

Abstract.—Trawl surveys of hoki, *Macruronus novaezelandiae* (Hector) in the Southland and subantarctic areas (Southern Plateau) of New Zealand's Exclusive Economic Zone were carried out in May 1992 and 1993. The proportion of females of each age that would spawn in the coming spawning season (July–August) was estimated on the basis of histological analysis of gonad samples and ageing data. Comparisons were made between numbers of fish at age in these surveys and numbers of fish at age in surveys in November–December 1991 and 1992 to estimate migration before May.

The results indicate that 66% (standard error [SE] of 3%) of females age 7 and over that were on the Southern Plateau in May 1992 would spawn in winter 1992, compared with 65% (SE 2%) in 1993. If the number of hoki estimated to have already migrated out of the survey area in May are included as prespawners, then up to 67% (SE 5%) of adult females were predicted to spawn in winter 1992 and 82% (SE 3%) in winter 1993.

This study confirms that the proportion of adult hoki that spawn in a given year is substantially less than 1. It is not known how much this varies, whether it is with or without trend, or whether it is correlated with any environmental variables. Fishery indicators such as stock and fishery risk are particularly sensitive to the annual proportion of adult hoki that spawn, and it is possible that its variation could obscure any underlying stock-recruitment relationship.

Estimating the annual proportion of nonspawning adults in New Zealand hoki, *Macruronus novaezelandiae*

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Hoki (*Macruronus novaezelandiae* Hector) form New Zealand's largest commercial fishery with an annual catch of about 200,000 metric tons (t). The fish are widely distributed throughout New Zealand's 200-mile Exclusive Economic Zone in depths of 50–800 m, but most commercial fishing is at depths of 200–800 m around the South Island (Fig. 1). Fishing effort is greatest during the July–August spawning season off the west coast and in Cook Strait but also occurs on the Chatham Rise and management areas south of Puysegur Point (hereafter referred to as the Southern Plateau) (Fig. 1) throughout the rest of the year.

Although managed as a single stock, hoki are assessed annually as two stocks (Sullivan and Cordue¹; Sullivan et al.²). There is no genetic evidence for a split, but because morphometric and growth rate differences have been found between the two spawning grounds (Horn and Sullivan, 1996; Livingston and Schofield, 1996), a cautious approach in determining yield has been taken. Hoki are assessed as two stocks by using stock reduction models (Sullivan et al.²). Abundance indices estimated from acoustic surveys, trawl surveys, and catch-per-unit-of-effort data on the spawning grounds have been the main inputs to the models (Sullivan et al.²).

Of the two stocks, the western stock, which resides primarily on the Southern Plateau and spawns off the west coast of the South Island, is substantially larger than the eastern stock, which resides primarily on the Chatham Rise and spawns in Cook Strait. Juvenile hoki (2–5 yr) of both stocks appear to reside and mix together on the Chatham Rise in relatively shallow water. As the fish reach maturity, it is assumed that they recruit to their respective stocks.

Winter surveys of the Southern Plateau and Chatham Rise have shown that significant numbers of mature-size hoki, both males and females, do not partake in the spawning migration in a given year (Livingston et al., 1991; Hurst and Schofield, 1995).

From trawl surveys of the Southern Plateau in July–August and November–December 1990, it was estimated that the ratio of recruited

¹ Sullivan, K. J., and P. L. Cordue. 1992. Stock assessment of hoki 1992. New Zealand Fisheries Assessment Res. Document 92/12, NIWA Greta Point library, Wellington, New Zealand, 43 p.

² Sullivan, K. J., P. L. Cordue, and S. L. Ballara. 1995. A review of the 1992–93 hoki fishery and assessment of hoki stocks for 1994. New Zealand Fisheries Assessment Research Document 95/5, NIWA Greta Point library, Wellington, New Zealand, 45 p.

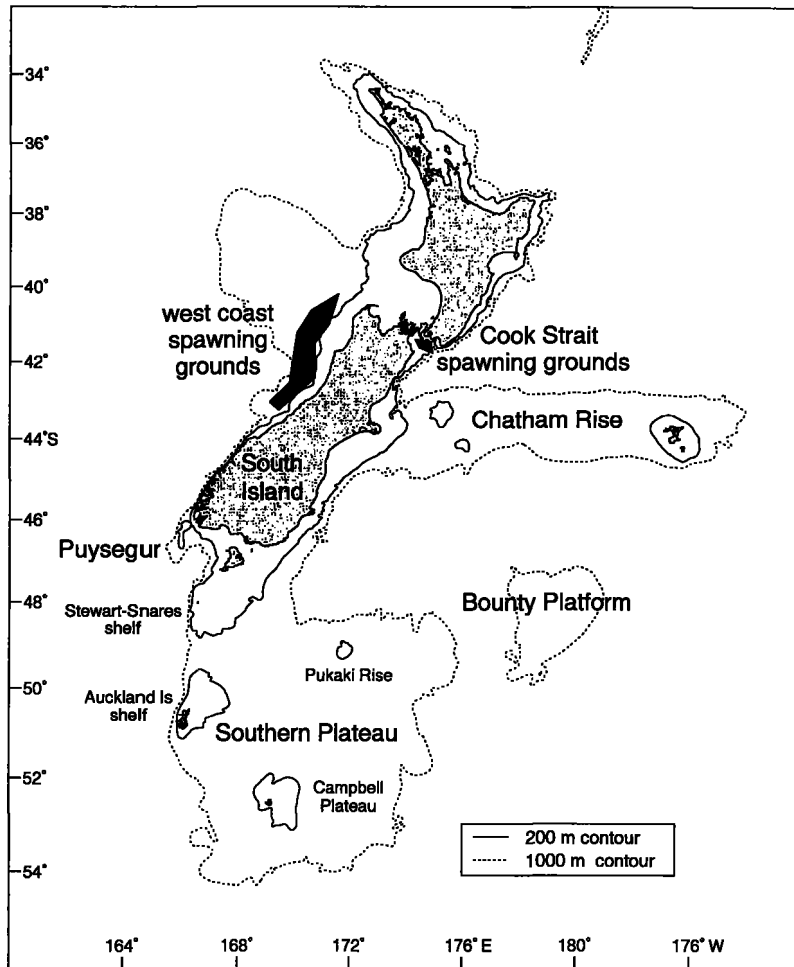


Figure 1

Map of New Zealand showing spawning and feeding grounds of hoki, *Macruronus novaezelandiae*.

biomass of western stock hoki present in winter to the recruited biomass of western stock hoki present in summer was 1:2.05 (Hurst and Schofield, 1995). Hurst and Schofield concluded that the total proportion of adult hoki that spawned in 1990 was between 60% and 75%.

The annual proportion of adult hoki that spawn was incorporated into the stock reduction analysis of hoki as a model parameter for the first time in 1992 (Sullivan and Cordue, 1992). A sensitivity analysis of the response of fishery indicators, such as stock and fishery risk to changes in various model parameters, found that they were particularly sensitive to the proportion of hoki that spawn in a given year (Sullivan and Cordue¹). In view of this sensitivity, a research program, to estimate more accurately the annual proportion of hoki that spawn and the maturity ogive of hoki at age in the western stock, was initiated.

The spawning season for hoki begins in late June and can extend into mid-September (Sullivan et al.²).

Large fish tend to spawn earlier than smaller fish, and on the west coast, spawning extends northwards as the season progresses (Langley, 1993). Hoki are not caught in quantity in the vicinity of the west coast outside the spawning season, and there is some evidence from commercial data and trawl survey data to suggest that hoki migrate to the west coast from the Southern Plateau during May–June (Ballara³). Female hoki gain up to 40% of their total body weight as their ovaries ripen (Kuo and Tanaka, 1984), but for the remainder of the year, the ovaries are small, weighing less than 1% of total body weight. Ovaries begin to ripen in April before female hoki migrate to their spawning grounds (van den Broek et al., 1981; Kuo and Tanaka, 1984).

Evidence of spawning at other times of the year has not been reported (Kuo and Tanaka, 1984). Preliminary histological work on hoki females collected throughout the spawning season indicates that hoki are either synchronous or group synchronous spawners. That is, their ovaries develop a single set of oocytes in a given season, and these oocytes are released in a single event (synchronous) or over several spawning events (group synchronous) (West, 1990). The same species in Tasmania develops a single set of oocytes in each season (Gunn et al., 1989). It is un-

known whether the proportion of hoki that spawn in a given year is determined by environmental conditions or whether it relates to a shallow recruitment curve or even some nonannual endogenous rhythm.

Our hypothesis was that if hoki develop their oocytes synchronously within each ovary, it should be possible to distinguish developing prespawners from nonspawners prior to the onset of the spawning season and thereby estimate both the proportion of fish that would spawn and a maturity ogive based on histological characterization.

In this study we collected monthly samples to monitor seasonal changes in the ovarian development of hoki prior to spawning. We also used random trawl surveys of the Southern Plateau in December and May in two consecutive years to determine 1) the

³ Ballara, S. 1995. Natl. Inst. Water and Atmospheric Res., P.O. Box 14-901 Kilbirnie, Wellington, New Zealand. Personal commun.

proportion of female hoki on the Southern Plateau in May that would spawn in the coming season and 2) the proportion of females that already have begun their spawning migration by May. In this paper, we detail 1) the histological basis for classifying hoki as either nonspawners or prespawners and 2) the analyses used to estimate the maturity ogive and the total proportion of fish that would spawn in July or August.

Materials and methods

Trawl surveys

Two sets of surveys were completed: 1) 12 November–23 December 1991 and 17 April–21 May 1992; 2) 14 November–22 December 1992 and 1 May–4 June 1993. The survey area (275,356 km²) incorporated depths of 300–800 m south of Puysegur Point, excluding rough ground and the Bounty Platform (Fig. 1). The surveys used a two-phase random stratification design (Francis, 1984), and because hoki tend to be near the seabed during daylight, coming up off the bottom to feed at night (Kerstan and Sarhrage, 1980), trawling was carried out during daylight hours only. Trawling procedure and standardization of gear, station, and stratum details are reported for each survey individually by Chatterton and Hanchet (1994), Schofield and Livingston (1994, a and b), and Ingerson et al. (1995).

Length-frequency samples of about 200 female hoki were collected from each tow on a random basis. The length-frequency distribution and the total numbers of fish were scaled up to the total stratum area by using the Trawlsurvey Analysis Program, as described by Vignaux.⁴ The scaling was done by assuming a catchability and vulnerability of 1.0 in all surveys. Because these assumptions were unlikely to be valid, the numbers of fish were used only in a relative sense.

Additional samples of 20 female hoki were collected from each tow to measure gonad and total body weight, to identify macroscopic gonad stage, and to obtain histological samples from ovaries. Otoliths were also collected from these fish for ageing. Maturing hoki in the later stages of vitellogenesis can be macroscopically distinguished from resting hoki. The ovaries at that point are swollen, and the individual oocytes, visible to the naked eye, are opaque and creamy pink. Resting and immature ovaries are

small and translucent and no oocytes are visible. Previous surveys of hoki in April–May (e.g. van den Broek et al., 1981) reported few hoki that were sufficiently developed to be identified macroscopically as maturing. We therefore obtained histological samples of ovaries as well as recorded their macroscopic appearance. The central portion of the ovary from each sample was preserved at sea in 8%–10% buffered formalin. Samples were later processed to produce thin sections that were stained with standard haemotoxylin and eosin preparations.

Histological staging

In developing a method to distinguish prespawning hoki from nonspawning 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 | The oocyte is surrounded by a few follicle cells and contains a large nucleus surrounded by a thin layer of cytoplasm. The nucleus has one large nucleolus and several small nucleoli. |
| Perinucleolar stage | The nucleus has multiple nucleoli at its periphery. Late perinucleolar oocytes may have vacuoles in the cytoplasm. |
| Yolk vesicle (cortical alveoli) stage | 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 is visible at this stage. |
| Vitellogenic (yolk) stage | Small yolk granules which gradually enlarge until they form fluid-filled spheres are typical. The spheres may eventually fuse to form a continuous mass of fluid yolk. |
| Ripe (mature) stage | The nucleus may be peripheral or may have disintegrated completely. |

Criteria to distinguish prespawners from nonspawners were developed from a subsample of ovary sections from each survey and from some commer-

⁴ Vignaux, M. 1994. Documentation of trawlsurvey analysis program. NIWA Greta Point Internal Report 225, NIWA Greta Point library, Wellington, New Zealand, 44 p.

cial samples collected from January through August (see below). These criteria (described in the Results section) were then used by an independent reader to classify May 1992 and May 1993 female hoki as prespawners or nonspawners.

Monthly samples were also collected from commercial vessels to monitor hoki development between January and September. Up to 40 ovary samples from a range of adult-size fish were preserved in 8% buffered formalin at the time of capture. Samples were processed in the laboratory, sectioned, and stained with standard haematoxylin and eosin preparations. Samples were collected mostly from Chatham Rise (Jan–May) and the west coast of the South Island (Jun–Jul) because these were the areas where commercial vessels were operating at that time.

Each fish was staged histologically (as described above) to determine the earliest month in which development began. Five of the most developed fish from each month were then selected for oocyte measurement to confirm that New Zealand hoki are synchronous or group synchronous like their Australian counterparts (Gunn et al., 1989). The mean diameter of 200 oocytes was measured (after Foucher and Beamish, 1980) from each of the five fish.

Ageing

It is unknown whether recruitment to the spawning fisheries is length-driven or age-driven. Observers from the west coast hoki fishery have found spawning hoki as young as 2 years and as small as 42 cm total length, in some years (Sullivan et al.²). Because the model used for stock assessment is an age-structured one (Sullivan et al.²), fish were aged as part of this study, and all analyses were carried out by using age data. It was also important to age fish so that comparisons of the numbers of fish in each cohort in December and May could be made.

Otoliths from each fish in the histological samples from the May surveys and from the biological samples in December were aged by using the validated ageing method described by Horn and Sullivan (1996). These data were also used to develop age-length keys. Where there were no fish in the sample of a given length, the age-length key was interpolated with nearby values of age.

Proportion of each age class developing to spawn

The proportion of fish in each age class that were classified as prespawners was estimated for each age stratum from the aged histological samples. The number of fish at each age in each stratum was esti-

mated from the age-length key and the length-frequency distribution in the stratum. For each age class the total number of prespawners was therefore estimated from the proportion of fish that were developing to spawn and from the total number of fish in each stratum. The standard error of these estimates was estimated by using a resampling technique, whereby in each stratum, a sample, the same size as the original sample, was selected (with replacement) from the original sample. The age-length key and proportion of prespawners were calculated from the combined sample of the 15 strata. This process was repeated 1,000 times. The standard error of the estimates was estimated from the standard deviation of the values in 1,000 replicates.

Proportion of adult spawning fish

An estimate \hat{p}_+ of the proportion of prespawners in the plus group of adult fish (p_+) can be obtained by using the method described above but by considering all adult fish as a single plus group. However, if some fish had already left the Southern Plateau to spawn before the survey in May, they also should be counted as prespawning fish. This means that the proportion of adult prespawners present on the Southern Plateau in May (p_+) is an underestimate of the total proportion of fish that will spawn (p) as

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

where s is the number of prespawners on the Southern Plateau in May, ns is the number of nonspawners on the Southern Plateau in May, and g is the number of fish that had left the Southern Plateau before May, presumably to spawn.

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 prespawners and nonspawners) that are still in the survey area when the second survey is done, then

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

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 because both trawl surveys will be subject to measurement error and because an unknown number of fish will have died naturally or have been caught between December and May. But to obtain the best estimate of x , the numbers of adult fish on the Southern Plateau in December and May were estimated from the total numbers of fish in the surveys and the proportion that were in the adult age group. The age distributions were estimated from the length-frequency distributions and the age-length keys were calculated from the samples collected for age determination.

In determining the number of fish that moved out of the survey area before May, 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 on the Southern Plateau between December and May in these two years was 10,595 t in 1992 and 8,339 t in 1993. Because the estimated size of the stock was 860,000 t in May 1992 and 1.3 million t in May 1993 (Cordue⁵), fishing mortality was considered 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 Southern Plateau to spawn. This number was used in Equation 2 to obtain an estimate \hat{x} of the migration ratio x . An estimate of the total proportion of fish that will spawn (p) was calculated by using \hat{x} and an estimate of \hat{p}_+ of p_+ in Equation 3. Standard errors of these numbers were calculated by a resampling procedure that included uncertainty regarding the total number of fish in the December and May surveys.

Procedure for estimating the total proportion of adult fish spawning

The estimation procedure for the proportion of adult spawning fish was as follows:

- 1 The total number of fish on the Southern Plateau 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. This number of fish was then distributed over the length-frequency distribution (assumed to be known exactly).

- 2 An age-length key (including ageing error) was generated by sampling with replacement from the fish in the age-length sample from the December survey and was applied to the December length-frequency distribution to estimate the number of adult fish in December, n_1 . The number of adult fish expected to be alive in May was calculated by applying the natural mortality M to n_1 , as $n_1 e^{-M5/12}$.
- 3 The same procedures described in 1 and 2 above were applied to the May surveys to obtain the total number of fish on the Southern Plateau in May (N_2) and the number of adult fish in May (n_2)

- 4 The number of fish apparently missing (n_m) was estimated as

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

- 5 Taken as a fraction of the number n_2 on the Southern Plateau in May, x (the migration ratio) was estimated by

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

- 6 \hat{p}_+ was calculated by using the simulated age-length key and the histological sample as described above. Hence \hat{p} was estimated as

$$\hat{p} = \frac{\hat{p}_+ + \hat{x}}{1 + \hat{x}}.$$

This process was repeated 1,000 times. The standard errors of each of the values was calculated from the standard deviation of the distribution of the 1,000 values.

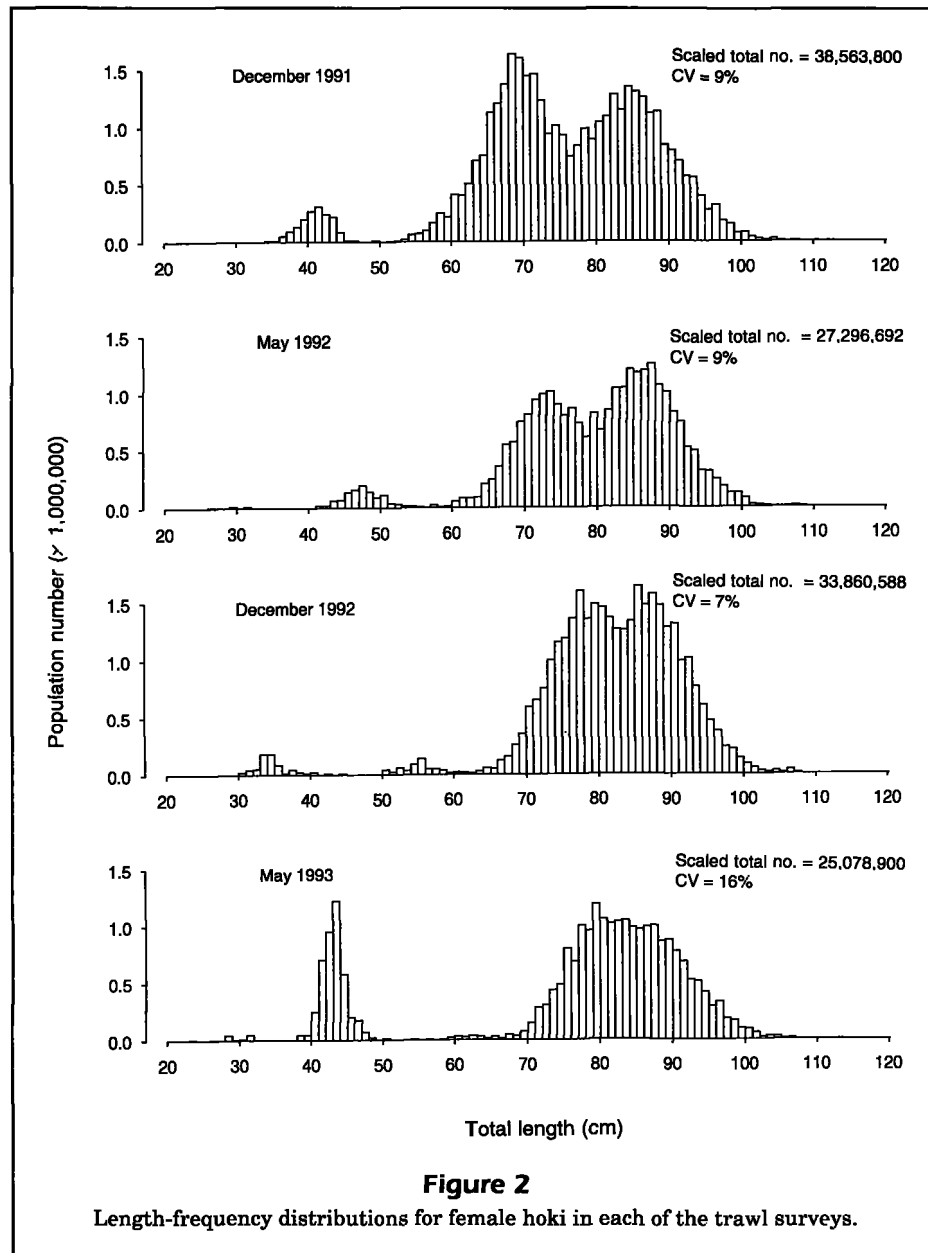
Results

Trawl surveys

The four surveys were successfully completed with a combined total of 495 stations sampled. Gear parameters were within the range necessary for survey standardization (Hurst et al.⁶), thereby permitting the direct comparison of survey results used for data analysis (Chatterton and Hanchet, 1994; Schofield and Livingston, 1994, a and b; Ingerson et al., 1995).

⁵ Cordue, P. 1996. Natl. Inst. Water and Atmospheric Res. P.O. Box 14-901 Kilbirnie, Wellington, New Zealand. Personal commun.

⁶ Hurst, R. J., N. Bagley, T. Chatterton, S. Hanchet, K. A. Schofield, and M. Vignaux. 1992. Standardisation of hoki/middle depth time series trawl surveys. NIWA Greta Point Internal Report 194, NIWA Greta Point library, Wellington, New Zealand, 87 p.



The numbers of hoki observed in the May surveys (26.8 million [1992], 24.4 million [1993]) were considerably less than in the December surveys (38.6 million [1991], 34.8 million [1992]) (Fig. 2). In addition, the length-frequency histograms show a decline in bimodality in the adult part of the distribution between May and December (Fig. 2). In December 1991, 56% of 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.

There were 541 fish in the histological sample in May 1992 and 1,136 fish in the sample in May 1993 (Table 1). In 1992, stratum 1 (300–600 m depth at

Puysegur) 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.

Ageing

There were very few young fish in most strata, and limited numbers of fish in the 1986 cohort, which appeared as age-6 fish in 1992 and as age-7 fish in 1993. Although fish were aged to a maximum age of 19 years, we combined them into a group of age 10⁺ and above. The ageing data were also used to develop age-length keys.

Table 1
Percentages of each histological stage observed in female hoki sampled from each survey.

Histological stage	Dec 1991	May 1992	Dec 1992	May 1993
Chromatin nucleolar	0	0	0	0.1
Perinucleolar	100	45.4	100	39.7
Yolk vesicle	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

Histology

Monthly samples of hoki from the Chatham Rise and west coast of the South Island showed little change in oocyte stage in January and February, all being classified as perinucleolar (Table 2). In April, May, and June, larger oocytes of the yolk vesicle and vitellogenic yolk stages were evident. By July and August, females sampled on the west coast of the South Island were vitellogenic or ripe and had hyaline oocytes (Table 2). Oocytes clearly developed as a synchronous group, evidenced by the separation in size of the developing clutch from the reserve fund of chromatin nucleolar and perinucleolar oocytes (Fig. 3).

During the December trawl surveys, most ovaries contained oocytes that could be classified as late perinucleolar (Fig. 4).

By May, however, a significant change in oocyte stage had occurred; many ovaries contained cortical alveoli organized into a ring structure and showed increased oocyte size and oil droplets forming around the nucleus (Fig. 5). Because the oocyte stage observed in summer appeared to be a natural holding point in development, we classified a fish with such a stage as perinucleolar. When we saw the same development in fish in the autumn surveys they were classified as nonspawners. Only those fish with a proliferation of cortical alveoli and oil droplets that had begun 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.

Table 1 shows the proportion of fish at each stage in each of the surveys. In both December samples, most or all fish were classified as perinucleolar. In contrast, in the May surveys, only 45.4% and 39.7% were in the perinucleolar stages in 1992 and 1993 respectively.

For fish caught during the trawl survey in May 1993, stage of development of the ovary of each fish in the histological sample was also evaluated mac-

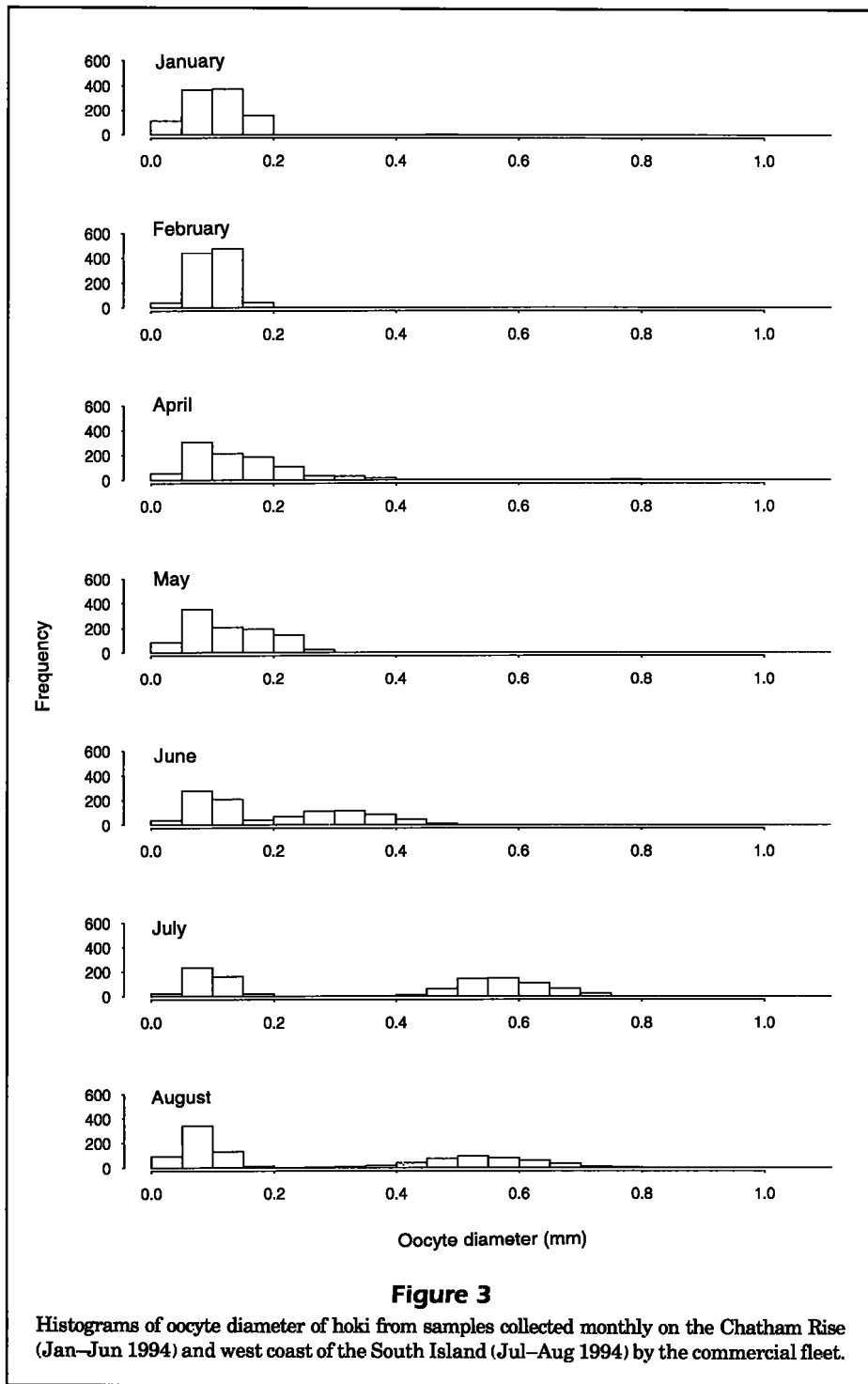
Table 2

Numbers of hoki monthly samples showing ovarian development on the Chatham Rise and west coast spawning grounds.

Region and month	Histological stage			
	Perinucleolar	Yolk vesicle	Vitellogenic	Ripe
Chatham Rise				
January	22	—	—	—
February	10	—	—	—
March	no sample			
April	6	9	1	—
May	10	9	1	—
West coast				
June	4	3	13	—
July	—	—	10	5
August	—	—	9	5

roscopically. The number of fish at each histological stage and at each stage of macroscopic gonad development are presented in Table 3. In total, of the 237 ovaries classified as maturing, only two were classified histologically as nonspawners. However, of the 899 ovaries classified as resting, 450 were classified histologically as nonspawners and 449 as prespawners. This finding confirms that physical development for spawning begins before it is apparent macroscopically in the ovaries and reinforces the requirement for histological methods of analysis.

The proportion of prespawners in each stratum was estimated from the aged histological samples from the May surveys (Table 4). If there were not at least two fish in a stratum of a particular age, the proportion was not estimated. Although there were many age-stratum combinations where the proportion of prespawners in a particular age class could not be estimated (mainly for the young fish and for the 1986 cohort), these were not generally found in strata that supported the greatest numbers of hoki of that age class (Table 4).



Proportion of each age class developing to spawn

Table 4 shows the estimated proportion of pre-spawners in each age class in the 1992 and 1993 May surveys. Table 4 also shows the percentage of fish at each age that were in strata where the proportion of

developing fish could be measured (i.e. had at least two fish in the sample). Where this is less than 50%, the estimate is based on fish from only a small fraction of the population, and should not be used. Where it is less than 66%, the estimate might be considered unreliable. In 1992 there were enough data to make a reliable estimate of the proportion of pre-spawners

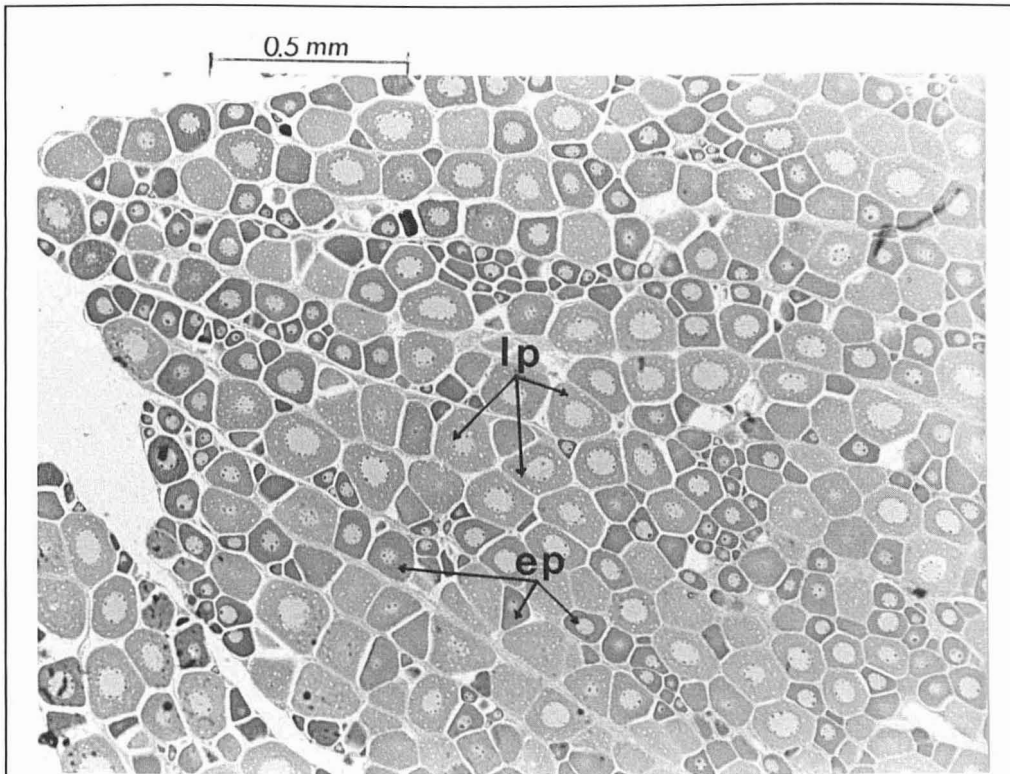


Figure 4

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)).

for ages 5, 7, 8, 9, and 10⁺, but age 6 (the 1986 cohort) and ages 1, 2, 3, and 4 could not be estimated because the strata with samples contained less than half of the total number of fish in the survey area. In 1993 there were enough data to make a reliable estimate of the proportion of prespawners for ages 5, 6, 8, 9, and 10⁺, but ages 3 and 7 (again, the 1986 cohort) were unreliable and ages 1, 2, and 4 could not be estimated.

The estimates of prespawners in each age class for the two surveys are shown in Figure 6. 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 prespawners. It is therefore likely that the ogive increases steeply below age 5 before levelling off.

Proportion of adult fish spawning

Figure 6 suggests that there may have been some increase in the proportion of prespawners up to age 8 in 1992 but that in 1993 the numbers of prespawners did not increase after age 5.

If we assume that any increase after age 7 is not significant, then the asymptotic values of the ogives

Table 3

Numbers of hoki classified in each histological stage compared with numbers of hoki classified in each macroscopic stage (May 1993).

Histological stage	Macroscopic stage		
	Resting	Maturing	Total
Nonspawners	450	2	452
Chromatin Nucleolar	1	0	1
Perinucleolar	449	2	451
Prespawners	449	235	684
Yolk Vesicle	154	1	155
Vitellogenic	295	197	492
Ripe	0	37	37
Grand total	899	237	1,136

in Figure 6 represent the measured proportion of adult prespawners (p_+) in the years 1992 and 1993. Following a procedure identical to that above, but considering only fish aged 7 and over, the proportion of adult prespawners in the survey area was estimated as 66% in 1992 (SE 3%) and 65% in 1993 (SE 2%).

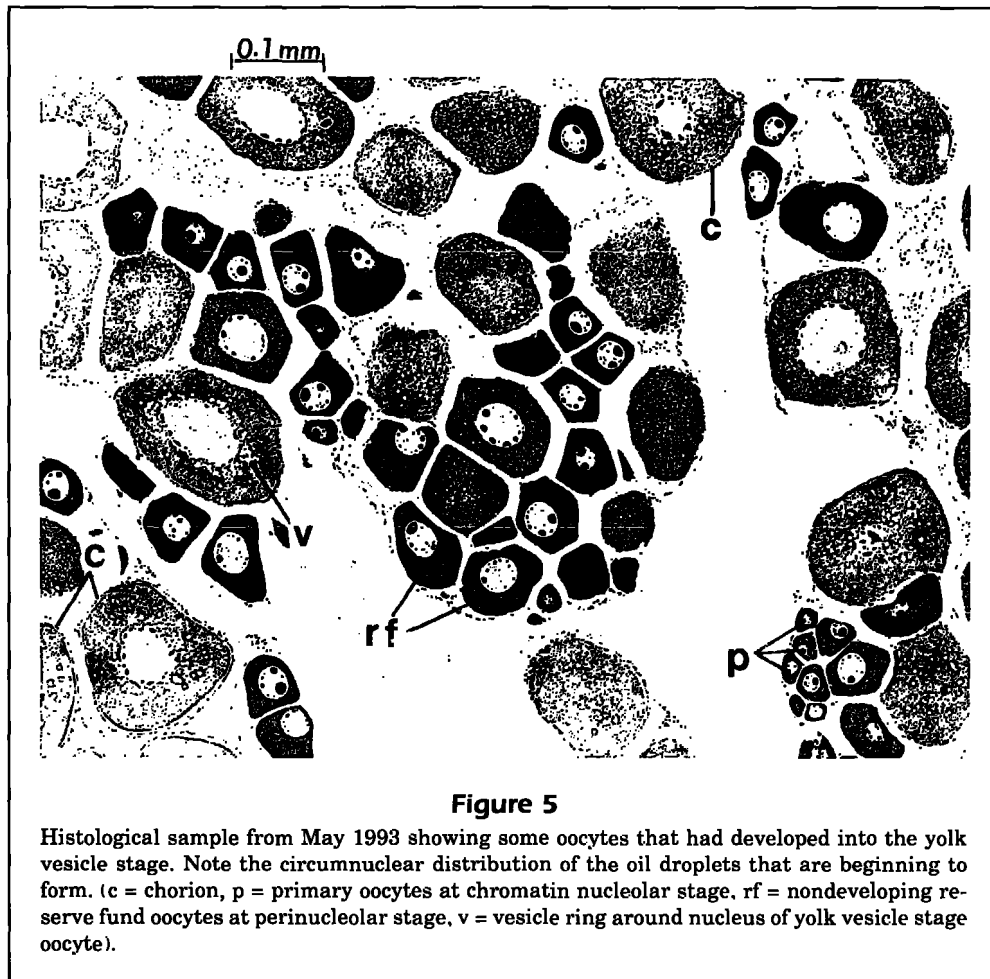


Figure 5

Histological sample from May 1993 showing some oocytes that had developed into the yolk vesicle stage. Note the circumnuclear distribution of the oil droplets that are beginning to form. (c = chorion, p = primary oocytes at chromatin nucleolar stage, rf = nondeveloping reserve fund oocytes at perinucleolar stage, v = vesicle ring around nucleus of yolk vesicle stage oocyte).

Table 4

Estimated total numbers of female fish, numbers of female fish in sampled strata, percentage of female fish in strata covered by sampling, numbers of prespawners, proportion of prespawners with standard error (SE), for each age class in the May surveys (NA indicates that the value could not be estimated). SE = standard error.

	Age class									
	1	2	3	4	5	6	7	8	9	10 ⁺
May 1992										
Total in survey (× 1,000)	54	1,182	0	1,648	7,645	557	2,101	6,025	3,407	4,150
In sampled strata	0.00	511	0	691	7,458	130	1,478	5,973	3,387	4,132
% in sampled strata	0	43	NA	42	98	23	70	99	99	100
Prespawners (× 1,000)	0.00	0.00	0.00	132	3,333	35	844	4,065	2,323	2,652
Proportion spawning	NA	0.00	NA	0.19	0.45	0.27	0.57	0.68	0.69	0.64
SE	NA	NA	NA	0.10	0.05	0.26	0.08	0.05	0.05	0.05
May 1993										
Total in survey (× 1,000)	95	3,573	142	135	2,614	6,986	338	1,777	4,340	4,447
In sampled strata	0	0	83	29	2,586	6,986	183	1,739	4,304	4,418
% in sampled strata	0	0	59	21	99	100	54	98	99	99
Prespawners (× 1,000)	0	0	0	0	1,649	3,928	123	1,143	2,967	2,782
Proportion spawning	NA	NA	0	0	0.64	0.56	0.67	0.66	0.69	0.63
SE	NA	NA	NA	NA	0.05	0.03	0.18	0.06	0.03	0.03

Table 5

Estimation of total proportion spawning (p) of age-7+ hoki based on (p_+) the proportion of prespawners on the Southern Plateau and on the number of hoki in the plus group on the Southern Plateau in December 1991, 1992, and May 1992, 1993. (n = number of hoki $\times 10^3$, SE = standard error; M = natural mortality).

Year	$M = 0$ n (SE)	$M = 0.25$ n (SE)	$M = 0.3$ n (SE)
1992			
Observed, December 1991	17, 945 (1,700)	17, 945 (1,700)	17, 945 (1,700)
Observed, May 1992	15, 682 (1,400)	15, 682 (1,400)	15, 682 (1,400)
Expected, May 1992	17, 945 (1,700)	16, 170 (1,500)	15, 837 (1,500)
Missing, May 1992	2, 263 (2,200)	488 (2,100)	155 (2,100)
Migration ratio	0.14 (0.16)	0.03 (0.14)	0.01 (0.14)
Proportion spawning	0.70 (0.05)	0.67 (0.05)	0.66 (0.05)
1993			
Observed, December 1992	23, 250 (1,800)	23, 250 (1,800)	23, 250 (1,800)
Observed, May 1993	10, 902 (1,700)	10, 902 (1,700)	10, 902 (1,700)
Expected, May 1993	23, 250 (1,800)	20, 950 (1,600)	20, 518 (1,600)
Missing, May 1993	12, 348 (2,400)	10, 048 (2,300)	9, 616 (2,300)
Migration ratio	1.13 (0.43)	0.92 (0.39)	0.88 (0.38)
Proportion spawning	0.84 (0.03)	0.82 (0.03)	0.81 (0.04)

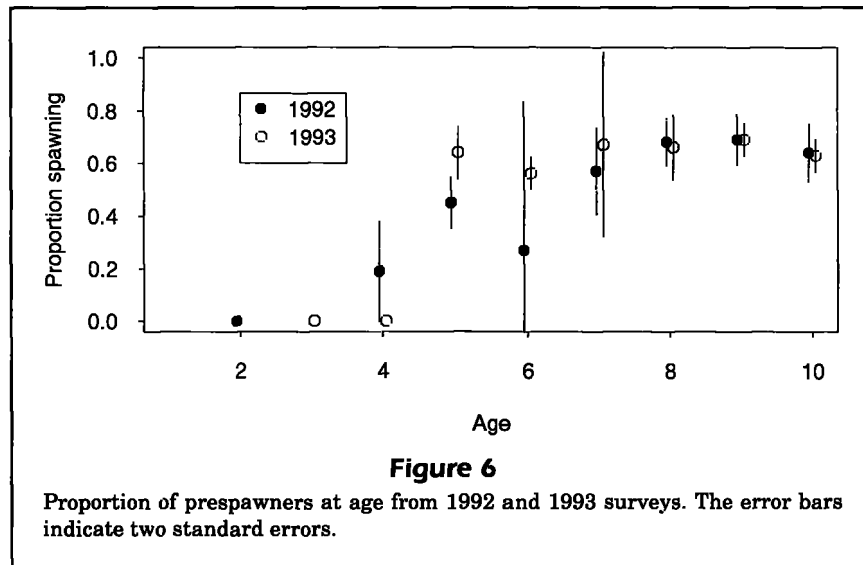
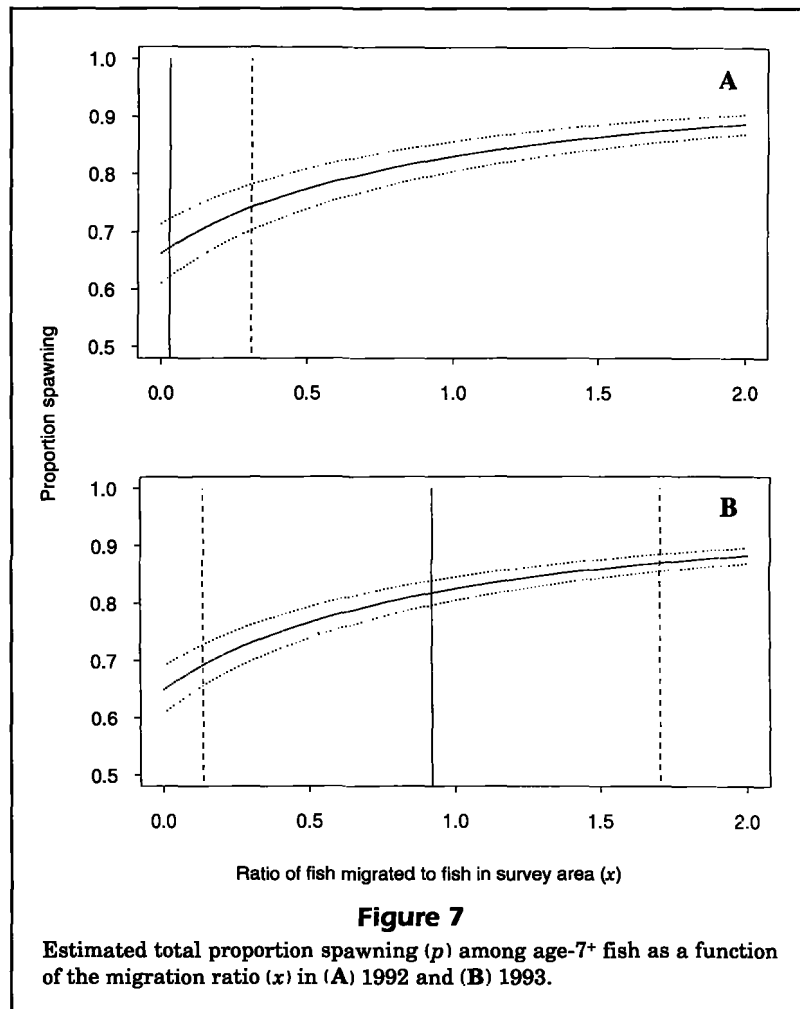


Table 5 shows the estimates of the total proportion of adult fish that will spawn (i.e. including those fish that have already left the area) calculated as above. The calculations were done with three estimates of natural mortality M , including the best estimate $M = 0.25$, and two bounding values $M = 0$ and $M = 0.3$ (Sullivan et al.²). Table 5 shows that this makes little difference to the estimate of \hat{p} . Standard errors of the estimates were calculated by using the resampling technique.

The best estimate of the total proportion of adult fish that would have spawned in the 1992 winter sea-

son was 0.67 (SE 0.05, with $M = 0.25$). If M is as high as 0.3 or as low as 0, the estimate of p decreases to 0.66 or increases to 0.70 respectively. The best estimate of the total proportion of adult fish that will spawn in the 1993 winter season was 0.82 (SE 0.03). If M is as high as 0.3 or as low as 0, the estimate of p is 0.81 or 0.84 respectively.

Figure 7 shows the effect of the estimate of \hat{x} on the estimate of \hat{p} for 1992 and 1993. In each plot there are three curves for \hat{p} as a function of \hat{x} . The solid curve is the function given the estimated value of \hat{p}_+ (0.66 in 1992 and 0.65 in 1993). The two dot-



ted curves are the functions at plus and minus two standard errors of this value.

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

Discussion

The number of studies that have attempted to measure the level of nonspawning in adult fish and to determine its effect on population estimates used for stock assessment appears to be few. It is often assumed that although the steepness of the maturity ogive varies among species, it will always level out at or near 100% spawning (e.g. Hislop, 1984). Species documented to reach less than 100% spawning

include orange roughy, *Hoplostethus atlanticus*, off southeast Australia at 55% (Bell et al., 1992), the brackish water burbot *Lota lota* (L) in the Baltic sea at 70% (Pulliainen and Korhonen, 1990), and the estuarine yellow-fin (surf) bream, *Acanthopagrus australis* at 50% (Pollock, 1984). Although the annual proportion of hoki that spawn is similar to that of these other species, the other studies did not adjust for population size or take migratory movements into account. Our estimates for hoki are close to the range indicated by Hurst and Schofield (1995) who did adjust for population size.

There were some potential sources of error that we could not measure. First, the number of undeveloped fish surveyed on the Southern Plateau in May that were classified as nonspawners, which could have developed late and gone on to spawn, is unknown. This would lead to an underestimate of the proportion of prespawners. Second, if a number of fish remained undeveloped but migrated to the spawning ground anyway, the number of fish that

would leave the Southern Plateau after May would be underestimated. Third, the number of developing fish in May that could have resorbed their eggs and not gone on to spawn after all could lead to an over-estimation of the total proportion spawning. Other sources of error concern changes in catchability and vulnerability between surveys and the difficulty of detecting any bias or size selectivity when sampling a population with the trawl.

With regard to the first source of error above, it was encouraging that hoki collected in April showed significant signs of development compared with those collected in February (Table 2). The most likely fish to be affected by late development are the younger, smaller fish because they spawn later in the season compared with the older, larger fish which spawn at the beginning of the season (Langley, 1993). Because we estimated the proportion of hoki age 7 years and above that were spawning, the problem was minimized.

With regard to the second source of potential error, undeveloped hoki of age 4 and greater are not caught on the spawning grounds during the spawning season (Langley, 1993), suggesting that there may be 100% spawning among hoki that migrate to the west coast spawning grounds. We have no data on the number of fish that could resorb their eggs before the spawning season, but none were found in the May samples in this study.

With regard to the trawl survey technique, it is possible that there are systematic changes in catchability or vulnerability between December and May. We considered it more likely, however, that the changes in fish numbers were real, and that some fish had already migrated away from the Southern Plateau before the May survey, particularly in 1993 when the survey took place later than in 1992.

The ratio of the number of missing fish to the number of fish present on the Southern Plateau (the migration ratio, x) can also be expressed in terms of the proportion of fish that have already migrated (p_m)

$$x = \frac{p_m}{1 - p_m}$$

or, equivalently

$$p_m = \frac{x}{1 + x}$$

Both x and p_m change as fish leave the Southern Plateau. 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 the 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 1993, when an estimated 82% of fish have gone

to spawn, \hat{p}_m is 0.82 and \hat{x} has increased to 4.6. Therefore, in May 1993, when $\hat{x} = 0.92$ and $\hat{p}_m = 0.48$, we can estimate that more than half (58.5%) of the fish that were going to spawn had already gone.

This is, of course, poorly estimated, as is x , but it is higher than was expected before the surveys were done. If the survey results are correct, they suggest that in May 1993, fish had already started to migrate in large numbers. The survey in May 1993 began two weeks later in the year than that in 1992, indicating that May is a critical time for the spawning migration of hoki. This interpretation is supported by the change in distribution of fish from the east to the west between December and May in 1993, but not in May 1992. If, however, our estimates of the numbers of fish that have migrated away from the Southern Plateau by May are incorrect (e.g. because of changes in catchability or vertical availability between December and May, or because not all fish have begun to develop by May), then the proportion of prespawners on the Southern Plateau in May could be used as a lower limit of the proportion spawning of the total population. Given that a standardized trawl survey technique was the best method available to us to sample the adult hoki population, we believe that it would be difficult to improve on the estimates of proportion spawning obtained.

The 4–6 yr age classes show different proportions of prespawners in each year, with more 4 year olds but with fewer 5 and 6 year olds developing to spawn in 1992 than those in 1993 (Fig. 6). Differences in the proportion of spawning fish in the younger age classes could also relate to the preceding spawning history of a particular age class.

Although every year many hoki spawn on the west coast of the South Island, it is clear that a large number of individuals do not. Species that exhibit such behavior usually have a major accessory activity that requires a significant amount of energy in addition to spawning itself (Bull and Shine, 1979). Hoki migrate over vast distances of about 1,500 km from the Southern Plateau to the west coast spawning grounds. The energy cost incurred during migration may be so high that there is not enough left for egg production the following year.

Lack of food and migration distance have been suggested as reasons for lack of spawning among orange roughy (Bell et al., 1992) and yellow fin bream (Pollock, 1984). However, Pulliainen and Korhonen (1990) found that nonspawning burbot maintained a condition similar to that of spawning burbot and ruled out low food supplies as an explanation for nonspawning adults.

Within species where different populations show different levels of nonspawning, it has been found

that the lowest frequencies are usually associated with increased stress, such as poorer quality habitat, food shortage, or a shorter growing season (Bull and Shine, 1979). Nonspawning condition has been induced experimentally for several species by reducing their food supply (e.g. haddock [Hislop et al., 1978]; Newfoundland winter flounder [Burton and Idler, 1987]; and plaice [Horwood et al., 1989]).

Nutrients are in good supply and do not limit primary production on the Campbell Plateau (which forms a major portion of the Southern Plateau survey area); however, chlorophyll concentrations over depths of 450 m or greater are generally low (Heath and Bradford, 1980). Heath and Bradford suggest that because of this and other characteristics of the area, there never will be a well-developed zooplankton community with a high biomass on the Campbell Plateau. Areas of higher productivity are found on the island shelves and shallow rises in the area, or downstream from the Campbell Plateau itself. The energetics of the food chain in the study area are not known. It is possible that the lack of high primary and secondary productivity in the area contributes toward nonreproduction in some hoki from year to year.

Whatever the cause, nonspawning among adult hoki has important implications for stock assessment and risk estimation in the management of New Zealand hoki stocks. The proportion of fish that migrate to spawn is a scaling factor that relates the number of fish observed during the spawning season (using tools such as CPUE and acoustics) to the total population. It also provides a buffer between the total stock and the population vulnerable in any one year to the greatest fishing effort that is applied during the spawning season. Further, it reduces the stock size, which is needed for calculating the stock-recruit relationship used in predicting future recruitment.

The effect of these factors may be minimal if the level of nonspawning fish is constant. If, however, the proportion spawning varies from year to year, as suggested by our study, the implications for modeling may be both complex and important.

It is likely that there are other species not necessarily related to hoki that could also have significant and variable proportions of nonspawning fish. There may therefore be major implications for the stock assessment of those species as well. Any stock assessment tool that is used to obtain an estimate of absolute abundance from a spawning population (e.g. acoustics, egg-production method) should take nonspawning into account. It is also important that the effect of nonspawning on any stock-recruitment relationship (assumed or measured) be taken into account because one of the more serious difficulties

in determining the stock-recruitment relationship of any species is obtaining a reliable measure of the spawning stock size (Hilborn and Walters, 1992). Further, the stock-recruitment dynamics of a population could be masked, particularly if the level of nonspawning is correlated to some environmental factor or autocorrelated because of some inherent life strategy, such as improved longevity or increased egg size.

We have shown that nonspawning among adult hoki is substantial, and it has important consequences for stock assessment. For these reasons, it is clear that a better understanding of its variability, and how widespread its occurrence might be among other species, would be useful for fisheries management worldwide.

Acknowledgments

We thank Peter Horn for ageing the samples; Kevin Sullivan, Patrick Cordue, and Len Tong for useful discussions; the scientific staff who participated in the trawl surveys; the officers and crew of GRV *Tangaroa*; and the scientific observers for collecting samples from commercial vessels. We also thank three anonymous reviewers for their comments and suggestions.

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