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Description and analyses of the 1995 orange roughy egg surveys at East Cape and Ritchie Bank (TAN9507), and reanalyses of the 1993 Ritchie Bank egg survey

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DESCRIPTION AND ANALYSES OF THE 1995 ORANGE ROUGHY EGG SURVEYS AT EAST CAPE AND RITCHIE BANK (TAN9507), AND REANALYSES OF THE 1993 RITCHIE BANK EGG SURVEY

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1. EXECUTIVE SUMMARY

1. This FARD describes analyses of the 1995 orange roughy egg production surveys at East Cape and Ritchie Bank (TAN9507) which formed the 1996 and 1997 stock assessments for those fisheries. The FARD also describes reanalyses of the 1993 Ritchie Bank (TAN9306) survey data. These reanalyses affect both the 1996 and 1997 East Cape and Ritchie Bank stock assessments.

2. The main egg production method used at East Cape and Ritchie Bank was the Daily Fecundity Reduction Method (DFRM). The DFRM determines the biomass of spawning females by dividing the daily rate of planktonic egg production (N_0), determined from quantitative plankton surveys, by the daily rate of decline in weight-specific egg number in the females (D) determined from trawl samples taken in the spawning area through the spawning season. This biomass is scaled to the stock biomass using the proportion of spawning females to all recruited fish (S) determined from a wide-area trawl survey made before the onset of seasonal spawning. A second method was used at East Cape, the Annual Egg Production Method (AEPM). The AEPM divides an estimate of integrated egg production over the whole spawning season by the annual (total season) fecundity of females to estimate spawning female biomass. This is then scaled up to estimate stock biomass, as for the DFRM.

3. The analyses are divided into three types: analyses of plankton data, fecundity and gonad stage data, and random trawl survey data. For the 1995 plankton data at East Cape and Ritchie Bank, analyses are described for standardisation of egg counts to eggs per m^2 sea surface area, at age. This took into account plankton net trajectory and development rate of eggs, both of which varied with depth. Next, the standardised counts were scaled up to estimate egg abundance at age over the whole survey area, accounting for survey stratification and advection of eggs out of the survey area. Then, these standardised abundances were used to calculate N_0 by back-calculating egg abundance at time of spawning and egg mortality rate (Z). Unrealistic (negative) Z values were obtained, and it was considered likely that extreme spatial and temporal patchiness in spawning were the causes. N_0 values were therefore calculated using 'best' estimates of Z, the latter derived from the 1993 Ritchie Bank survey.

4. Fecundity and gonad stage data were collected from a series of trawls made by *Tangaroa* and commercial vessels both before and during the East Cape and Ritchie Bank plankton surveys. At each tow, the ovaries from a random sample of female fish were staged macroscopically. For most tows, ovaries were taken from a subsample of the staged fish for estimation of fecundity and histological analysis. For each trawl, the product: proportion actively spawning times the numbers of mature oocytes kilogram of female, was regressed against date to estimate D.

5. Random trawl survey data were used to calculate S for East Cape and Ritchie Bank stock areas. The base case stock area for East Cape was assumed to be the area of the wide area trawl survey (Cape Runaway to Gisborne) and for Ritchie Bank it was assumed to be areas 2A, 2B, and 3A.

6. Reanalysis of the 1993 Ritchie Bank survey indicated that turnover of spawners (in the form of spent females leaving the survey area before spawning was finished) was occurring in the spawning area during the DFRM trawl survey. Turnover violates the assumption implicit in the DFRM approach that all spawners of the year are in the trawl survey area and available to the trawl, regardless of ovarian condition, at all times during the fecundity reduction sampling period. This reanalysis was further refined for the 1996 stock assessment using a more formal correction method. No evidence of turnover was found in the East Cape survey, and it is hypothesised that this was related to the absence of commercial fishing during the spawning season at East Cape whereas there was commercial fishing at Ritchie Bank in 1993 and 1995.

7. The recruited biomass estimate (*c.v.%*) for the 1996 stock assessment for the Ritchie Bank using the 1993 survey was 32 000 t (40) and for the 1995 survey it was 7 500 t (50), both corrected for turnover. The Ritchie Bank 1995 survey estimate is considered unreliable because of low and incomplete plankton station coverage during the survey. The estimate for East Cape was 40 000 t (67). Estimates for East Cape using the AEPM were also given, although these were not used in the stock assessment.

8. For the 1997 stock assessment, two corrections were made to the 1996 estimates for East Cape and Ritchie Bank. First, an error in the 1993 Ritchie Bank survey Z estimate was corrected, leading to a revision in the 1995 East Cape Z and N_0 estimates (since the East Cape 'best Z estimate' was that from the 1993 Ritchie Bank survey). Second, an updated estimate of turnover was used, which incorporated turnover estimates from the 1996 'Graveyard' egg production survey, and affected both the East Cape and Ritchie Bank biomass estimates. For Ritchie Bank in 1993 the 1997 stock assessment biomass estimate (c.v.%) was 22 000 t (49) and for the 1995 survey it was 7000 t (50), both corrected for turnover. For East Cape in 1995 the biomass estimate was 29 000 t (69).

2. INTRODUCTION

In 1994 a new fishery for orange roughy developed off East Cape. Although orange roughy had been taken in the area for several years, there has been a dramatic increase in effort and landings as aggregations of pre-spawning and spawning fish are targeted in autumn and winter. A catch level of 3000 t was set for the 1995–96 fishing year, although little is known about stock size or long-term sustainable yield. At the Ritchie Bank, biomass was estimated using an egg production survey in 1993 (Field *et al.* 1994). This information resulted in a two year stepped reduction in TACC (from 10 333 t to 2500 t) between 1993–94 and 1995–96.

Two egg production surveys were conducted in June and July 1995 (voyage TAN9507, Zeldis (1995)) to provide a first biomass estimate for East Cape and to update the Ritchie Bank estimate. Two types of egg production survey were used. The main type used at East Cape and Ritchie Bank was the Daily Fecundity Reduction Method (DFRM). The DFRM determines the biomass of spawning females by dividing the daily rate of planktonic egg production (N_0), determined from quantitative plankton surveys made during all or part of the spawning season, by the daily rate of decline in weight-specific egg number in the females (D), determined from trawl samples taken in the spawning area through the spawning season. The spawning female biomass is scaled to the stock biomass using the proportion of spawning females to all recruited fish (S), determined from a wide-area trawl survey made before the onset of seasonal spawning. The principal disadavantage of the DFRM is that it is subject to bias if turnover of spawners occurs during the spawning season.

The second method used at East Cape was the Annual Egg Production Method (AEPM). In the AEPM an estimate of integrated egg production over the whole spawning season is derived from a series of quantitative plankton surveys made through the spawning season. This is divided by the annual (total season) weight-specific fecundity of females, derived from trawl samples made before spawning but after annual ovarian egg complement is fully mature, to estimate spawning female biomass. This is then scaled up to estimate stock biomass, as for the DFRM. The principal disadvantage of the AEPM is that planktonic egg production needs to be measured through all, or most of, the spawning season, unlike the DFRM. For this reason, the AEPM was not applied at Ritchie Bank in 1995 when only 5 days were available for the plankton survey.

The following five sections of this report refer to the analysis that was carried out for the 1996 stock assessment. This includes revisions made to the original 1994 Ritchie Bank assessment (Field *et al.* 1994), based on the 1993 Ritchie Bank survey (Zeldis *et al* 1997a). Further refinements to the analysis for the 1997 stock assessment are described in Section 8.

3. REVISIONS TO 1993 RITCHIE BANK SURVEY

A number of revisions were made to both the data and analyses for 1993 Ritchie Bank egg production survey since it was documented in Field *et al.* (1994), for use in the 1996 assessments of the Ritchie Bank and East Cape orange roughy fisheries (Zeldis *et al.*1997).

3.1 Estimation of Egg Production, N_0, and Egg Mortality Rate, Z

A number of factors contributed to revisions of the N_0 and Z values from the 1993 Ritchie Bank survey.

- During the plankton survey for Ritchie Bank egg production on TAN9306 two additional strata were occupied when it was discovered that 1) there was some spawning on North

Hill, about 12 km north of Ritchie Hill, and 2) eggs were advecting into and through the southwestern corner of the original survey area. Inclusion of data from these strata altered the egg production and mortality rates.

- An error in the egg abundance data was corrected.
- Errors in the determination of maximum ages of egg stages were corrected.
- 'Curved' correction factors were used to convert egg counts, for each plankton tow and egg stage, to densities (eggs per m^2 of sea surface) (Appendix 1).

The nett effects of the four changes outlined above were to change N_0 from 13.9×10^9 to 17.0×10^9 eggs per day (*c.v.* 42%) and Z from 0.88 to 0.95 (95% c.i. 0 to 2.0).

3.2 Ovarian Wall Weight

The rate of fecundity reduction D (eggs per kg per day), or daily fecundity, in the orange roughy spawning female population is determined by the slope of the relationship between R_i (eggs per kg) and the day of the spawning season. The estimates of R_i used in Field *et al.* (1994) took no account of the biasing effects of ovarian wall weight in calculation of weight-specific fecundity The correction due to the ovarian wall weight (described by Zeldis *et al.* (1997)) changed the Field *et al.* (1994) D estimate from 733 to 787 eggs per kg per day.

3.3 Turnover

Reanalysis of the 1993 Ritchie Bank survey indicated that turnover of spawners (in the form of spent females leaving the survey area before spawning was finished) was occurring in the DFRM trawl survey area during the survey (Zeldis *et al.* 1997a). Turnover violates the assumption implicit in the DFRM approach that all spawners of the year are in the trawl survey area and available to the trawl, regardless of ovarian condition, at all times during the fecundity reduction sampling period. The evidence for turnover, and the methods applied to correct for it, were described by Zeldis *et al.* (1997a). These corrections changed the value of D from 787 to 1106 eggs per kg per day (a *c.v.* was not estimated for the corrected value).

3.4 Estimation of S

To estimate the recruited biomass (B_{rec}, defined as the biomass of fish over 32 cm long) an estimate of the ratio B_{rec}/B_{spf}, was needed, where B_{spf} is the biomass of spawning females. We denote this ratio as S. This ratio allows for recruited females that did not spawn, and females that did spawn but were under 32 cm, as well as the sex ratio.

The data needed for S were obtained from the March-April 1993 wide-area east coast trawl survey. In Field *et al.* (1994) it was assumed that all females in stage 3 (late vitellogenic) in these trawls would spawn in winter 1993 (Bell *et al.* 1992). However, histological examination of ovaries from randomly selected females from these trawls showed that 4.5% of them were undergoing complete atresia (resorbtion) of their oocyte complement and would not spawn that year (Zeldis *et al.* 1997a). In addition, an analysis error was found in the calculation for S. When corrections were applied for atresia and the analysis error, the value for S was changed from 2.07 (Field *et al.* 1994) to 1.85 (Zeldis *et al.* 1997a).

4. ANALYSIS OF 1995 PLANKTON DATA

The end point of the analysis of the plankton data is estimates of the numbers of eggs produced per day or per spawning season. This analysis proceeds in three stages. First, the raw egg counts (numbers of eggs, of each stage, caught in each plankton tow) are standardised to eggs per m^2 of sea surface. Second, the standardised egg counts are combined to obtain, for each egg stage and each subsurvey or combination of subsurveys, estimates of mean abundance in the whole survey area. Third, from these abundances, estimates of mean daily planktonic egg production (i.e., the number of eggs spawned per day) are made for the whole survey area and for each subsurvey, or combination of subsurveys.

4.1 Standardisation of Egg Counts

The standardisation from egg count to egg density (eggs per m) uses the formula, density = count x correction factor.

The correction factor takes into account the area of the mouth of the net and the volume of water filtered by it. With a vertical haul, the correction factor is 0.5 (because the net mouth area = 2 m^2). Because the vessel drifted during shooting and hauling, hauls were not vertical and so the correction factors were always less than 0.5.

Correction factors were calculated for two sets of assumptions:

a) 'straight' - assuming that the path of the net during hauling was straight, and that at the start of hauling the net was vertically below the position of the vessel when the net was deployed, and

b) 'curved' - using changes in vessel position, warp length, depth, and current data to infer the path of the net during hauling.

In the following analyses, the 'curved' factors are used for 'base case' estimates because the assumptions underlying them are likely to be a better approximation to the truth. The 'straight' factors were calculated as a sensitivity analysis because it was these factors that were used in the analysis of the 1993 Ritchie Bank egg survey in the 1994 and 1995 stock assessments (Field *et al.* 1994, Annala 1995).

For the straight path, the time spent by the net in any given depth layer is strictly proportional to the thickness of that layer. Because of this, the 'straight' correction factor for a particular plankton tow is the same for each egg stage. However, with the 'curved' path, there is a different correction factor for each combination of plankton tow and egg stage.

i) 'Straight' correction factors

The 'straight' correction factors were calculated as the maximum depth of the tow divided by the product of the net mouth area (2 m^2) and the distance hauled (this product is the volume of water filtered). The distance hauled was calculated using Pythagoras' Theorem from the maximum depth of the tow and the distance that the ship drifted from deployment to recovery of the net, determined using Global Positioning System (nominal precision 80 m). It was assumed that, at the start of hauling, the net was below the position of the vessel when deployment began, i.e., the net dropped vertically through the water during deployment.

ii) 'Curved' correction factors

The calculation of the correction factors that convert egg counts to egg density (eggs per m^2) for when the path of the net during hauling is assumed to be curved is described in Appendix 1. The following data on water currents (Table 1) and the depth distribution of eggs of different stages (Table 2) were used in the calculations.

Water current velocity profiles (velocity as a function of depth) were calculated for the East Cape and Ritchie Bank areas by a) calculating mean geostrophic velocity profiles using CTD data and assuming zero velocity at 1000 m, and b) correcting these profiles so that the 100 m velocities matched that measured by buoys drogued to 100 m.

Table 1: Depth profiles of water current velocities for East Cape and Ritchie Bank area

	East Cape		Ritchie Bank	
Depth (m)	Speed ($m.s^{-1}$)	Bearing (deg)	Speed ($m.s^{-1}$)	Bearing (deg)
0	0.390	180	0.210	24
100	0.357	180	0.201	24
200	0.322	180	0.198	15
300	0.280	180	0.168	11
400	0.254	180	0.162	6
500	0.230	180	0.149	3
600	0.209	180	0.170	354
700	0.190	180	0.169	347
800	0.166	180	0.148	337
900	0.146	180	0.131	318
1000	0.123	180	0.119	301

Data on egg development rate as a function of temperature, buoyancy by stage, and temperature as a function of depth were used to calculate the age and depth range for each egg stage in each area using the methods of Zeldis *et al.* (1995).

Table 2: Egg age by depth for East Cape and Ritchie Bank

	East Cape				Ritchie Bank			
Stage	Min age	Max age	Max depth	Min depth	Min age	Max age	Max depth	Min depth
1	0.0	4.6	850	787	0.0	5.4	850	779
2	4.6	7.5	787	748	5.4	8.7	779	734
3	7.5	10.2	748	711	8.7	11.9	734	692
4	10.2	12.8	711	675	11.9	15.0	692	650
5	12.8	15.3	675	640	15.0	18.0	650	610
6	15.3	17.7	640	607	18.0	20.8	610	572
7	17.7	20.0	607	575	20.8	23.5	572	535
8	20.0	22.2	575	544	23.5	26.1	535	499
9	22.2	24.2	544	514	26.1	28.5	499	465
10	24.2	26.2	514	486	28.5	30.9	465	432
11	26.2	30.9	486	418	30.9	36.3	432	354
12	30.9	37.2	418	323	36.3	43.7	354	246
13	37.2	42.3	323	242	43.7	49.5	246	158
14	42.3	46.5	242	175				
15	46.5	49.9	175	118				
16	49.9	52.8	118	70				

The 'curved' correction factors were typically much greater than the 'straight' factors for the early egg stages, but about the same for the later stages (Figure 1). The reason for this can be seen in a comparison of the straight and curved paths for a selection of stations (Figure 2). The closer the net path is to vertical, the larger is the correction factor (with a factor of 0.5 for a vertical path). In the deeper water, where stage 1 eggs are found, the curved path is typically much closer to vertical than the straight path. However, the paths are approximately parallel in the shallow water (where stage 15 eggs are found). The distance the vessel drifted as the net was hauled also affected correction factors. Estimated net paths, and hence correction factors, were more dissimilar as drift distance increased (Figure 2).

In summary, the ratio of the curved/straight correction factors was dependent on both drift distance and egg stage (Figure 3). Curved correction factors were approximately proportional to drift distance for young egg stages, and much less affected by drift for the later stage eggs.

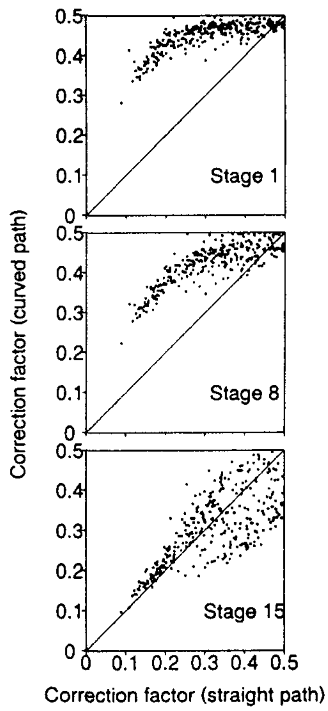

Figure 1: Comparison of "straight" and "curved" egg count correction factors for early, middle, and late stage eggs at East Cape. Each point represents one station.

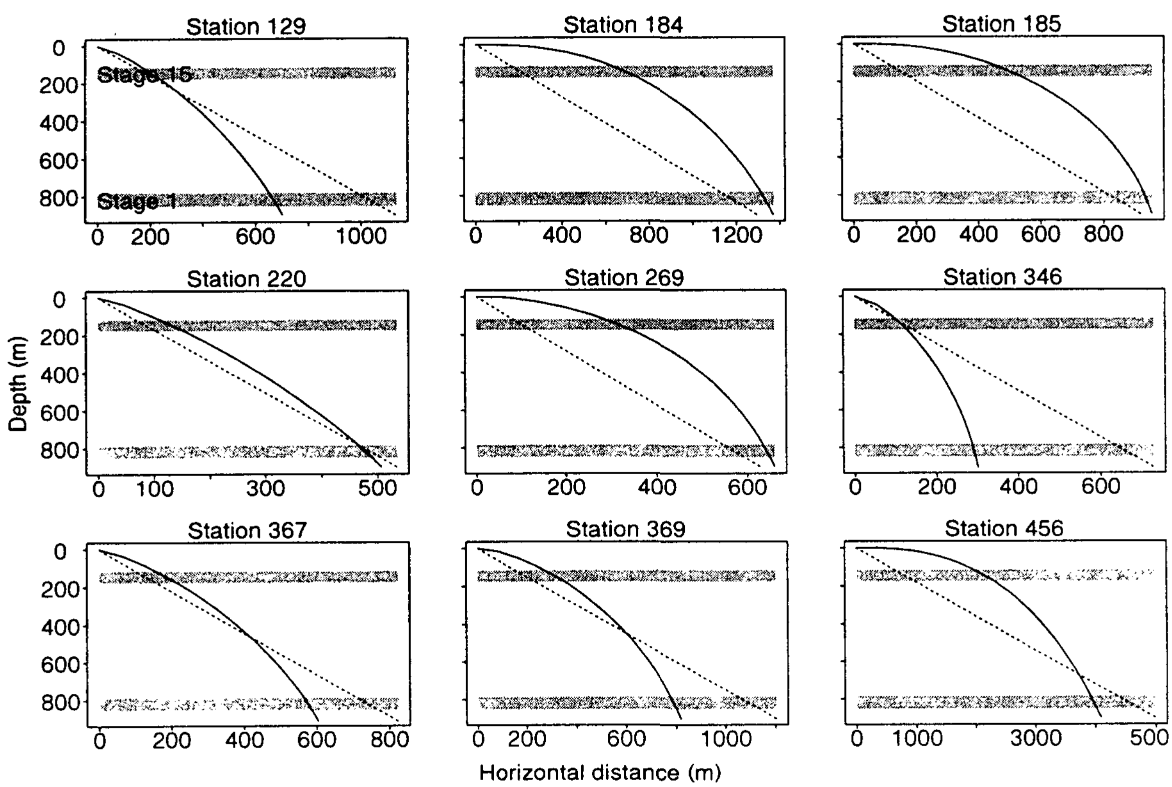

Figure 2: Comparison of "straight" (dotted line) and "curved" (solid line) net paths for nine randomly chosen stations at East Cape. The shaded bands in each panel show the depth range occupied by stage 1 (lower) and stage 15 (upper) eggs.

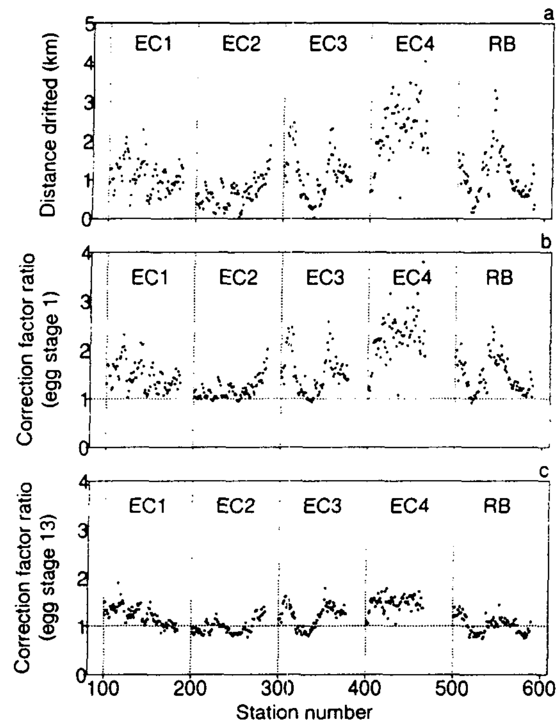

Figure 3: Illustration of how the ratio of curved/straight correction factors for a particular plankton tow is largely a function of the distance the vessel drifted while hauling the net. Panel a shows distance drifted for each tow; panels b and c show the ratio of correction factors for early (stage 1) and late (stage 13) stage eggs, respectively. Each point represents one tow.

4.2 Calculation of Egg Abundance

The calculation of egg abundances by stage in the survey area (N_a) was made by multiplying the mean egg density at age in each stratum by stratum area, and summing across strata. The *c.v.* of N_a was calculated using the standard deviation of egg density at age, weighted by stratum area. The definition of strata, combining of egg stages, and likely advection out of the survey area which contribute to the calculation of egg abundance are described below.

In calculating egg abundance we assumed no diel periodicity in spawning. Attempts to find evidence of diel periodicity using simple graphical methods were unsuccessful.

4.2.1 Strata by subsurvey

The strata occupied in the East Cape and Ritchie Bank surveys varied from snapshot to snapshot as information about currents became available, and in response to time constraints (Figure 4).

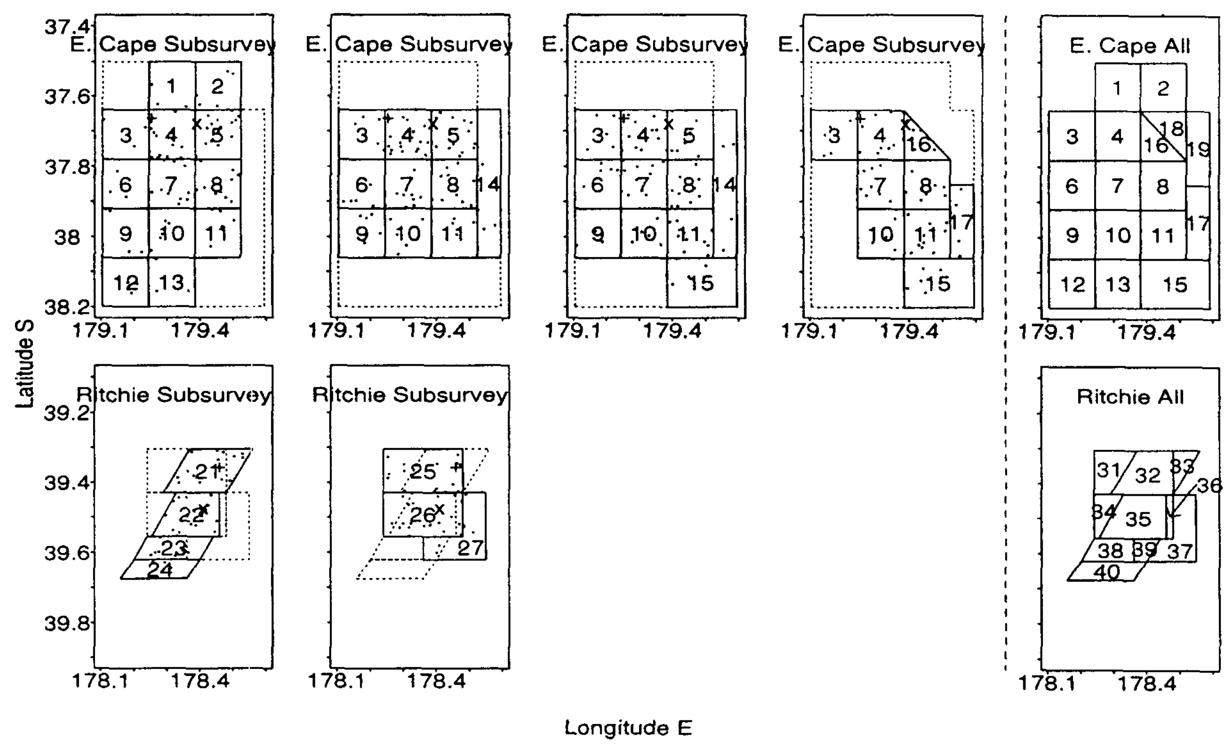

Figure 4: Stratum boundaries, station positions ('.'), and location of spawning hills ('x','+') for East Cape and Ritchie Bank. Panels to the left of the vertical broken line show stratum boundaries and station positions by subsurvey; panels to the right show the final stratifications for each area (defined post-survey to allow data from all subsurveys to be combined). 'x' marks the main spawning hill in each area; '+' marks Hill 3 at East Cape and North Hill at Ritchie Bank.

In some of the analyses presented below data from several subsurveys were combined. When this was done, the stratification was modified so that the area of each of the original strata was equal to the union of one or more of the new strata. For East Cape this required only two changes: stratum 5 was split into strata 16 and 18; and stratum 14 was split into strata 17 and 19. The number of stations occupied in each of the new strata, for each subsurvey are given in Appendix 2.

4.2.2 Composite egg stages

Early stage eggs which could not be staged precisely because of damage during hauling (Zeldis *et al.* 1995) were assigned negative stage numbers (Table 3). The distinction between stage -3 and -2 damaged eggs was made by the degree of coalescence of the oil droplet: by the four cell stage, the oil droplet is completely coalesced (Zeldis *et al.* 1997b.). Unfertilised eggs were recorded as stage 0. Of the 8750 eggs caught, only 13 were unfertilised (9 at East Cape and 4 at Ritchie Bank).

Two composite egg stages were used in egg production calculations (Table 4). The few stage -1 eggs were split in the ratio 1:3 between composite stages A and B.

Table 3: Stages assigned to damaged early stage eggs

Negative stage	Corresponding stages	Total number caught
-3	1 to 3 (pre germ disc to 2 cell)	988
-2	4 to 7 (4 cell to 32 cell)	1697
-1	3 to 6 (2 cell to 16 cell)	31

Table 4: Composite egg stages used in egg production calculations

Composite stage	Recorded stages
A	-3, 0, 1, 2, 3
B	-2, 4, 5, 6, 7

4.2.3 Advection of eggs

Egg abundance was calculated only for those stages for which it appeared that advection out of the survey area by water movement was negligible (Table 5) (a loss of eggs by advection would cause a negative bias in N_a).

Advection was examined by: 1) calculating expected egg paths originating at known spawning hills from the current velocity profiles and egg age and depth data (see above; Figures 5a and 5b); 2) plotting centroids (centre of gravity, Zeldis *et al* 1997a)) of successive egg stages from egg density data (Figures 5c and 5d); and 3), plotting egg density by stage against latitude and longitude to detect stages which had a high density near a boundary of the survey area.

It is not to be expected that these two approaches would give precisely the same picture. The expected path analysis ignores any horizontal and temporal variation in currents; the centroid analysis is affected by both types of variation, is sensitive to single large catches of eggs, and is biased for any stage for which some eggs have been advected out of the survey area.

In the East Cape survey area there was a southward drift of eggs (Figures 5a and 5c) but no significant advection across the southern boundary for stages less than 16 (Figure 6a). Advection across the eastern and western boundaries was not substantial (Figure 6b).

For Ritchie Bank, advection is clearly to the north for the early stages (stages A, B, 8–10; Figure 5d) which suggests that the great most of spawning took place on Ritchie Hill. All stages less than 10 do not appear to have crossed the northern boundary of the survey area to any great extent (Figure 6c). Eggs of stage 13 appear to have been advected into the area across the southern boundary, suggesting either that there is another spawning area nearby to the south or that there is a gyre which advects eggs out of the survey area to the north and then back into it from the south. The bathymetry of the area and the lack of any substantial fishing effort nearby to the south suggest that the latter explanation is correct.

Table 5: Egg stages included in the estimation of egg production (*see* Table 5 for stages included in the composite stages A and B)

Area	Stages included
East Cape	A, B, 8, 9, 10, 11, 12, 13, 14, 15
Ritchie Bank	A, B, 8, 9

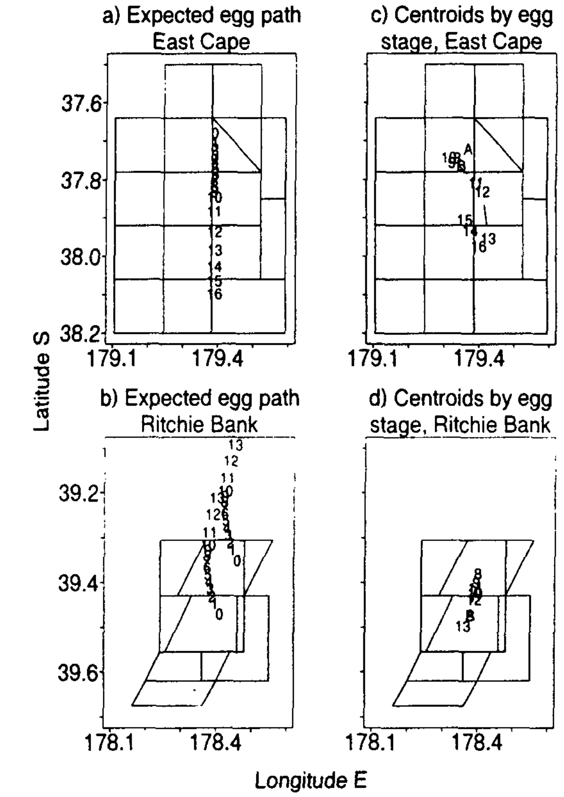

Figure 5: Expected and observed advection of eggs at East Cape and Ritchie Bank. Left panels show expected egg paths from the main spawning hills as calculated from current profiles and shown as expected position of eggs at stages 0 to 16; for Ritchie Bank (lower left panel) an expected path from North Hill is also shown. Right panels show observed paths as inferred by the centroids of egg density for stages A, B, 9,...13.

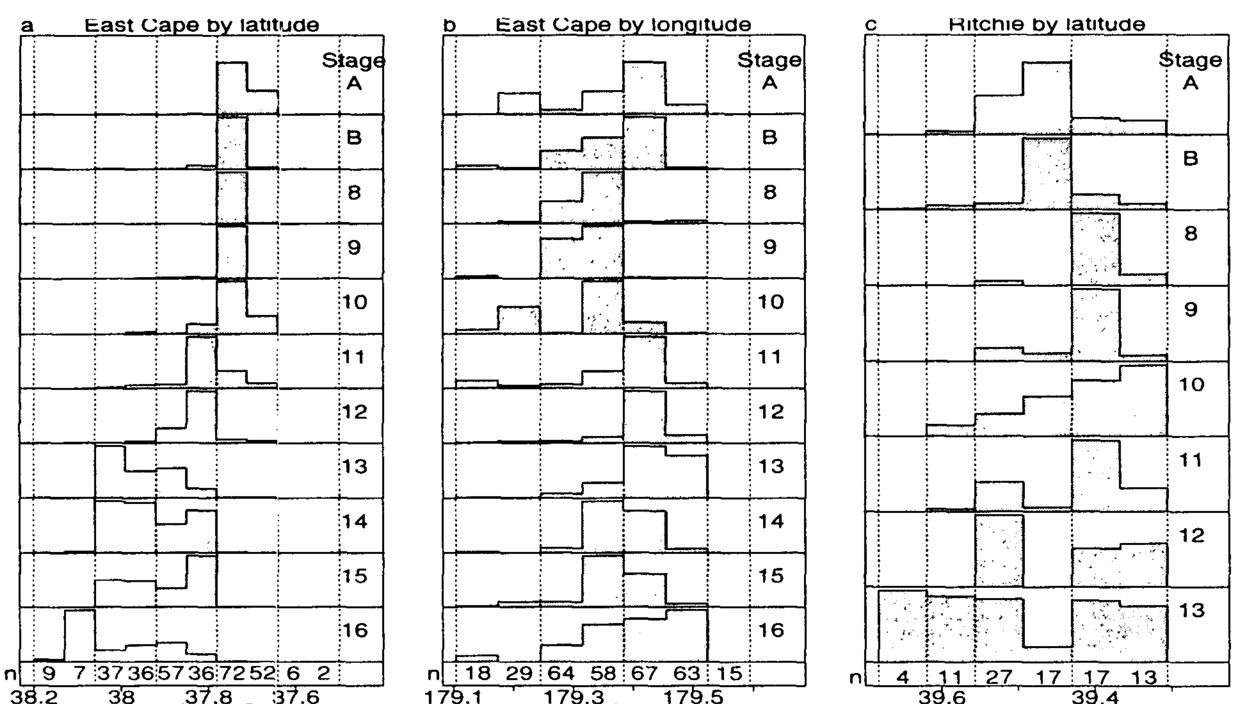

Figure 6: Mean egg density by stage and latitude or longitude: a) East Cape by latitude; b) East Cape by longitude; c) Ritchie Bank by latitude. Broken vertical lines indicate stratum boundaries; *n* = number of plankton stations in each latitude or longitude slice.

4.2.4 Abundance by egg stage and subsurvey

For each egg stage, and each subsurvey, two estimates of abundance were calculated using the 'straight' and 'curved' correction factors (Appendix 2). The estimated *c.v.*s of the abundance estimates were typically high (median about 0.5; Figure 7a). The ratio of "curved:straight" estimates ranged from 0.8 to 2.3 but was usually greater than 1, varied greatly between subsurveys, and tended to decrease with increasing stage (Figure 7b).

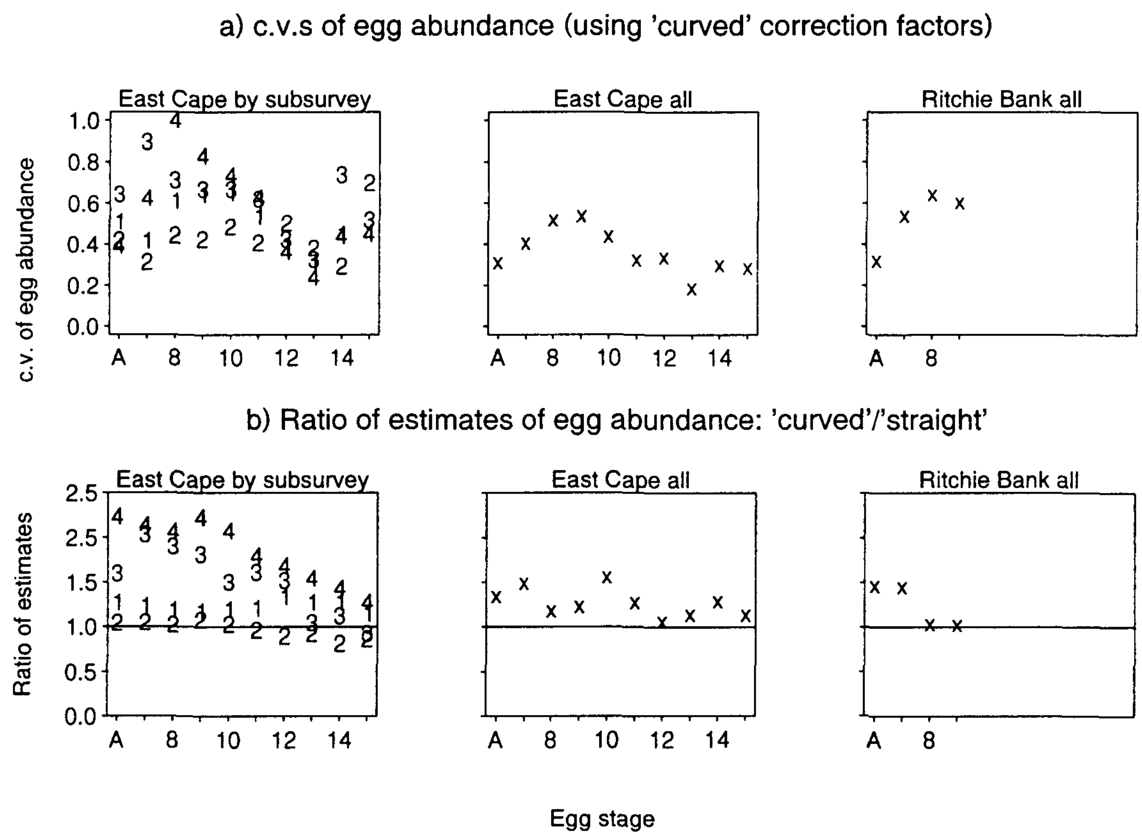

Figure 7: Two aspects of egg abundance estimates for East Cape and Ritchie Bank surveys in 1995: a) estimated *c.v.*s (calculated using the "curved" correction factor), and b) ratio of "curved"/"straight" estimates of abundance. Results are shown by subsurvey for East Cape (left panels, plotting symbol

4.3 Estimation of Planktonic Egg Production

4.3.1 Initial estimates of daily planktonic egg production

An attempt was made to estimate daily egg production using the same maximum likelihood model as was used for the 1993 Ritchie Bank survey (Zeldis *et al.* 1997a). Note that, for a given egg stage, the abundance divided by the stage duration is an estimate of the daily production of eggs of that stage. This model uses these values, together with the age range for each stage, to back-calculate the production at age 0. It assumes that, for the period considered (a subsurvey, or group of subsurveys), daily egg production (N) and egg mortality (Z) were (reasonably) constant.

The fit of this model to the data is shown in Figure 8 (the estimates of N are the y-intercepts of the curves). These initial estimates of N and Z for each subsurvey and using the 'straight' and 'curved' correction factors are given in Table 6. In three of the four East Cape subsurveys (and for the combined East Cape data set, 'ECall') the maximum likelihood estimates of Z were negative, implying thategg abundance increased as the eggs aged. This is clearly unsatisfactory. Several possible causes of this result were investigated and are discussed below.

Before doing this it is worth commenting on the effect of the two types of correction factors. Note that, except for snapshot EC2, the estimates using the 'curved' correction factors were substantially higher than those using the 'straight' correction factors. This is to be expected, given the patterns in Figure 7a.

Table 6: Initial estimates of egg production (N, billions.day^{-1}) and egg mortality (Z, day^{-1}) for "straight" and "curved" correction factors.

	"Straight"		"Curved"	
Subsurveys	N	Z	N	Z
East Cape:				
EC1	6.4	0.4	8.1	0.5
EC2	1.8	-0.3	2.1	-0.1
EC3	0.4	-1.5	0.8	-1.2
EC4	0.2	-1.7	0.6	-1.4
all strata	2.3	-0.5	2.8	-0.5
Ritchie:				
all strata	6.4	2.0	10.3	2.4

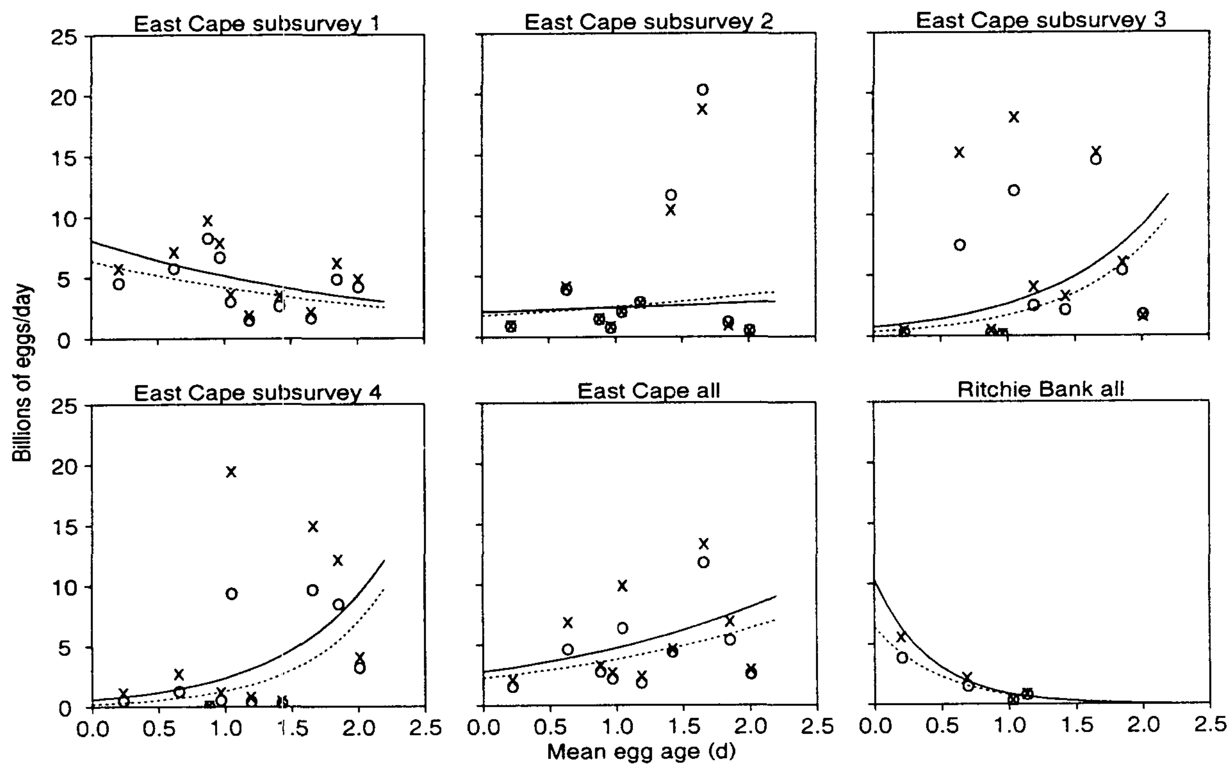

Figure 8: Initial estimates of daily planktonic egg production (N) for each subsurvey at East Cape and for all data at East Cape and Ritchie Bank. The estimate of N is the intercept of the plotted curves on the y-axis. Estimates are given using both the "curved" ('x' and solid lines) and "straight" ('o' and broken lines) correction factors.

4.3.2 Could negative Zs have occurred by chance?

It could be that the negative estimates of Z occurred by chance. In other words, although the true egg abundance (corrected for stage duration) declined with increasing age, it could be that, because of the high *c.v.*s associated with egg catches, *estimated* abundance increased with age. Simulations carried out for a range of values for the true Z and for the *c.v.* of the egg abundance estimates (assumed to be the same for all egg stages) showed that this was most unlikely (Table 7). Although negative estimates of Z occurred, the probability that they were less than -0.8 was very small. In the four East Cape subsurveys, two estimates were less than -0.8 (the estimates of Z for East Cape using the 'curved' data were: EC1 0.45; EC2 -0.13; EC3 -1.21; EC4 -1.39; all strata -0.54).

Table 7: Proportions of simulated survey results where the estimated Z was < 0 or < -0.8

	P(Estimated $Z < 0$)				P(Estimated $Z < -0.8$)			
c.v.	Z=0.3	Z=0.5	Z=0.7	Z=0.9	Z=0.3	Z=0.5	Z=0.7	Z=0.9
0.0	0.52	0.44	0.43	.039	0.00	0.01	0.00	0.02
0.1	0.37	0.42	0.39	0.40	0.00	0.00	0.02	0.03
0.3	0.05	0.12	0.29	0.29	0.00	0.00	0.00	0.01
0.5	0.00	0.07	0.08	0.12	0.00	0.00	0.00	0.01
0.7	0.00	0.00	0.02	0.10	0.00	0.00	0.00	0.00
0.9	0.00	0.00	0.01	0.01	0.00	0.00	0.00	0.00

4.3.3 Did egg production change gradually during the East Cape survey?

The preceding result implies that the constant-N, constant-Z model does not work for East Cape. One way in which this model might fail is if Z were constant and N changed gradually over the period of the survey (e.g., if N increased steadily, or increased and then decreased).

One way to investigate the possibility of this gradual change is to consider all instances when eggs from adjacent stages were caught in the same plankton tow. Suppose, for example, N steadily decreased throughout the survey period. Then, more often than not, we would expect that the older adjacent stage would be more abundant than the younger one (after correcting for volume of water filtered and stage duration). This is because the older stage eggs were spawned slightly earlier than the younger stage eggs caught in the same haul. Other patterns would be observed for different changes in egg production during the survey.

Figure 9 is a graphical presentation of the results of such an analysis. That the same (or similar) patterns are not seen in all panels of this figure suggests that the data are not consistent with a "constant-Z, gradual-N" model (although this analysis ignored Z (which should tend to make later stages less abundant than earlier stages), when the analysis was repeated with a correction for an assumed Z of 1 (day^{-1}) there was very little change in the graph).

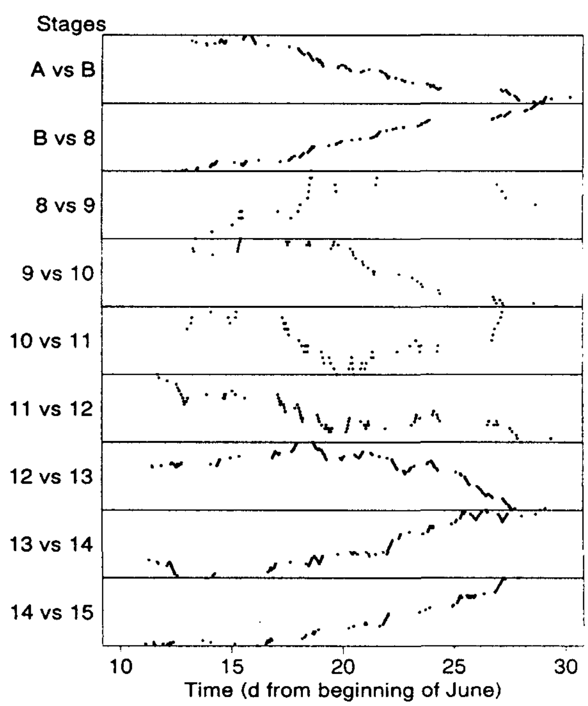

Figure 9: Results of comparing abundances of adjacent egg stages to infer trends in egg production (N). A rising/falling line implies rising/falling production. Each dot corresponds to a tow at which both stages were caught. The x-axis records the mean time of spawning for the two stages. On the vertical scale the dot is placed 1 unit higher than the preceding tow if the older stage eggs are more abundant than the younger stage eggs, and 1 unit lower if younger eggs are more abundant.

4.3.4 Time - Space Patterns in Egg Production

Another explanation for the pattern of increasing egg abundance with age observed in subsurveys 2, 3, and 4 (Figure 9) is that spawning and distributions of young eggs at East Cape were very patchy in both space and time.

I) Spatial patchiness

Abundance estimates below the true mean could occur more frequently for younger eggs than older eggs if the true spatial distributions of young eggs were more clumped than those of older eggs. Most of the eggs at East Cape arise from a small source of production on the northwest side of a small hill (*see* Figure 4) which was also the only area which showed an orange roughy acoustic mark during the survey. The spatial distribution of spawning and the size of the patch of young eggs was therefore probably extremely small relative to the strata containing it. Most young eggs (stages 1–10) occurred in two strata (4 and 5) which contained spawning hills 1 and 3; Figures 4 and 6). In contrast, most older stages (11–15) were more widely distributed over the southern strata (7, 8, 10, 11). Presumably, as the eggs ascended the water column, variations in ascent rate and development rate would widen the distribution of eggs-at-age vertically (Zeldis *et al.* 1995) and as they encountered increasing horizontal flow velocities, horizontal shear and turbulent diffusion the egg distributions would become increasingly 'smeared' horizontally.

This hypothesis would imply that the *c.v.*s of the younger eggs should have been higher than those of older eggs. This appeared to be so for most of the East Cape data (*see* Figure 7a), even though more samples were taken in the strata where young eggs occurred than in strata where older eggs occurred (*see* Figure 4 and Appendix 2)

ii) Temporal patchiness

Patchiness of spawning in time also could have caused large underestimates of young egg abundance. Section 4.3.3 showed that it was unlikely that egg production varied gradually through the spawning season. However, if egg production was *pulsed* (for example, on the scale of less than or equal to 0.5 day) it could have been missed by much of the sampling near the spawning hill. The likelihood of such pulses being missed by the sampling will increase as the duration and frequency of the pulses decrease, if the temporal sampling rate stays constant. If spawning had occurred in rapid pulses, would the sampling that was actually done at East Cape have effectively sampled it?

To examine this, the times that older egg stages (10, 12, 13, 14, 15) would have occurred as young eggs (stages 1–7), were graphed for the four subsurveys against the actual times stations were occupied in strata 4 and 5 (the strata which yielded the young eggs) (Figure 10). This was done for all stations where these older stages were abundant (defined as occurring in densities greater than or equal to 1 egg per m^2 per h). This showed that there were frequent and extended periods with no sample coverage of these strata. Furthermore, the back calculated times when the abundant older eggs would have been young were wholly or partly during these times of no sample coverage in strata 4 and 5. This indicates that *if* egg production by the East Cape spawners did occur synchronously across the population in a few pulses of short duration, there was ample opportunity for the plankton sampling to have missed it. In contrast, the sampling in strata 7, 8, 10, and 11 which yielded the more dispersed older eggs was more dispersed in time (Figure 10) because it was done over a wider area. This could have lessened the likelihood that older eggs which arose from spawning pulses would be missed by the sampling.

In summary, the very clumped spatial distribution of spawning at East Cape could have caused the imprecise estimates of Z because it may have led to the undersampling of young eggs more frequently than older eggs. This would be exacerbated if spawning occurred in brief and infrequent pulses synchronously throughout the population, which would have had a high likelihood of being missed by the relatively infrequent sampling in the strata containing the spawning hills.

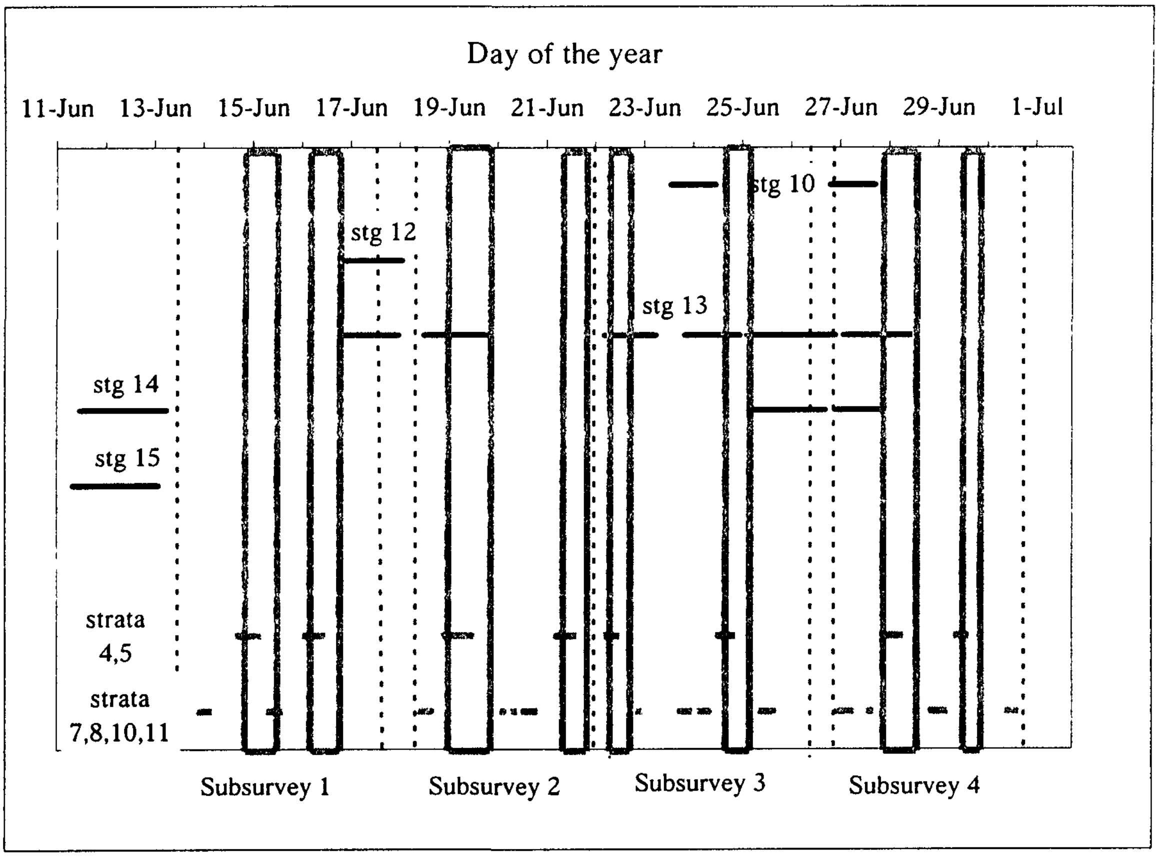

Figure 10: Times of East Cape plankton sampling compared to times when young eggs would have been abundant in strata 4 and 5 (estimated by back-calculating from egg stages 10–15). Times when indicated egg stages would have been young (≤ stage 7) are shown by black horizontal bars. Times when indicated strata were occupied are shown by stippled horizontal bars. Time intervals when strata 4 and 5 were occupied are encased in stippled rectangles, showing that there was little overlap of time of occupation with times when young eggs would have been present in those strata. Times when strata containing older eggs (strata 7, 8, 10, 11) were occupied are also shown. Vertical dotted lines show time intervals of plankton subsurveys 1 to 4.

4.3.5 'Best', 'lower bound', and 'upper bound' *Z* values

To obtain more reliable estimates of egg production *Z* values were taken from the probability distribution for *Z* from the 1993 Ritchie Bank orange roughy egg production survey (Zeldis *et al.* 1997a) and applied to the current egg abundance data. The estimate for Ritchie Bank in 1995 was not used because of low sample numbers and inconsistent spatial and temporal coverage by the subsurveys.

The mean *Z* estimate for the 1993 orange roughy survey was 0.95 and the lower and upper 2.5% cutoffs on this distribution were zero and 2.0, respectively. These estimates for *Z* were used below to estimate *N*, assuming a 'variable-*N*, constant-and-known-*Z*" model for both the East Cape and 1995 Ritchie Bank surveys.

4.3.6 Estimates of daily planktonic egg production

The maximum likelihood model was used to estimate daily planktonic egg production, N, for three values of Z: 0.95, 0, 2.0 (Figure 11). These estimates are shown together with the initial estimates (see 4.3.1) in Table 8. Baseline estimates were taken as those for East Cape 'all strata' and Ritchie Bank 'all strata' with $Z = 0.95$. Estimates with $Z = 2.0$ and $Z = 0$ were used as upper and lower bounds, respectively.

Table 8: Initial and final estimates of daily planktonic egg production (N, billions day^{-1}) and egg mortality (Z, day^{-1})

	Initial		Z=0.95	Z=0	Z=2.0
Subsurveys	N	Z	N	N	N
East Cape:					
EC1	8.1	0.5	15.3	4.5	58.7
EC2	2.1	-0.1	7.5	2.5	25.5
EC3	0.8	-1.2	14.2	4.0	57.1
EC4	0.6	-1.4	13.7	3.8	55.8
all strata	2.8	-0.5	20.8	5.7	85.4
Ritchie:					
all strata	10.3	2.4	4.5	2.6	8.1

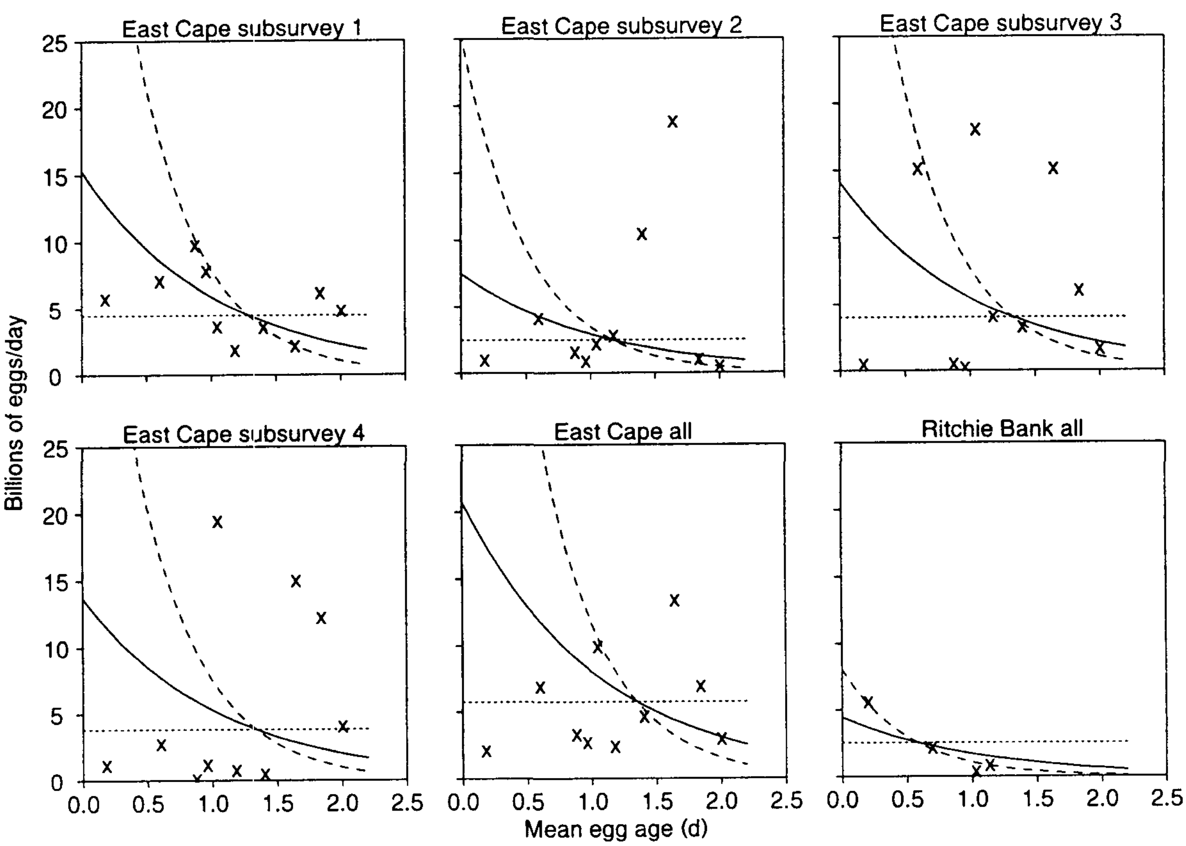

Figure 11: Illustration of estimates of daily planktonic egg production (N) for three values of Z: 0.95 (solid lines), 0 (dotted lines), and 2.0 (broken lines). Results are shown for each subsurvey at East Cape and for all data at each of East Cape and Ritchie Bank. The estimate of N is the intercept of the plotted curves on the y-axis.

4.3.7 Estimates of total egg production at East Cape

The value of N_{tot}, the total egg production for East Cape, was estimated as the area under the solid line in Figure 12a, i.e. 550 billion eggs. This uses the 'EC all, Z = 0.95' estimate of planktonic egg production (see 4.3.6) for the period of the survey (about 12–30 June) and assumes that production increased linearly to this level from the start of spawning (3 June) and then decreased linearly from this level until the end of spawning (8 July). Lower and upper bounds on production, derived from the 'Z = 0' and 'Z = 2.0' estimates in Section 4.1.3.5 were 150 and 2250 billion eggs. An alternative estimate using the individual EC1, EC2, EC3 and EC4 N values (with Z = 0.95) (dotted line in Figure 12a) is 350 billion eggs.The date of the start of spawning was that on which the proportion of ovulated fish from trawl samples (described below) became 0.05, and was interpolated between samples taken on 2 June and 6 June 1995. The date for the end of spawning was estimated by fitting a probit curve to the plot of percentage stage 6 vs day and using this to estimate the day at which percentage stage 6 reached 95 (Figure 12b).

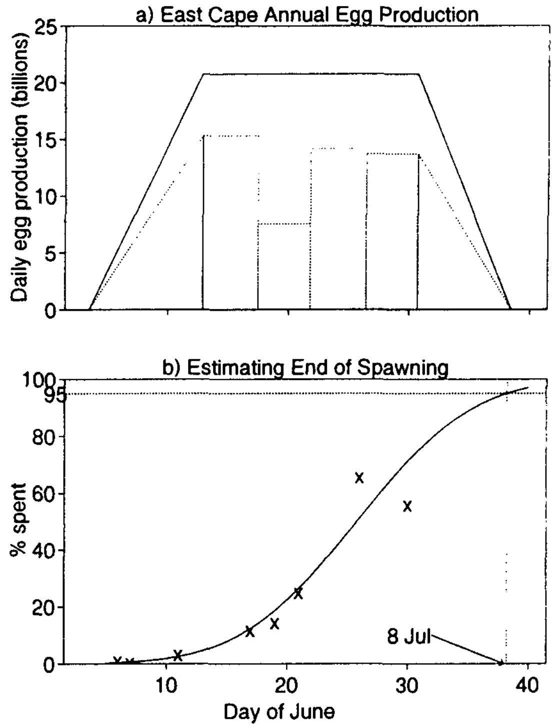

Figure 12: Illustration of a) estimating the total annual egg production (N_{tot}), and b) end of spawning, for East Cape. N_{tot} is the area under solid line in the upper panel (it would be the area under the broken line if each subsurvey was analysed separately). The end of spawning is defined as the day 95% of fish are spent, which is estimated by a fitting a probit curve to the gonad stage data.

4.4 *c.v.*s and Bootstrap Distributions for *N*

Coefficients of variation (*c.v.*) for N were calculated using the following ad hoc procedure. The starting point was the set of estimates of egg abundance — one estimate (together with a *c.v.*) for each egg stage: 1000 simulated sets of abundance data were generated from lognormal distributions with the original values as means and a common *c.v.* equal to the median *c.v.* of the original data. Each simulated data set was paired with a Z value from the bootstrap distribution for Z from the 1993 Ritchie Bank survey. For each simulated data set the maximum likelihood value of N was calculated, given the associated Z value. Coefficients of variation calculated from each set of 1000 values of N were 49% for Ritchie Bank and 65% for East Cape.

These *c.v.*s must be treated with caution because of the ad hoc nature of the method by which they were calculated. One unsatisfactory aspect of this method is that the baseline estimates are nowhere near the middle, or even the mean, of the bootstrap distributions: they are at the 73rd and 82nd quantiles of the distributions, for East Cape and Ritchie Bank, respectively. This problem persists when the estimate of N is converted to recruited biomass, B_{rec}.

5. ANALYSIS OF 1995 FECUNDITY AND GONAD STAGE DATA

Gonad stage and fecundity data were collected from a series of trawls carried out by *Tangaroa* before and during the East Cape egg survey, and by commercial vessels at East Cape and Ritchie Bank. A random sample of fish from each tow was sexed and staged macroscopically. At most tows ovaries were taken from a subsample of the staged fish for estimation of fecundity and histological analysis. Only tows on or near the main spawning hills were used in these analyses. The number of these samples available is given in Table 9.

Table 9: Number of tows from which gonad stage (and fecundity) data were available for analysis

Area	Tangaroa	Commercial
East Cape	9 (9)	6 (3)
Ritchie Bank	0 (0)	46 (38)

5.1 Pre-spawning Fecundity

Pre-spawning fecundity was higher at Ritchie Bank than at East Cape (Table 10, Figure 13), and higher at Ritchie Bank during 1995 than 1993.

Table 10: Mean fecundity of stage 3 females early in the spawning season (7 tows before 12 June for 1995 East Cape; 5 tows before 12 June for 1993 Ritchie Bank; 13 tows before 17 June for 1995 Ritchie Bank)

		Total fecundity ('000 eggs/female)	Relative fecundity, R_0 ('000 eggs/kg)
East Cape:	1995	44.0	26.5
Ritchie Bank:	1993	53.9	30.7
	1995	61.4	32.9

5.2 Daily Fecundity Reduction

Estimates of D, the daily fecundity reduction (eggs $kg^{-1}day^{-1}$) are 1047 for East Cape and 965 for Ritchie Bank (*c.v.* = 11% for both). These numbers were estimated as the slopes (ignoring sign) of the lines in Figure 14 using weighted linear regression. Each point in this figure represents one or more tows on that day.

5.3 Spent Fish

In calculating the daily fecundity reduction, D, it was assumed that all spent fish had no eggs left in their ovaries. This appeared to be the a reasonable assumption for East Cape, where the mean fecundity of spent fish was only 321 (range 0 to 2709, n = 35). However, the assumption was not as good for Ritchie Bank, where the corresponding figure was 7041, though the sample was small (n = 6: 0, 498, 824, 9887, 11 249, 19 793). It appears that half of this sample should have been staged as 5 or 8, rather than 6. Almost all ovaries from East Cape (and all those of stage 6) were staged on *Tangaroa*; all those from Ritchie Bank were staged by observers.

When these fecundities were used in calculating D, the estimate reduced by 1% for East Cape and by 2.5% for Ritchie Bank. However, the latter figure is imprecise because so few stage 6 ovaries were sampled and there is uncertainty about the gonad staging for this area (note that the ovary count sample was much larger than the gonad stage sample: there were 166 stage 6 fish in the latter at Ritchie Bank).

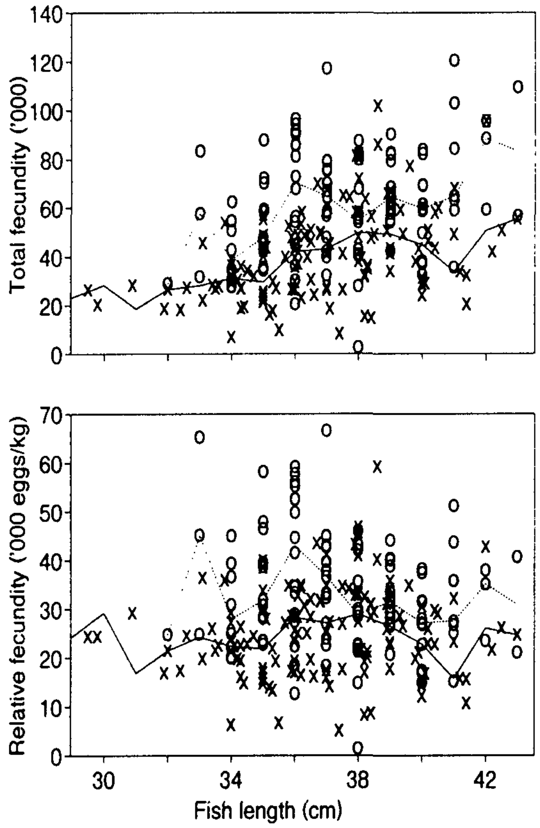

Figure 13: Comparison of a) total fecundity and b) relative fecundity at East Cape (x, ——) and Ritchie Bank (0, ········) (lines indicate median fecundity at length). Data are from stage 3 ovaries from early to midJune (before 12 June for East Cape, before 17 June for Ritchie Bank).

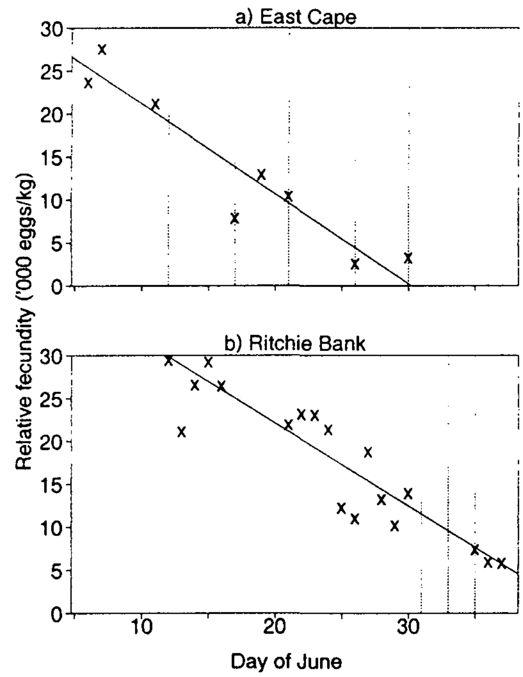

Figure 14: Estimation of *D*, the daily fecundity reduction for a) East Cape and b) Ritchie Bank. *D* is the absolute value of the slope of the plotted line, which was obtained by a weighted linear regression with weights equal to the size of the combined gonad stage sample for each day. The vertical broken lines show the start and end of each subsurvey in each area.

6. ANALYSIS OF 1995 RANDOM TRAWL SURVEY DATA

The data analysed above allow the estimation of the biomass of females spawning, B_{spf}, at East Cape and Ritchie Bank. To estimate recruited biomass (B_{rec}, defined as the biomass of fish of length greater than or equal to 32 cm) we need an estimate of the ratio B_{rec}/B_{spf}, which we denote S. This ratio allows for recruited females that did not spawn, and females that did spawn but were less than 32 cm (very few), as well as the sex ratio.

To calculate S we need data from the whole area which provides spawners for the two spawning areas. For East Cape, we used data from the random trawl survey carried out on TAN9506 (4–21 May 1995; Clark 1995). For Ritchie Bank, there was no survey in 1995 but data were available from surveys of the Ritchie/Wairarapa/Kaikoura area (TAN9203, 16 March – 11 April 1992; TAN9303, 15 March – 12 April 1993; and TAN9403, 16 March – 11 April 1994).

6.1 Estimates of *S*

S was estimated using

$$S = \frac{\sum_{i} (P_{rec,i} X_i)}{\sum_{i} (P_{spf,i} X_i)}$$

where $P_{rec.i}$ is the proportion, by weight, of the catch at station *i* that is recruited; $P_{spf.i}$ is the proportion, by weight, of the catch at station *i* that is female and of gonad stage 3 or greater; and X_i is a weighting factor calculated as $X_i = C_i A_j / n_j$, where C_i is the catch rate at station *i* (t/km), A_j is the area of the stratum containing station *i*, and n_j is the number of stations in stratum *j*. Estimates of *S* are given in Table 11.

*c.v.*s for *S* were calculated by the same bootstrap procedure used for the 1993 Ritchie egg survey (Zeldis *et al.* 1997a)

The calculation of $P_{spf.i}$ was complicated beacuse for some stations in some of the Ritchie Bank surveys not all fish that were sexed and measured were staged. Because of this, the following formula was used:

$$P_{spf} = \frac{W'_{spf}}{W'_f} \times \frac{W_f}{W_{tot}}$$

where *W* refers to a weight calculated for fish in the length-sex sample, *W'* refers to the weight of the staged subsample, the subscript *f* refers to females, and *spf* refers to females of gonad stage 3 or greater.

Table 11: Estimates of *S*, the ratio (by biomass) of recruited fish to spawning females, and *SF*, the female spawning fraction (proportion, by biomass, of mature females that will spawn in a given year) for various assumptions of spawning ground catchment areas

Area	Year	Number of stations	*S*	*c.v* (%)	*SF*	*c.v* (%)
East Cape:						
all strata	1995	87	2.02	(9)	0.68	(11)
hills 1-8 only	1995	46	2.01	(4)	0.90	(2)
all except C. Runaway	1995	76	1.83	(9)	0.77	(9)
Ritchie Bank:						
2A,2B,3A	1992	162	1.99	(7)	0.49	(8)
2A,2B,3A	1993	196	1.85	(3)	0.52	(6)
2A,2B,3A	1994	194	2.14	(5)	0.42	(7)
2A	1992	101	1.81	(8)	0.65	(7)
2A	1993	91	1.74	(5)	0.60	(7)
2A	1994	70	1.72	(5)	0.62	(5)
2B	1992	26	2.39	(15)	0.36	(16)
2B	1993	55	1.92	(6)	0.62	(7)
2B	1994	69	2.61	(7)	0.36	(12)
3A	1992	35	2.98	(26)	0.18	(24)
3A	1993	50	2.18	(13)	0.24	(20)
3A	1994	55	3.34	(17)	0.16	(24)

For East Cape, the base case estimate of *S* was taken as 2.02 which assumed that the catchment area for this spawning ground was the whole survey area. For Ritchie Bank, the catchment area was also assumed to be the whole survey area (2A, 2B, 3A) and the estimates from the three years for this area were averaged to give a value of 1.99.

6.2 Estimates of Female Spawning Fraction

The quantity S is needed to calculate B_{rec} but has no straightforward biological meaning. A quantity that has more biological relevance is the spawning fraction — the proportion of mature females (stage greater than or equal to 2) that spawn in a given year (i.e., that have stage greater than or equal to 3 in the months leading up to spawning. This fraction is not used in estimating biomass from egg surveys but is useful in understanding spawning activity. Estimates are given in Table 11. For both East Cape and Ritchie Bank the spawning fraction was higher near the spawning sites and decreased with increasing distance from them.

7. ADJUSTING RITCHIE BANK SURVEYS FOR TURNOVER

An assumption of the DFRM is that there is no "turnover" of spawning fish during the period of the survey, that is, it is assumed that no (female) spawners enter or leave the spawning area during this period. Some evidence of turnover during the 1993 Ritchie Bank egg survey, and an attempt to correct for this, are detailed in Section 3 above. In this section further evidence of turnover is presented (for both the 1993 and 1995 Ritchie Bank surveys) and a more formal way of correcting for it is described. This results in revisions to the estimates of daily fecundity reduction, D, for these surveys.

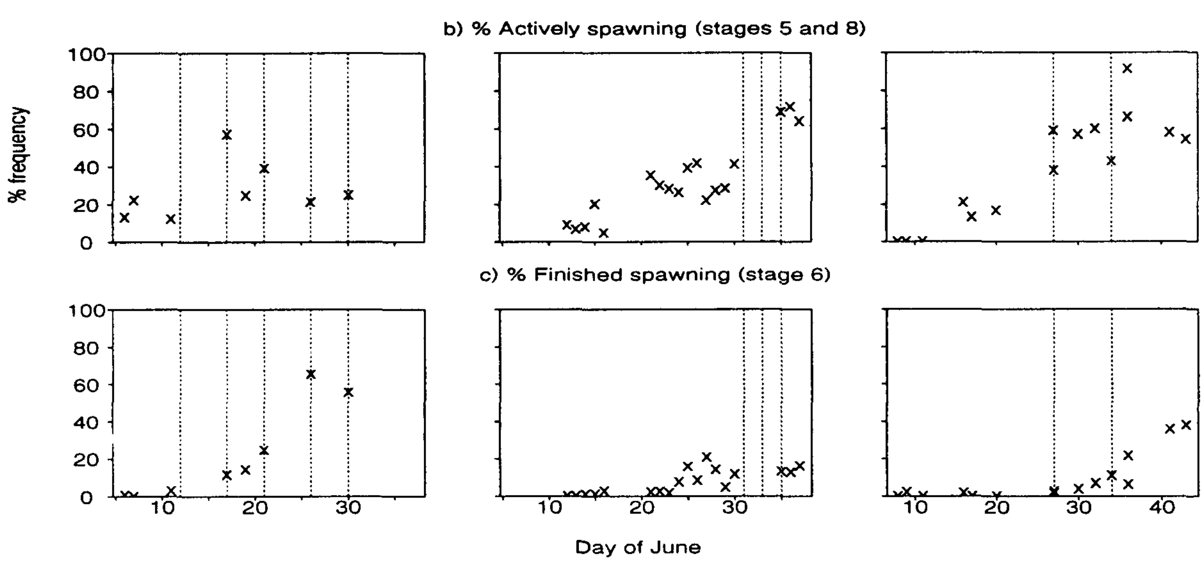

Figure 15: Comparison of gonad stage frequencies plotted against time for three surveys: East Cape, Ritchie Bank 1995, and Ritchie Bank 1993: a) preparing to spawn (stages 3 and 4), b) actively spawning (stages 5 and 8), and c) finished spawning (stage 6). The vertical broken lines show the start and end of each subsurvey in each area.

Evidence of turnover is seen in a comparison of gonad stage frequency data between the three egg surveys (Figure 15). At East Cape the active stages rarely exceeded 30–40% and more than 50% of fish were spent by the end of the survey. This is the pattern that has been observed in other spawning areas (e.g., the Chatham Rise and Challenger Plateau (Francis 1996)). By contrast, at the end of both of the Ritchie Bank surveys active fish exceeded 60% and there were few spent fish. This pattern suggests that in both 1993 and 1995 spent fish were leaving the Ritchie Bank survey area before the survey was over, that is, turnover was occurring. That a high proportion of fish were spent at the end of the East Cape survey suggests that little or no turnover occurred there. A possible reason for this difference in behaviour is that during both surveys at Ritchie Bank there were other boats fishing in the area, whereas this was not true at East Cape. The following model was developed to estimate the amount of turnover on Ritchie Bank and adjust for it.

7.1 Model Assumptions

The main model assumption is that all females leave the survey area d days after they have finished spawning (i.e., after they are spent, or stage 6). Secondary assumptions are that the the proportion of females of stages 3 and 6 at time t, $p_3(t)$ and $p_6(t)$, can be described by

$$p_3(t) = 1 - F\left(\frac{t - \mu_3}{\sigma_3}\right) \quad \text{and}$$

$$p_6(t) = F\left(\frac{t - \mu_6}{\sigma_6}\right)$$

where F is the cumulative distribution function of the standard normal distribution. Thus the model has five parameters: d, μ_3, σ_3, μ_6, σ_6 (Figure 16) and the proportion of fish that have left the survey area at time t is given by

$$p_{dep}(t) = F\left(\frac{t_i + d - \mu_6}{\sigma_6}\right)$$

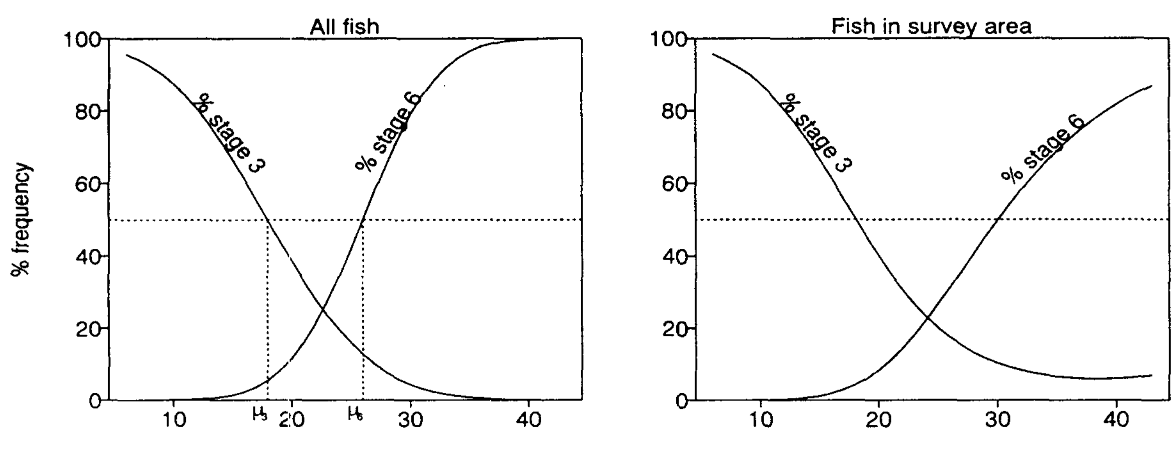

Figure 16: Turnover model. The time trajectories of the percentages of female fish of stages 3 and 6 are shown for all fish (left panel) and for fish in the survey area (right panel), assuming that fish leave the survey areas 2 days after finishing spawning (i.e., d = 2). The parameters μ_3, μ_6 describe the date at which 50% of female fish are of stages 3 and 6, respectively. The time between these dates is the mean active time (MAT).

The above equations describe the gonad stage frequencies for *all* spawning females (Figure 16a). The frequencies within the survey area (Figure 16b) are biased because they exclude fish that have spawned and left the area.

7.2 Interpretation of Model Parameters

The model assumptions imply that the date at which an individual female finishes spawning (i.e., reaches stage 6) is normally distributed with mean μ_6 and standard deviation σ_6. However, the meanings of μ_3 and σ_3 depend on whether, during the spawning season, any females revert to stage 3 from the active stages 4, 5, or 8.

If there is no reversion, the interpretation is clear. The model assumptions then imply that the date at which an individual female leaves stage 3 is normally distributed with mean μ_3 and standard deviation σ_3. If there *is* reversion, some females will leave stage 3 more than once and these parameters will describe the distribution of the *mean* date at which this occurs for each individual.

A quantity of interest is the mean spawning time (MST), which is defined as the mean time from first spawning to spent (stage 6). It is not possible to estimate MST with the data available but we can estimate the mean active time (MAT), which is defined as the mean time a female spends in one of the active stages, 4, 5, or 8. The MAT is simply $\mu_6 - \mu_3$.

If there is no reversion, and if there is not much delay between first entering stage 4 and first spawning, then MAT $\approx$ MST. If there is reversion (and if there is not much delay between first entering stage 4 and first spawning) then MAT $<$ MST.

7.3 Fitting the Model

In principle, it is possible to fit this model to the survey data by maximum likelihood (assuming the gonad stages in each sample are distributed multinomially). In practice, however, it is not possible to estimate d from our data. This is because it is possible to obtain fits to the data that are almost equally good using widely different values of d. However, for a given value of d it is possible to obtain estimates of the other four parameters. Further, any "large" value of d (i.e., greater than the duration of the survey, and so implying no turnover) results in the same values for the other four parameters.

To fit the model it was first assumed that no turnover occurred at East Cape (so d was "large"). This resulted in an estimate of 18.6 d for MAT. Second, it was assumed that MAT was about the same in all areas. Setting MAT to 18.6 d produced estimates of d = 2.1 d in 1995, and d = 1.2 d in 1993, for Ritchie Bank. Averaging these values (i.e., setting d = 1.6) and refitting the model resulted in the final parameter estimates (Table 12).

Table 12. Parameter estimates for turnover model. Units for μ_3 and μ_6 are days from the start of June; all other parameters have units days

Survey	μ_3	σ_3	μ_6	σ_6	d	MAT
East Cape 1995	7.2	6.3	25.8	7.6	"large"	18.6
Ritchie Bank 1995	13.5	10.4	30.0	9.1	1.6	16.5
Ritchie Bank 1993	15.8	6.7	36.5	7.4	1.6	20.7

7.4 Adjusting D for Turnover

Daily fecundity reduction, D (eggs per kg d), is calculated as the slope (ignoring sign) of the regression of R_i on t_i, where R_i is the mean fecundity per kg of spawning female in sample i and t_i is the date of sample I (*see* Figure 14). When there is turnover (as described by the above model), R_i will be overestimated because it will not include spent females that have left the survey area. Furthermore, the percentage overestimate will increase with increasing t_i so that D will be underestimated.

Once the turnover model is fitted it is possible to correct each R_i by multiplying it by $(1-p_{dep}(t_i))$ and thus adjust D for the effects of turnover. This was done for both Ritchie Bank surveys using the turnover parameter values in Table 12. The effect was to increase D by 23% for the 1995 survey (from 965 to 1188) and 25% for the 1993 survey (from 788 to 989).

8. ESTIMATES OF BIOMASS FOR THE 1996 STOCK ASSESSMENT

This section brings together all orange egg survey biomass estimates used in the 1996 stock assessment (Annala & Sullivan 1996). Thus, it includes the revisions to the 1993 Ritchie Bank egg survey (Section 3), the results from the two 1995 surveys (Sections 4–6), and turnover adjustments for the two Ritchie Bank surveys (Section 7). The results of the 1995 Ritchie Bank survey are considered unreliable because of low and incomplete plankton station coverage. Also presented, for completeness, are the AEPM estimate of biomass for East Cape (not used in the stock assessment) and values of the parameters from which all biomass estimates were calculated. These results are given in Table 13.

Table 13. Estimates of biomass and associated parameters as used in the 1996 stock assessment (c.v.s in parentheses, where available). For the Ritchie Bank surveys estimates are given with ("Adj.") and without ("No adj'") adjustment for turnover

A. Using daily fecundity reduction method (DFRM)

Survey	Egg production N (eggs d^{-1})	Biomass ratio S	Fecundity reduction D (eggs kg^{-1} d^{-1})		Recruited biomass B_{rec} (t)	
			No adj.	Adj.	No adj.	Adj.
Ritchie Bank 1993	17×10^9 (42)	1.85 (3)	788 (11)	989 (7)	40 000 (45)	32 000 (40)
Ritchie Bank 1995	4.5×10^9 (49)	1.99 (5)	965 (11)	1188 (8)	9 200 (51)	7 500 (50)
East Cape 1995	21×10^9 (65)	2.02 (9)	1047 (11)	–	40 000 (67)	–

B. Using annual egg production method (AEPM)

Survey	Egg production N_{tot} (eggs)	Biomass ratio S	Fecundity R_0 (eggs kg^{-1})	Recruited biomass B_{rec} (t)
East Cape 1995	550×10^9	2.02 (9)	26 500	42 000

Recruited biomass was calculated as $B_{rec} = (N \times S)/D$ for the DFRM and $B_{rec} = (N_{tot} \times S)/R_0$ for the AEPM.

9. REVISIONS FOR THE 1997 STOCK ASSESSMENT

The above egg survey biomass estimates for Ritchie Bank and East Cape were revised for use in the 1997 stock assessment. The revisions arose for two reasons. First, an error was found in the analysis of the 1993 Ritchie Bank survey. This led to changes in the biomass estimates from the 1995 surveys of East Cape and Ritchie Bank because these were based on the estimate of egg mortality, *Z*, from the 1993 survey. Second, the analysis of the 1996 Graveyard egg survey provides an update on the turnover correction for the Ritchie Bank biomass estimates.

9.1 Correction of Error

The error in the analysis of the 1993 survey concerned the central stratum in the plankton survey which was covered twice for each snapshot. Mean egg abundances for each pair of occupations of this stratum were *summed*, whereas they should have been *averaged*. This means that the overall egg abundance was overestimated (particularly for the younger eggs, which were most abundant in the inner stratum). As a result, both *N* and *Z* were overestimated. This overestimation of *Z* for the 1993 survey caused an under-estimation of *N* in the 1995 surveys (Table 14).

Table 14. Original and revised estimates of egg production (*N*, billions of eggs/day) and egg mortality (*Z*, day^{-1}) with *c.v.s* (%) in parentheses. '-' = not estimated for this survey

	Original		Revised	
Survey	*N*	*Z*	*N*	*Z*
Ritchie Bank 1993	17.0 (42)	0.96 (53)	10.9 (46)	0.70 (69)
Ritchie Bank 1995	4.5 (49)	-	3.8 (50)	-
East Cape 1995	20.8 (65)	-	14.8 (66)	-

9.2 Turnover Corrections

The turnover corrections for the two Ritchie Bank surveys were based on a model that assumed that each female left the survey area *d* days after it had completed spawning. It was not possible to estimate *d* directly for these surveys so the following further assumptions were made:

- that *d* was the same in both years, and
- that the mean active time (MAT) at Ritchie Bank in these two years was similar to that at East Cape in 1995.

The MAT is the time a female spends in the active stages, 4, 5, and 8. This could be estimated at East Cape because it appeared that there was no turnover there. The estimated value was 18.6 d. With the above assumptions this produced a value of *d* = 2.1 d for the two Ritchie Bank surveys.

The second of the above two assumptions was reasonable at the time because there was only one spawning area where MAT had been estimated. However, now that the 1996 Graveyard egg survey has been analyzed (Francis *et al.*, 1997.) there is a second estimate of MAT — 25.7 d. Given this new estimate it seems reasonable to modify the above assumption to say that the MAT for Ritchie Bank is similar to the mean of the two estimates, i.e., 22.2 d. With this value the revised estimate of d for Ritchie Bank is 2.8 d. This decreases the estimates of daily fecundity reduction, D, as shown in Table 15.

Table 15. Original and revised estimates of turnover-corrected daily fecundity reduction (D, eggs kg^{-1} day^{-1}) with *c.v.*s (%) in parentheses. Estimates of D without turnover correction (unchanged by these revisions) are included for completeness. Current best estimates are underlined. '-' = this survey unaffected by turnover

Survey	Corrested for turnover		Uncorrected for turnover
	Original	Revised	
Ritchie Bank 1993	989 (7)	912 (8)	788 (11)
Ritchie Bank 1995	1188 (8)	1103 (9)	965 (11)
East Cape 1995	-	-	1047 (12)

9.3 Summary of Revisions

The effect of these two sets of revisions on estimates of recruited biomass is shown in Table 16. The main effect has come from the revisions to N. This effect is slightly reduced for the Ritchie Bank surveys by the revised turnover corrections.

Table 16. Estimates of biomass and associated parameters as used in the 1997 stock assessment (*c.v.*s in parentheses, where available). For the Ritchie Bank surveys estimates are given with ("Adj.") and without ("No adj'") adjustment for turnover

A. Using daily fecundity reduction method (DFRM)

Survey	Egg production N (eggs d^{-1})	Biomass ratio S	Fecundity reduction D (eggs kg^{-1} d^{-1})		Recruited biomass B_{rec} (t)	
			No adj.	Adj.	No adj.	Adj.
Ritchie Bank 1993	11 x 10^9 (46)	1.85 (3)	788 (11)	912 (8)	26 000 (50)	22 000 (49)
Ritchie Bank 1995	3.8 x 10^9 (50)	1.99 (5)	965 (11)	1103 (9)	8 000 (52)	7 000 (50)
East Cape 1995	15 x 10^9 (66)	2.02 (9)	1047 (12)	–	29 000 (69)	–

B. Using annual egg production method (AEPM)

Survey	Egg production N_{tot} (eggs)	Biomass ratio S	Fecundity R_0 (eggs kg^{-1})	Recruited biomass B_{rec} (t)
East Cape 1995	390 x 10^9	2.02 (9)	26 500	30 000

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APPENDIX 1: CALCULATION OF 'CURVED' CORRECTION FACTORS

This appendix describes the calculation of the correction factors that convert egg counts to egg density (eggs per m^2) when the path of the net during hauling is assumed to be curved

The approach taken was to calculate, for each plankton tow,

a) the position of the net at the start of hauling;
b) the position of the net at a series of equally spaced times during hauling;
c) the flow of water through the net at each of these times; and
d) a correction factor for each of these times.

Finally, interpolation was used to calculate the correction factor when the net was at the mid-point of the depth layer associated with each egg stage. This was taken as the correction factor for that egg stage at that plankton tow.

First, the assumptions behind these calculations and some notation are defined.

A1.1 Assumptions and Notation

The calculations required the following assumptions.

1. The vessel drifted at a constant velocity while shooting and while hauling.
2. While shooting, the net dropped at a constant speed.
3. While hauling, the warp was always straight and decreased in length at a constant rate.
4. The net mouth was always perpendicular to the warp.
5. The water velocity varied only with depth (not with longitude, latitude, or time).
6. The following are known exactly:
    a) the vessel position at the time of shooting and the start and finish of hauling,
    b) the net depth and warp length at the start of hauling, and
    c) the water velocity profile.

Two further assumptions are described in Sections A1.2 and A1.3

Let $\underline{P}_n(t)$ and $\underline{P}_v(t)$ be 3-dimensional vectors describing the position of the net and the vessel at time t, where time and position are measured relative to the time and vessel position when the net was shot, and the three coordinates give distances, in metres, to the east, north, and downwards, respectively. (In this Appendix, vectors are underlined to distinguished them from scalars.). Let t_1 and t_2 stand for the times at the start and finish of hauling.

Let the water velocity at depth z be described by the vector $\underline{C}(z)$, and the mean water velocity between the surface and depth z by $\underline{C}'(z)$. Denote the net depth and the warp length at time t by $z_n(t)$ and $w(t)$, respectively (note that $z_n(t)$ is the depth coordinate of $\underline{P}_n(t)$).

Where it is convenient, the symbols t_1 and t_2 will be replaced by subscripts 1 and 2, so that, for example, $\underline{P}_n(t_1)$, $z_n(t_1)$, and $\underline{P}_v(t_2)$ may be written as $\underline{P}_{n1}$, z_{n1}, and $\underline{P}_{v2}$, respectively.

From the above assumptions, $\underline{P}_{v1}$, $\underline{P}_{v2}$, z_{n1}, and w_1 are known, as are $\underline{C}(z)$ and $\underline{C}'(z)$ for all z. Also, of course, $\underline{P}_{n2} = \underline{P}_{v2}$.

A1.2 Calculating $\underline{P}_{nl}$

In calculating the position of the net at the start of hauling it was assumed that, while the net was sinking before hauling, its horizontal velocity was the sum of the water velocity and some fraction c of the vessel velocity (the latter component being caused by drag from the warp). Thus,

$$(A1) \qquad \underline{P}_{nl} = c\,\underline{P}_{vl} + t_l\underline{C}'(z_{nl}) + \underline{Z}_{nl}$$

where $0 < c < 1$, and $\underline{Z}_{nl}$ is the 3-dimensional vector, $(0,0,z_{nl})$. Also, from assumptions 3 and 6,

$$(A2) \qquad |\underline{P}_{nl} - \underline{P}_{vl}| = w_l$$

The value of c (and thus $\underline{P}_{nl}$) can be calculated by solving the simultaneous equations (A1) and (A2). Geometrically, this is equivalent to finding a point of intersection of the horizontal line defined by (A1) and the horizontal circle defined by (A2) (both are at depth z_{nl}).

Substituting for $\underline{P}_{nl}$ from (A1) in (A2) and expanding, we get the quadratic equation in (c-1)

$$(A3) \qquad (c-1)^2|\underline{P}_{vl}|^2 + 2(c-1)\,t_l\,\underline{P}_{vl}\bullet\underline{C}'(z_{nl}) + t_l^2|\underline{C}'(z_{nl})| + z_{nl}^2 - w_l^2 = 0$$

which is solved using the usual formula (• denotes the vector dot product).

Where there were two solutions for c (at all but a few stations), the one using the negative square root was chosen because it was usually the one that satisifed the condition $0 < c < 1$.

For the few stations where (A3) had no real solution (i.e., the line and circle did not intersect) $\underline{P}_{nl}$ was taken to be the point on the circle closest to the line. It may be shown that this $\underline{P}_{nl}$ is given by

$$(A4) \qquad \underline{P}_{nl} = r\frac{\underline{P}_{cl}}{|\underline{P}_{cl}|} + \underline{P}_{vl} + \underline{Z}_{nl}$$

where r is the radius of the circle and $\underline{P}_{cl}$ is the point, on the surface vertically above the line, that is closest to the shot position, and is given by

$$(A5) \qquad \underline{P}_{cl} = t_l\underline{C}'(z_{nl}) - \frac{t_l\underline{C}'(z_{nl}) \bullet \underline{P}_{vl}}{|\underline{P}_{vl}|^2}\underline{P}_{vl} \; .$$

Stations where (A3) did not have a real solution, or where c did not satisfy $0 < c < 1$, were assumed to be instances where the above assumptions did not hold. The assumptions clearly did not hold at the 13 stations where $z_{nl} > w_l$. For these stations, z_{nl} was set equal to w_l, and $\underline{P}_{nl}$ was taken to be vertically below $\underline{P}_{vl}$.

A1.3
Calculating the Net Path During Hauling

From assumptions 1 and 3 the position of the vessel and length of the warp at any time during hauling was calculated using

$$(A6) \qquad \underline{P}_v(t) = \frac{(t_2 - t)\,\underline{P}_{v1} + (t - t_1)\,\underline{P}_{v2}}{(t_2 - t_1)}$$

and

$$(A7) \qquad w(t) = \_\underline{P}_v(t) - \underline{P}_n(t)\_ = \frac{(t_2 - t)\,w_1}{(t_2 - t_1)} \; .$$

To calculate the position of the net during hauling we make one further assumption: that the velocity of the net is the sum of the water velocity and a vector in the direction of the warp. Using this assumption, an iterative procedure was used to calculate $\underline{P}_n(t)$ at times $t_1 + \delta t$, $t_1 + 2\delta t$, etc, for a small time interval δt. The basis of this procedure is the ability to calculate $\underline{P}_n(t+\delta t)$ once $\underline{P}_n(t)$ is known. This is done as follows.

The velocity assumption may written approximately as

$$(A8) \qquad \frac{\underline{P}_n(t + \delta t) - \underline{P}_n(t)}{\delta t} = p(t)\,\frac{\underline{P}_v(t) - \underline{P}_n(t)}{|\underline{P}_v(t) - \underline{P}_n(t)|} + \underline{C}(z_n(t))$$

where $p(t)$ is an unknown scalar which varies with t. Replacing t by $t + \delta t$ in (A7) we get

$$(A9) \qquad |\underline{P}_v(t + \delta t) - \underline{P}_n(t + \delta t)| = \frac{(t_2 - t - \delta t)\,w_1}{(t_2 - t_1)}$$

and substituting for $\underline{P}_n(t+\delta t)$ from (A8), (A9) may be rewritten as

$$(A10) \qquad |p(t)\underline{A} + \underline{B}| = \frac{(t_2 - t - \delta t)\,w_1}{(t_2 - t_1)}$$

where

$$(A11) \qquad \underline{A} = -\frac{(t_2 - t_1)\delta t}{w_1 (t_2 - t)}\,(\underline{P}_v(t) - \underline{P}_n(t))$$

and

$$(A12) \qquad \underline{B} = \underline{P}_v(t + \delta t) - \underline{P}_n(t) - \delta t\,\underline{C}(z_n(t)) \; .$$

Expanding (A10), we get the quadratic equation

$$(A13) \qquad \underline{A}\bullet\underline{A}p(t)^2 + 2\underline{A}\bullet\underline{B}p(t) + \underline{B}\bullet\underline{B} = \left[\frac{(t_2 - t - \delta t)\,w_1}{(t_2 - t_1)}\right]^2$$

which may be solved for $p(t)$ in the usual manner.

In solving (A13), the solution using the positive square root was ignored because it led to large values of $p(t)$ and large vertical oscillations in the net path.

A1.4 Flow of Water Through the Net

Since, by assumption 4 above, the net mouth was always perpendicular to the warp, the flow of water through the net at time t (in m^3s^{-1}) is given by

$$(A14) \qquad F(t) = 2\underline{V}_{nw} \bullet \underline{U}_{wp}$$

where $\underline{V}_{nw}$ is the velocity of the net relative to the water, given approximately by

$$(A15) \qquad \underline{V}_{nw} = \frac{\underline{P}_n(t+\delta t) - \underline{P}_n(t)}{\delta t} - \underline{C}(z_n(t)) \ ,$$

$\underline{U}_{wp}$ is a unit vector in the direction of the warp, given by

$$(A16) \qquad \underline{U}_{wp} = \frac{\underline{P}_v(t) - \underline{P}_n(t)}{|\underline{P}_v(t) - \underline{P}_n(t)|} \ ,$$

and the factor 2 is the net mouth area in metres squared.

A1.5 Calculation of Correction Factors

The correction factor associated with a horizontal layer of water is given by

$$(A17) \qquad \mathrm{CF} = \frac{\text{Thickness of layer}}{\text{Volume of water filtered by net within layer}} \ .$$

Thus, for the layer of water that the net passed through between times t and $t + \delta t$, the correction factor is given approximately by

$$\frac{z_n(t) - z_n(t+\delta t)}{F(t)\delta t} \ .$$

which is treated as the correction factor associated with depth $z_n(t)$. Thus, for each plankton tow, correction factors for depths $z_n(t_I)$ $(=z_{nI})$, $z_n(t_I+\delta t)$, $z_n(t_I+2\delta t)$, etc, were calculated.

Finally, the correction factor for a given egg stage at a given plankton tow was calculated, by interpolation, as the correction factor at the mid-point of the depth layer asociated with that egg stage.

APPENDIX 2: STRATUM DATA BY SUBSURVEY

Table 17: Number of stations completed in each of the new strata, by subsurvey, at East Cape and Ritchie Bank

						Subsurvey
	Stratum	1	2	3	4	All
East Cape:	1	3	0	0	0	3
	2	5	0	0	0	5
	3	3	5	5	5	18
	4	15	20	10	10	55
	6	3	5	5	0	13
	7	10	10	10	10	40
	8	10	10	10	8	38
	9	5	5	3	0	13
	10	5	5	5	5	20
	11	5	5	10	10	30
	12	3	0	0	0	3
	13	3	0	0	0	3
	15	0	0	5	5	10
	16	5	7	6	8	26
	17	0	3	2	5	10
	18	10	8	4	0	22
	19	0	2	3	0	5
Ritchie Bank:	31	0	5			5
	32	11	10			21
	33	4	0			4
	34	0	2			2
	35	20	15			35
	36	0	3			3
	37	0	5			5
	38	7	0			7
	39	1	2			3
	40	4	0			4

Table 18: Abundance (millions of eggs) by egg stage and subsurvey for East Cape and Ritchie Bank using "straight" and "curved" correction factors

						"straight"					"curved"
	Egg stage	1	2	3	4	All	1	2	3	4	All
East Cape:	A	1 924	382	115	211	668	2 442	400	183	469	887
	B	2 341	1 579	3 030	517	1 884	2 886	1 658	6 146	1 105	2 790
	8	751	132	23	3	254	888	135	43	6	297
	9	554	62	8	43	181	649	67	14	95	220
	10	250	171	994	779	530	299	175	1 495	1 617	821
	11	290	556	481	82	367	352	535	775	147	463
	12	690	3 055	552	69	1 150	922	2 731	838	116	1 206
	13	353	4 318	3 070	2 051	2 504	448	3 982	3 201	3 169	2 828
	14	841	207	933	1 483	942	1 074	169	1 048	2 120	1 201
	15	589	76	244	449	367	676	65	225	571	413
Ritchie Bank:	A					1897					2750
	B					726					1042
	8					37					38
	9					81					82