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**Effects of sea surface temperature, adult size and adult condition on
spatial variability in egg volumes of three pelagic species from the
southern Benguela**

Applied Marine Science Course-work Masters Degree: Mini-Dissertation.

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(February 2007)

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1. Abstract

Spatial variability in egg volume was investigated for anchovy, sardine and round herring in the southern Benguela in 1998, 2000 and 2001. The relationship between sea surface temperature (SST) and egg volume was determined and the parental condition hypothesis was investigated through the relationships of adult size and condition with egg volume. General linear models for each species were used to determine the factors that were significantly related to egg volume at the scale of sample collection. Visual interpretation of the effects of adult size and condition on egg volumes was done on a large scale. Spatial variability in egg volume occurred for all three species ($p \leq 0.001$), related to differing factors for each species for each of the years. Spatial variability in round herring egg volume could not be related to any of the measured factors for any of the three years. Anchovy egg volumes in 1998 and 2000 were related to SST but not in 2001. Sardine eggs from Continuous Underway Fish Egg Sampler samples were larger than those from California Vertical Egg Tow net (CalVET) samples. Sardine CalVET sampled egg volumes were not related to SST, adult size or adult condition. The high variability of key processes in the southern Benguela at small scales of space and time to some extent masks long-term large-scale spatial variations in egg volume.

2. Introduction

Egg quality can be generally defined as the egg's potential to produce viable fry (Kjørsvik *et al* 1990), and it can be one of the causes of variability in recruitment. If egg quality is poor the survival potential of the hatched larva decreases, thereby impacting reproductive success. Adult body condition appears to affect egg quality, and according to the "parental condition" hypothesis, large females and females in good condition, i.e. with large lipid reserves, will produce larger eggs than those in poor condition (Palumbi 2004).

In addition to spawner condition, environmental conditions like temperature and food availability can affect egg size and batch fecundity (Funamoto and Aoki 2002, Mukhametova 2004). Riveiro *et al.* (2004) observed two parental strategies over the spawning period of the European sardine, *Sardina pilchardus* and concluded that sardine employ a parental strategy that adapts the organic content of eggs to the evolution of the temperature in the area during the spawning period. Eggs of high organic content were produced in the coldest months and were therefore bigger than those produced in warm months (Riveiro *et al.* 2004). It was also found that egg size decreased as the spawning season progressed and the quantity of available food increased (Riveiro *et al.* 2004). Similar results were found by Castro (2004) for anchovy off the Chilean coast, i.e. egg size tended to decrease with the progression of the spawning season. The same results were found for the Japanese anchovy off the Pacific coast by Funamoto and Aoki (2002).

The reproductive potential of pelagic fish populations, like other fish populations, have generally been assessed using spawning stock biomass and egg quantities/fecundity (Solemndal 1997). However, recent research in the Far East, Norway, Chile and Spain has illustrated the influence of spawner condition and age/size on egg quality and fecundity, where fish in better condition produce better and/or more eggs, thereby affecting the viability of the offspring (Morimoto 1996, Solemndal 1997, Riveiro *et al.* 2004) (Figure 1).

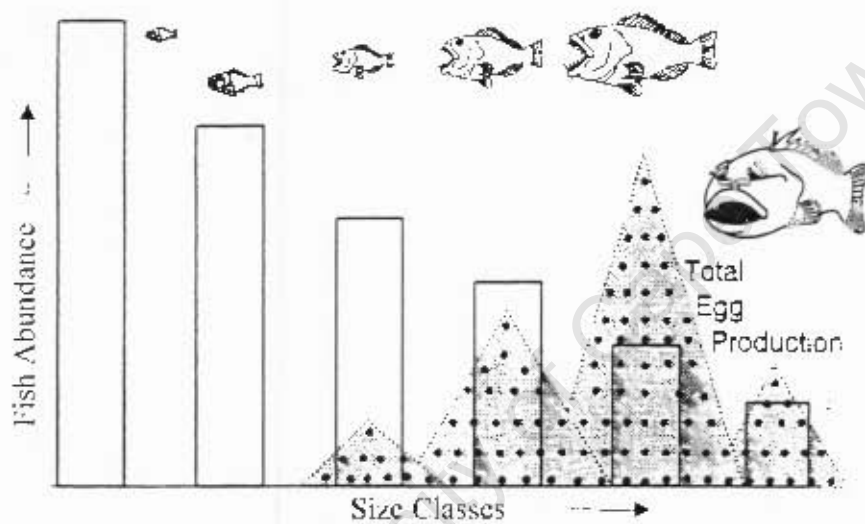


Figure 1: Population size structure and total egg production in a hypothetical unfished fish population (Bohnsack 1990).

The fecundity of large fish and the improved viability of their offspring have implications for fisheries management, especially with regard to closed seasons and closed areas at the time of the spawning season. The current minimum size limits, implemented using mesh size restrictions for the pelagic fishery, protect those fish contributing little to recruitment, whereas old, large and "good condition" females are targeted. Fishing not only removes biomass, which is the major factor for the pelagic fishery, but also truncates

the age and size structure of fish populations and often results in localized depletions (Berkeley *et al.* 2004) (Figure 2).

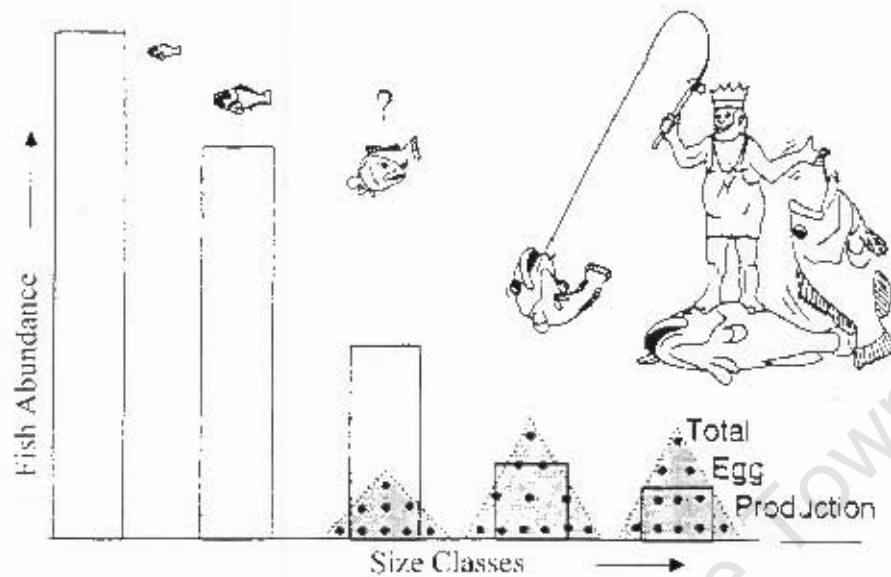


Figure 2: Hypothesised effects of intense fishing on population size and total egg production (Bohnsack 1990).

Fishing can decrease peaks of abundance and prolong times of low abundance, possibly preventing a period of potential high abundance (Hutchings *et al.* 2000). One of the ecological issues for the small pelagics fishery in South Africa is the recruitment problem, for which one of the indicators is condition of adults (Shannon *et al.* 2006). Pelagic fish species are commercially important and the South African pelagic fishery is the largest by mass of fish landed although it has a lower economic value than the demersal trawl fishery due to the low unit value (Booth and Hecht 2000). Anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*) and the round herring (*Etrumeus whiteheadi*) are the three most important species caught and landed by pelagic vessels (Griffiths *et al.* 2004).

Historically, sardine was the dominant fish harvested and processed by the canning industry, but since 1966 anchovy has been the dominant species landed and is primarily used for fishmeal and oil (Booth and Hecht 2000). Anchovy remains the largest component of the pelagic fishery, followed by sardine and round herring (Griffiths *et al.* 2004). The anchovy and sardine stocks are considered to be fully utilised (Bergh and Butterworth 1987, Butterworth *et al.* 1993), but round herring is considered to be under-utilised (Roel and Armstrong 1992).

In addition to fisheries implications, pelagic fish species are ecologically important. Sardine-anchovy systems have been called “wasp-waist” ecosystems by Bakun (1996). This is because they prey on a high diversity of planktonic organisms and are preyed upon by a large number of predators. As Schwartzlose *et al.* (1999) explain, transfer of energy from plankton to predators is mainly through a few species of forage fish thereby forming a wasp-waist in terms of species diversity. Therefore changes in relative abundance of the forage fish influences species at both lower (food) and higher (predator) trophic levels.

Recruitment variability is believed to be important in determining overall variability of the pelagic fish stocks. Egg and larval viability could play a role in determining recruitment and this study aimed to investigate links between egg size (as a proxy for egg quality) and biotic and abiotic factors. Sardine eggs have a wide perivitelline space between the chorion and yolk. Therefore a relationship between egg volume, yolk volume and oil globule volume was assessed to determine whether egg volume measurements accurately represent egg quality, i.e. bigger eggs should have more yolk and a bigger oil

globule. Egg volume has been shown to be inversely affected by SST elsewhere (Le Clus 1992). In South Africa, SST increases from west to east along the South African coastline. The warm Agulhas Current occurs off the east coast and wind-driven coastal upwelling results in cold temperatures on the west coast. This relationship was investigated for anchovy, sardine and round herring eggs sampled along the South African coast in 1998, 2000 and 2001. In addition to abiotic influences, adult size and condition have been shown to influence egg volume, where an increase in adult size and lipid content results in bigger better eggs being spawned (Funamoto and Aoki 2002, Llanos-Riviera and Castro 2004, Palumbi 2004, Berkely *et al.* 2004, Kalmer 2005 and Llanos-Riviera and Castro 2006); this is known as the “parental condition hypothesis. In South Africa, fish size (Barange *et al.* 1999), and condition vary spatially for both anchovy (van der Lingen and Hutchings 2005), and sardine (van der Lingen *et al.* 2006) with a movement east as they get bigger and improve in condition. Adult size and lipid content results in bigger, better eggs being spawned. The “parental condition” hypothesis was tested for anchovy and sardine to determine whether it can be supported by data collected from the southern Benguela on egg volume and adult size and condition. An objective of this study was to determine the effects that the eastward shift with fish age (and thus size) had on egg volume in 1998, 2000 and 2001.

3. Materials and Methods

Factors affecting spatial variability in egg volume of round herring, anchovy and sardine in the southern Benguela were investigated for 1998, 2000 and 2001. The egg samples were collected during the annual pelagic spawner biomass surveys conducted in

November/ December 1998, 2000 and 2001 by the Department of Environmental Affairs and Tourism (DEAT), branch Marine and Coastal Management (MCM) on board FRS *Algoa* and FRS *Africana*. The surveys are designed to coincide with the peak spawning period of anchovy, although sardine and round herring are also known to spawn during that time. The surveys covered the continental shelf area from Hondeklip Bay on the west coast of South Africa to Port Alfred on the east coast (Figure 3). The survey track consisted of gridlines perpendicular to the coast extending over the 200m isobath.

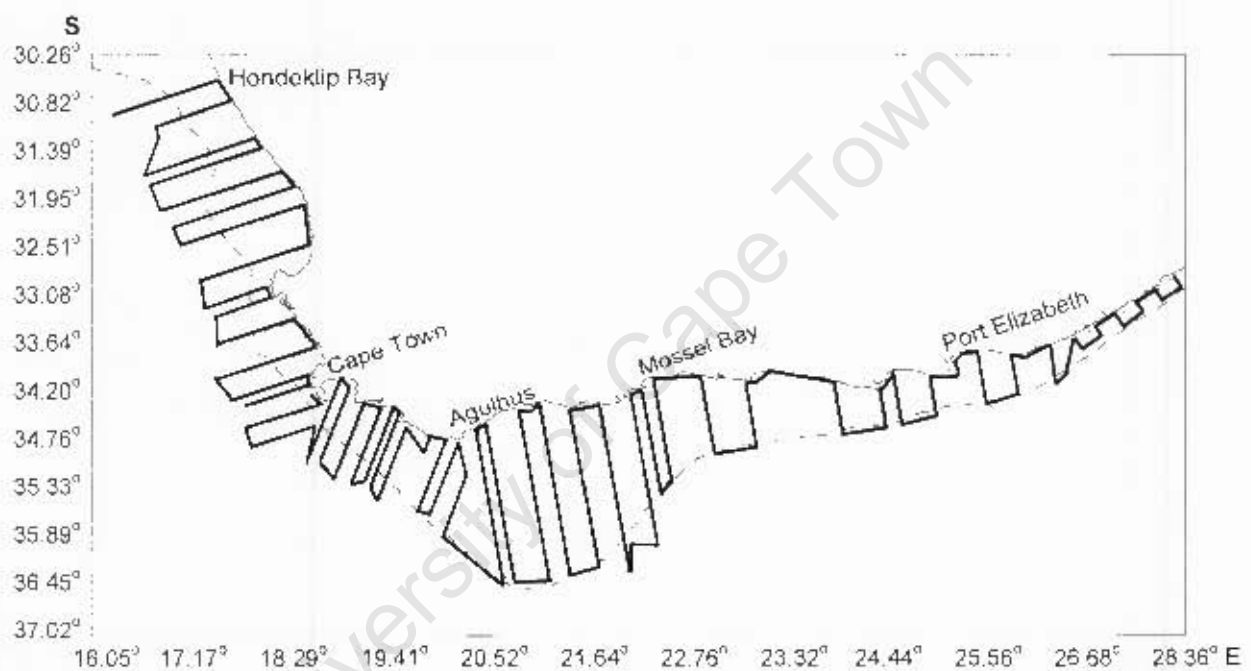


Figure 3. Map showing the area that was sampled during the annual spawner biomass survey in 1998. The dashed line indicates the 200m isobath.

Egg samples were collected using the Sardine California Vertical Egg Tow (CalVET) net, which is hauled vertically from 5m off the bottom or from a depth of 100m every 5 or 10 nautical miles (nmi) (van der Lingen *et al.* 2001), and the Continuous Underway Fish Egg Sampler (CUFES), which sieves eggs from the water at varying intervals depending on their abundance: 0.13nmi at high abundance and 4nmi at low abundance. Samples were put into plastic jars and immediately preserved in 5% buffered formalin (previous

studies on anchoveta eggs have reported no egg size shrinkage or shape changes with formalin preservation (Fisher, 1958) after which the eggs were identified extracted in the laboratory using a light microscope. The extracted eggs were counted and preserved in 5% buffered formalin in separate plastic vials for further analysis.

The data collected at each station of the spawner biomass surveys consisted of longitude and latitude co-ordinates and a sea surface temperature (SST) for each egg sample. Although each cruise followed a similar survey track, the samples were taken at different positions each year. The samples were assigned to $0.5^{\circ} \times 0.5^{\circ}$ grids according to their latitude and longitude co-ordinates (Figure 4), and the grids were used as a spatial variable in the analyses.

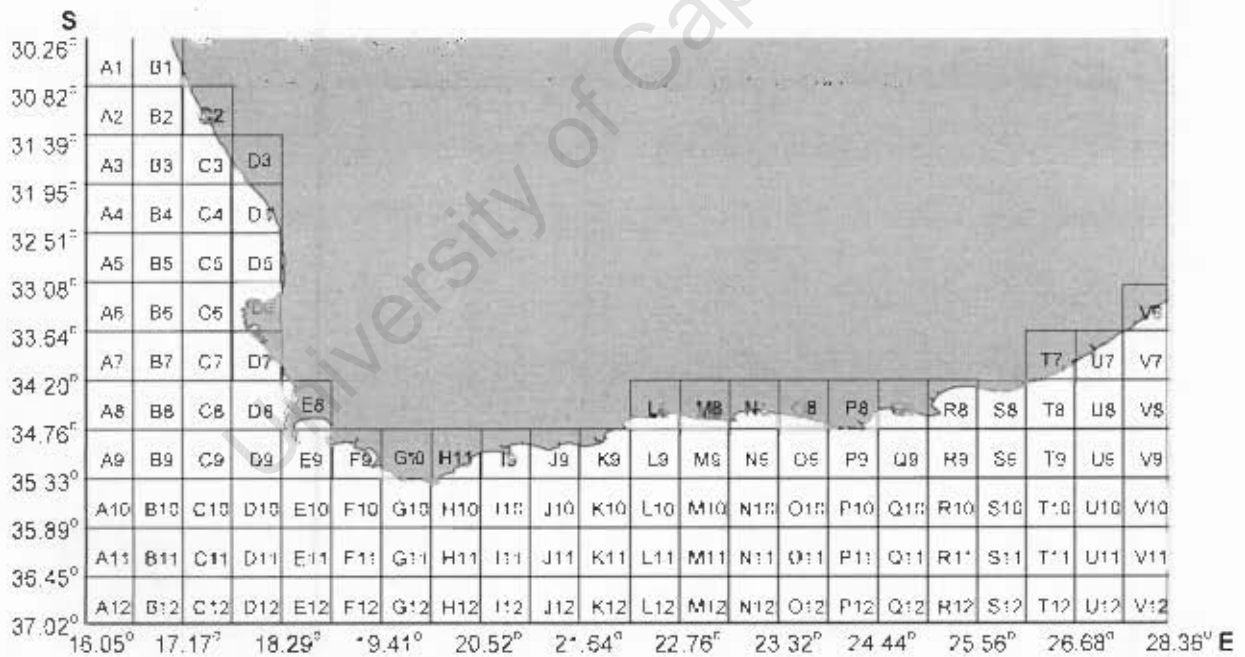


Figure 4. Grids, $0.5^{\circ} \times 0.5^{\circ}$, resulting from the equal division of latitudes 30°S - 37.02°S and longitudes 16.05°E - 28.36°E .

SST data were collected with each sample by means of a TSG probe mounted at hull depth, i.e. 6m. Adults were collected by means of a trawl net when shoals were detected

via the echo-sounder system. Adult samples were sub-sampled, identified, measured and weighed and each trawl sample was assigned to a grid (Figure 4). In each grid the proportions of big, average and small adults, was calculated, using the size classes in Table 1.

Table 1. Size (cm) of round herring, anchovy and sardine adults in each of three classes.

Class	Species		
Size	Round Herring	Anchovy	Sardine
Small	14.5-16.5cm	8.5-10.0cm	15.5-17.0cm
Average	16.6-19.5cm	10.1-12.0cm	17.1-20.0cm
Big	19.6-22.0cm	12.1-14.5cm	20.1-22.0cm

Fat stage data were obtained via visual assessment of mesenteric fat for anchovy and sardine from the biomass surveys of 1998, 2000 and 2001, but there were no fat stage data for round herring. The fat stage data (fat stages one to five) for anchovy were divided into three categories: *Thin*, *Average* and *Fat* (Table 2) and expressed as proportions of thin and fat adults in each grid.

Table 2. Fat content (FS: Fat Stage and LLC: Log Lipid content (%WBM)) of anchovy and sardine adults in each of three classes.

Fat Content	Round Herring	Anchovy	Sardine
Thin	-	FS 1	LLC 0-0.728
Average	-	FS 2-4	LLC 0.729-1.911
Fat	-	FS 5	LLC 1.912 +

Sardine fat stage (fat stages one to seven) was converted to lipid content (expressed as % wet body mass, WBM), which is a better estimate of body lipid content than fat stage in sardine (van der Lingen and Hutchings 2005), using the following equation (Table 3) (de Goede & van der Lingen, 2005):

$$\text{Lipid content (\%WBM)} = a_{(\text{fat stage})} + b(\text{fish mass(g)}) + c(\text{fat stage} * \text{fish mass}) + d$$

Equation A

where a , b , c and d are parameters in the equation.

Table 3: Parameter values used to convert fat stage and fish mass into body lipid content.

Fat stage	Parameter value			
	a	b	c	d
1	-2.58	0.097	-0.080	3.23
2	-2.46	0.097	-0.067	3.23
3	-2.01	0.097	-0.040	3.23
4	-1.31	0.097	-0.035	3.23
5	-0.42	0.097	-0.037	3.23
6	-0.05	0.097	-0.012	3.23
7	0.0	0.097	0.0	3.23

Lipid content was log transformed and the proportions of *Thin* and *Fat* sardine adults was determined for each grid (Table 2).

Sardine eggs that were obtained sampled using both the CalVET net and CUFES from the 1998, 2000 and 2001 spawner biomass surveys were measured. Egg measurements were done by taking two diameter measurements perpendicular to each other using an ocular micrometer at 40x magnification. Volumes (mm^3) were calculated using the formula for a sphere:

$$V = \frac{4\pi r^3}{3}$$

Equation B

where r is the radius (mm), taken as the average of the two diameter measurements.

The same procedure was followed for round herring eggs obtained from CalVET net samples. Samples had different numbers of eggs per station. For stations where there were more than 100 eggs, a sub-sample was taken and 100 eggs were measured. In total,

3130 CalVET sampled sardine eggs were measured from 1998, 2000 and 2001 with the total number of stations being 279. For sardine, 148430 eggs were measured from 1137 CUFES sampled stations, and for round herring, 1002 eggs were measured from 145 stations.

Egg diameter, oil globule diameter and yolk diameter were measured for 195 sardine eggs as described above. This sub-sample consisted of measurements from both survey and archived samples. Egg-, yolk- and oil globule volume were determined using Equation A. The three volumes were transformed using a logarithmic transformation and correlation tests were done to establish whether egg volumes were related to yolk volumes and oil globule volumes, using STATISTICA 7 software (Statsoft Inc., 2004).

Anchovy eggs from the 1998, 2000 and 2001 CalVET net samples were measured by taking a length and width measurement for each, using an ocular micrometer at 40x magnification.

The volumes (mm³) were determined using the formula for a prolate spheroid:

$$V = \frac{4\pi}{3} \frac{a}{2} \frac{b}{2} \frac{c}{2} \quad \text{Equation C}$$

where a is the length (mm), b is the width (mm) and c is the depth (mm), and c (not measured) is assumed to be equal to b (measured).

A total of 10855 anchovy eggs were measured from a total of 234 stations from 1998 to 2001.

To assess large-scale pattern, the log egg volumes for the three species were plotted on maps and overlaid with SST data and the proportions of Small and Big fish. The same was done for proportions of *Thin* and *Fat* fish for anchovy and sardine, where the sizes of the circles represented the proportion of adults in that category. These analyses were done using Surfer 8 software (Golden Software, Inc., 2002).

General linear models (GLMs) were used to determine which factors were related to egg volume, using STATISTICA 7 software. All GLMs were constructed using Type VI (unique) sums of squares. Residuals were visually checked to ensure that the assumption of normality was satisfied. Egg volumes were transformed (log (EV)) using a log transformation to normalise the residuals. Explanatory variables were *Grid* number, *Gear* (in the case of sardine), and *Year* as categorical variables and *SST* as the only continuous variable. Two way interactions were included in the models. The GLMs for each of the species were:

Round Herring

$$\text{Log}(\text{EV (mm}^3)) = \beta + \text{Grid} + \text{year} + \beta_1 \text{SST} + \text{Grid} * \text{SST} + \text{Year} * \text{SST} + \text{Grid} * \text{Year} + E$$

Equation D

Anchovy

$$\text{Log}(\text{EV (mm}^3)) = \beta + \text{Grid} + \text{year} + \beta_1 \text{SST} + \text{Grid} * \text{SST} + \text{Year} * \text{SST} + \text{Grid} * \text{Year} + E$$

Equation E

Sardine

$$\text{Log}(\text{EV (mm}^3)) = \beta + \text{Grid} + \text{year} + \beta_1 \text{SST} + \text{Gear} + \text{Grid} * \text{SST} + \text{Year} * \text{SST} + \text{Grid} * \text{Year} + E$$

Equation F

where E is the error term.

Because I was interested in the *Grid*Year* interaction, only those grids in which eggs occurred in all three years were used in the analysis (Figure 6). The adjusted R^2 and p values were noted for each GLM in addition to all main and interaction effects. In addition post-hoc analyses (Tukey tests) were done to show which levels of the various factors were significantly different.

4. Results

SSTs for the whole survey showed the coldest waters were on the west coast, and warmest offshore of Mossel Bay and Port Elizabeth in 1998 (Figure 5a). In 2000 a similar pattern occurred, when the coldest waters occurred on the west coast and increased in temperature offshore in a south-easterly direction, with the highest temperatures occurring offshore between Mossel Bay and Port Elizabeth (Figure 5b). In addition, in 2000 a cool ridge of cold water extended over the Agulhas Bank in a south-westerly direction from mid-way between Cape Agulhas and Mossel Bay (Figure 5b). The SSTs for 2001 followed the same pattern as 2000, except that the cold ridge was a warm ridge because the surrounding waters being cooler (Figure 5c).

4.1 Round Herring

In 1998, log egg volume for round herring was lowest over the central and eastern Agulhas Bank increasing offshore (Figure 6a). The largest eggs were found on the northern west coast and offshore from Cape Town and Mossel Bay in a southerly

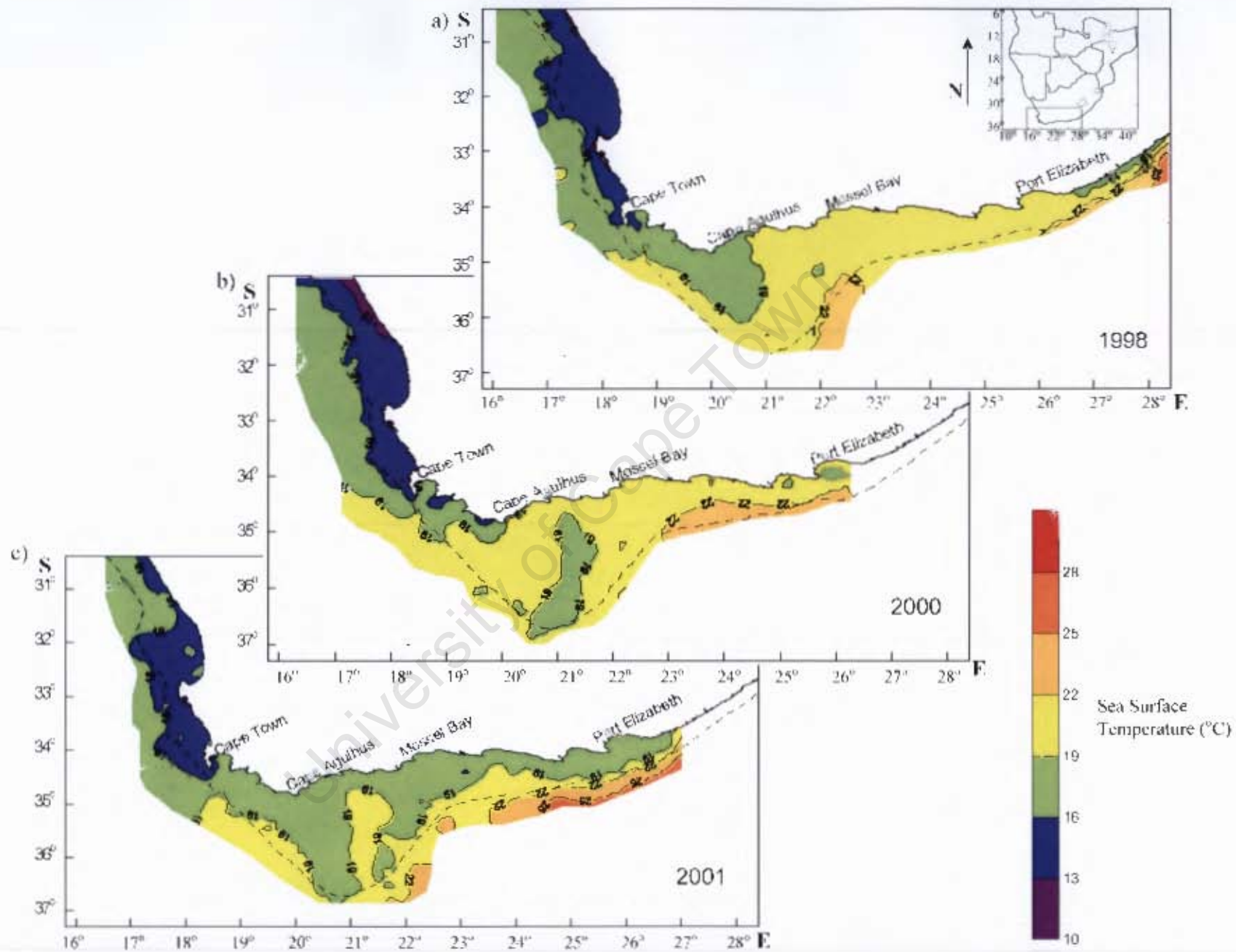


Figure 5. Sea surface temperature (SST) recorded during the spawner biomass surveys conducted in 1998, 2000 and 2001. The 200m depth contour is indicated as the dotted line and SST ($^{\circ}\text{C}$) values on contour lines are oriented to have warmer temperatures above the label, which are represented on each of the maps to follow.

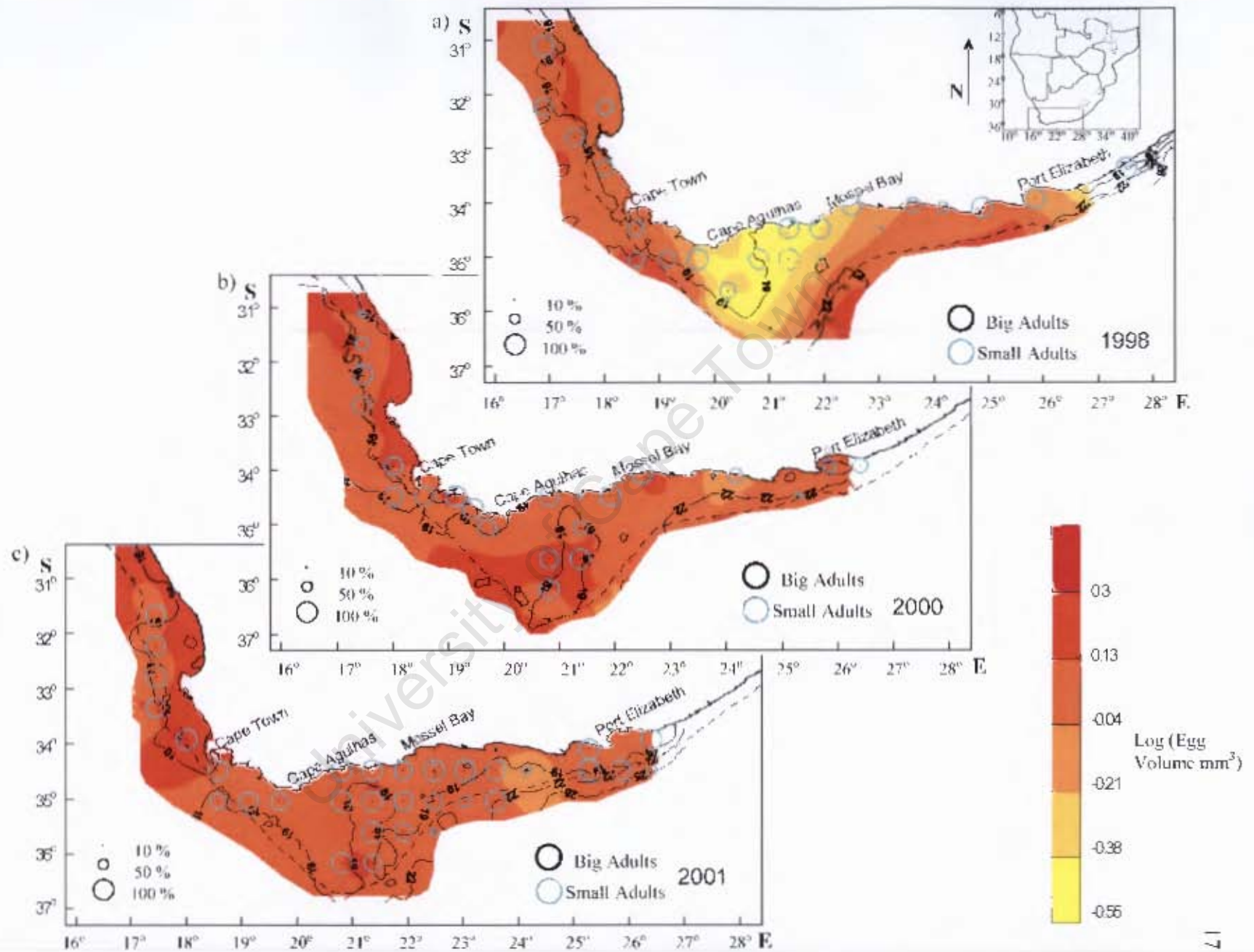


Figure 6. Spatial distribution of round herring egg volumes (shown as colour contours) in 1998, 2000 and 2001. Percentages big (black rings) and small (blue rings) adults, in each grid where % refers to a total comprised of big, average and small adults. The 200m depth contour is indicated as the dotted line and SST as solid contour lines with labels oriented to have warmer temperatures above the label, warmer temperatures above the label.

direction, and Port Elizabeth, in a south westerly direction (Figure 6a). In 2000 the biggest eggs were found on the west coast, south west of Cape Town, south of Mossel

Bay and over the offshore areas of the Agulhas Bank (Figure 6b). The smallest eggs were found inshore mid-way between Mossel Bay and Port Elizabeth (Figure 6b). In 2001 the biggest eggs were found west of Cape Town and the smallest again south of approximately mid-way between Mossel Bay and Port Elizabeth, thereby decreasing from west to east (Figure 6c).

In 1998 small round herring adults were found along the whole coastline, with increased abundance inshore on the west and south western coasts (Figure 6a). Both small and big adults were found along the whole coastline in 2000 but occurred closer inshore, with fewer occurring between Mossel Bay and Port Elizabeth (Figure 6b).

In addition, their distribution didn't extend as far beyond Port Elizabeth as it did in 1998 and adults appeared to occur on the cold ridge with only one area where the proportion of big adults was greater than that of small adults (Figure 6b). The distribution for 2001 on the west coast is similar to that of 1998 and extended to a similar eastern point as 2000 (Figure 6c). There were, however, more adults over the central and eastern Agulhas Bank in 2001 with the highest proportion of big adults occurring mid-way between Mossel Bay and Port Elizabeth (Figure 6c). Although the largest proportion of big adults occurred in this area, it wasn't greater than the proportion of small adults in this area (Figure 6c).

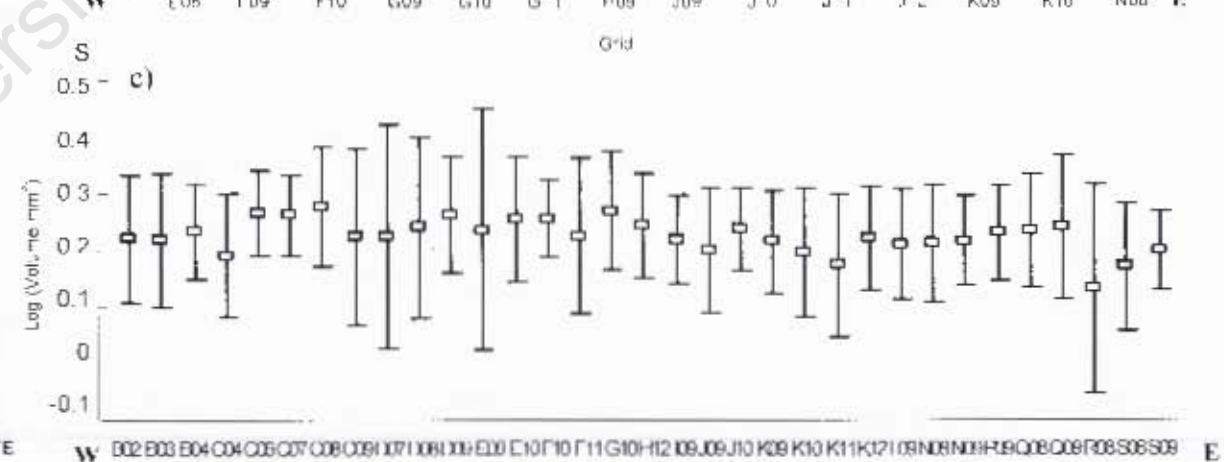
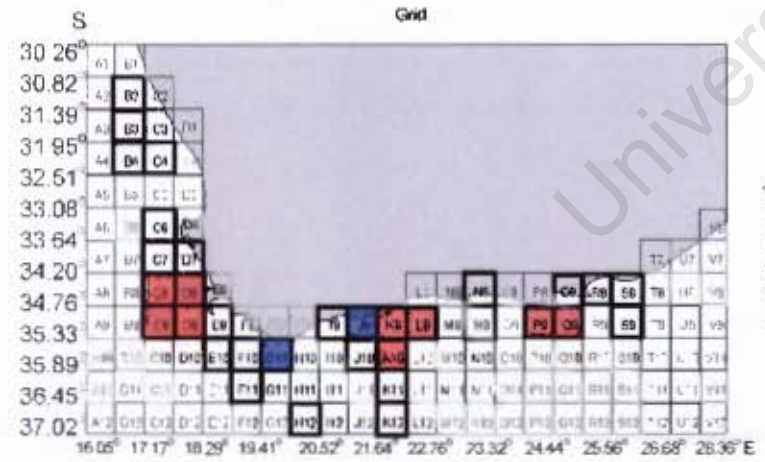
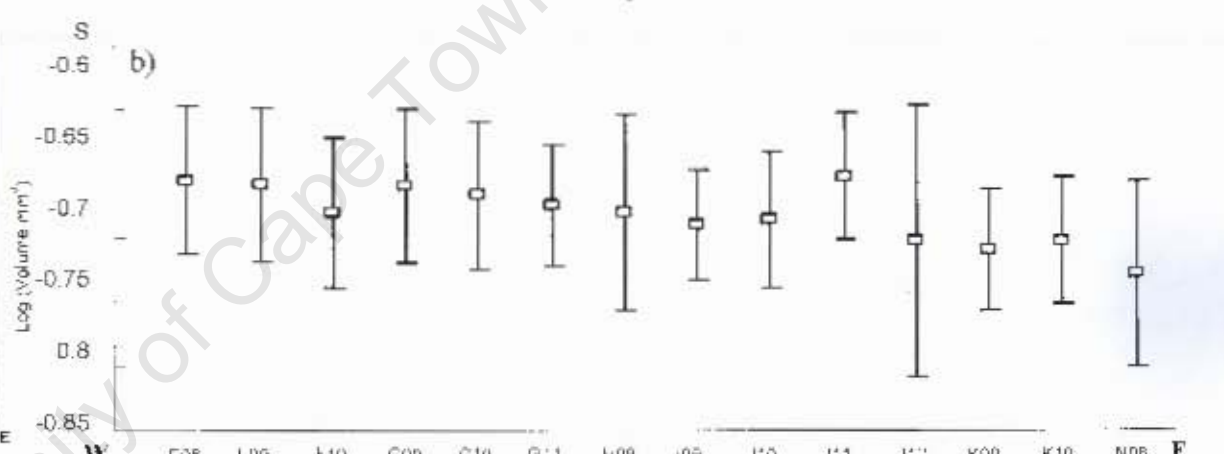
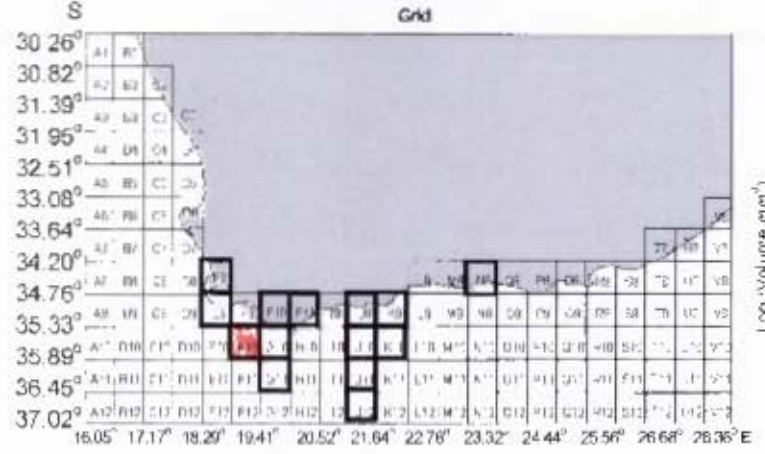
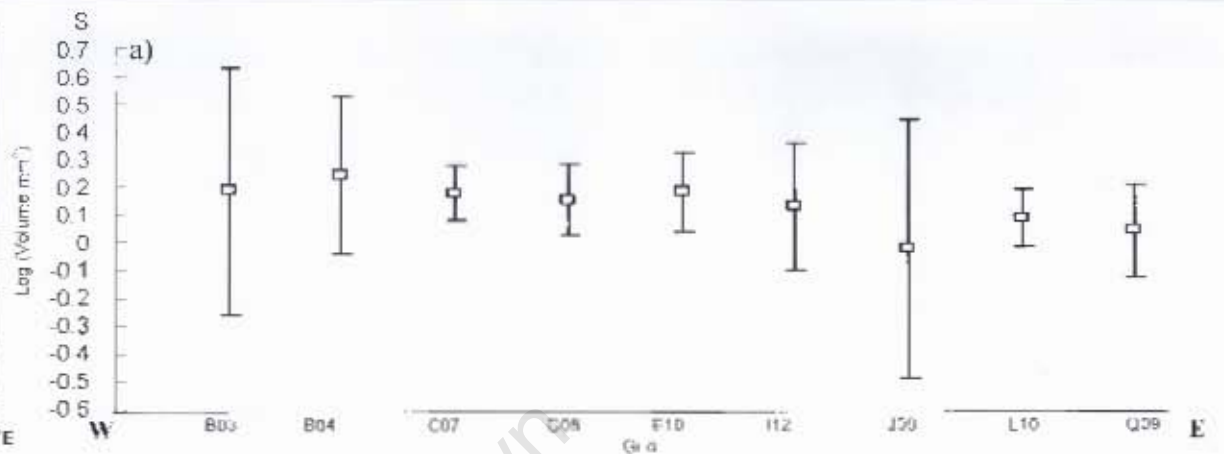
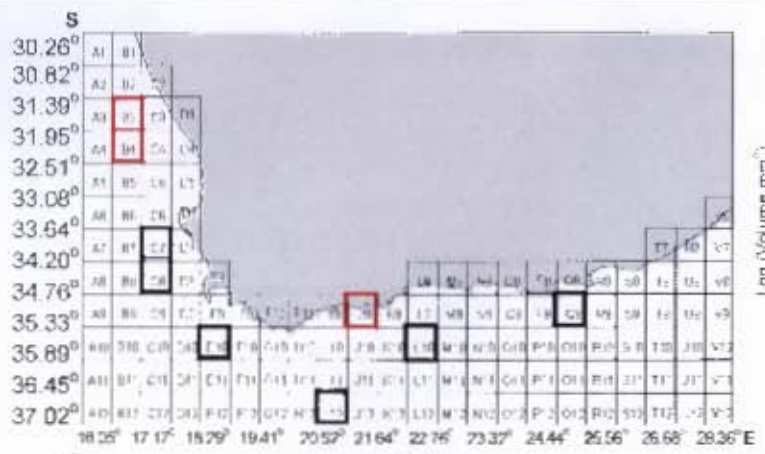


Figure 7. Results of the GIMs showing the observed means (\pm standard error) of egg volumes for each grid, arranged in order from west to east and inshore to offshore for a) Round Herring, b) Anchovy and c) Sardine. The grids used in the GIMs are indicated in bold on the maps in the left hand panel.

Round herring eggs were smallest in 1998. Eggs on the west coast increased in size from 1998 to 2001 and decreased in size on the eastern south coast. There was an increase in the distribution of small adults from 1998 to 2001, as well as a decrease in the western and eastern extent.

The GLM for round herring explained 36% of the variability in egg volume, where egg volumes differed significantly among areas but not among years or with SST (Table 4). Egg volume in one grid, J09, was significantly lower than those in grids B03 and B04 (Figure 7a). Egg volume decreased from west to east with a patchy but extensive distribution, stretching from the west coast to the eastern south coast for all three years (Figure 7a).

Table 4. General Linear Model results for Round Herring (Adjusted $R^2=0.30$) showing the contributions of the different variables to determining egg volume.

Factor	df	F	% Var	p
Intercept	1	0.729		0.394
<i>Grid</i>	8	2.679	3.90	0.007
<i>SST</i>	1	0.763	0.14	0.383
<i>Year</i>	2	1.641	0.60	0.195
<i>Gear</i>	-	-	-	-
<i>Grid*SST</i>	8	2.675	3.90	0.007
<i>Year*SST</i>	2	1.438	0.52	0.239
<i>Grid*Year</i>	16	4.048	11.80	<0.001
Model	37		36.65	<0.001
Error	348		63.35	
Total	385			

The main interaction effects are shown, together with univariate statistics of the parameter values. $R^2 = R^2$ from test of SS whole model vs. SS residual.
df= degrees of freedom, F= F-ratio, % Var.= % variance explained= $100 \times SS_{effect}/SS_{tot}$.

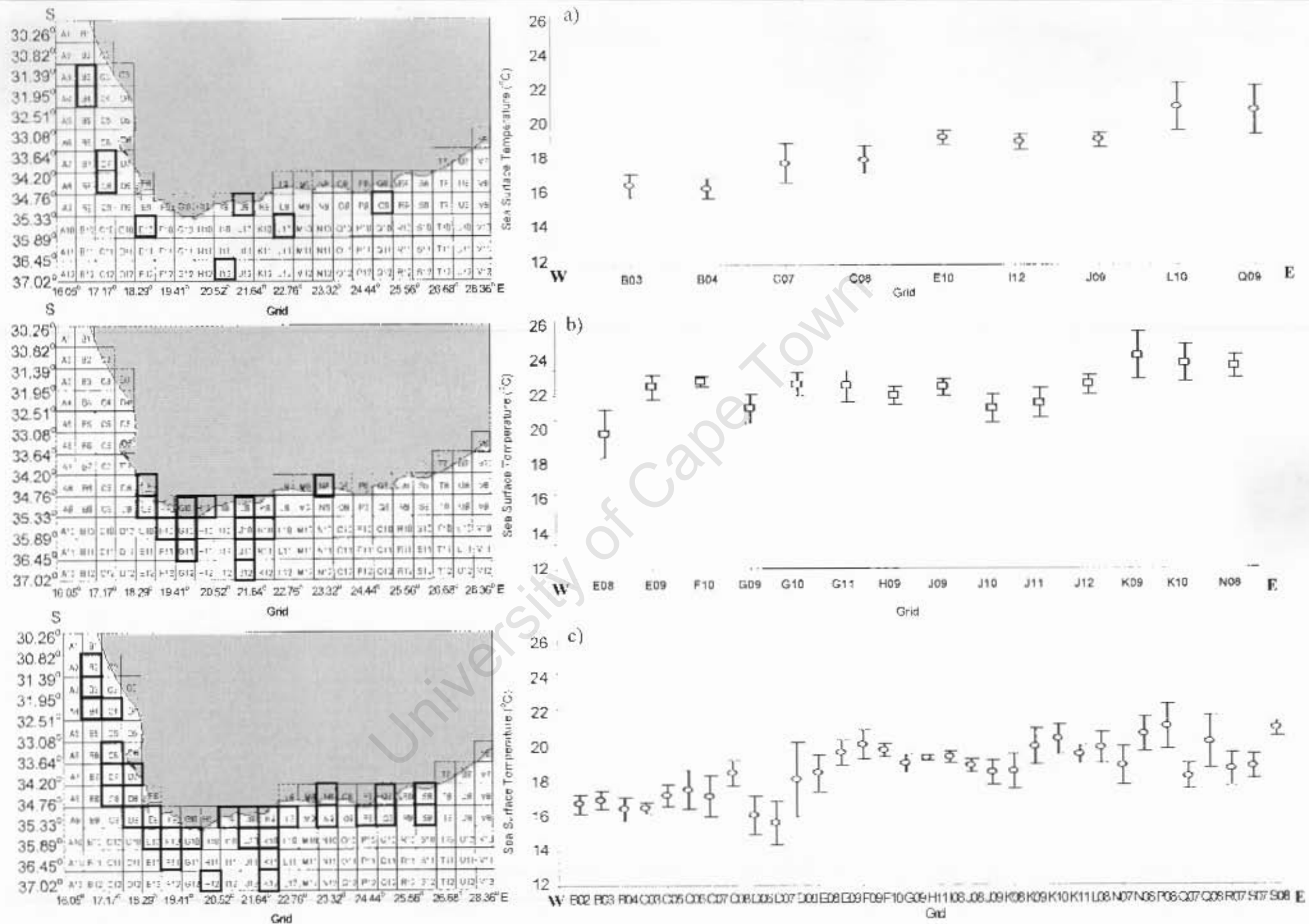


Figure 8. Relationships between mean sea surface temperature (°C) and grids, arranged in order from west to east and inshore to offshore, for a) Round Herring, b) Anchovy and c) Sardine. The grids used in the GLMs are indicated in bold on the maps in the left hand panel

There was a significant *Grid*SST* effect that explained 3.90% of round herring egg volume variability (Table 4). SST increased from west to east for the grids in which eggs occurred for all three years (Figure 8a).

4.2 Anchovy

Anchovy eggs were largest mostly west of the middle of the central Agulhas Bank (Figure 9a and 10a). They were smallest mostly east of the middle of the central Agulhas Bank (Figure 9a and 10a). In 2000 there was a patchy distribution of egg volumes with the biggest eggs being found at the two extremes of the coverage, and the smallest eggs being found south of Mossel Bay (Figure 9b and 10b). The biggest anchovy eggs in 2001 were found inshore on the central Agulhas Bank and the smallest on the west coast (Figure 9c and 10c).

In 1998 small anchovy adults were in greater proportions than big adults inshore, but the reverse occurred offshore (Figure 9a) with the highest proportion of big adults occurring on the eastern Agulhas Bank (Figure 9a). In 2000 the distribution of anchovy adults extends further west than 1998 (Figure 9b). The western areas were dominated by greater proportions of small adults than large, which dominate from this point eastwards (Figure 9b). In 2001 the adult distribution extended from the west coast to beyond Port Elizabeth, covering the majority of the area sampled from inshore to offshore (Figure 9c). The entire area except one grid, J12, had a higher proportion of small adults (Figure 9c), therefore 2001 was the year of smallest egg volumes and increased occurrence of small fish.

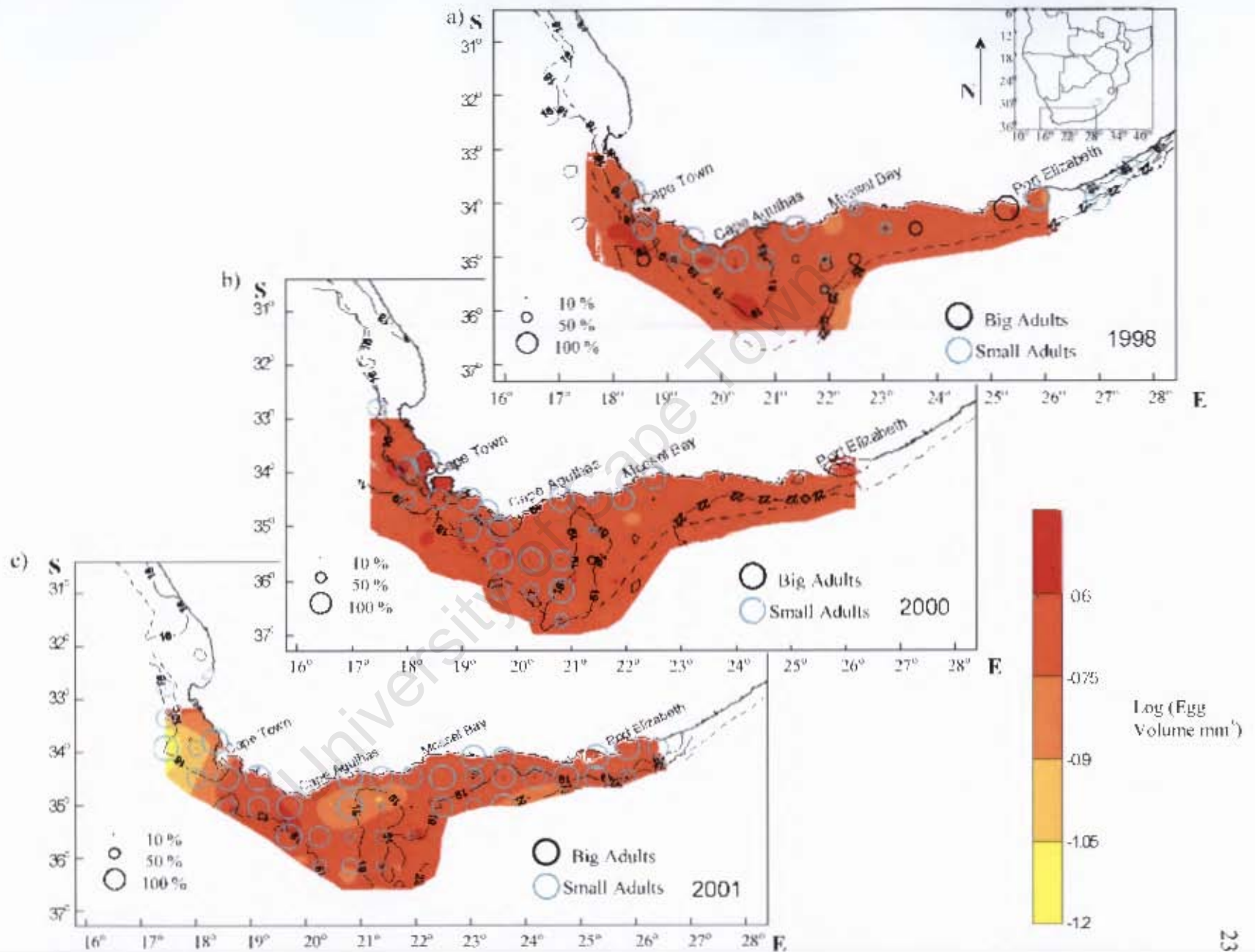


Figure 9. Spatial distribution of anchovy egg volumes (shown as colour contours) in 1998, 2000 and 2001. Percentages big (black rings) and small (blue rings) adults, in each grid where % refers to a total comprised of big, average and small adults. The 200m depth contour is indicated as the dotted line and SST as solid contour lines with labels oriented to have warmer temperatures above the label.

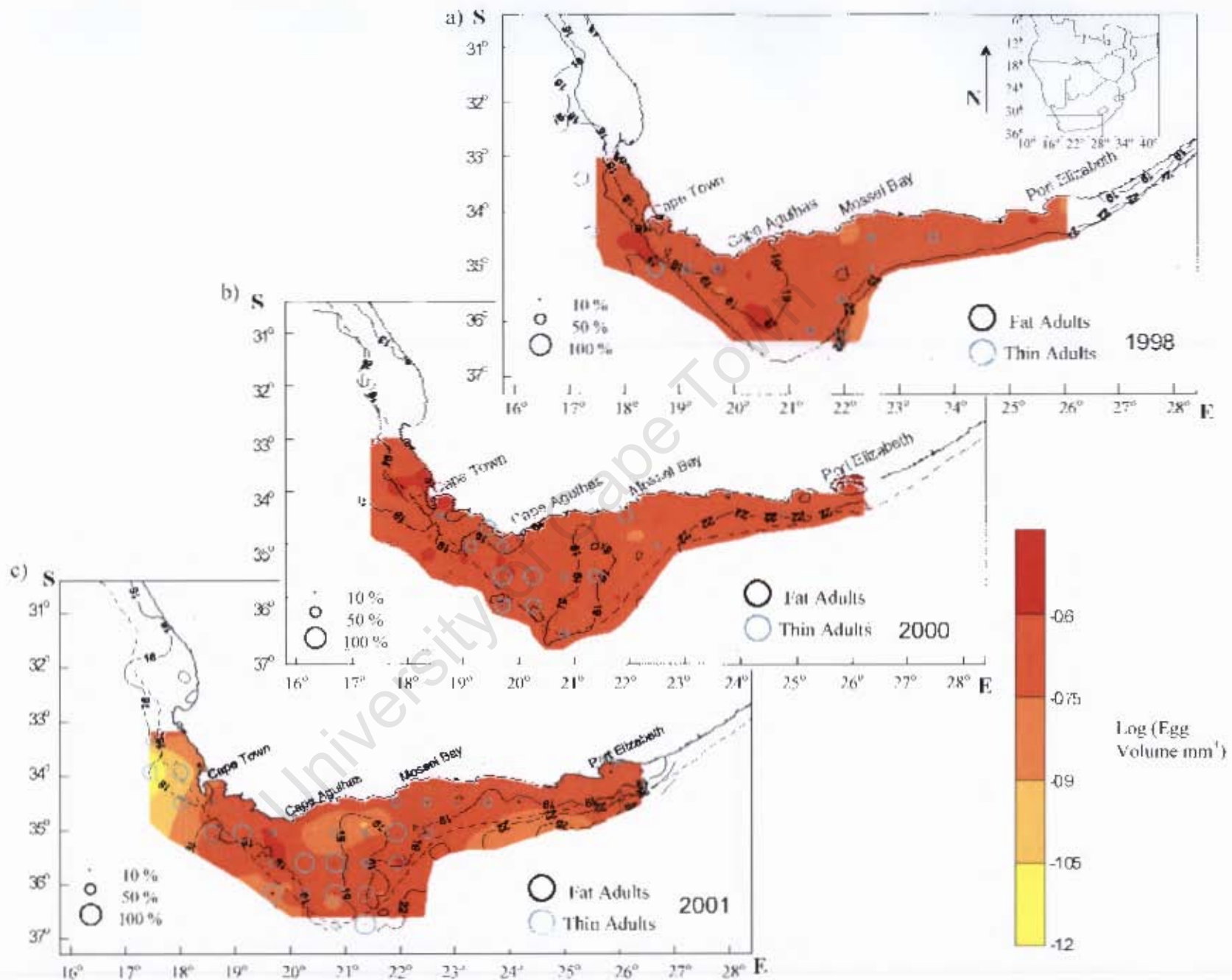


Figure 10. Spatial distribution of anchovy egg volumes (shown as colour contours) in 1998, 2000 and 2001. Percentages fat (black rings) and thin (blue rings) adults, in each grid where % refers to a total comprised of fat, average and thin adults. The 200m depth contour is indicated as the dotted line and SST as solid contour lines with labels oriented to have warmer temperatures above the label.

The largest proportions of thin anchovy were seen south of Mossel Bay with only three areas having a higher proportion of fat adults in 1998 (Figure 10a). The distribution of these adults appeared divided into a western and eastern distribution, both of which have the largest proportion of thin adults offshore and lowest inshore (Figure 10a). In 2000 there was a more concentrated distribution than in 1998, with the majority of adults found on the western and central Agulhas Bank (Figure 10b). As for 1998, only three areas had higher proportions of fat adults than thin adults, which in 2000 occurred in the eastern areas (Figure 10b). The distribution in 2001 extended from offshore on the west coast to east of Port Elizabeth, again dominated by thin adults (Figure 10c). Their distributions extended offshore, with fat fish only occurring at the extremes of the coverage (Figure 10c).

Anchovy egg volume decreased between 2000 and 2001 with little, if any, change between 1998 and 2000. The smallest eggs were found in 2001 off the west coast. Adult distribution increased from 1998 to 2001. The distribution of adults shifted from furthest east in 1998 to further west in 2000 and back towards the east again in 2001. The proportions of thin and fat adults increased from 1998 to 2001. In 1998 few thin and/or fat adults occurred over the central Agulhas Bank, which was the area where there were increased proportions of both in 2000 and 2001.

The GLM for anchovy explained 15% of the variability in egg volume, where egg volumes differed significantly among areas (Table 5). Egg volume decreased from west to east with a clumped distribution around the Agulhas Bank (Figure 7b)

Table 5. General Linear Model results for Anchovy (Adjusted $R^2=0.15$) showing the contributions of the different variables to determining egg volume.

Factor	df	F	%Var	p
Intercept	1	6.378	0.09	0.012
<i>Grid</i>	13	6.045	1.17	<0.001
<i>SST</i>	1	0.900	0.01	0.343
<i>Year</i>	2	4.001	0.12	0.018
<i>Gear</i>	-	-	-	-
<i>Grid*SST</i>	13	6.146	1.19	<0.001
<i>Year*SST</i>	2	4.517	0.13	0.010
<i>Grid*Year</i>	26	7.558	2.92	<0.001
Model	57	18.534	15.72	<0.001
Error	5666		84.28	
Total	5963			

The main interaction effects are shown, together with univariate statistics of the parameter values. $R^2 = R^2$ from test of SS whole model vs. SS residual.

df= degrees of freedom, F= *f*-ratio, % Var.= % variance explained= $100 \times SS_{\text{effect}}/SS_{\text{tot}}$.

Anchovy egg volume significantly differed among years (Table 5). The smallest mean egg volume occurred in 1998, whereas the largest occurred in 2000 and 2001 where 2001 had the highest variability (Figure 11).

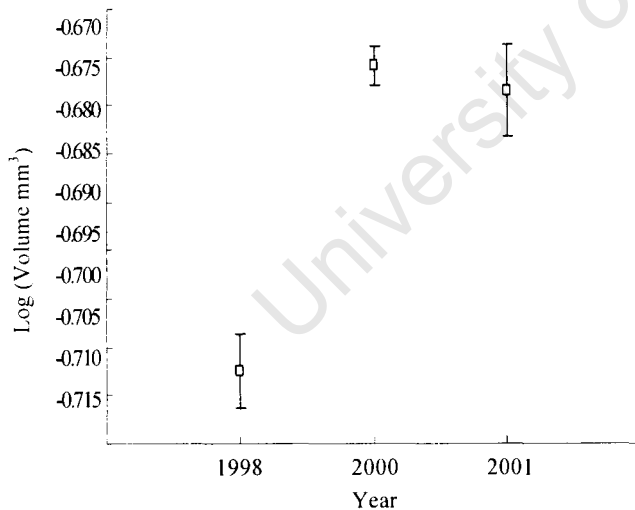


Figure 11. Results of the GLM showing the differences in observed mean log egg volume between 1998, 2000 and 2001 for anchovy, with the 95% confidence intervals illustrated by the error bars.

There was a significant *Grid*SST* effect on anchovy egg volume (Table 5). SST increased from west to east for the grids in which eggs occurred in all three years (Figure 8b). In addition, there was a significant *Year*SST* effect on egg volume (Table 5). SSTs in grids where eggs occurred had an increased range for anchovy in 2000, when egg volumes were large, and decreased for both from 1998 to 2001 (Figure 12).

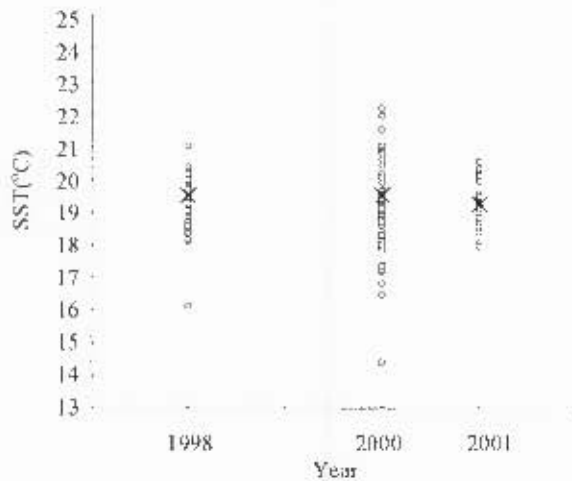


Figure 12. Observed SST measurements for 1998, 2000 and 2001 in the grids where eggs occurred, illustrated by the open circles, for anchovy, with the annual mean temperature illustrated by the bold crosses.

4.3 Sardine

Sardine egg volume and yolk volume were positively related to each other ($p < 0.001$, $R = 0.332$, $n = 195$), as were egg volume and oil globule volume ($p = 0.015$, $R = 0.173$, $n = 195$). There was a great deal of unexplained variability in these data (Figure 13), probably related to the precision with which measurements could be made, but they indicate that measurements of egg volume indicate the energetic content of the eggs.

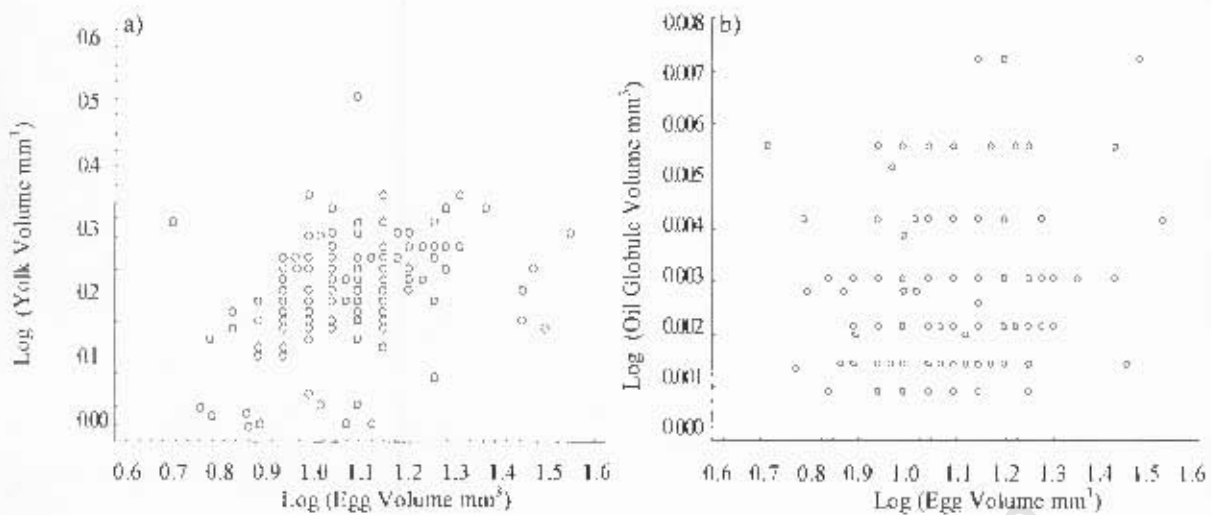


Figure 13. (a) Log (yolk volume mm^3) and (b) log (oil globule volume mm^3) relationships with log (egg volume mm^3), where the open circles represent individual measurements.

Sardine CalVET egg volume in 1998 was lowest in the western and central areas, and highest from the western Agulhas Bank towards eastern areas (Figure 14a and 15a). In 2000 the lowest egg volume for the CalVET samples occurred around Cape Agulhas, increasing offshore (Figure 14b and 15b). In 2001 a different pattern was seen with the majority of the eggs surrounding Cape Town (Figure 14c and 15c). The largest eggs were found south east of Mossel Bay (Figure 14c and 15c).

The 1998 sardine CUFES eggs were largest offshore in eastern areas (Figure 16a and 17a) and the smallest eggs were found offshore from Mossel Bay (Figure 16a and 17a). In 2000, the largest eggs were found offshore on the northern west coast, and the smallest from the western to the central Agulhas Bank (Figure 16b and 17b). The smallest eggs for 2001 occurred on the west coast in patches, as well as offshore from Mossel Bay in

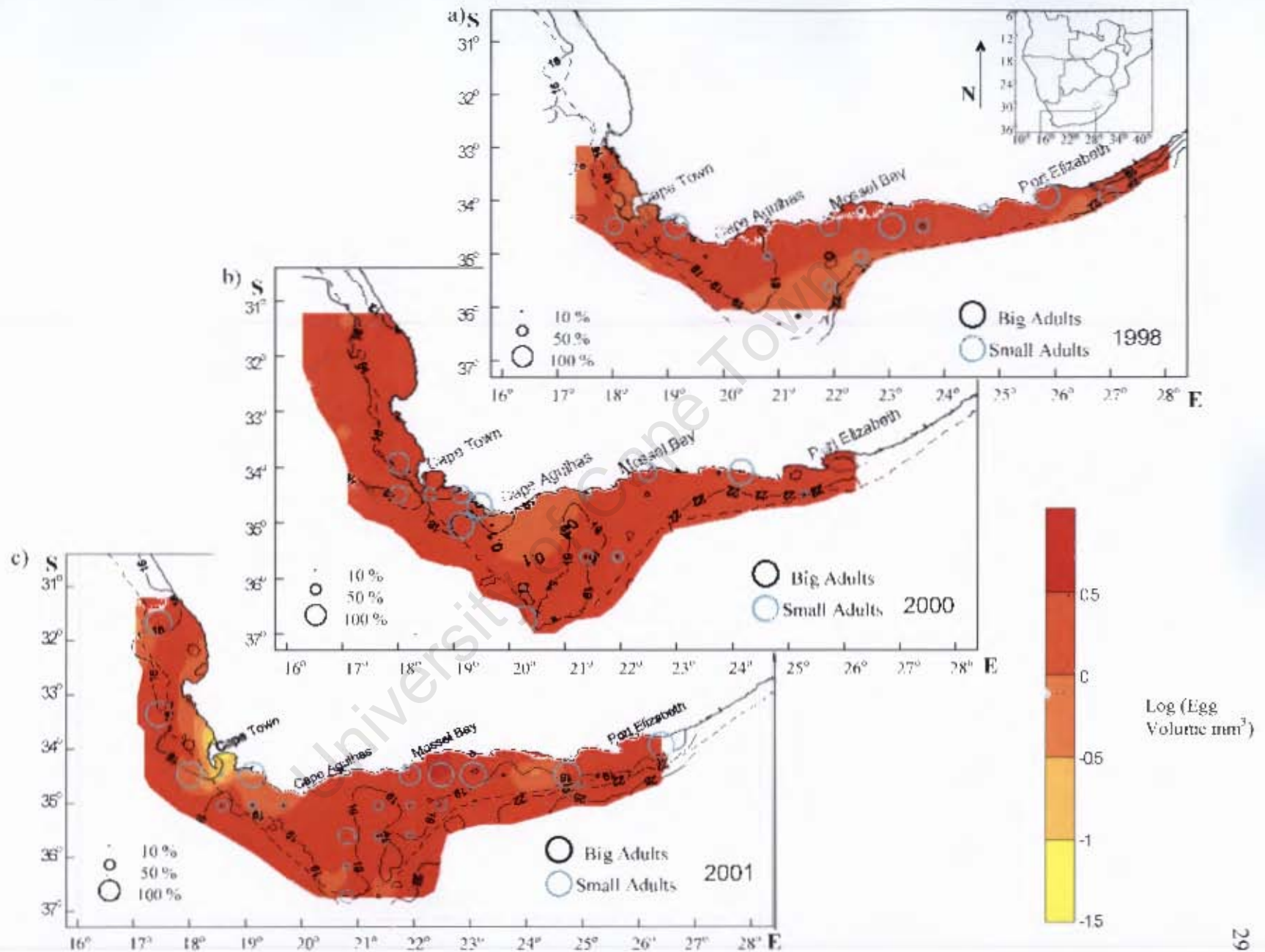


Figure 14. Spatial distribution of CalVIET sampled sardine egg volumes (shown as colour contours) in 1998, 2000 and 2001. Percentages big (black rings) and small (blue rings) adults, in each grid where % refers to a total comprised of big, average and small adults. The 200m depth contour is indicated as the dotted line and SST as solid contour lines with labels oriented to have warmer temperatures above the label.

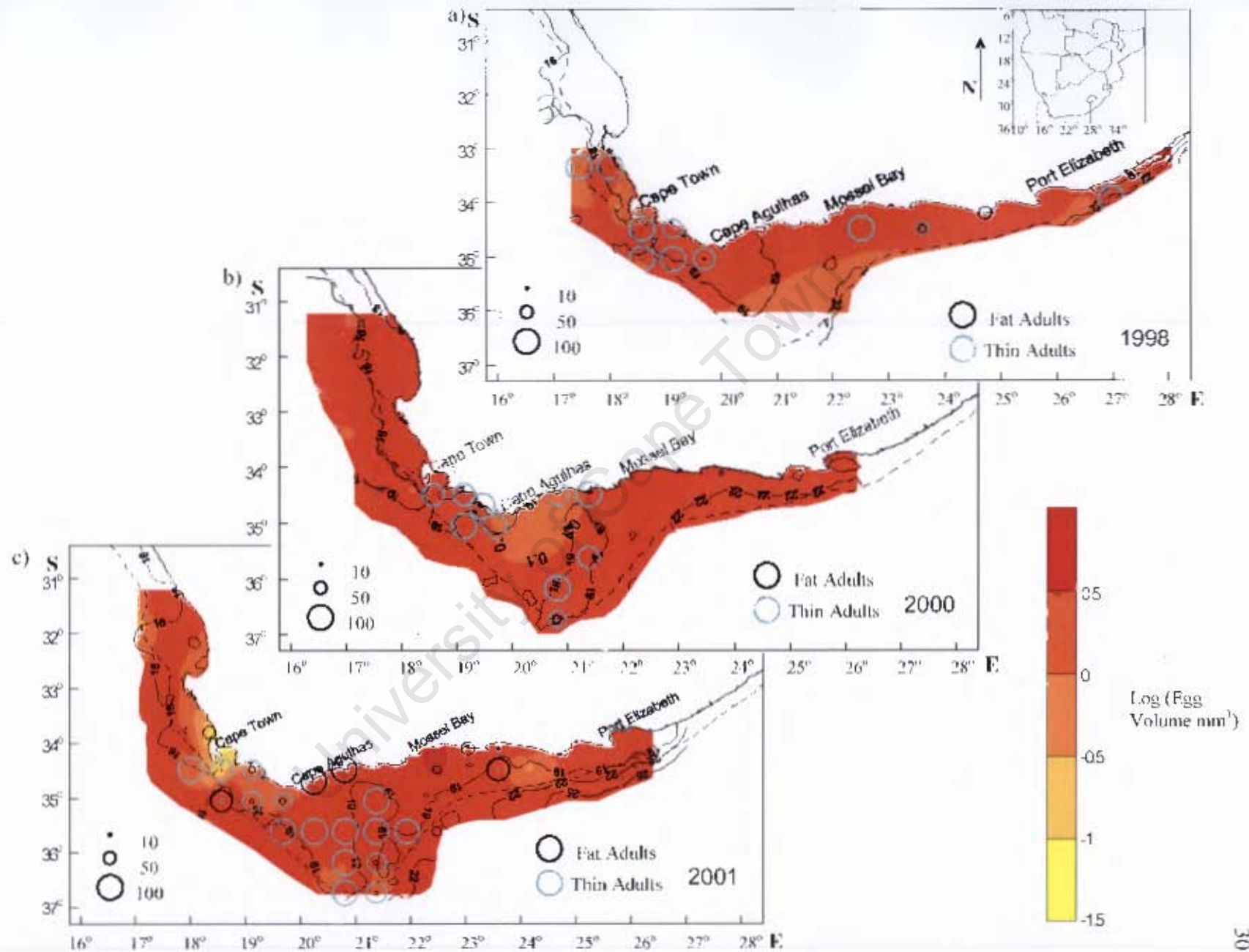


Figure 15. Spatial distribution of CalVET sampled sardine egg volumes, contours, and proportions of fat and thin adults, black and blue circles, during the spawner biomass surveys conducted in 1998, 2000 and 2001. The 200m depth contour is indicated as the dotted line and SST as solid contour lines with labels oriented to have warmer temperatures above the label.

patches (Figure 16c and 17c). The largest eggs were found extending from offshore on the west coast to inshore from Cape Town eastwards (Figure 16c and 17c).

In 1998 small sardine adults occurred on the west coast and extended to east of Port Elizabeth with the greatest proportions occurring over the central and eastern Agulhas Banks (Figure 14a and 16a). Big adults had the same distribution as the small adults but were in higher proportions offshore in the western areas (Figures 14a and 16a).

In 2000 adults were found from the northern west coast to east of Port Elizabeth with proportions of small adults being higher than those of big adults, mostly over the western Agulhas Bank (Figure 14b and 16b). Big adults were found in higher proportions over the central Agulhas Bank (Figure 14b and 16b).

Sardine adults in 2001 were distributed from the northern west coast to east of Port Elizabeth with two concentrated groups, one in the western to central areas and the second in the central and eastern areas (Figures 14c and 16c). The proportion of large adults only exceeded that of the small adults in one area in the western concentration, and in four areas in the eastern concentration (Figures 14c and 16c). The proportion of thin adult sardines, i.e. low lipid content, exceeded that of fat sardines in all but one area, west of Port Elizabeth (Figures 15a and 17a).

There was a concentration of sardine adults from Cape Agulhas up the west coast (Figures 15a and 17a). Thin and fat adults in 2000 were distributed over the central and western Agulhas Bank (Figure 15b and 17b). In all areas the proportion of thin adults

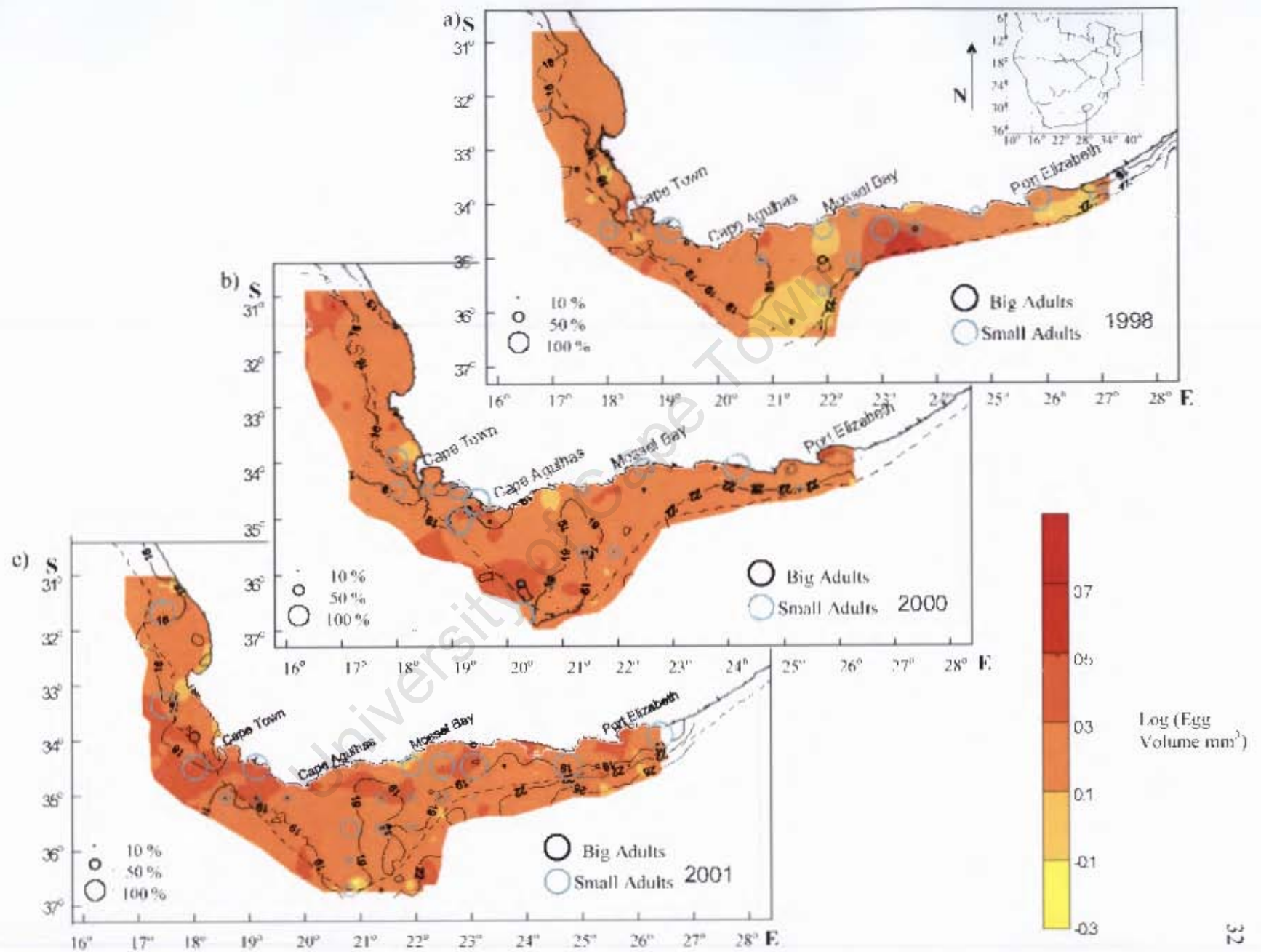


Figure 16. Spatial distribution CUFES sampled sardine egg volumes (shown as colour contours) in 1998, 2000 and 2001. Percentages big (black rings) and small (blue rings) adults, in each grid where % refers to a total comprised of big, average and small adults. The 200m depth contour is indicated as the dotted line and SST as solid contour lines with labels oriented to have warmer temperatures above the label.

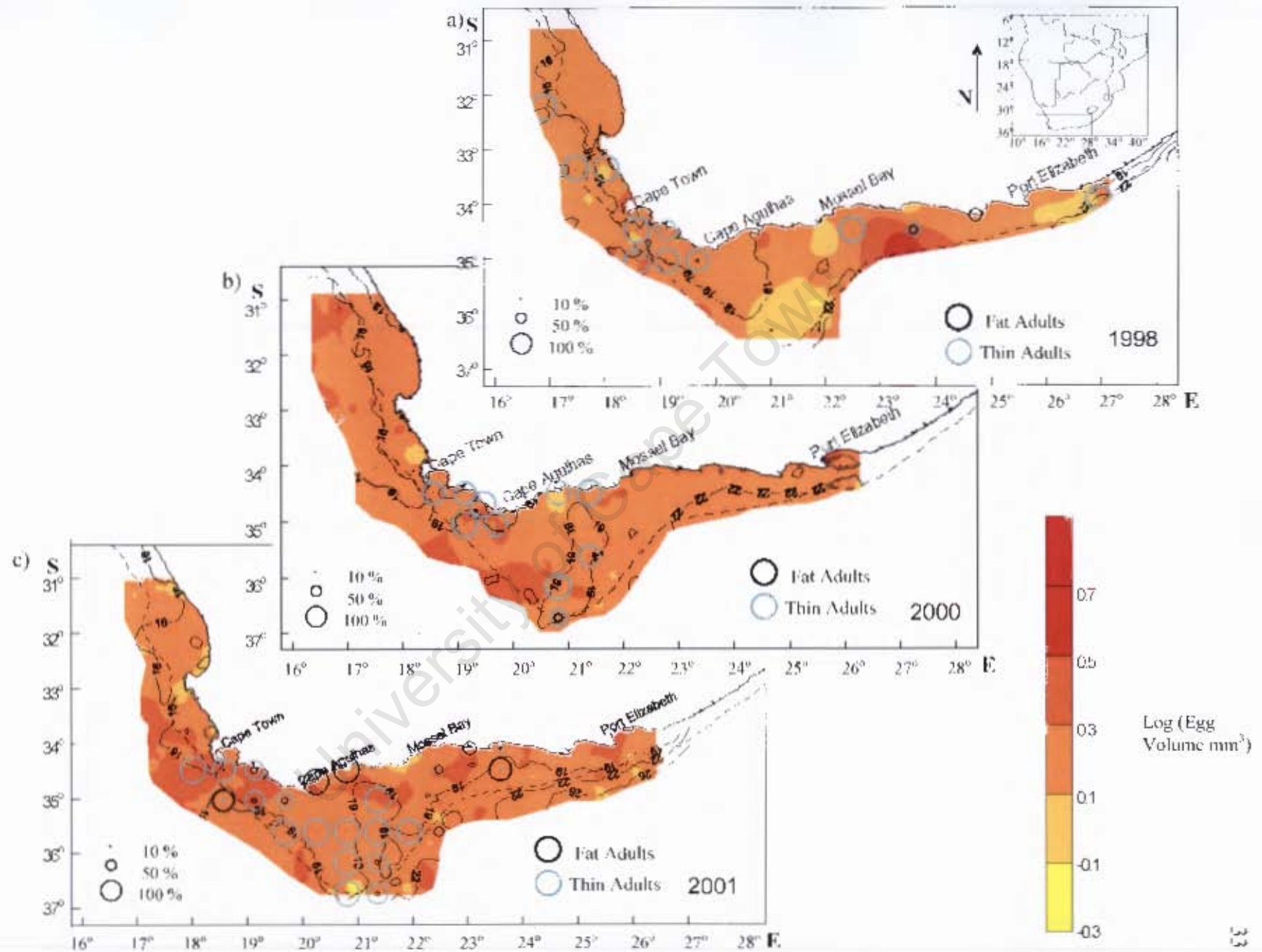


Figure 17. Spatial distribution of CUFFS sampled sardine egg volumes (shown as colour contours) in 1998, 2000 and 2001. Percentages fat (black rings) and thin (blue rings) adults, in each grid where % refers to a total comprised of fat, average and thin adults. The 200m depth contour is indicated as the dotted line and SST as solid contour lines with labels oriented to have warmer temperatures above the label.

exceeded that of the fat adults with the largest proportion of fat adults occurring at the southernmost point of the Agulhas Bank (Figures 15b and 17b). In 2001 a similar distribution pattern to 2000 was seen but extended slightly further west and further east (Figures 15c and 17c). Numerous areas had higher proportions of fat adults than thin, and most were inshore in central to eastern areas (Figures 15c and 17c).

Adult distributions for sardine extended furthest east in 1998 and furthest west in 2001. In addition, the proportions of adults and area of occurrence increased from 1998 to 2001. Thin and fat adult distributions extended furthest west and east in 1998, increasing in abundance and proportion from 1998 to 2001. Egg volumes were smallest and biggest in 2001 for the CalVET volumes and largest in 1998 for the CUFES.

The GLM for sardine explained 14% of the variability, showing that egg volumes differed significantly among areas for all three years (Table 6). Egg volume decreased from west to east over an extensive area stretching from the west coast to the eastern south coast (Figure 7c).

Table 6. General Linear Model results for sardine (Adjusted $R^2=0.14$) showing the contributions of the different variables to determining egg volume.

Factor	df	F	%Var	p
Intercept	1	2.393	0.013	0.122
<i>Grid</i>	32	5.722	0.989	<0.001
<i>SST</i>	1	6.844	0.037	0.009
<i>Year</i>	2	14.661	0.158	<0.001
<i>Gear</i>	1	40.285	0.218	<0.001
<i>Grid*SST</i>	32	6.044	1.045	<0.001
<i>Year*SST</i>	2	13.017	0.141	<0.001
<i>Grid*Year</i>	64	13.204	4.566	<0.001
Model	134			<0.001
Error	15700			
Total	15834			

The main interaction effects are shown, together with univariate statistics of the parameter values. $\text{Adj.}R^2 = \text{Adjusted } R^2$ from test of SS whole model vs. SS residual.
 $\text{df} = \text{degrees of freedom}$, $F = f\text{-ratio}$, $\% \text{ Var.} = \% \text{ variance explained} = 100 \times \text{SS}_{\text{effect}}/\text{SS}_{\text{tot}}$.

Sardine egg volume significantly differed among years (Table 6). The smallest mean egg volumes occurred in 1998 increasing to its highest in 2001 (Figure 18). Sardine egg volumes from samples measured using CUFES and CalVET nets were different for *Gear* (Table 6), with CalVET net samples having significantly smaller eggs than those sampled by the CUFES (Figure 19).

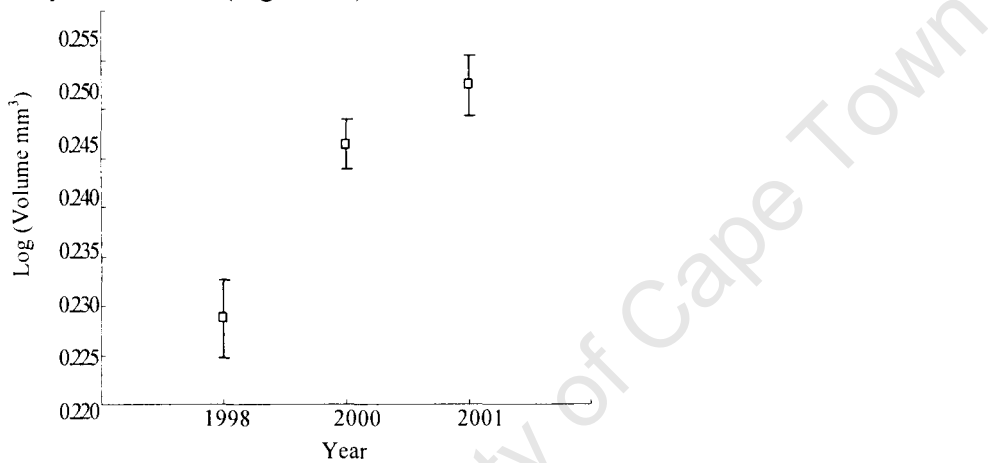


Figure 18. Results of the GLM showing differences in observed mean log egg volume between 1998, 2000 and 2001 for sardine, with the 95% confidence intervals illustrated by the error bars.

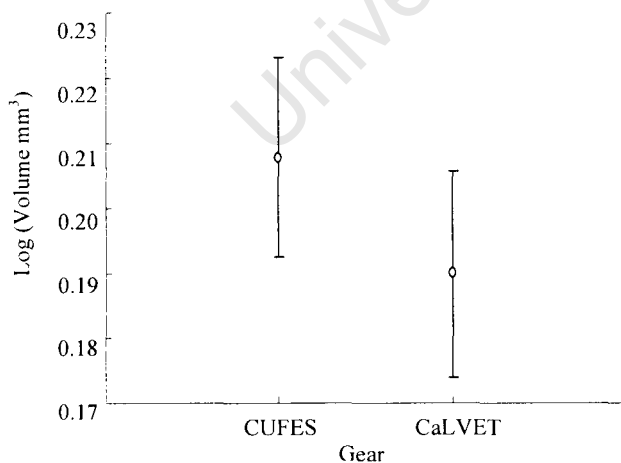


Figure 19. Least squared mean log volume for the different gears used to sample sardine eggs in 1998, 2000 and 2001, with the vertical bars denoting the 95% confidence intervals.

For sardine, SST explained very little of the variability in egg volume (0.037%) and increased from west to east for the grids in which eggs occurred for all three years (Figure 8c). There was a significant *Year*SST* effect on the sardine egg volumes where the mean decreased from 1998 to 2001. Sardine eggs occurred in a wider range of temperatures than anchovy (Figure 20).

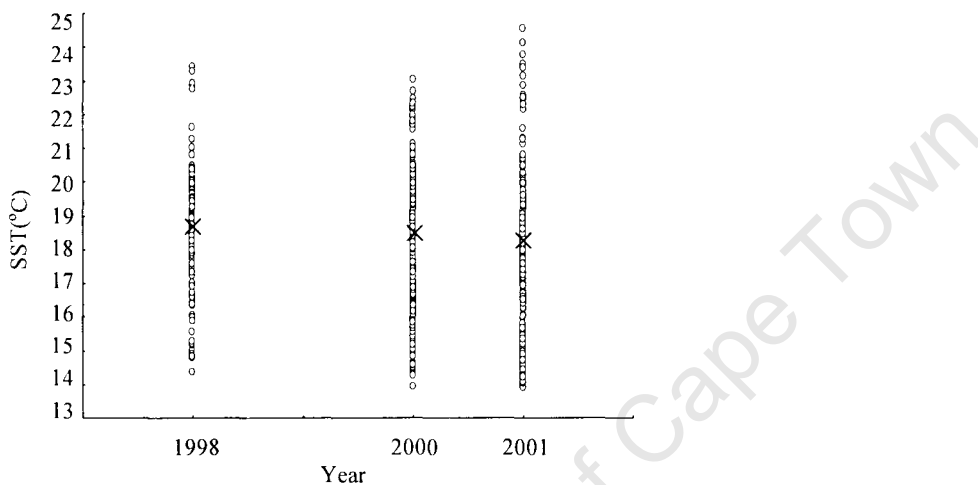


Figure 20. Observed SST measurements for 1998, 2000 and 2001 in the grids where eggs occurred, illustrated by the open circles, for sardine, with the annual mean temperature illustrated by bold crosses.

5. Discussion

Recruitment variability is believed to be important in determining overall variability of pelagic fish stock strength. Egg and larval viability could play a role in determining recruitment. It has been shown that a parental effect is exerted on egg volume for pelagic species elsewhere (Hunter and Leong 1981, Pauly and Pullin 1988, Kjørsvik *et al* 1990, Solemdal 1997, Funamoto and Aoki 2002, Riveiro *et al.* 2004, Mukhametova 2004, Rivera and Castro 2004, Kalmer, 2005). In South Africa, fish size (Barange *et al.* 1999) and condition vary spatially for both anchovy (van der Lingen and Hutchings 2005), and

sardine (van der Lingen *et al.* 2006), with a movement east as they get bigger and improve in condition. In addition, sea surface temperature (SST) increases from west to east. As a result of these findings spatial variability in egg volume was investigated to determine links between egg size and biotic and abiotic factors. Simple relationships were not expected because the southern Benguela system is a dynamic, non-linear system. The main results relate to scale, spatial variability, adult size and or condition variability and SST.

Sardine egg volume was confirmed to be correlated with yolk- and oil globule volume. These data showed large variability, which was probably the result of measurement error, as the oil globule, especially, was very small in comparison to the egg and yolk. A possible solution to the problem is to measure the egg, yolk and oil globule at a higher magnification. This was not possible for this study for technical reasons related to decreased precision, introduced by poor depth of field resolution, at high magnifications.

Egg volume was confirmed to vary spatially, and was generally found to decrease from west to east for anchovy, round herring and sardine. A limiting factor in obtaining these results was the small number of grids that could be used in the analyses, particularly for round herring and anchovy. Only grids that contained eggs in all of the three years were used in the GLMs, to try and control interannual variability in the results.

5.1 Round Herring

The null hypotheses that SST and year had no systematic relationships with egg volume were accepted for round herring; there was no effect of SST and no significant differences in egg volume among years. If egg volume decreases with an increase in temperature (Funamoto & Aoki 2002, Riveiro *et al.* 2004, Kamler 2005), then egg volume should decrease from west to east. In contrast, the smallest round herring eggs occurred on the Agulhas Bank in 1998, and egg volume did not vary with the observed temperature changes in 2000 and 2001.

The largest round herring eggs for all three years were consistently found on the west coast and the smallest on the Agulhas Bank in 1998 and between Mossel Bay and Port Elizabeth in 2000 and 2001. Large proportions of small adults were found along the west coast for all three years, which would suggest that there might have been some mismatch between sampling of eggs and adults for round herring, or that adult size did not have a strong relationship with round herring egg volume in these three years.

In 1998, zooplankton concentrations were very high offshore on the western Agulhas Bank, with dense swarms of copepods over most of the central Agulhas Bank (Coetzee *et al.* 1999). This would suggest that round herring egg volume should be higher in these regions if energy from food is allocated to reproduction i.e. to the eggs, which was not the case. There are three possible explanations for these results. First, the food available might not have been suitable for or available to round herring. Second, the history of feeding (in other areas) might be more important in determining egg size than the food

environment in the spawning area. Finally, lipid content of round herring might determine egg size, as proposed by the parental condition hypothesis; the adult condition was not determined for round herring. Round herring distributions in 2000 and 2001 were dominated by small adults, which did not specifically coincide with either large or small eggs. The largest proportion of big adults in 2001 was found in an area of small eggs, which might suggest that very fecund large adults produce small eggs (Berkely *et al.* 2004, Palumbi 2004), but the smallest eggs in 2000 were found in a similar area with a very small proportion of large adults. The presence of big adults in this area in 2001 may therefore be coincidence. Food availability was not described in 2000 and 2001.

When large scale changes in round herring egg volumes over the three years are considered (Figure 12), the west coast showed an increase in volume from 1998 to 2001 and the eastern south coast a decrease. Temperature on the west coast decreased from 1998 to 2001 and increased on the eastern south coast. This suggests that temperature might have an inverse effect on egg volume at a larger scale than that considered in the GLMs. In addition, proportions of round herring adults and distribution of adults increased from 1998 to 2001, which could suggest that biomass increased from 1998 to 2001. An increase in biomass could result in a decrease in food availability and consequently a decrease in fat content of adults. According to the parental condition hypothesis, this would result in a decrease in egg volume. The year with the lowest biomass was 2001 and the highest biomass occurred in 2000 (Coetzee *et al.* 2001), but these years did not correspond with largest and smallest egg volumes.

5.2 Anchovy

SST had an inverse relationship with anchovy egg volume in 1998 and 2000, i.e. when SST decreased, egg volume increased. Similar findings were reported by Funamoto and Aoki (2002) for the Japanese anchovy (*Engraulis japonicus*) and Llanos-Riviera and Castro (2004 & 2006) for the Chilean anchovy (*Engraulis ringens*). Large eggs are expected to have more reserves, which are required in cold water because of the increased time of development required before hatching (Llanos-Riviera and Castro 2004).

Anchovy adult condition is estimated well via visual assessment of mesenteric fat, and is allocated to one of five fat stages for each individual (van der Lingen and Hutchings 2005). Adult condition appeared to have little or relationship with anchovy egg volume (Figure 14). Most of the big eggs occurred in proximity to small adults and small eggs were found near big adults (Figure 13). Large fish produce more eggs than do small fish (Berkely *et al.* 2004, Palumbi 2004), which might explain why the area of small eggs is larger than expected in comparison to the proportion of large fish.

In 2001, anchovy egg volume was not related to SST, adult size or fat stage. Anchovy eggs were smallest on the west coast and the Agulhas Bank and largest south west of Cape Agulhas. Neither areas of big or small eggs were dominated by either big or small adults or fat or thin adults. It would be expected that areas containing the smallest eggs would be in the proximity of big and/or thin adults and areas with the biggest eggs in the proximity of small and/or fat adults (Funamoto and Aoki 2002, Llanos-Riviera and Castro 2004, Palumbi 2004, Berkely *et al.* 2004, Kalmer 2005 and Llanos-Riviera and Castro 2006). This is the case for the big eggs but does not hold for the small eggs. SSTs

for both the areas in question were nearly identical. Adults were numerous, but most of the adults were small and thin so food may have been an important factor in determining egg size (Hunter and Leong 1981).

At a larger scale, anchovy egg volumes showed little change between 1998 and 2000 but showed a large decrease from 2000 to 2001. SST decreased from 1998 to 2001, and appeared to influence egg volume in those years but not in 2000. There was a large increase in anchovy biomass from 1998 to 2000 (Coetzee *et al.* 2006), which suggests favourable conditions in 2000 that might be expected to produce good condition eggs. By 2001, density dependent effects on food availability might have been important, decreasing egg volume and accounting for the differences between the years 2000 and 2001.

5.3 Sardine

At a small spatial scale SST has a significant positive relationship with sardine egg volume which is contrary to what has been reported in the literature, but this may be due to fat large adults occurring in warmer waters. However on a larger scale in 1998, 2000 and 2001, there was no relationship between sardine egg volumes from CalVET samples and SST, adult size or condition. SST, adult size and adult condition showed no direct relationships with the egg volumes due to the smallest eggs occurring in cold and warm water and in areas in which both big and small and thin and fat adults occurred.

General trends in sardine egg volumes showed a large change between 1998 and 2000 and little increase from 2000 to 2001. SST decreased from 1998 to 2001, and appeared to influence egg volume in all three years. This is supported by the literature, where increases in temperature have been shown to result in decreases in egg volume for other sardine species (Pauly and Pullin 1988, Le Clus and Malan 1995, and Kalmer 2005). There was a large increase in sardine biomass from 1998 to 2000 (Coetzee *et al.* 2006), which suggests favourable conditions in 2000 that might be expected to produce good condition eggs. By 2001, density-dependent effects on food availability might have been important (van der Lingen *et. al.* 2006), slowing the increase in egg volume and accounting for the minimal differences between the years 2000 and 2001.

The above sardine results are for the eggs sampled by the CalVET nets, which were significantly smaller than the eggs sampled by the CUFES. The probable reason for the difference in egg volumes was buoyancy, which is a function of egg size. Large eggs should rise to the surface faster than small eggs. The CUFES was sampling at a shallow depth of 6m and should be biased toward large eggs, whereas the CalVET net samples vertically from 100m to the surface, providing a representative sample of all size eggs, but decreasing the mean volume when compared with CUFES samples. The CUFES increases the spatial resolution of sardine egg distributions, which are very patchy (Lo *et al.* 2001) and samples many more sardine eggs. Even though more eggs were sampled by the CUFES, which should result in a more representative result, there is a clear bias illustrated by the results. Therefore no attempt was made to establish relationships between these egg volumes and SST, adult size and adult condition.

Assumptions in this study were made for numerous factors. SST is the temperature taken at 6m throughout the study. Therefore the temperature at which most eggs were spawned is not the temperature at hull depth, and could be much cooler. Sampling occurred from west to east over a period of 4 to 10 weeks thereby exerting a temporal effect. Small eggs might be expected to be produced at the end of the spawning season, i.e. the end of the survey (Hunter and Leong 1981, Hinckley 1990, McEvoy and McEvoy 1991, Le Clus and Malan 1995, Baynes and Howell 1996, Solemdal 1997, Riveiro *et al.* 2004, Llanos-Rivera and Castro 2004, Berkeley *et al.* 2004, Kalmer 2005). This can't be corrected for, as the only means to accomplish that is to use more than one vessel to complete the survey, each starting at a different place which is not financially or logistically viable. The general survey cruise track from west to east probably also coincides with the migratory movement of adults, introducing the possibility of sampling some adults more than once. However, eggs spawned in the areas sampled can hatch up to four days after spawning, which makes the assumption valid that some of the adults in the vicinity spawned those eggs. An improved sampling method might be to obtain adults eggs from those fish that are about to spawn, which would give a direct correlation between adult size and condition and egg volume. Another option is to raise and spawn adults in captivity, but this has yet to be achieved in South Africa.

6. Conclusions

Egg volume varied spatially for round herring, anchovy and sardine, decreasing from west to east for all three species. Sea surface temperature (SST) had no significant effect on round herring egg volumes in any of the years or on a large scale. It had an inverse

effect on anchovy egg volume in 1998 and 2000 but not for 2001. For sardine, SST had no effect egg volumes sampled by the CalVET net for any of the years. On a larger scale SST showed a direct effect on egg volume for 1998 and 2001. Adult size did not influence round herring egg volume, anchovy egg volume, or sardine egg volume. Parental condition was unknown for round herring and may have been a contributing factor in determining egg volume, in conjunction with food availability. Parental condition had no effect on anchovy egg volume but had an effect in 2000 on sardine CalVET sampled eggs. In addition to the three factors looked at, food availability and biomass were contributing factors that require further investigation.

Due to small scale variability of a large number of parameters it is not possible to predict the effects of sea surface temperature (SST), adult size and condition on egg volume from year to year. At least some of these factors act in concert or alone to affect egg volume and thereby recruitment. When wanting to predict changes in egg size or determine the effects of physical and biological factors it is important to incorporate all factors affecting egg production, e.g. food availability and biomass. This study attempted to find relationships at sea which have been demonstrated in controlled laboratory studies conducted at small scales. The results have proved to be useful in identifying spatial and temporal patterns in egg volume, but were inconclusive in relating these to possible causal factors. Hence in order to have some predictive capacity it is desirable to collect data that can provide a clear, logical test of the predictions. This will probably necessitate dedicated at-sea studies on the appropriate time and space scales. In the meantime, it is important to continue monitoring these variables to try and identify events that are likely to have a significant impact on recruitment.

7. Acknowledgements

This study was partly supported by the Sea and Coast II programme of the South African Network for Coastal and Oceanic Research, funded by the National Research Foundation and Marine and Coastal Management, MCM. Logistic and financial support from the Marine Biology Research Centre (UCT), the Harry Crossely Foundation and the K.W Johnston Foundation are gratefully acknowledged. A big thank you to my supervisors, Dr Coleen Moloney and Dr Carl van der Lingen for their endless help and time! In addition, I would like to acknowledge the assistance of University of Fort Hare students: Mr Xolani Charlie, Ms Nontando Tshiwose, Ms Nontsikelo Sitsha, Ms Natasha Tose, Ms Pamela Memani, Mr Xolela Wellem (in 2005) and Ms Lebo Malefane, Ms Sinazo Peter, Ms Zandie Mnyakama, Ms Babalwa Bara, Mr Daniel Mazungula (in 2006) Ms Nomfundiso Mtalana processed the anchovy egg volume data for 1998 and 2000. Lastly I would like to thank Mrs Futter for her useful comments on the first draft, and Mr Futter (MPhil Marine Law) for useful discussions.

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