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**Spawning fraction and maturity ogive estimates of female hoki, western stock, 1992 and 1993**

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## Spawning Fraction and Maturity Ogive Estimates of Female Hoki, Western stock, 1992 and 1993

M. Vignaux, M.E. Livingston, & K.A. Schofield,

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### 1. Executive Summary

Trawl surveys of hoki in the Sub-Antarctic area were carried out in May 1992 and 1993 to estimate the proportion of females of each age that would spawn in the coming spawning season (July–August) based on a histological analysis of gonad samples and ageing data. Comparisons were made of numbers of fish at age between these surveys and surveys in November–December 1991 and 1992 to estimate migration before May.

Females were classified as spawners if the most developed oocytes in their gonads had moved beyond the resting (perinucleolar) stage, and begun secondary development (yolk vesicle formation). Secondary development begins before the gonads can be seen macroscopically to develop from the resting to the maturing stage.

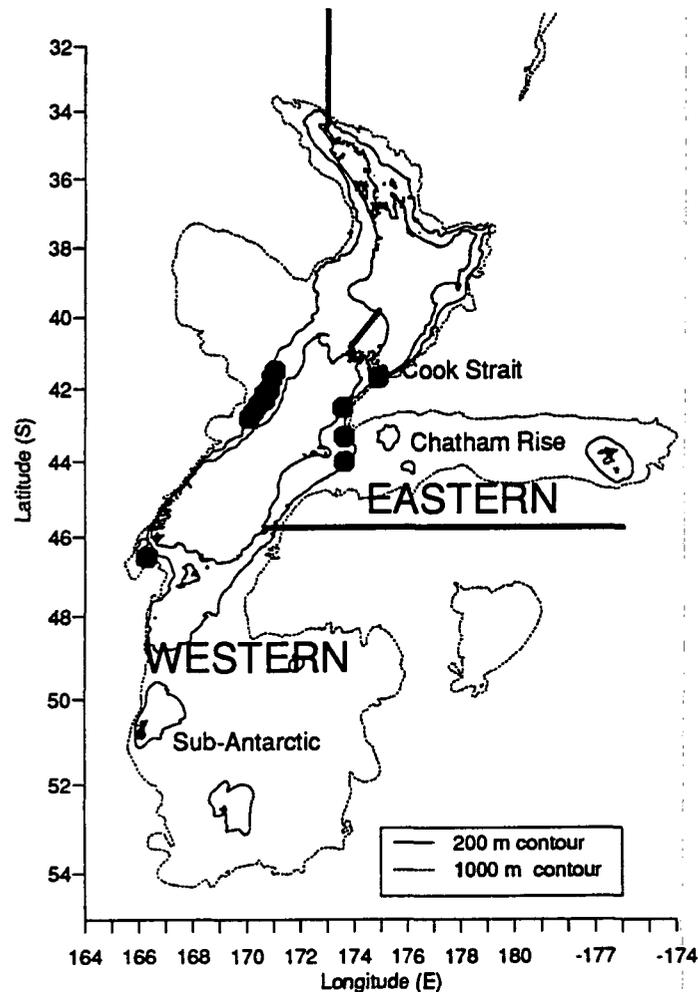
A maturity ogive was estimated for both 1992 and 1993 for most ages above 5 years. Apart from age 5 fish, which appeared more likely to spawn in 1993 than 1992, the two maturity ogives are very similar, and reach the same level for fish of age 8 and above.

The results of this study indicate that 65% (standard error (*s.e.*) of 3%) of females of age 6 and over that were in the Sub-Antarctic area in May 1992 would spawn in winter 1992, compared with 61% (*s.e.* 2%) in 1993. If the estimated number of fish that had already migrated from the Sub-Antarctic area to spawn between December 1991 and May 1992 are included as spawners then up to 78% (*s.e.* 3%) of mature females would have spawned in winter 1992. Similarly, 77% (*s.e.* 4%) of mature females would have spawned in winter 1993.

### 2. Introduction

The current TACC for hoki (202 155 t) applies to all parts of the EEZ (HOK 1) except around the Kermadec Islands (HOK 10). However, in recent years, modelling for stock assessment has treated the fishery as two separate stocks, or fishery units, and estimated the yield for each unit separately (Sullivan & Cordue 1992, 1994, Sullivan *et al.* 1994). The two units (Figure 1) are as follows.

1. A western stock in which the adult population spends most of the year in the Sub-Antarctic area, migrating north to Puysegur Bank and the west coast of the South Island to spawn in winter.



**Figure 1:** Map showing the western and eastern hoki stocks with the known spawning grounds shown as the black areas.

2. An eastern stock which resides most of the year on the Chatham Rise, migrating west to the east coast of the South Island and Cook Strait to spawn in winter.

Although there is no genetic basis for this split, support for treating the two units separately comes from morphometric and growth rate differences found between Cook Strait and west coast spawners which match similar differences between Chatham Rise and Sub-Antarctic area fish (Livingston *et al.* 1992).

Data collected from trawl surveys from 1975 to 1992 have identified the Chatham Rise as the only significant nursery ground for juvenile hoki (Livingston *et al.* 1992). As there do not appear to be any other major sources of juvenile hoki for the western stock, the current view is that hoki recruit to the western stock from the Chatham Rise as they reach 4–5 years old.

From trawl surveys carried out in the Southland and Sub-Antarctic areas in July–August and November–December 1990 it was estimated that the recruited biomass of hoki present in winter and the recruited biomass present in summer was in the ratio 1:2.05 (Hurst & Schofield 1991). Therefore it seems that not all fish of recruited size leave to spawn every winter. This may be due to a shallow maturity ogive (i.e., some fish do not spawn until they are quite old, but then spawn every year), or to non-annual spawning among fish which have already recruited to the fishery, or to some combination of these two hypotheses.

Because such a high proportion of hoki appear not to spawn in a given year, recent modelling for the hoki stock assessment (Sullivan *et al.* 1994) has assumed that there is a proportion,  $p$ , which is less than 100% even for mature fish, that will spawn in a particular year. A maturity ogive which reaches 100% for females age 6 and above was then estimated from the relative catches of male and female hoki of ages 4 and 5 in the 1991 and 1992 west coast fisheries (Sullivan & Cordue 1994). The maturity ogive is multiplied by the proportion spawning  $p$  of mature fish, to give the proportion of fish of each age that will spawn in a given year. Hence, if 42.9% of females of age 5 are assumed to be mature and  $p\%$  of mature fish will spawn, then  $p\%$  of 42.9% of age 5 females will spawn in a given year.

The trawl surveys of the western stock in winter and summer 1990 suggested that  $p$  was most likely to be between 60 and 75% (Hurst & Schofield 1991). Therefore proportion spawning became an important factor in the model of the western stock. To improve our estimate of  $p$  for the western stock, trawl surveys of hoki in the Sub-Antarctic area were carried out in May 1992 and 1993. Comparisons of numbers of fish-at-age between these surveys and surveys in November–December 1991 and 1992 were made to estimate migration before May.

This report describes the histological basis that was used to distinguish female spawners from non-spawners, and how the survey data were used to estimate a maturity ogive and the proportion spawning  $p$  of mature females of the western stock.

This project aimed to distinguish female spawners from non-spawners using histological methods to determine the threshold between the two. The data were then used to estimate a maturity ogive and the proportion spawning of mature females in the western stock.

### 3. Methods

In order to estimate a maturity ogive and  $p$  for the western hoki stock, it is necessary to:

1. develop a method for distinguishing spawners from non-spawners;
2. survey hoki in summer when female fish are mostly resident in the Sub-Antarctic area and resting, and again in autumn when their gonads have begun to develop but migration for spawning has not begun; and
3. develop a method to analyse the data by age class.

### 3.1 Trawl surveys

Two sets of surveys were carried out; December 1991 and May 1992, December 1992 and May 1993 (Table 1). The survey area incorporated depths of 300–800 m in the Southland and Sub-Antarctic areas, excluding the Bounty Platform. The random trawl survey design used in the December 1991 and 1992 surveys (Chatterton *et al.* 1993, Chatterton & Hanchet 1994) was also used in the May 1992 and 1993 surveys (Schofield & Livingston 1994a, 1994b) except that the Bounty Platform stratum (which was not sampled in the December 1991 survey) and one stratum at Puysegur in 800–1000m depth (which contributed less than 0.1% of total hoki biomass for the December 1991 survey) were omitted. These strata were also omitted from analyses of the December surveys for the purposes of this study. The surveys used a two-phase design, which aimed to sample from all strata in the first phase, and to return in a second phase to those strata found to have a high coefficient of variation, to improve the sampling (Francis 1984).

The number of stations in the May surveys was considerably less than in the December surveys because of fewer daylight hours (*see* Table 1). The gear and its configuration and the sampling procedures were the same in each of the surveys (Hurst *et al.* 1992).

**Table 1: Survey dates and number of stations used in this study**

Survey	Survey reference	Dates	No. of	
			Stations	Strata
TAN9105	December 1991	12.11.91–23.12.91	150	15
TAN9204	May 1992	17.4.92–21.5.92	90	15
TAN9211	December 1992	14.11.92–22.12.92	155	15
TAN9304	May 1993	1.5.93–4.6.93	100	15

The length frequency distribution and the total numbers of fish were scaled up to the total stratum area using the Trawlsurvey Analysis Program as described by Vignaux (1994). The scaling was done assuming a catchability and vulnerability of 1.0 in all surveys. As this was unlikely to be true, the numbers of fish were always used in a relative sense only.

### 3.2 Ageing

To obtain an ogive of proportion spawning at age, and to identify fish in the age 6+ age class, otoliths from each fish in the histological samples from the May surveys were aged using the validated ageing method described by Horn & Sullivan (1994). These data were also used to develop age-length keys for the two May surveys. Where there were no fish in the sample of a given length, the age-length key was interpolated using nearby values of age.

### 3.3 Histology

In developing a methodology to distinguish spawning hoki from non-spawning hoki we classified ovaries into the stages given by West (1990). Ovaries were classified according

to the most advanced oocyte present in the ovary. A summary of these stages (as given by West) is as follows:

**Chromatin nucleolar stage.** This is a stage of primary growth. The oocyte is surrounded by a few follicle cells with a large nucleus surrounded by a thin layer of cytoplasm. The nucleus has a single large nucleolus.

**Perinucleolar stage.** As oocyte growth begins the nucleus enlarges and multiple nucleoli generally appear at its periphery. Late perinucleolar oocytes may have vacuoles in the cytoplasm which usually characterise the yolk vesicle stage.

**Yolk vesicle (cortical alveoli) formation.** This stage is characterised by the appearance of large numbers of yolk vesicles in the cytoplasm. They increase in size and number to form several peripheral rows. The chorion often appears at this stage.

**Vitellogenic (yolk) stage.** Small yolk granules which gradually enlarge until they form fluid filled spheres are typical of this stage. The spheres may eventually fuse to form a continuous mass of fluid yolk.

**Ripe (mature) stage.** This stage prepares the oocyte for its final release into the ovarian lumen. It starts by the peripheral migration of the nucleus and the disintegration of its membrane.

Hoki ovaries have 'group synchronous' development with a single group of oocytes developing to maturity in the spawning season (our unpublished data). Hoki spawn in winter, with the females gaining up to 40% of their total body weight as their gonads ripen (Kuo & Tanaka 1984). For the remainder of the year, the gonads are small, weighing less than 1% of total body weight. Ovaries begin to ripen in April before the female hoki migrate to their spawning grounds (van den Broek *et al.* 1981, Kuo & Tanaka 1984).

Hoki ovaries are routinely staged macroscopically during research surveys and by scientific observers on commercial vessels. A summary of these stages of macroscopic gonad development is as follows:

**Immature/resting (Stage 1).** The ovaries are small (< 5 cm long, < 0.5 cm in diameter) and translucent and have thin walls. Immature ovaries are clear; resting ovaries are lightly speckled inside.

**Maturing (Stage 2).** The ovaries are swollen with oocytes that are opaque and have a creamy/pink colour. The ovary walls are thin with numerous blood vessels.

**Ripening (Stage 3).** The ovaries are swollen and hyaline oocytes are present within the creamy/pink egg mass.

**Running ripe (Stage 4).** The ovaries are swollen, making up to 40% of the total body weight. Hyaline oocytes flow freely out of the ovary under very light pressure.

**Fully spent (Stage 5).** The ovaries are no longer swollen, and have a deep purple or red colour. The ovary walls are thick, but flaccid.

Macroscopic stages 1 and 2 probably incorporate West's (1990) chromatin nucleolar, perinucleolar, and yolk vesicle stages, and possibly the early vitellogenic stage. To distinguish the new season's spawners from non-spawners, histological sectioning of individual ovaries is required, as the macroscopic development of the ovary does not enter Stage 3 until the oocytes are much further developed. We tested this assumption by comparing macroscopic stages with the histological assessment.

In December 1991 and May 1992 whole gonads from biological samples were preserved in 10% buffered formalin. In December 1992 and May 1993 the gonads were sectioned at sea and preserved in 8% buffered formalin. Histological sections from each gonad were cut and stained using standard H & E preparations.

Histological sectioning shows that during the resting phase hoki ovaries contain large numbers of primary oocytes. Like other teleosts, the oocytes at this time are small and are not developed beyond the perinucleolar stage. Many of the oocytes had vacuoles scattered through the cytoplasm, characteristic of late perinucleolar, early yolk-vesicle stage (Figure 2). Secondary growth, usually signalled by the proliferation of cortical alveoli, and the appearance of oil droplets around the nucleus begins to occur by late April or early May (Figure 3). Yolk granules are more visible in the oocytes of the more developed ovaries (Figure 4). By July, hoki on the spawning grounds have fully mature ovaries and have begun to spawn. Fish remaining in the Sub-Antarctic area in July are largely undeveloped, although there are some, particularly in the Auckland Islands area, which have maturing gonads (Hurst & Schofield 1991). The oocytes would be vitellogenic under the staging system above.

To estimate the spawning fraction in a given year, the hoki in the Sub-Antarctic area should ideally be sampled after secondary oocyte growth has begun (i.e., entering the yolk-vesicle or later stage) but before the fish migrate away to their spawning grounds. Because hoki arrive at their spawning grounds from the end of June, we chose May as the latest time to survey them in the Sub-Antarctic area (*see* Table 1).

During the summer resting phase, most ovaries contained oocytes that could be classified as either late perinucleolar or early yolk vesicle stage (*see* Figure 2). By autumn, though, a significant change in oocyte stage had occurred with many ovaries containing cortical alveoli organised into a ring structure, increased oocyte size, and oil droplets forming around the nucleus. As the oocyte stage observed in summer appeared to be a natural holding point in development, we classified such fish as perinucleolar. When we saw the same development in fish in the autumn surveys they were classified as non-spawners (Figure 5). Only those fish with a proliferation of cortical alveoli and oil droplets beginning to form around the nucleus were classified as being at or beyond the yolk vesicle stage, and therefore counted as spawners for the coming season.

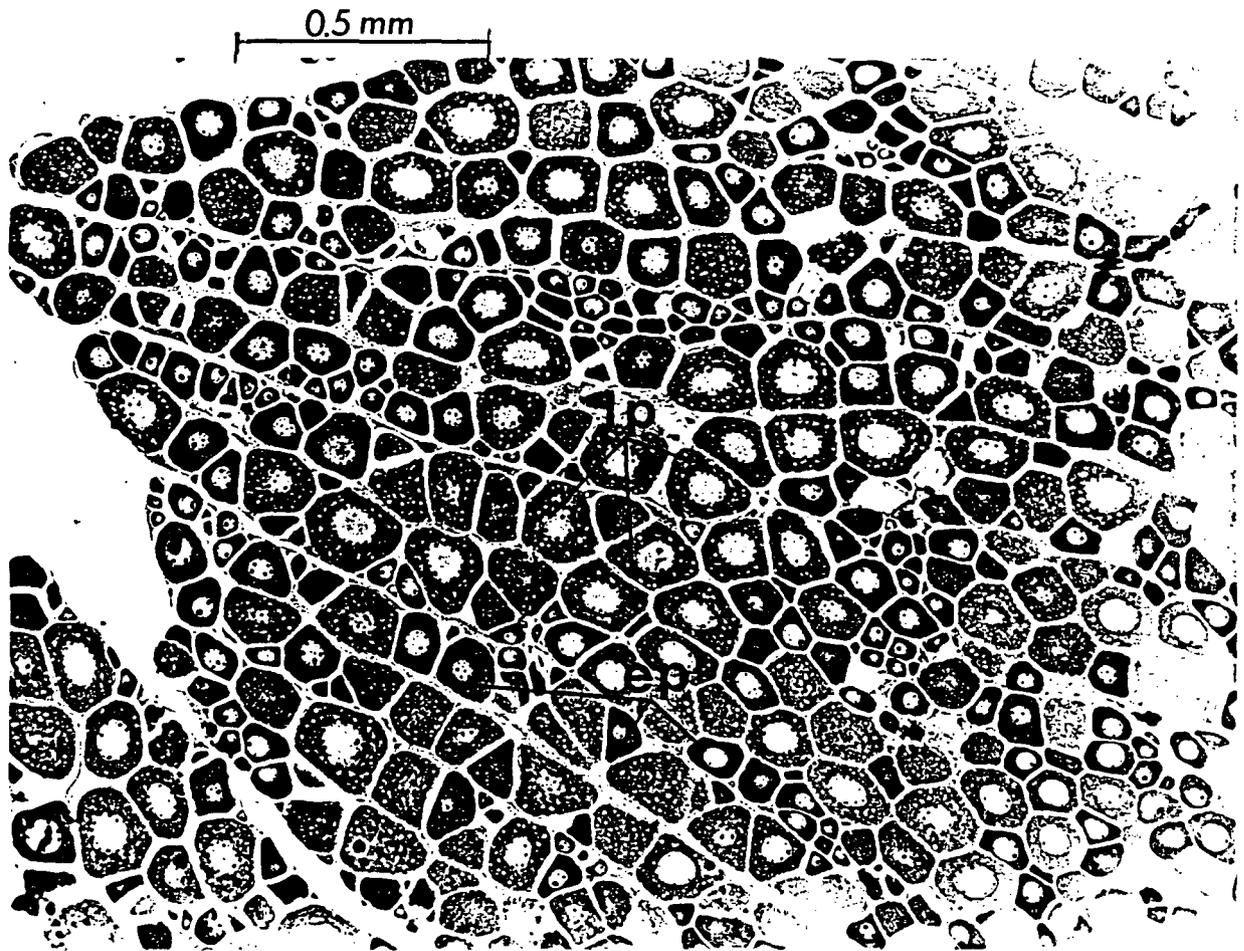


Figure 2: Resting ovary with oocytes in the late perinucleolar stage, December 1991.

ep = early perinucleolar stage oocyte

lp = late perinucleolar stage oocyte (some yolk vesicles present)

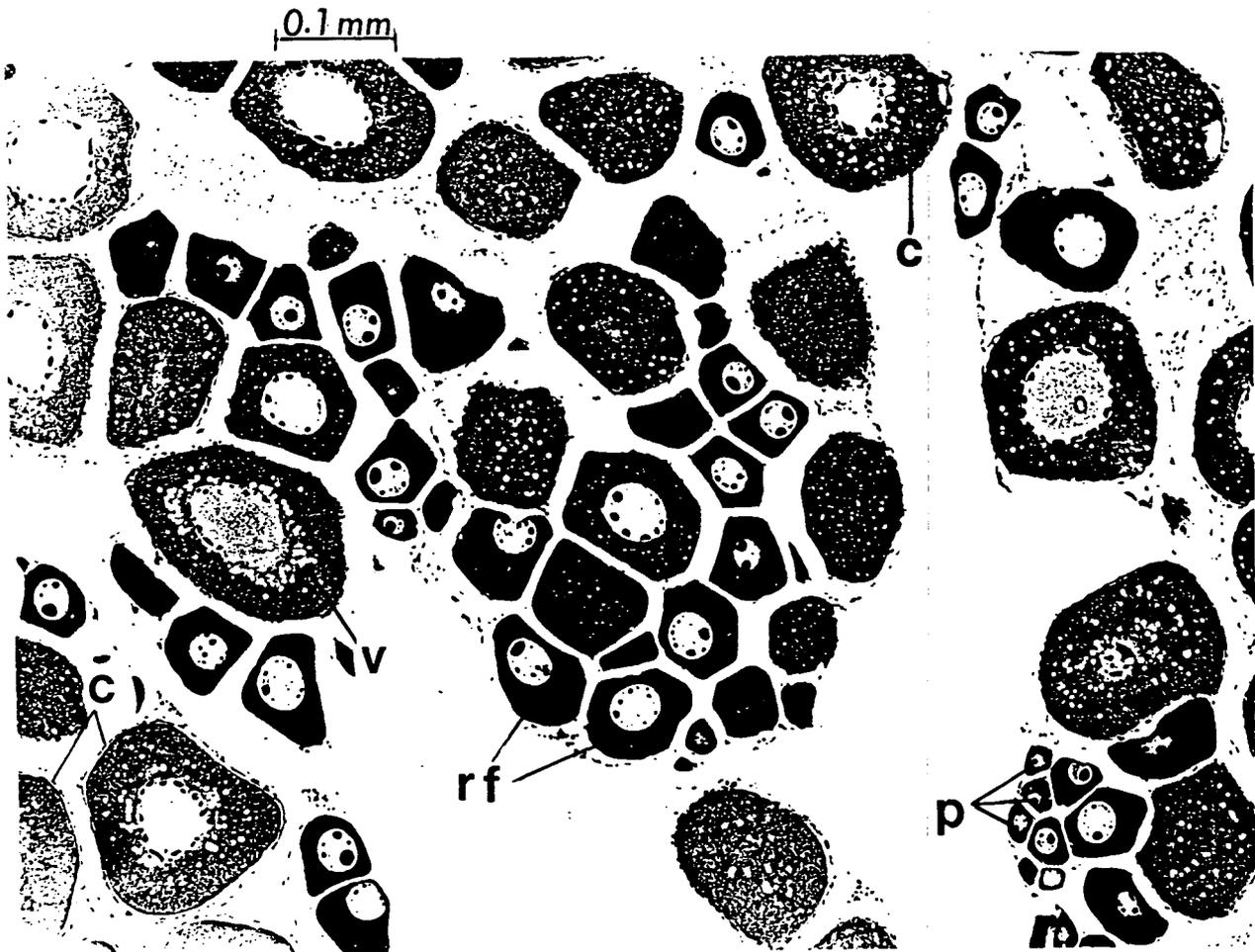


Figure 3: Histological sample from May 1993 showing some oocytes that had developed into the yolk vesicle stage. Note the circumnuclear distribution of the oil droplets beginning to form.

c = chorion

p = primary oocytes at chromatin nucleolar stage

rf = non-developing reserve fund oocytes at perinucleolar stage

v = vesicle ring around nucleus of yolk vesicle stage oocyte

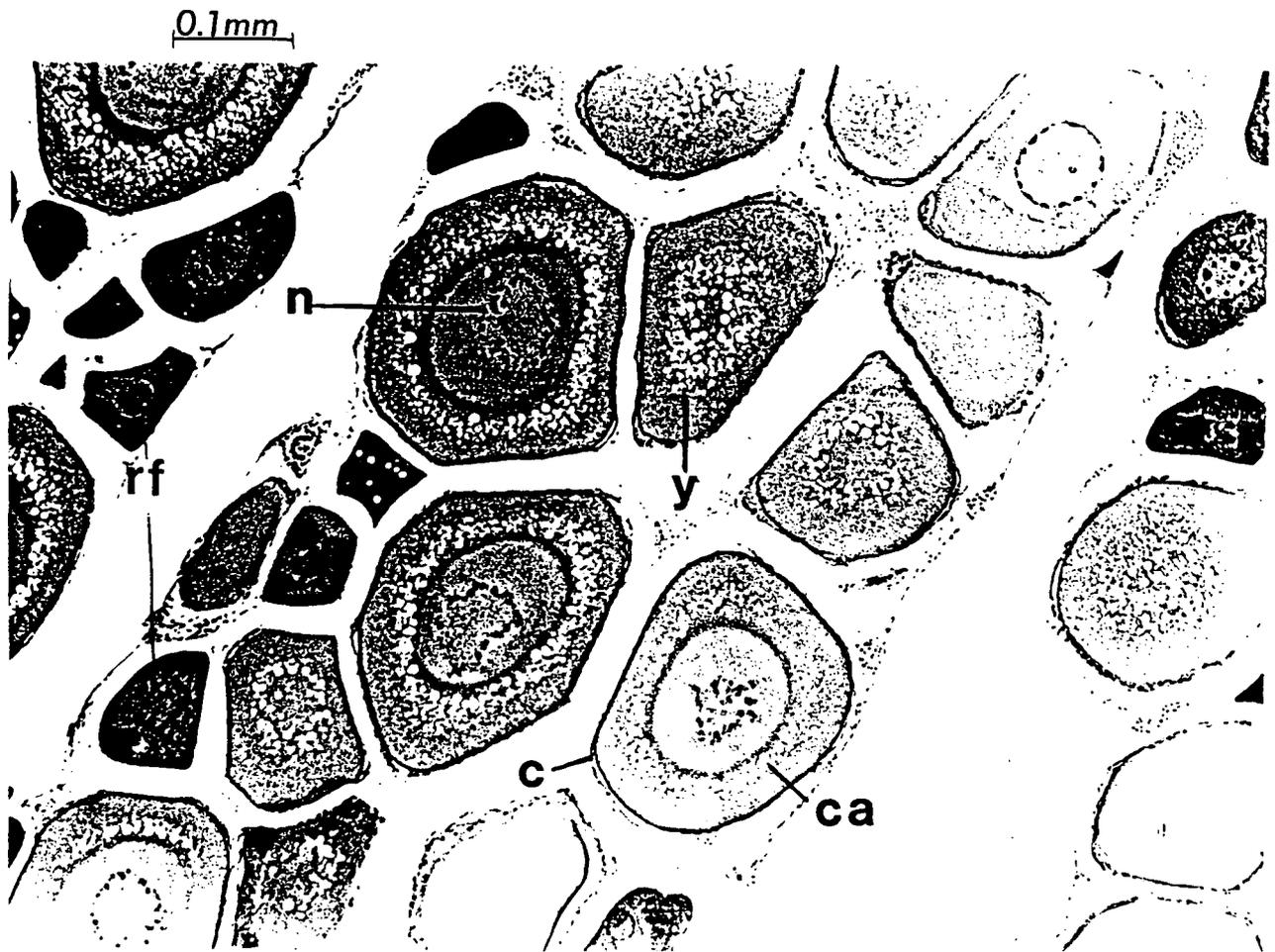


Figure 4: Histological sample from May 1993 showing oocytes in the early vitellogenic stage, with some yolk granules in the cytoplasm.

c = chorion

ca = cortical alveoli with oil droplets

n = nucleoli in a ring inside nucleus

rf = non-developing reserve fund oocytes at perinucleolar stage

y = yolk granules developing in cytoplasm

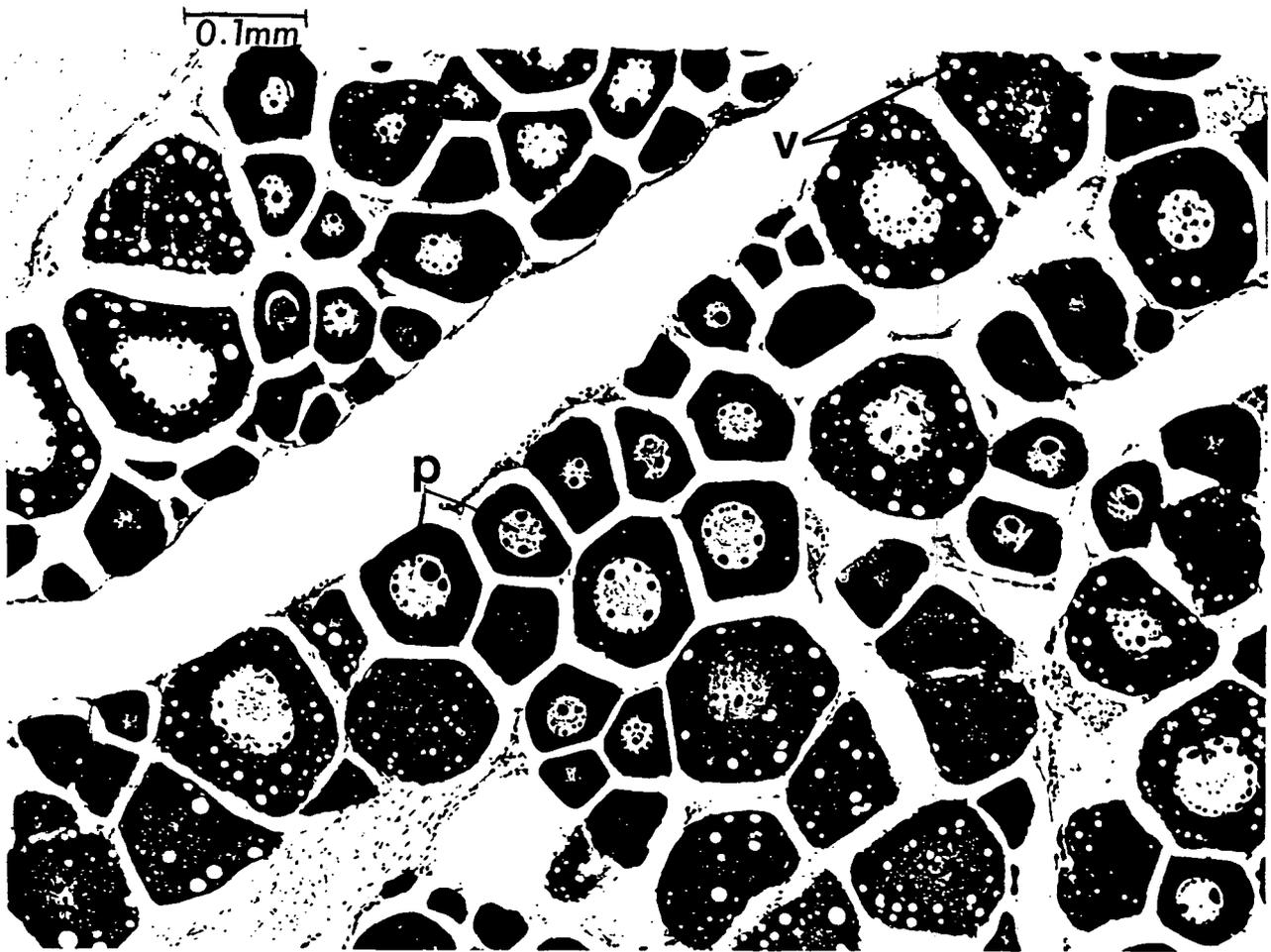


Figure 5: Histological sample from May 1993 showing non-developing ovary classified as perinucleolar stage.

p = perinucleolar stage oocytes

v = yolk vesicles present in perinucleolar oocytes

### 3.4 Analysis

#### 3.4.1 Proportion spawning by age class

The proportion of fish at each age that would spawn in each stratum was estimated from the aged histological samples. The number of fish at each age in each stratum was estimated from the age-length key and the length frequency distribution in the stratum. For each age class the total number of fish spawning was therefore estimated from the proportion spawning and the number of fish in each stratum.

The standard error of these estimates was estimated using a resampling technique. In each stratum, a sample was selected (with replacement) from the actual sample, of the same size as the actual sample. Ageing error was simulated by adding or subtracting up to 2 years to each of the ages according to the probabilities given in table 7 of Horn & Sullivan (1994). The age-length key and proportion spawning were calculated from the combined sample of the 15 strata. This process was repeated 1000 times. The standard error of the estimates was estimated from the standard deviation of the values in 1000 replicates.

#### 3.4.2 Measured proportion spawning of mature fish

The proportion spawning for mature fish ( $p_+$ ) can be estimated using the method described above, but considering all adult fish as a single plus group.

However, if some fish had already left the Sub-Antarctic area to spawn before the survey in May, they should presumably be counted as spawning fish. This means that the measured proportion spawning of mature fish ( $p_+$ ) is an underestimate of the true proportion spawning  $p$  as

$$p_+ = \frac{s}{s + ns} \leq \frac{s + g}{s + ns + g} = p \quad (1)$$

where  $s$  is the number of spawners in the Sub-Antarctic area in May,  $ns$  is the number of non-spawners in the Sub-Antarctic area in May,  $g$  is the number of fish that had left the Sub-Antarctic area to spawn before May.

If we define a migration ratio

$$x = \frac{g}{s + ns} \quad (2)$$

to be the ratio of the number of fish which have gone to spawn to the number of fish (both spawners and non-spawners) that are still in the survey area when the second survey is done, then

$$p = \frac{s + g}{s + ns + g} = \frac{p_+ + x}{1 + x} \quad (3)$$

where  $\frac{s}{s+ns}$  is the measured proportion spawning of mature fish and  $p = \frac{s+g}{s+ns+g}$  is the true proportion spawning. Thus  $p$  equals  $p_+$  when  $x$  is zero, and increases towards an asymptote of 1 when  $x$  is very large.

The migration ratio,  $x$ , cannot be estimated very precisely, as both trawl surveys were subject to experimental error, and an unknown number of fish will have died naturally or been caught between December and May. But to get the best estimate of  $x$ , the numbers of adult fish in the Sub-Antarctic area in December and May were estimated from the total numbers of fish in the surveys and the proportion that were in the adult (age 6+) age group. The age distribution in the May survey was estimated from the length frequency distribution and the age-length key calculated from the aged sample. As there was no age-length key for the December surveys, an age-length key from the spawning fishery the previous July was applied to the length frequency distribution in December (because there is less growth between July and December than between December and May).

In determining the number of fish that moved out of the Sub-Antarctic area before the May surveys, it is necessary to account for fish that died between December and May. Five months of natural mortality was applied to the number of fish observed in the December surveys to estimate the number of fish that would be expected in the May surveys. The catch taken in the Sub-Antarctic area between December and May in these 2 years was only 10 595 t in 1992 (8% of the total estimated catch on the western stock in the 1991–92 fishing year) and 8339 t in 1993 (7% of the total), so fishing mortality was assumed to be negligible.

The discrepancy between the number of fish expected in the May survey and the number observed was the maximum number of fish that could be considered to have left the Sub-Antarctic area to spawn. This number was converted to a fraction  $x$  of fish in the Sub-Antarctic area in May using Equation 2, and the true proportion spawning  $p$  was calculated using Equation 3 and the value of  $p_+$  as calculated in Section 3.4.1.

Standard errors of these numbers were calculated using a resampling procedure which included the uncertainty about the total number of fish in the December and May surveys and the uncertainty in the age-length keys.

**Estimation procedure for the measured proportion spawning for mature fish**  
The estimation procedure for the measured proportion spawning of mature fish is as follows.

1. The total number of fish in the Sub-Antarctic area in December,  $N_1$  was selected from a normal distribution with mean equal to the estimated value for this survey and with standard deviation equal to the standard error of this estimate (Vignaux 1994).
2. This number of fish was distributed over the length frequency distribution from that December survey (assumed to be known exactly)
3. An age-length key (including ageing error) was generated by sampling with replacement from the fish in the age-length sample from the spawning fishery in the previous July.
4. This age-length key was applied to the December length frequency distribution to estimate the number of fish age 5+ in December,  $n_1$ .

5. The number of fish of age 6+ expected to be alive in May was calculated by applying  $M$  to  $n_1$ , as  $n_1 e^{-M5/12}$
6. The total number of fish in the Sub-Antarctic area in May,  $N_2$  was selected from a normal distribution with mean equal to the estimated value for this survey and with standard deviation equal to the standard error of this estimate
7. This number of fish was distributed over the length frequency distribution from that May survey (assumed to be known exactly)
8. An age-length key (including ageing error) was generated by sampling with replacement from the fish in the age-length sample.
9. This age-length key was applied to the May length frequency distribution to estimate the number of fish age 6+ in the Sub-Antarctic area in May,  $n_2$
10. The number of fish apparently missing is estimated as

$$n_m = n_1 e^{-M5/12} - n_2$$

11. Taken as a fraction of the number  $n_2$  in the Sub-Antarctic area in May,  $x$  (the migration ratio) is estimated by

$$x = \frac{n_m}{n_2}$$

12.  $p_+$  is calculated using the simulated age-length key and histological sample as described in Section 3.4.1.
13. Hence  $p$  is estimated as

$$p = \frac{p_+ + x}{1 + x}$$

This process was repeated 1000 times. The standard errors of each of the values was calculated from the standard deviation of the distribution of the 1000 values.

## 4. Results

### 4.1 Trawl surveys

The surveys were all completed successfully, and were described by Chatterton *et al.* (1993), Chatterton & Hanchet (1994), and Schofield & Livingston (1994a, 1994b).

The total scaled number ('000) of female fish in each of the surveys was:

Survey	Stations	Number of fish ( <i>c.v.</i> )
December 1991	150	38 563 (0.09)
May 1992	90	26 768 (0.09)
December 1992	155	34 792 (0.07)
May 1993	100	24 450 (0.16)

The number of fish observed in May is clearly less than the number observed the previous December. While it is possible that there are systematic changes in catchability or vulnerability between December and May, it is assumed that some fish have already migrated away from the Sub-Antarctic area before the May survey.

In December 1991, 56% of adult females (over 50 cm) were in strata west of 170° E. In May 1992, 59% were west of this line. In December 1992, 49% were in the west and in May 1993 68% were in the west. These figures suggest that there had been some net movement of fish from the east to the west between December and May, at least in 1993, which supports the assumption that fish were already migrating to spawn in May.

Length frequency distributions for the two May surveys are in Figure 6. The number of fish of each age in each stratum was estimated from the age-length key and the length frequency distribution in the stratum for the May 1992 and 1993 surveys (Tables 2 and 3).

There were 541 fish in the histological sample in May 1992 and 1 136 fish in the sample in May 1993 (Tables 4 and 5). In 1992 stratum 1 was not sampled and female fish from every second station in the other strata were sampled. In 1993 female fish from every station in all 15 strata were sampled.

#### 4.2 Ageing

Otoliths from each fish in the histological samples from the May 1992 and May 1993 surveys were aged using the validated ageing method described by Horn & Sullivan (1994) (see Tables 4 and 5). There were very few young fish in most strata, and limited numbers of fish in the 1986 cohort, which is known to be very small (Horn & Sullivan 1994). This cohort appears as age 6 fish in 1992 and age 7 fish in 1993. Although fish were aged up to a maximum age of 19 years, they are combined here into a plus group of age 10 and above. These data were also used as age-length keys for the two May surveys (Figure 7).

Where there were no fish in the sample of a given length, the age-length key was interpolated using nearby values. Thus in the 1992 key, fish up to 57 cm were assigned age 2, fish of 59 and 60 cm were assigned age 4, fish of 64 cm were divided equally between ages 4 and 5, and fish of more than 100 cm were placed in the plus group. In 1992 there were no fish that were assigned age 2. In 1993, fish up to 60 cm were assigned age 2, and fish over 100 cm were placed in the plus group. The age 2 group represents juveniles that cannot be distinguished with the age-length keys.

#### 4.3 Histology

In both December samples, most or all fish were classified as perinucleolar (Table 6). Some fish in the December 1991 sample were classified in the yolk vesicle stage, but most had few vesicles evident around the nucleus and no chorion. In contrast, in the May surveys only 45.4% and 39.7% were in the perinucleolar stages.

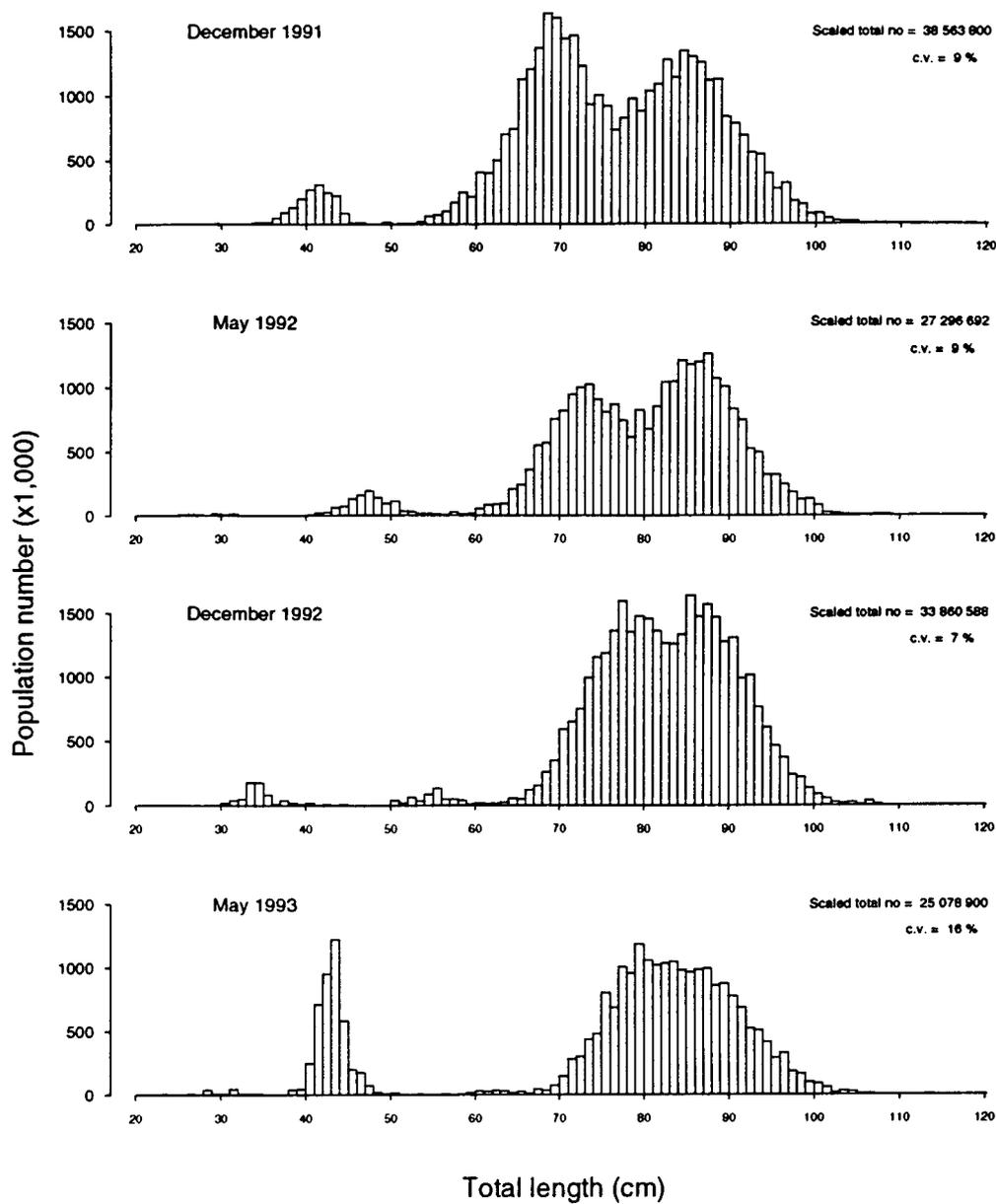


Figure 6: Length frequency distributions for female fish in each of the trawl surveys.

**Table 2: Total number ('000) of female fish from each age and stratum in the May 1992 survey**

Stratum	Age									Total
	2	3	4	5	6	7	8	9	10+	
1	722	0	246	162	2	3	9	0	2	1 145
2	514	0	18	22	0	3	5	4	3	569
3	20	0	53	142	5	16	37	14	10	296
4	0	0	240	1 192	84	268	787	392	454	3 418
5	0	0	71	285	25	82	243	129	178	1 014
6	5	0	362	792	37	83	196	65	41	1 580
7	0	0	24	262	29	92	229	86	63	785
8	0	0	208	1 216	76	223	555	314	324	2 915
9	0	0	219	1 050	71	232	614	314	307	2 807
10	0	0	42	353	41	174	516	268	276	1 671
11	0	0	43	487	59	227	705	437	562	2 520
12	0	0	9	105	22	119	449	345	534	1 583
13	0	0	153	810	80	293	863	475	528	3 201
14	0	0	135	717	49	169	457	226	220	1 972
15	0	0	26	271	27	130	388	207	242	1 291
Total	1 260	0	1 849	7 865	606	2 113	6 053	3 277	3 743	26 768

**Table 3: Total number ('000) of female fish from each age and stratum in the May 1993 survey**

Stratum	Age									Total
	2	3	4	5	6	7	8	9	10+	
1	3 130	63	49	211	212	4	15	34	41	3 760
2	63	4	2	6	7	0	1	3	2	89
3	88	15	47	290	268	8	36	66	48	865
4	394	14	36	364	608	24	115	263	321	2 140
5	0	0	11	215	539	20	99	212	180	1 275
6	13	0	7	142	373	13	61	131	100	839
7	0	0	0	56	203	9	46	101	84	499
8	0	0	12	463	993	42	211	512	488	2 719
9	0	6	36	673	1 804	78	383	865	638	4 484
10	30	0	7	139	368	19	89	213	209	1 074
11	0	0	0	34	305	28	165	486	646	1 664
12	0	0	0	89	371	24	152	409	482	1 528
13	0	0	0	53	278	31	149	422	455	1 388
14	0	0	4	127	361	18	102	235	199	1 045
15	0	0	0	88	356	23	112	265	236	1 081
Total	3 719	101	210	2 949	7 047	340	1 737	4 218	4 129	24 450

**Table 4: Number of female fish of each age in each stratum in the May 1992 histological sample**

Stratum	Age									Total
	2	3	4	5	6	7	8	9	10+	
1	0	0	0	0	0	0	0	0	0	0
2	3	0	3	4	0	1	1	0	1	13
3	0	0	0	7	0	0	1	0	1	9
4	0	0	1	11	1	7	11	4	6	41
5	0	0	2	2	0	3	6	5	2	20
6	0	0	0	7	2	0	7	3	5	24
7	0	0	1	7	1	3	5	2	4	23
8	0	0	3	15	0	4	10	11	12	55
9	0	0	7	15	2	0	13	4	4	45
10	0	0	1	16	1	6	17	8	12	61
11	0	0	0	6	1	6	11	6	12	42
12	0	0	0	4	0	5	16	17	16	58
13	0	0	3	10	1	1	7	6	7	35
14	0	0	3	19	0	4	22	13	9	70
15	0	0	0	8	2	4	12	4	15	45
Total	3	0	24	131	11	44	139	83	106	541

**Table 5: Number of fish of each age in each stratum in the May 1993 histological sample**

Stratum	Age									Total
	2	3	4	5	6	7	8	9	10+	
1	0	6	3	8	11	0	3	0	1	32
2	0	2	1	3	13	0	2	4	7	32
3	0	0	0	7	13	0	1	9	5	35
4	0	1	1	13	34	2	5	24	25	105
5	0	0	0	7	18	0	3	8	6	42
6	0	0	0	12	17	1	5	13	14	62
7	0	0	0	4	25	0	7	12	8	56
8	0	0	0	11	49	3	5	14	15	97
9	0	0	1	19	30	1	8	34	23	116
10	0	0	0	11	33	2	3	21	27	97
11	0	0	0	0	19	2	11	15	40	87
12	0	0	0	4	14	4	15	27	43	107
13	0	0	0	3	7	2	9	30	21	72
14	0	0	0	11	33	2	15	27	36	124
15	0	0	0	3	30	0	9	18	12	72
Total	0	9	6	116	346	19	101	256	283	1 136

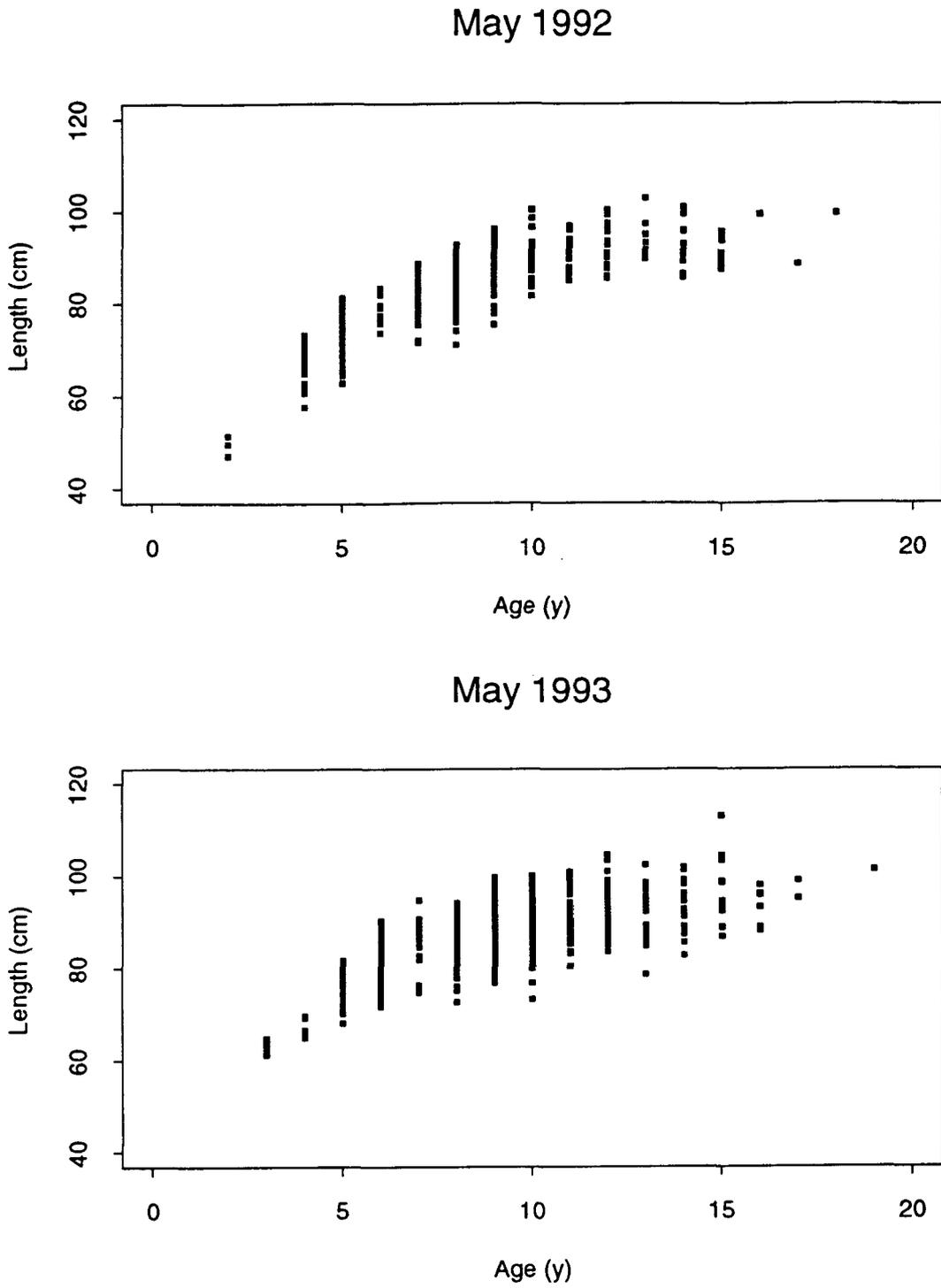


Figure 7: Distribution of length at age of female fish from the May 1992 and 1993 surveys.

**Table 6: Percentages of fish at each histological stage in each survey**

	Dec 1991	May 1992	Dec 1992	May 1993
Chromatin nucleolar	0	0	0	0.1
Perinucleolar	81.0	45.4	100	39.7
Yolk vesicle	19.0	27.1	0	13.6
Vitellogenic	0	27.5	0	43.3
Ripe	0	0	0	3.3
Number in sample	452	541	1 039	1 136

The stage of development of the ovary of each fish in the histological sample was also evaluated macroscopically when caught during the trawl surveys in May 1993. The number of fish at each histological stage and at each stage of macroscopic gonad development are presented in Table 7. In total, of the 237 ovaries classified as maturing, only 2 were classified histologically as non-spawners. However, of the 899 ovaries classified as resting, 450 were classified histologically as non-spawners and 449 as spawners. This confirms that development for spawning is apparent in the oocytes before it becomes apparent macroscopically in the ovaries, and reinforces the requirement for this analysis to be done using the histological data at this time of year.

**Table 7: Numbers of fish at each histological stage and at each stage of macroscopic gonad development (May 1993)**

Histological stage	Macroscopic appearance		Total
	Resting	Maturing	
Non-spawners	450	2	452
Chromatin Nucleolar	1	0	1
Perinucleolar	449	2	451
Spawners	449	235	684
Yolk vesicle	154	1	155
Vitellogenic	295	197	492
Ripe	0	37	37
Grand total	899	237	1 136

The proportion of fish that would spawn in each stratum was estimated from the aged histological samples from the May surveys (Tables 8 and 9). If there were not at least two fish in the stratum of that age, the proportion was not estimated. Although there were many age-stratum combinations where the proportion spawning could not be estimated (mainly for the young fish and for the 1986 cohort), these were not generally in strata which contributed greatly to the biomass of that age class (see Tables 2 and 3).

#### 4.4 Proportion spawning by age class

Tables 10 and 11 show the estimated proportion spawning in each age class in the 1992 and 1993 surveys. Standard errors were estimated using a resampling technique. The tables also show the proportion of fish at each age that were in strata where the proportion

**Table 8: Proportion spawning from each age and stratum from the May 1992 sample (NA indicates that the value could not be calculated)**

Stratum	Age									Total
	2	3	4	5	6	7	8	9	10+	
1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2	0	NA	0.00	0.50	NA	NA	NA	NA	NA	0.28
3	NA	NA	NA	0.57	NA	NA	NA	NA	NA	0.60
4	NA	NA	NA	0.64	NA	0.43	0.91	0.75	0.83	0.67
5	NA	NA	0.50	0.50	NA	1.00	0.67	0.80	0.50	0.71
6	NA	NA	NA	0.57	1	NA	0.43	0.33	0.20	0.70
7	NA	NA	NA	0.29	NA	0.00	0.20	0.00	0.50	0.46
8	NA	NA	0.33	0.13	NA	0.75	0.80	0.64	0.83	0.26
9	NA	NA	0.00	0.53	0	NA	0.77	0.75	0.75	0.56
10	NA	NA	NA	0.19	NA	0.33	0.41	0.50	0.67	0.53
11	NA	NA	NA	0.33	NA	0.83	0.73	1.00	0.58	0.41
12	NA	NA	NA	0.25	NA	0.60	0.94	0.59	0.63	0.67
13	NA	NA	0.00	0.60	NA	NA	0.57	1.00	0.57	0.60
14	NA	NA	0.33	0.53	NA	0.75	0.59	0.38	0.56	0.53
15	NA	NA	NA	0.25	0	0.25	0.67	0.25	0.47	0.42
Total	0	NA	0.13	0.41	0.45	0.54	0.67	0.60	0.60	0.54

**Table 9: Proportion spawning from each stratum and age from the May 1993 sample (NA indicates that the value could not be calculated)**

Stratum	Age									Total
	2	3	4	5	6	7	8	9	10+	
1	NA	0	0	0.50	0.27	NA	0.33	NA	NA	0.28
2	NA	0	NA	0.33	0.38	NA	1.00	0.50	0.71	0.47
3	NA	NA	NA	0.57	0.77	NA	NA	0.89	1.00	0.80
4	NA	NA	NA	0.69	0.76	1.00	0.80	0.88	0.80	0.78
5	NA	NA	NA	0.57	0.83	NA	0.67	0.50	0.67	0.69
6	NA	NA	NA	0.92	0.94	NA	1.00	1.00	0.50	0.85
7	NA	NA	NA	0.25	0.56	NA	0.14	0.75	0.63	0.54
8	NA	NA	NA	0.73	0.51	0.33	0.80	0.64	0.47	0.56
9	NA	NA	NA	0.74	0.46	NA	0.63	0.50	0.87	0.60
10	NA	NA	NA	0.45	0.33	0.50	0.67	0.57	0.59	0.48
11	NA	NA	NA	NA	0.42	1.00	0.64	0.87	0.55	0.60
12	NA	NA	NA	0.25	0.71	0.75	0.60	0.78	0.63	0.66
13	NA	NA	NA	0.33	0.71	1.00	0.56	0.73	0.52	0.64
14	NA	NA	NA	0.36	0.52	0.00	0.67	0.63	0.33	0.48
15	NA	NA	NA	1.00	0.20	NA	0.67	0.78	0.75	0.53
Total	NA	0	0	0.60	0.53	0.63	0.63	0.71	0.60	0.60

spawning could be measured (i.e. had at least two fish in the sample). Where this proportion is less than 50%, the estimate is based on fish from only a small proportion of the population, and should not be used. Where this proportion is less than 66%, the estimate might be considered unreliable.

In 1992 there are enough data to make a reliable estimate of the spawning fraction for ages 5, 7, 8, 9 and 10+, but age 6 (the 1986 cohort) and ages 2, 3, and 4 cannot be estimated as the strata with samples contain less than half of the total number of fish in the survey area. In 1993 there are enough data to make a reliable estimate of the spawning fraction for ages 5, 6, 8, 9 and 10+, but ages 3 and 7 (again, the 1986 cohort) are unreliable and ages 2 and 4 cannot be estimated.

The reliable proportion spawning by age class estimates are shown in Figure 8 for the two surveys. Although there were too few samples to obtain reliable estimates for fish of age 4 and under, it is clear that this proportion would be small. Only 3 of 42 (7%) fish in the sample that were age 4 or younger were classified as spawners. It is therefore likely that the the ogive increases steeply below age 5 before levelling off.

#### 4.5 Measured proportion spawning for mature fish

Sullivan *et al.* (1994) assumed that the proportion spawning increases with age to a constant value of  $p$  for females of age 6 and over. Figure 8 suggests that there may have been some increase in the proportion spawning up to age 8 in 1992, but that in 1993 the proportion spawning did not increase after age 5.

If we assume that any increase after age 6 is not significant, then the asymptotic values of the ogives in Figure 8 represent the measured proportion spawning of mature fish  $p_+$  for adult females in the 2 years 1992 and 1993. Following a procedure identical to that described in Section 3.4.1, but considering only fish aged 6 and over, the proportion spawning of adult females in the survey area was estimated as:

$$1992 p_+ = 0.65 \text{ (s.e. 0.03)}$$

$$1993 p_+ = 0.61 \text{ (s.e. 0.02)}$$

However, the results of the trawl survey (*see* Section 4.1) suggest that some fish had already left the Sub-Antarctic area to spawn before the survey in May, so it was considered necessary to include these fish as potential spawners. The numbers of adult fish in the Sub-Antarctic area in December and May were therefore estimated from the total numbers of fish counted in the surveys and the proportion that were in the adult (age 6+) age group.

Tables 12 and 13 show the estimated true proportion spawning of mature fish based on the measured proportion spawning of mature fish and the estimated number of mature fish that had already left the Sub-Antarctic area.

As there was no age-length key available for the December surveys, the age-length key from the WCSI spawning fishery the previous July (Horn & Sullivan 1994) was used

**Table 10: Estimated total numbers of female fish, numbers of female fish in sampled strata, percentage of female fish in strata covered by sampling, numbers of spawners, proportion spawning, and standard error of proportion spawning, for each age class in the May 1992 survey (NA indicates that the value could not be estimated)**

	Age class								
	2	3	4	5	6	7	8	9	10
Total in survey ( $\times 1000$ )	1 261	0	1 849	7 865	606	2 114	6 053	3 277	3 743
In sampled strata ( $\times 1000$ )	514	0	803	7 704	135	1 484	6 003	3 258	3 728
% in sampled strata	41	NA	43	98	22	70	99	99	100
Spawners ( $\times 1000$ )	0	0	150	3 428	37	842	4 092	2 242	2 389
Proportion spawning	0	NA	0.19	0.44	0.27	0.57	0.68	0.69	0.64
<i>s.e.</i>	NA	NA	0.09	0.05	0.27	0.08	0.05	0.05	0.05

**Table 11: Estimated total numbers of female fish, numbers of female fish in sampled strata, percentage of female fish in strata covered by sampling, numbers of spawners, proportion spawning, and standard error of proportion spawning, for each age class in the May 1993 survey - NA indicates that the value could not be estimated**

	Age class								
	2	3	4	5	6	7	8	9	10
Total in survey ( $\times 1000$ )	3 719	101	210	2 949	7 047	340	1 737	4 218	4 129
In sampled strata	0	66	49	2 915	7 047	185	1 701	4 183	4 088
% in sampled strata	0	65	24	99	100	54	98	99	99
Spawners ( $\times 1000$ )	0	0	0	1 861	3 966	125	1 121	2 889	2 574
Proportion spawning	NA	0.00	0.00	0.64	0.56	0.67	0.66	0.69	0.63
<i>s.e.</i>	NA	NA	NA	0.05	0.03	0.17	0.06	0.03	0.03

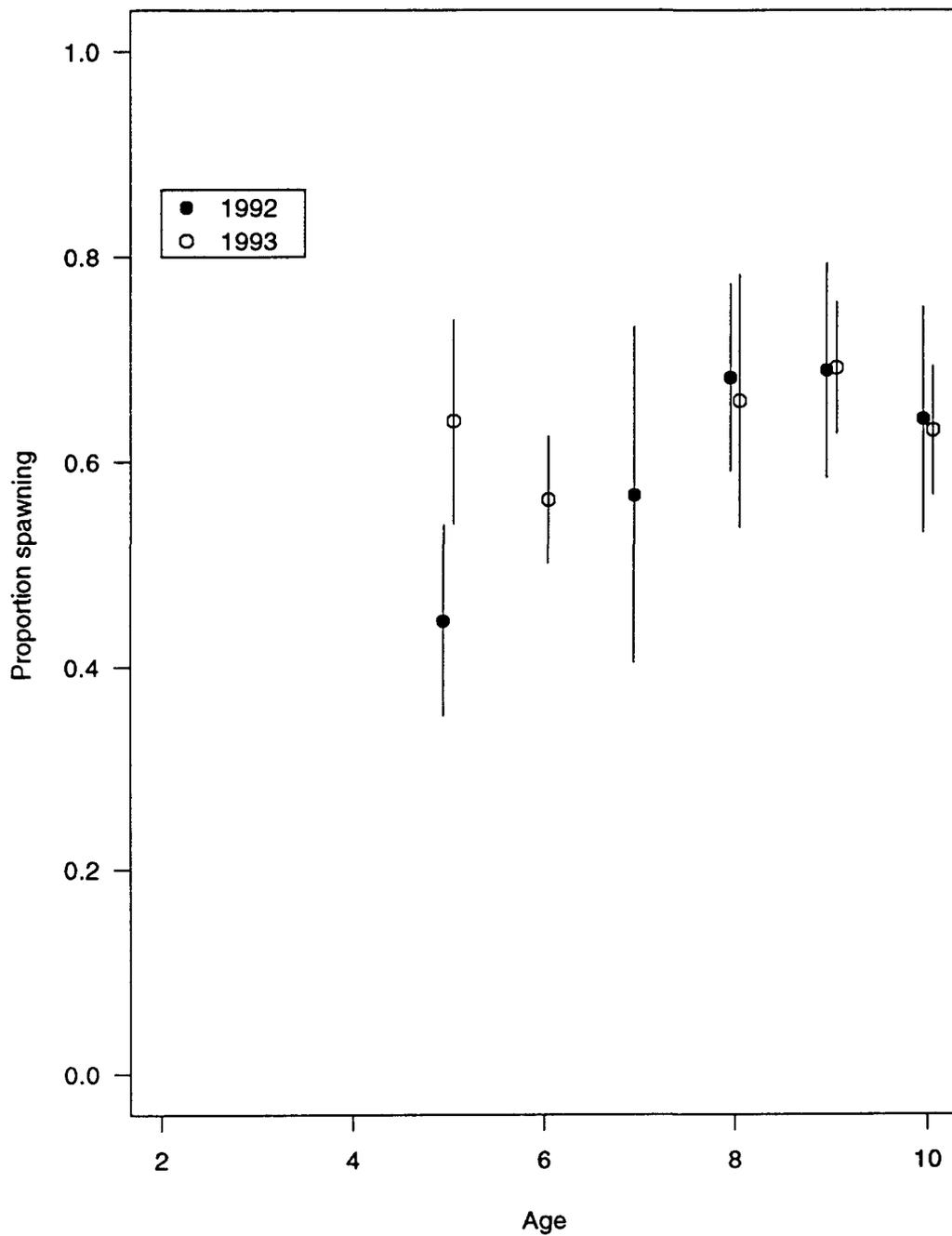


Figure 8: Maturity ogives from 1992 and 1993 surveys. The error bars indicate two standard errors.

**Table 12:** Estimation of true proportion spawning  $p$  of age 6+ fish based on  $p_+$ , the measured proportion spawning, and the number of fish in the plus group in the Sub-Antarctic area in December 1991 and May 1992. The first column gives the estimates based on applying an age-length key (ALK) derived from the July 1991 fishing season to fish in the December 1991 trawl survey. Numbers represent thousands of fish. The standard error of this estimate is given in parentheses. The second column gives the estimates based on applying an ALK derived from the May 1992 trawl survey. Estimates based on values of the natural mortality  $M$  of 0, 0.25 and 0.3 are shown

		Estimate ALK July 91	Estimate ALK May 92
	Observed December 1991	27 157 (2600)	30 549
	Observed May 1992	15 793 (1500)	15 793
$M = 0.25$	Expected May 1992	24 470 (2300)	27 527
$M = 0.25$	Missing May 1992	8 678 (2800)	11 734
$M = 0.25$	Migration ratio	0.55 (0.21)	0.74
$M = 0.25$	Proportion spawning	0.78 (0.04)	0.80
$M = 0$	Expected May 1992	27 157 (2600)	30 549
$M = 0$	Missing May 1992	11 364 (3000)	14 756
$M = 0$	Migration ratio	0.72 (0.24)	0.93
$M = 0$	Proportion spawning	0.80 (0.03)	0.82
$M = 0.30$	Expected May 1992	23 966 (2300)	26 960
$M = 0.30$	Missing May 1992	8 173 (2700)	11 167
$M = 0.30$	Migration ratio	0.52 (0.21)	0.71
$M = 0.30$	Proportion spawning	0.77 (0.04)	0.79

**Table 13:** Estimation of true proportion spawning  $p$  of age 6+ fish based on  $p_+$ , the measured proportion spawning, and the number of fish in the plus group in the Sub-Antarctic area in December 1992 and May 1993. The first column gives the estimates based on applying an ALK derived from the July 1992 fishing season to fish in the December 1992 trawl survey. The standard error of this estimate is given in parentheses. The second column gives the estimates based on applying an ALK derived from the May 1993 trawl survey. Estimates based on values of the natural mortality  $M$  of 0, 0.25 and 0.3 are shown

		Estimate ALK July 92	Estimate ALK May 93
	Observed December 1992	32 176 (2200)	32 421
	Observed May 1993	17 471 (2800)	17 471
$M = 0.25$	Expected May 1993	28 993 (2000)	29 214
$M = 0.25$	Missing May 1993	11 522 (3400)	11 744
$M = 0.25$	Migration ratio	0.66 (0.32)	0.64
$M = 0.25$	Proportion spawning	0.77 (0.04)	0.76
$M = 0$	Expected May 1993	32 176 (2200)	32 421
$M = 0$	Missing May 1993	14 705 (3600)	14 951
$M = 0$	Migration ratio	0.84 (0.35)	0.86
$M = 0$	Proportion spawning	0.79 (0.04)	0.79
$M = 0.30$	Expected May 1993	28 395 (2000)	28 612
$M = 0.30$	Missing May 1993	10 924 (3400)	11 141
$M = 0.30$	Migration ratio	0.63 (0.31)	0.64
$M = 0.30$	Proportion spawning	0.76 (0.04)	0.76

with the length frequency distribution from the December surveys to estimate the age distribution in the December surveys. Comparison of the mean lengths at age in the May surveys with the mean lengths in December (Sullivan *et al.* 1994) and the mean lengths at age in July (Horn & Sullivan (1994)) indicated that there was less growth between July and December than between December and May. For example, the 1990 cohort had mean length 34.5 cm in July 1991, 40.0 cm in December 1991 and 49.3 cm in May 1992. So the previous fishing season's age-length key would be more appropriate than that from the following May. As a sensitivity analysis, the calculations were also made using the age-length key from the survey the following May. These are shown in the second column. Tables 12 and 13 show that this makes little difference to the estimates of  $p$ . The true values are likely, however, to be intermediate between the two estimates in Tables 12 and 13.

The first two rows of Tables 12 and 13 show the estimates of the numbers of female fish in the 6+ age class observed in the December and May surveys. The number expected to have been observed in May (after applying natural mortality to the number observed in December) is compared with the number observed in May to find the number of fish apparently missing. The number missing is expressed as a fraction of the number observed in the May survey to find  $x$ , the migration ratio. The true proportion spawning of mature fish is calculated (from  $x$  and the histological proportion spawning  $p_+$ ) using Equation 3.

These calculations were done with three estimates of the natural mortality,  $M$ , including the best estimate  $M = 0.25$ , and two bounding values  $M = 0$  and  $M = 0.3$ . Tables 12 and 13 show that this makes little difference to the estimate of  $p$ . Standard errors of the estimates were calculated using a resampling technique. They are shown in parentheses.

The best estimate of the true proportion spawning for mature fish in the July 1992 season is 0.78 (*s.e.* 0.04). If the age-length key from May 1992 is used the best estimate is 0.80. If  $M$  is as high as 0.3 or as low as 0, the estimate of  $p$  decreases to 0.77 or increases to 0.80 respectively.

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Figure 9 shows the effect of the estimate of  $x$  on the estimate of  $p$  for 1992 and 1993. In each plot there are three curves for  $p$  as a function of  $x$ . The solid curve is the function given the estimated value of  $p_+$  (0.65 in 1992 and 0.61 in 1993). The two dotted curves are the functions at plus and minus two standard errors of this value.

The solid vertical lines show the value of  $x$  assuming  $M = 0.25$ . The two dashed vertical lines shown are at plus or minus two standard errors of this value. Clearly the value of  $x$  is not at all well known. However, the function is changing slowly over this range, so it is still possible to obtain a useful estimate of  $p$ .

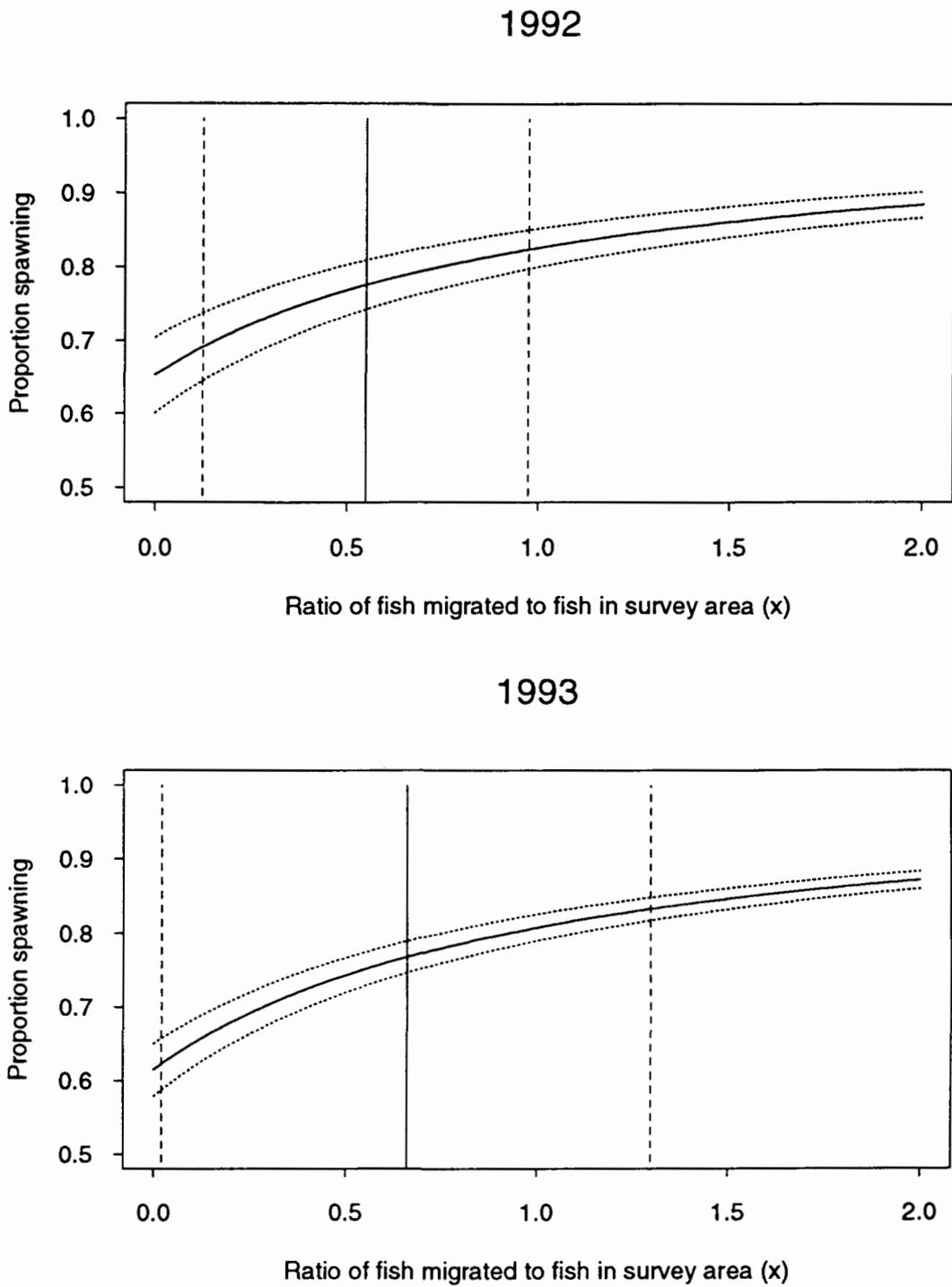


Figure 9: Estimated true proportion spawning ( $p$ ) of age 6+ fish as a function of the fraction of the migration ratio ( $x$ ) in 1992 and 1993.

## 5. Discussion

In both December samples most fish were classified as perinucleolar, i.e., in resting condition. By May, most of these fish had progressed to the yolk vesicle or a later vitellogenic stage. As the perinucleolar stage seemed to be the natural holding stage for fish in the summer, the yolk vesicle stage was taken to be the first stage of secondary development. Although some fish in the December 1991 sample were classified as at yolk vesicle stage, they were at an early stage of development compared to the yolk vesicle stage fish in the May surveys. In the December gonad samples, generally only one or two oocytes were showing signs of vacuole development around the nucleus; in May, gonads which had begun to develop generally had much higher proportions of developing oocytes. The possibility of subdividing the yolk vesicle stage should be investigated.

Gonads developed into the yolk vesicle stage before they were seen (macroscopically) to be maturing. Even for fish in the vitellogenic stage, more than half were classified (macroscopically) as resting. This reinforces the need for histological analysis to determine proportion spawning when the fish are at this stage of development.

There were enough data to estimate a proportion spawning for most ages above age 4, except for the 1986 cohort (age 6 in 1992 and age 7 in 1993). The curves are very similar above age 8, but age 5 fish appear to have been more likely to spawn in 1993 than in 1992.

If we interpret the proportion spawning by age curves as two estimates of the maturity ogive for female hoki (modified by an unknown proportion spawning for mature fish), then it seems that the ogive for female hoki must be steep, with age 5 fish nearly as likely to spawn as age 10+ fish. In the 1992 curve, age 5 fish are 69% as likely to spawn as age 10+ fish (44% compared with 66%) while in the 1993 curve, age 5 fish are just as likely to spawn as age 10+ fish (64% compared with 63%).

Although age classes less than 4 years were poorly sampled in the surveys, it is clear that the proportion spawning of 2 years or less was almost zero and very low at 3 and 4 years. The ogive then climbs steeply at age 5 and flattens out again from ages 7 or 8.

As the ogive is steep rather than shallow, the many fish of recruited size observed by Hurst & Schofield (1991) to be resident in the Sub-Antarctic area during winter is unlikely to be due to virgin fish which have not yet recruited to the fishery. It could be due to a proportion of infertile fish which will never become mature, but this proportion is likely to be small because it would be biologically inefficient for the species. It is more likely that mature fish which have already recruited to the fishery and spawned do not spawn annually.

The ogive is steeper than the ogive used in the 1994 assessment shown in Table 14 (estimated from the relative catches of male and female hoki of ages 4 and 5 in the 1991 and 1992 west coast fisheries) in which the proportion of age 5 fish that spawn is only 40% of the proportion of age 10+ fish that spawn (Sullivan *et al.* 1994). However, as the proportion spawning at age 5 is measured from a sample of age 5 fish that have already

**Table 14: Comparison of three maturity ogives for female hoki, as used in the 1994 assessment, as estimated from the 1992 proportion spawning at age curve, and as estimated from the 1993 proportion spawning at age curve. The estimates are the proportion spawning at age relative to the age 10+ value**

Source of ogive	Age									
	1	2	3	4	5	6	7	8	9	10+
1994 assessment	0	0	0	0.1	0.4	1.0	1.0	1.0	1.0	1.0
1992 estimate	NA	NA	NA	NA	0.7	NA	0.9	1.1	1.1	1.0
1993 estimate	NA	NA	0	NA	1.0	0.9	1.0	1.0	1.1	1.0

migrated to the Sub-Antarctic area, it may not be truly representative of all age 5 fish in the western stock; some of these may still be on the Chatham Rise or in the process of migrating south. If we were able to include these more slowly developing fish in the sample, it is likely that the proportion spawning of the younger cohorts would decrease.

The cohort age 5 in 1993 which had such a high proportion spawning (64%) is the 1988 year class. This year class, which appeared to be relatively strong on the Chatham Rise in 1991 and 1992 (Sullivan *et al.* 1994) were expected to recruit to the Sub-Antarctic area in 1993. However they did not do so, and the high proportion may reflect precocious fish within the cohort that have recruited ahead of the remainder of the year class.

Despite the difficulty in interpreting the proportion spawning for the younger ages, it is clear that the proportion spawning for the older ages was very similar in 1992 and 1993. If we assume (as in Sullivan *et al.* (1994)) that the true maturity ogive reaches 100% mature at age 6, then it is possible to estimate the overall proportion spawning for mature fish. This proportion was also very similar in 1992 and 1993 (65% with a *s.e.* of 3% and 61% with *s.e.* of 2%). If we also estimate migration of age 6+ fish away from the Sub-Antarctic area between December and May, then the true proportion spawning is estimated as 78% (*s.e.* 4%) in 1992 and 77% (*s.e.* 4%) in 1993. These estimates are not significantly different, nor are they sensitive to the exact form of the age-length key used for the December surveys or to estimates of natural mortality  $M$ .

The ratio of the number of missing fish to the number of fish present in the Sub-Antarctic area (the migration ratio,  $x$ ) can also be expressed in terms of the proportion of fish that have already migrated ( $p_m$ ).

$$x = \frac{p_m}{1 - p_m} \quad (4)$$

or, equivalently

$$p_m = \frac{x}{1 + x} \quad (5)$$

Both  $x$  and  $p_m$  change as fish leave the Sub-Antarctic area. In December, when no fish have migrated, both  $x = 0$  and  $p_m = 0$ . If a survey were to be done at a point when 33% of fish had migrated, or  $p_m = 0.33$ , there would be one fish missing for every two fish still in the survey area, and  $x$  would be 0.5. By July, when 78% of fish have gone to spawn,  $p_m$  is 0.78 and  $x$  has increased to 3.5. So when in May,  $x = 0.55$  and  $p_m = 0.35$ , we can

estimate that nearly half (45%) of the fish that were going to spawn had already gone. This is, of course, poorly estimated, as is  $x$ , but seems to be higher than was expected before the surveys were done, and suggests that fish may start to migrate in autumn, rather than early winter as had been hypothesised.

If the estimates of the numbers of fish that have migrated away from the Sub-Antarctic area by May are incorrect (perhaps because of changes in catchability or vertical availability between December and May, or because not all fish have begun to develop by May), the measured proportion spawning of mature fish (65% in 1992 and 61% in 1993) is a lower limit to the true proportion spawning.

Hurst & Schofield (1991) estimated that the most probable proportion of adult hoki spawning in 1990 was of the order of 60–75%, which is again similar to the true proportion spawning estimated in 1992 and 1993.

A proportion spawning for adult fish that is less than 100% may be thought to be unusual. Hislop (1984) showed in a study of four Northern Hemisphere gadid species that the shape of the ogive (i.e., proportion spawning at age) differed between species, but that all species reached 100% spawning after a certain age or size. However, up to 30% of the adult population of burbot, *Lota lota* (L.), a brackish water gadiform which occurs in the Baltic Sea, do not spawn in a given year (Pulliainen & Korhonen, 1990). No explanation was given. The authors concluded that adult burbot appear to have rest years, but that these are not for nutritional reasons.

The biological advantage for hoki of the proportion spawning being less than 100% is unclear. Possibly it reduces the mortality caused by the stress of a lengthy migration or of the spawning process itself. This could be achieved by an inbuilt cycle that incorporated rest years, or by a mechanism that responded to the condition of the individual fish each season. These possibilities require further investigation.

## 6. Acknowledgments

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