram of females<br>(batch fecundity) f f  $(eggs.g^{-1})$ (batch fecundity) Re Rc Instantaneous rate of egg cannibalism ( h ) ( h ) Eggs in sea per m from most recent Eggs in m nights spawning most recent (eggs.m-2) ED and  $(eggs.m<sup>-2</sup>)$  $ED(t)$  : nights spawning



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 $\hat{\boldsymbol{\beta}}$