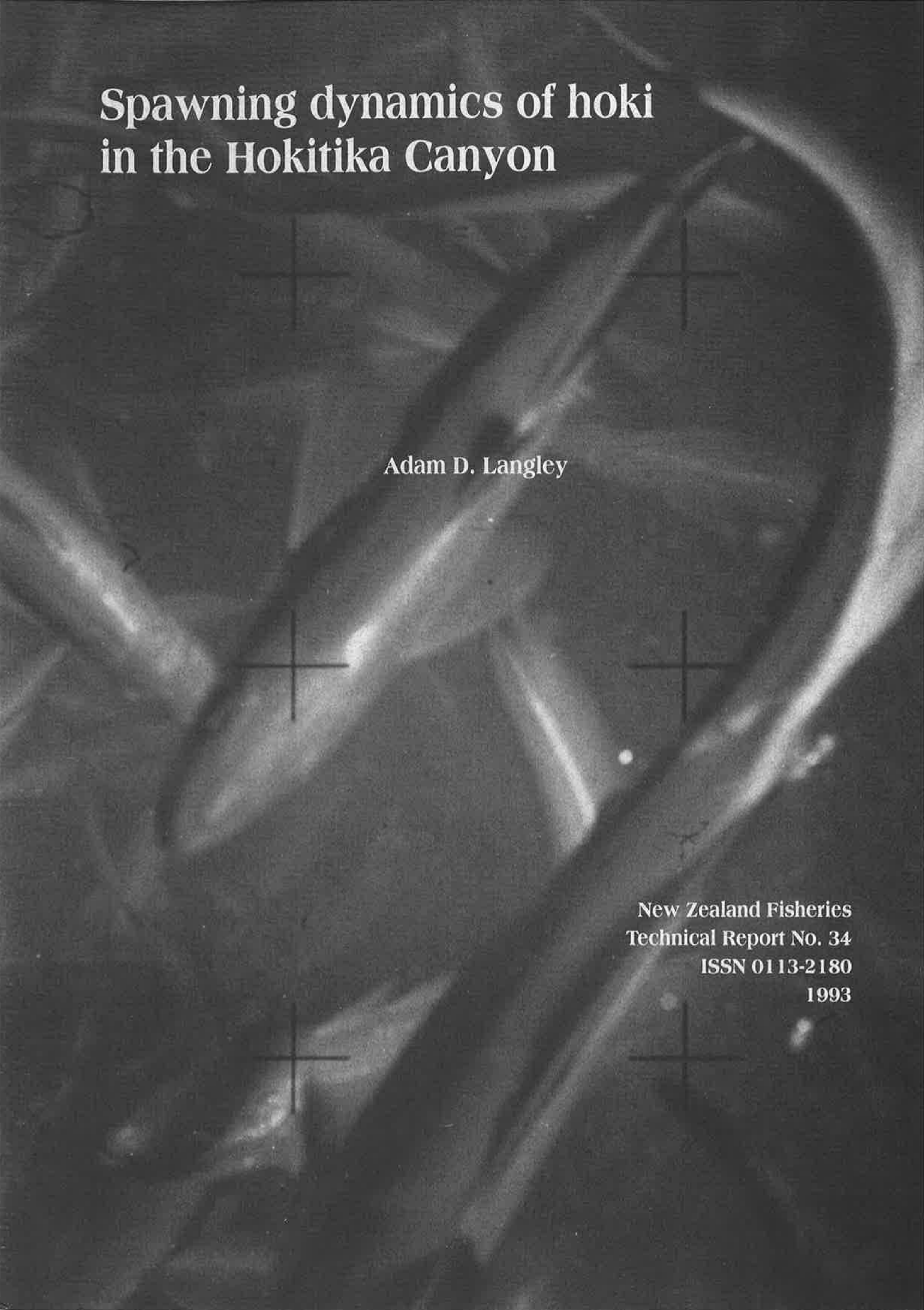
Spawning dynamics of hoki in the Hokitika Canyon



Adam D. Langley

New Zealand Fisheries
Technical Report No. 34
ISSN 0113-2180
1993

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Published by MAF Fisheries
Wellington
1992

ISBN 0-477-08660-8

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P.O. Box 297, Wellington,
New Zealand.

MAF Fisheries is the fisheries group of the New Zealand Ministry of Agriculture and Fisheries. The name MAF Fisheries was formalised on 1 November 1989 and replaced MAFFish, which was established on 1 April 1987. MAFFish combined the functions of the old Fisheries Research Division and Fisheries Management Division and the fisheries functions of the old Economics Division.

The *New Zealand Fisheries Technical Report* series in part continues the *Fisheries Research Division Occasional Publication* series. The *New Zealand Fisheries Occasional Publication* series contains mainly conference proceedings and bibliographies.

Edited by S. J. Baird

Set in 10 on 11 Times Roman

Typeset by Datacom *express*

Printed by Madison Printing Company Limited

Cover: A school of hoki at a depth of 460 m in Cook Strait. The photograph was taken with MAF Fisheries' stereo camera system by Alistair MacDiarmid.

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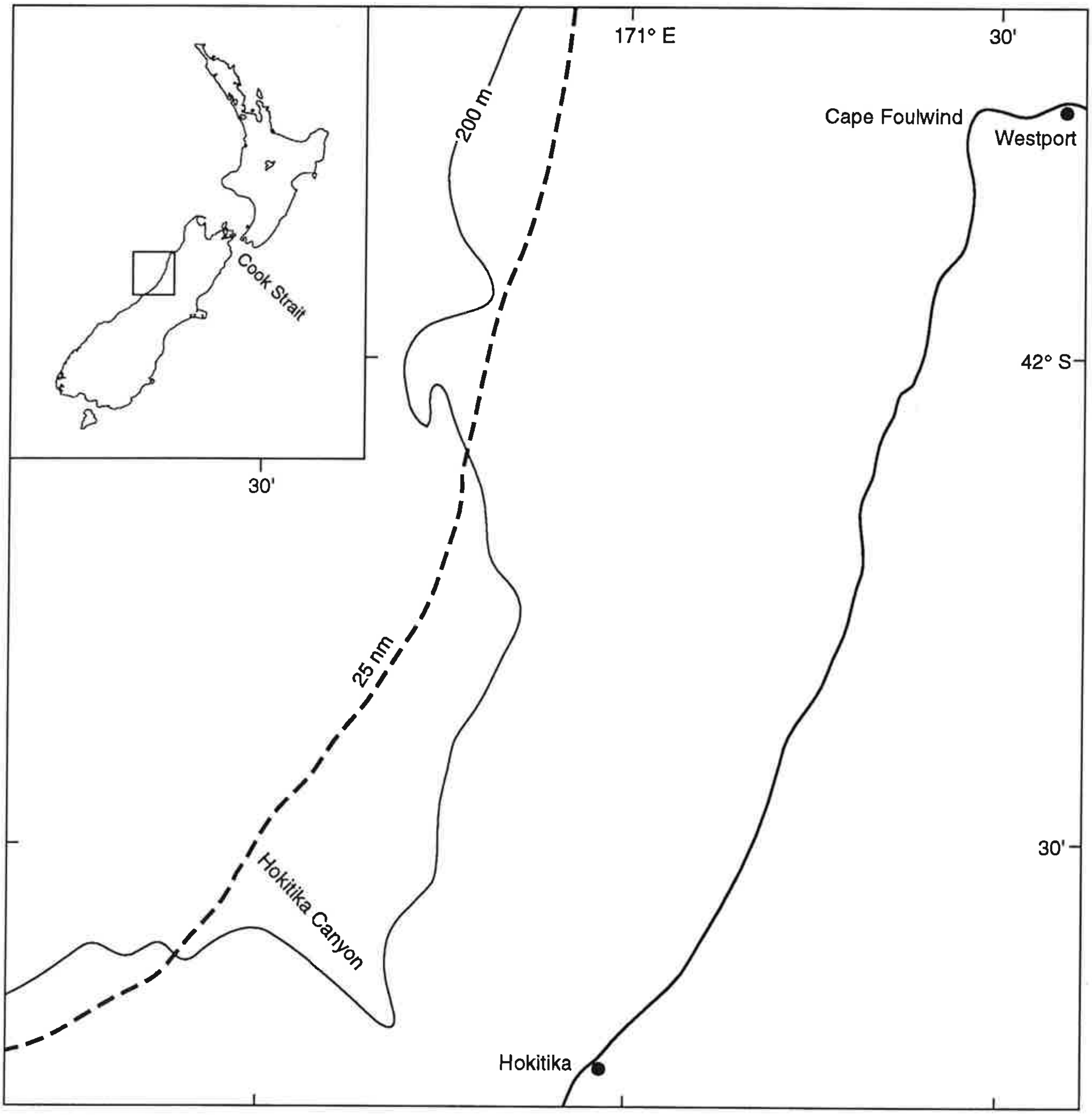

Figure 1: Chart of the northern west coast of the South Island indicating major features of the hoki fishing grounds mentioned in the text.

Abstract

Langley, A. D. 1993: Spawning dynamics of hoki in the Hokitika Canyon. *N.Z. Fisheries Technical Report No. 34.* 29 p.

During the 1989, 1990, and 1991 fishing seasons ovarian development stages of hoki (*Macruronus novaezelandiae*) were recorded by MAF Fisheries scientific observers working with the west coast South Island hoki fleet. The fishing season operates from mid June to early September and is centred on prespawning and spawning aggregations of hoki around the Hokitika Canyon. Early in the season the fleet fishes deeper water (500–900 m), and fish with maturing ovaries dominate catches of female hoki. As the season progresses the fleet fishes shallower water, and ripe, ovulated, and spent fish become increasingly predominant in the catch. In the Hokitika Canyon spawning is at its maximum between late July and late August, in 400–600 m.

The time taken for fish to spawn was estimated by use of two techniques. Estimates of minimum spawning time ranged from 14 to 27 days; however, estimates of 20–27 days are considered most reliable. Maturation time takes 5–6 days, so female hoki may spawn 3–5 batches of eggs during this period. Ovulated females were caught throughout the day, though a daily maximum in ovulated females may occur during 1800–2400 h. This suggests that female hoki may ovulate at any time of the day or remain ovulated for more than 1 day before spawning. Diurnal vertical migrations of hoki spawning aggregations appear independent of ovarian development. This report proposes a model which describes seasonal changes in hoki spawning dynamics in the Hokitika Canyon, and also discusses the implications of the work with respect to stock assessment techniques to determine hoki biomass.

Introduction

The fishery for hoki (*Macruronus novaezelandiae*) on the west coast of the South Island (WCSI) is New Zealand's largest commercial fishery in terms of total catch. Despite the importance of this fishery the reproductive biology and spawning behaviour of hoki are poorly understood. Biological data collected from the hoki fishery by the MAF Fisheries Scientific Observer Programme provided an opportunity to examine spawning behaviour. This report summarises the data collected, describes aspects of the seasonal spawning dynamics of hoki, and provides an estimation of the time hoki remain on the spawning grounds. Methods used in annual stock assessments for the hoki fishery include assumptions about spawning behaviour. This report discusses issues which will help test these assumptions.

The annual hoki catch dramatically increased after the increase in Total Allowable Catch (TAC) to 250 000 t in 1986. From 1 October 1990 the TAC was redefined as Total Allowable Commercial Catch (TACC), and this was reduced in 1990 to 200 000 t. Most of the hoki catch has been taken from the spawning aggregations on the west coast of the South Island. This fishery is centred around the Hokitika Canyon, though spawning fish are caught as far north as Cape Foulwind (Figure 1).

The reported WCSI hoki catch peaked at 220 000 t in 1988, but subsequently declined to 165 000 t reported in 1990 (Sullivan 1991). The fleet is dominated by large chartered factory trawlers fishing with midwater gear. During the middle of the season up to 60 vessels may fish on the main spawning aggregations. Fishing activity of the fleet is constrained by a restriction zone which excludes vessels over 43 m length from within 25 n. miles of the coast. The line truncates the head of the Hokitika Canyon (*see* Figure 1) and was introduced to protect the inshore domestic fishery from competition with larger vessels.

Spawning occurs in winter, and the hoki migrate to submarine canyons, where they school in large aggregations. There are major spawning grounds on the west coast of the South Island and in Cook Strait. Hoki also spawn in smaller aggregations outside these areas (Livingston 1990). The WCSI hoki spawning season is a predictable annual event.

Hoki begin to aggregate on the spawning grounds from late June, reach a peak in abundance between late July and early August, and most fish have dispersed from the grounds by early September (Sullivan 1991).

Hoki are multiple batch spawners which produce several batches of eggs during a spawning season (M. E. Livingston, MAF Fisheries pers. comm.). All batches are thought to be produced from one group of primary oocytes (synchronous development). Before spawning, each batch of eggs undergoes vitellogenesis, hydration, and ovulation. Ovulated (running ripe) fish are thought to spawn eggs at night (Zeldis in press).

In general, female hoki must reside in the spawning area for a minimum time to ripen and spawn all batches of eggs. However, it is possible that some females arrive in an ovulated state with a batch ready to spawn, whereas others may leave without spawning all batches of eggs. A reduction in the mean length of fish over the spawning season (Sullivan & Cordue 1990, Sullivan 1991) shows that turnover occurs as smaller fish replace larger fish in the spawning population. This implies that the spawning hoki population continually changes and fish immigrate and emigrate throughout the season.

The concept of turnover has important implications for stock assessment. Recent stock assessments for the WCSI hoki stock have focused on obtaining a series of relative biomass estimates by use of three methods:

1. random trawl surveys of fish in the dispersed phase;
2. catch per unit of effort data;
3. acoustic surveys of spawning aggregations.

The relative abundance indices are then applied in a stock reduction analysis to model changes in hoki biomass (Cordue *et al.* 1992).

Indices of the relative biomass of fish on the spawning grounds were obtained from acoustic surveys. Surveys of WCSI aggregations were carried out in 1985 and then annually from 1987 to 1991. These surveys were designed to take a series of sample transects of the grounds to produce an "instantaneous snapshot" of the spawning biomass. The resulting estimates of relative abundance were fitted to a model of expected hoki spawning biomass. The model assumes hoki biomass varies over time; there is a build-up during the early season to a plateau, then a decrease towards the end of the season.

The series of snapshots taken during the season provide estimates of the mean season plateau height, which allow the season's spawning biomass to be modelled (Cordue 1991). The total spawning biomass is equivalent to the integral of biomass against time. To obtain the actual stock biomass, total spawning biomass is divided by mean residence time. Residence time is unknown, but is assumed to be constant between seasons (Cordue 1989), and, therefore, mean plateau height can be used as a relative annual index of stock abundance. The validity of this assumption is unknown, but the assumption is crucial for the assessment of hoki spawning stocks.

There is also potential to assess hoki stocks from egg production surveys (Zeldis in press). Estimates of daily egg production made during the spawning season are used to estimate biomass. Different egg production methods require the determination of different parameters of hoki reproduction: annual fecundity, daily spawning fraction, batch fecundity, and the population sex ratio (Parker 1985, Zeldis in press). These can be adequately determined only when the spawning dynamics of hoki are understood.

The biological data collected by scientific observers enable investigation of the spawning behaviour of hoki. The objectives of this report are to document the spawning dynamics of hoki in relation to the WCSI fishery and to estimate the time that hoki reside on the spawning grounds.

Methods

Data collection

Since 1986, vessels which fish for hoki on the WCSI spawning fishery have been allocated scientific observers to collect biological data from the commercial catch. The primary aim of this sampling programme is to determine the size and age frequency of the catch. Female hoki ovarian development stage data were collected during the 1989, 1990, and 1991 spawning seasons, and these data are the basis of this report.

Ovarian staging

Gonad maturation in hoki is complex and there are many different states of development (M. E. Livingston, MAF Fisheries pers. comm.). An unambiguous hoki ovarian development staging scheme was needed to ensure ovarian development data were accurate and meaningful. The criteria used for the definition of gonad maturity are described in Appendix 1. The stages were defined as follows: stage 1, immature or resting; stage 2, ripening or maturing; stage 3, ripe; stage 4, running ripe (ovulated); stage 5, spent.

The stages are identified by either the condition of the eggs or the physical structure of the ovary. A maturing ovary is a solid mass of opaque eggs, and the ripening of this ovary is defined by the presence of hyaline eggs within the egg mass.

Female hoki are batch spawners, and the ovaries of each fish develop through stages 2, 3, and 4 several times until all batches are ripened and spawned. Consequently, stages 2 and 3 include first time spawners and fish which have already spawned one or more batches of eggs.

Sampling procedure

Scientific observers were asked to establish a sampling point from which all length frequency samples were collected, and fish could not be sorted by size before reaching that point. Sampling points were usually established at fish ponds or on factory conveyors.

Observers were to take samples at specified random times each day (the random times were defined by MAF Fisheries Greta Point scientists). If no fish were available from the chosen sampling point at the given time, the sample was taken from the next tow. One random sample was usually selected from each 12 h of fishing.

At least 100 fish were measured to the nearest centimetre below total length for each length frequency sample. All fish were sexed and the gonads of female fish were staged. Date, time, latitude, longitude, bottom depth, and groundrope depth were recorded for the start and end of each trawl. Headline height, gear type, and catch weights were also recorded.

Sample frequency

The number of samples collected during the season was roughly proportional to the size of the commercial catch. More length frequency samples were collected in July and August than in late June and September (Figure 2). The collection of samples is related to the distribution of the fleet, which varies between seasons. Although the fleet is generally centred on the Hokitika Canyon, in 1989 and 1991 the fishery operated more on the northern grounds late in the season and this is reflected in the sample distribution.

Data analysis

Ovarian stage analysis

For initial analysis, samples were summarised as the percentage of fish in each sample at each ovarian development stage.

Samples collected early in the spawning season were used to assess the reliability of the staging. At this time, hoki ovaries are predominantly maturing (stage 2), and few gonads are at other stages. Consistency between individual observers was assessed by examining the variance within a day between sample percentages of each stage. Samples taken on days on which there were very high variances were considered spurious and examined further. However, only one set of observer data was inconsistent, and the stages collected from that trip were excluded from the data set. Ovarian stage 1 (juvenile and resting) fish were also omitted from further analysis.

Ovarian development stages were analysed for diurnal, seasonal, and depth trends in hoki spawning behaviour. The percentage at each stage was plotted against relevant variables recorded at each trawl station. Where appropriate, the data were also divided into subsets to allow further analysis of possible relationships. The strength of apparent trends was assessed by use of linear regression.

Annual subsets of samples from the Hokitika Canyon were used to examine spawning as a seasonal event. The Hokitika Canyon was defined as between 42° 25′ and 42° 45′ S. Daily mean percentages for each stage were calculated from all samples collected from the Hokitika Canyon. These were then converted to relative numbers of fish

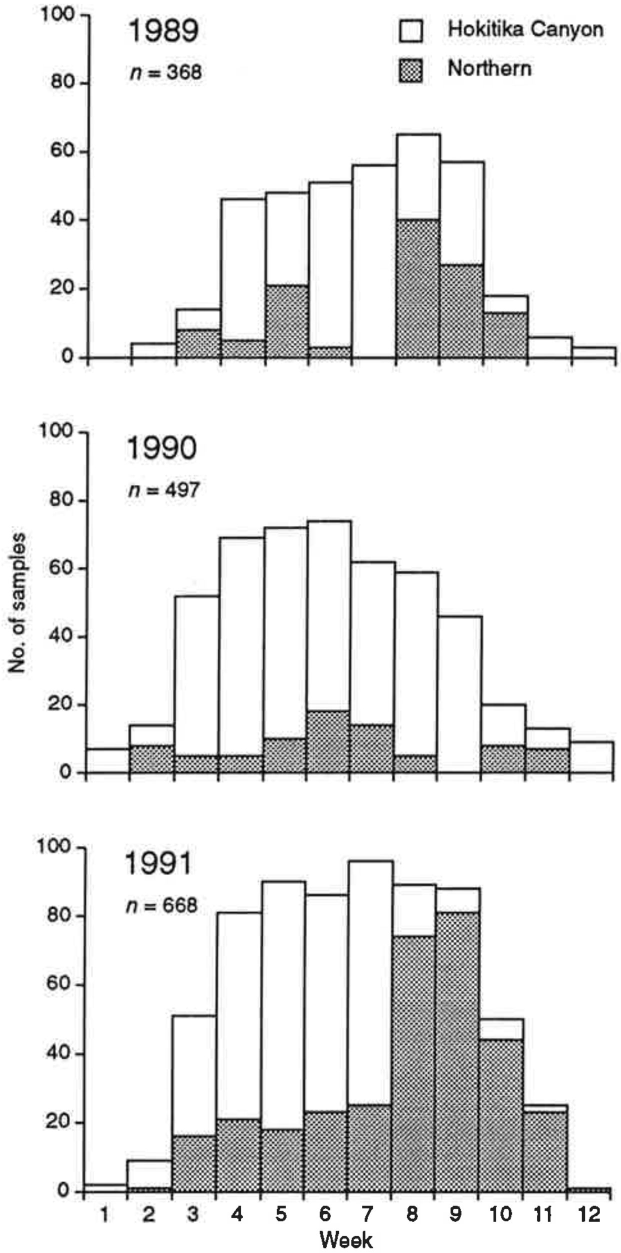

Figure 2: Weekly frequency of sample collection from the Hokitika Canyon and Northern (north of 42° 25′) fishing grounds during 1989, 1990, and 1991. (Weeks are consistent across years, Week 1 commenced on 15 June; *n* = total number of samples.)

caught at each stage by scaling to the smoothed total daily catch taken from the Hokitika Canyon. Smoothing of catch data was performed *after* Cleveland (1979). The median season day and the day interquartile range were calculated for each season for the relative numbers of stage 2 and stage 5 fish.

Length-based analysis

Samples collected from the Hokitika Canyon were pooled to produce composite daily length frequencies for each stage. The mean length and variance of each daily length frequency were calculated.

The mean lengths for stage 2 and stage 5 fish were regressed against the day of the season; each datum was weighted in the regression by the inverse variance of the mean length. The regression lines fitted to these data approximate the seasonal trend in mean length for both stages. The time taken by fish in the Hokitika Canyon to spawn can be estimated by the offset between regression lines. Because the regression lines are not parallel, the mean spawning time was calculated across the range of mean lengths observed during the spawning season. For each day of the season, the mean length of stage 2 fish was calculated from the regression. Spawning duration was then calculated from the time delay before fish of that mean length occurred in the stage 5 regression. To determine the mean season spawning time for the Hokitika Canyon, each spawning period was weighted by an estimate of the relative number of stage 2 fish caught in the Hokitika Canyon on that day of the season.

To calculate the standard error for the annual estimates of spawning time, the stage 2 and stage 5 regression lines were assumed to be parallel. The variance was then calculated as the sum of the variance of the two intercepts divided by the square of the mean slope for the regression lines. This technique probably underestimates the true standard error because it does not incorporate all sources of variance from the regressions.

The length-based analysis was restricted to data from the 1990 and 1991 seasons because insufficient data were collected from the Hokitika Canyon in 1989.

Results and discussion

Spawning behaviour

Between tow variation

The percentage of male fish in individual samples varied from 0 to 100% (Figure 3). In 1989 the sex ratio of the hoki catch was almost 50 : 50 over the spawning season. However, the percentage of male fish in the catch declined in subsequent years. A series of median tests (Mood 1950) showed that the distributions of the sampled sex ratios were significantly different between all years (chi-square test, $p < 0.05$). There was no apparent trend in mean daily sex ratio over the spawning seasons.

During the spawning season there was a general trend of diminishing proportions of stage 2 fish and an increase and subsequent decrease in the proportion of stage 3 and stage 4 fish. Towards the end of the season stage 5 fish were more prevalent in the catch (Figure 4). There was wide variation in these data. The proportion of fish at any ovarian development stage varied markedly between samples on a single day. This suggests that there were different stages of ovarian development between the aggregations fished.

The extent of between aggregation variation may be underestimated by the sampling programme. Sample collection depends on the fishing activities of the commercial fleet. Vessels often carry out long tows and fish through several aggregations of fish, and this could dilute the variation that is there.

There were obvious annual differences in the maximum percentages of stage 4 and stage 5 fish in ovarian samples (*see* Figure 4). In 1991, these stages accounted for a much smaller proportion of the sampled catch than in 1989 and 1990. This may reflect an actual change in the availability of these fish to the fleet in 1991.

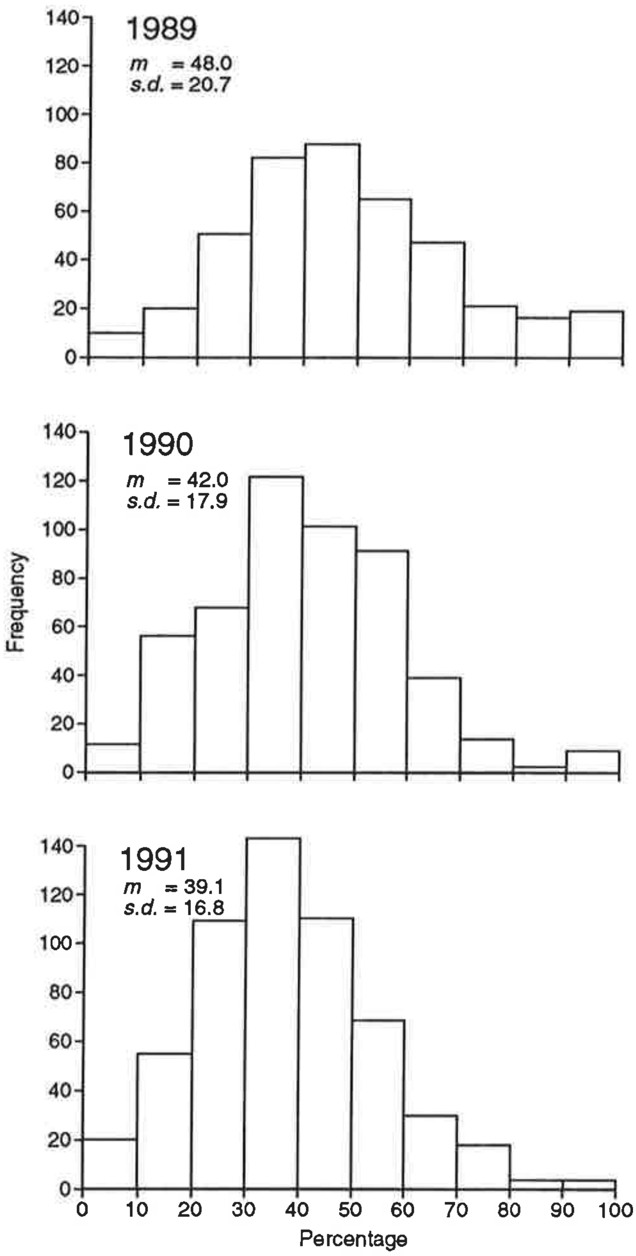

Figure 3: Frequency distribution of the percentage of males in each sample collected from the 1989, 1990 and 1991 WCSI hoki fishery (m = mean of sample percentages, sd = standard deviation of sample percentages).

Diurnal patterns

The hoki ovarian development stages showed no strong diurnal trend in spawning behaviour. Ovulation is probably the most discrete phase of the spawning cycle and, therefore, the most likely to reveal diurnal changes. There was no significant increase or decrease in the proportion of ovulated fish caught during any day period (Figure 5a). However, when only short tows (less than 3 h) were examined there were fewer samples with no ovulated fish between 1800 and 2400 h (Figure 5b).

Depth pattern

Spawning aggregations of hoki in the Hokitika Canyon are generally fished in 300–600 m, though some fishing does occur in deeper water (600–1000 m). Most deepwater fishing occurs before late July, and the fleet concentrafort in shallower water for the rest of the spawning season (Figure 6).

The spawning condition of fish caught on the bottom varied with bottom depth (Figure 7). Maturing (stage 2) fish dominated catches in 550–800 m depth range. However, the proportion of

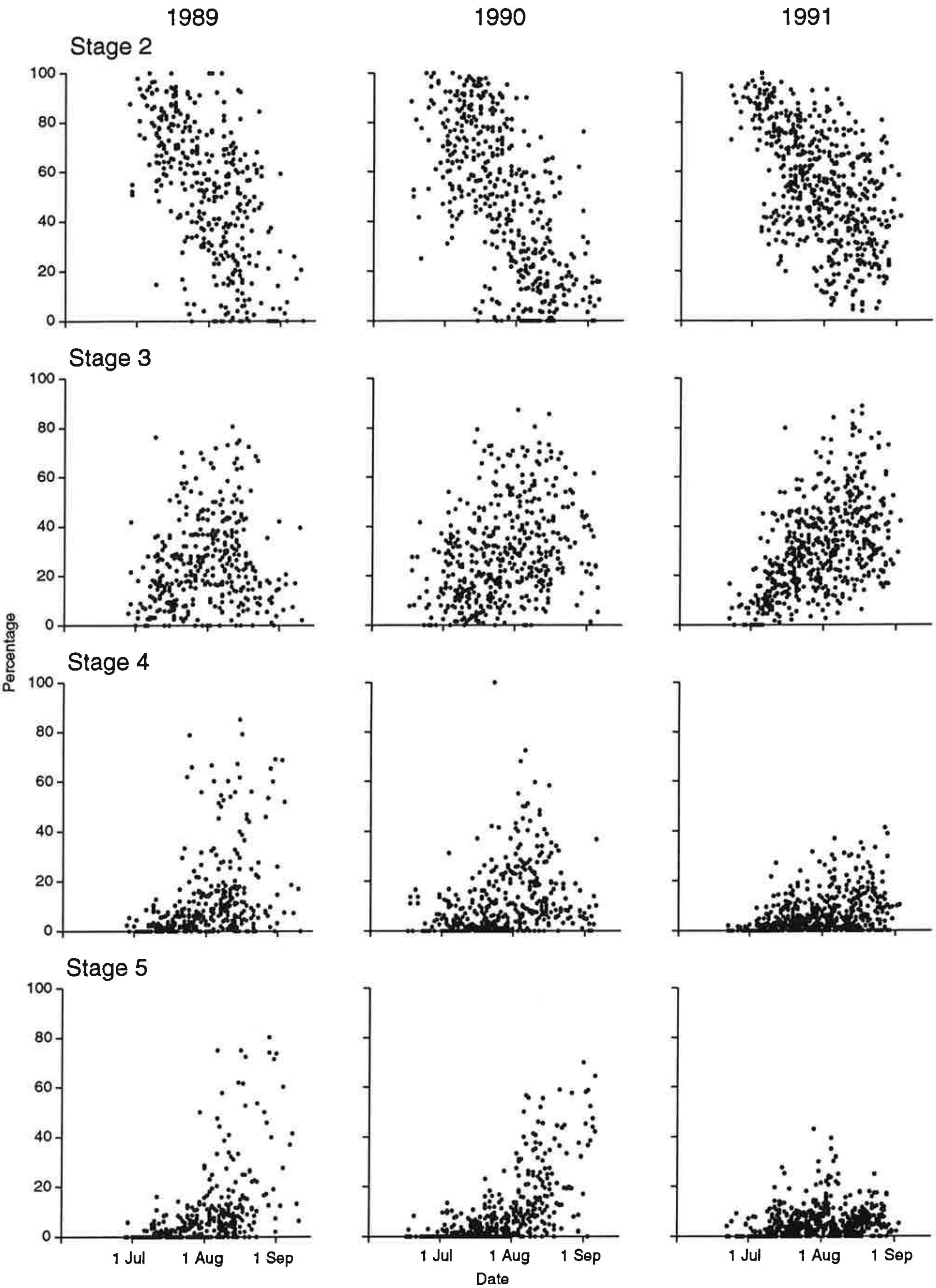

Figure 4: Percentage of each ovarian stage in samples during the 1989, 1990, and 1991 hoki WCSI spawning seasons.

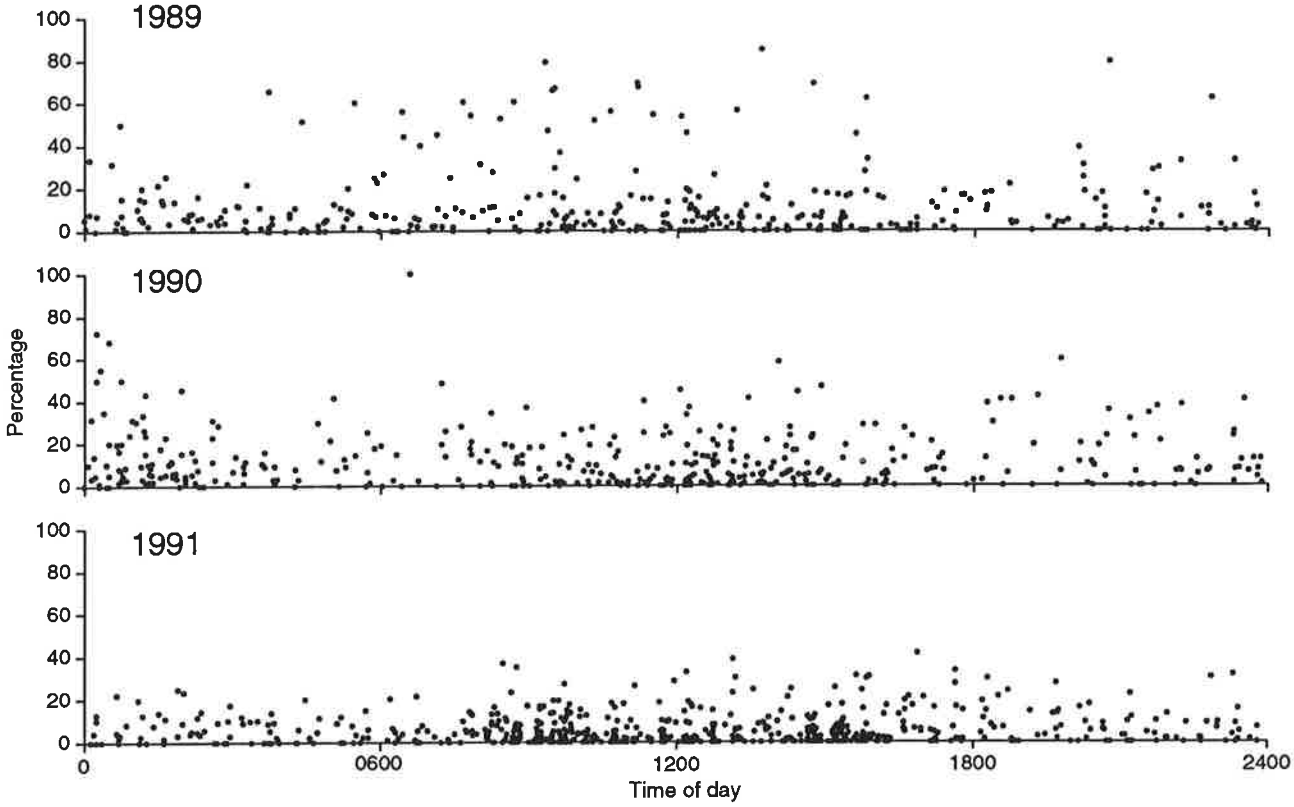

Figure 5a: Percentage of ovulated fish (stage 4) in ovarian samples against time of day sample taken (mid time of tow) for 1989, 1990, and 1991 hoki spawning seasons.

maturing fish declined as bottom depth decreased and there was an increase in the proportion of spawning or spent fish caught in shallower water.

Most ovulated fish were found in 400–600 m. There may also be substantial spawning in shallower water, but the extent of this is not known because the fishing fleet and, therefore, the sampling programme, is constrained by the 25 n. mile restriction zone. This line truncates the Hokitika Canyon at depths which range from 300 to 500 m and so restricts fishing in shallower depths.

The ovarian development stage data suggest that maturing hoki enter the spawning ground from deep water (700–800 m) and move to shallower water as their ovaries ripen to spawn. Vessel movement usually relates directly to actual fish abundance; the fleet fishes on aggregations of fish to maintain high catch rates. From late July spawning is at its peak in the Hokitika Canyon and the fleet concentrates fishing activity in shallower water. The absence of tows in deeper water after late July may be because aggregations of fish previously in these depths have moved into shallower water and the major migration of fish into the Hokitika Canyon has ceased.

The proportion of each ovarian development stage was also examined against height fished above the sea floor (bottom depth minus net depth) (Figure 8). Earlier results suggested that spawning occurred at night (*see* Figure 5b), when hoki aggregate in mid water. However, even when the analysis was restricted to samples taken from tows conducted at night, there was no obvious trend for any stage. The large proportion of maturing fish caught in mid water suggests that vertical migrations are probably independent of ovary condition.

The strength of any trend in ovarian development stage is obscured by inaccuracy of depth recordings. Fishing in and around submarine canyons means the depth fished and the height of gear above the bottom may vary greatly during a tow. Because fish may be taken over a wide range of depths, the sampling programme does not have sufficient power to detect a significant relationship with ovarian development stage.

More tows were made near the bottom in 1990 and 1991 than in 1989 (10.3, 48.6, and 64.9% for 1989, 1990, and 1991 respectively). This change in the vertical distribution of sampled tows is a result of a change in fishing activity between these years; since 1990 midwater gear was used closer to the bottom.

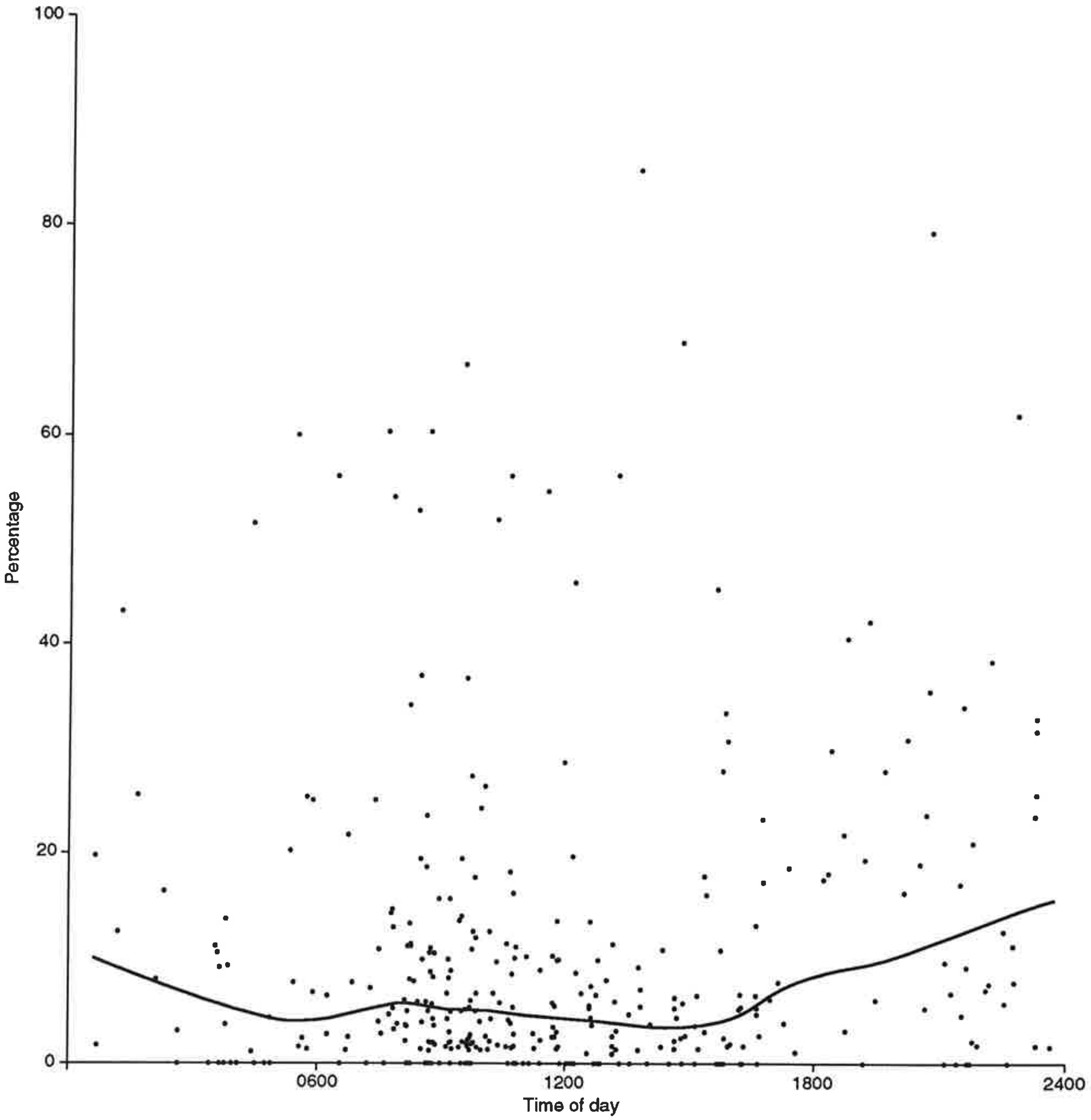

Figure 5b: Percentage of ovulated fish (stage 4) in ovarian samples against time of day sample taken (mid time of tow) for all tows of less than 3 h duration (combined from 1989, 1990, and 1991 hoki spawning seasons). Plotted line represents the trend in the data produced by use of a lowess smoothing function (*see* Cleveland 1979).

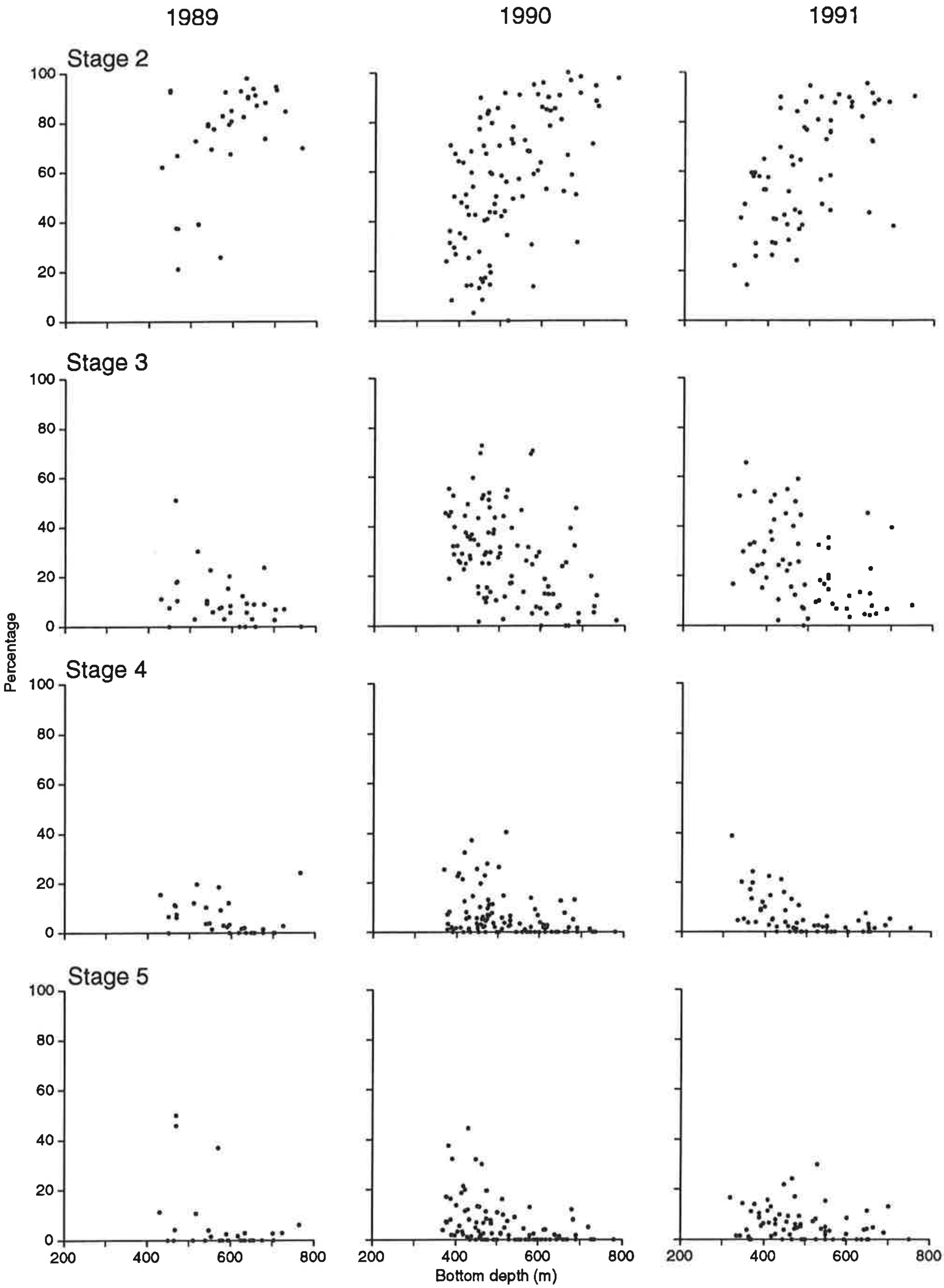

Figure 6: Percentage of each ovarian stage against bottom depth from bottom tows (groundrope less than 30 m above bottom) for the 1989, 1990, and 1991 hoki spawning seasons.

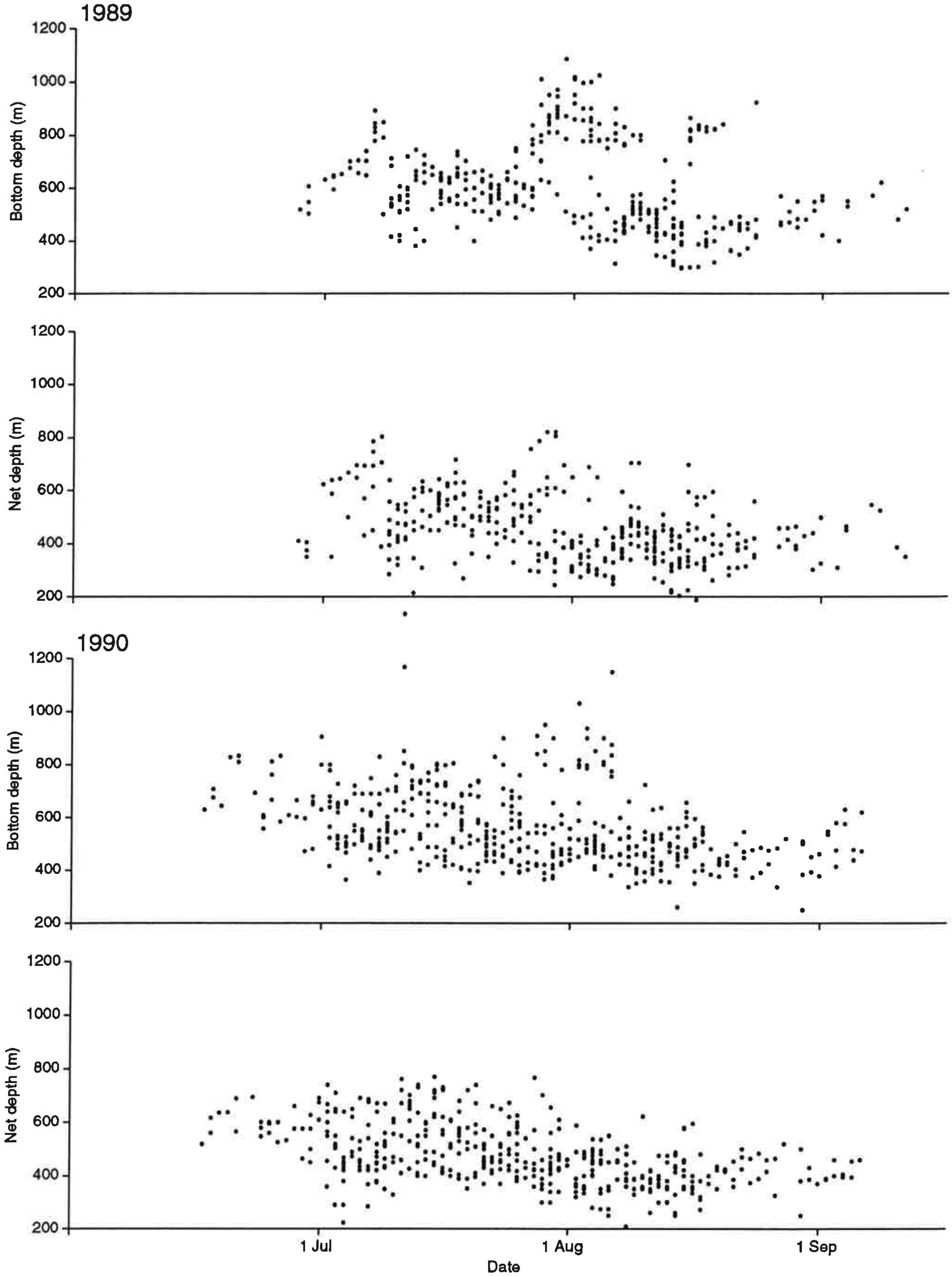

Figure 7: Bottom depth and net depth (groundrope) of tows from which hoki samples were taken during the 1989, 1990, and 1991 hoki spawning seasons.

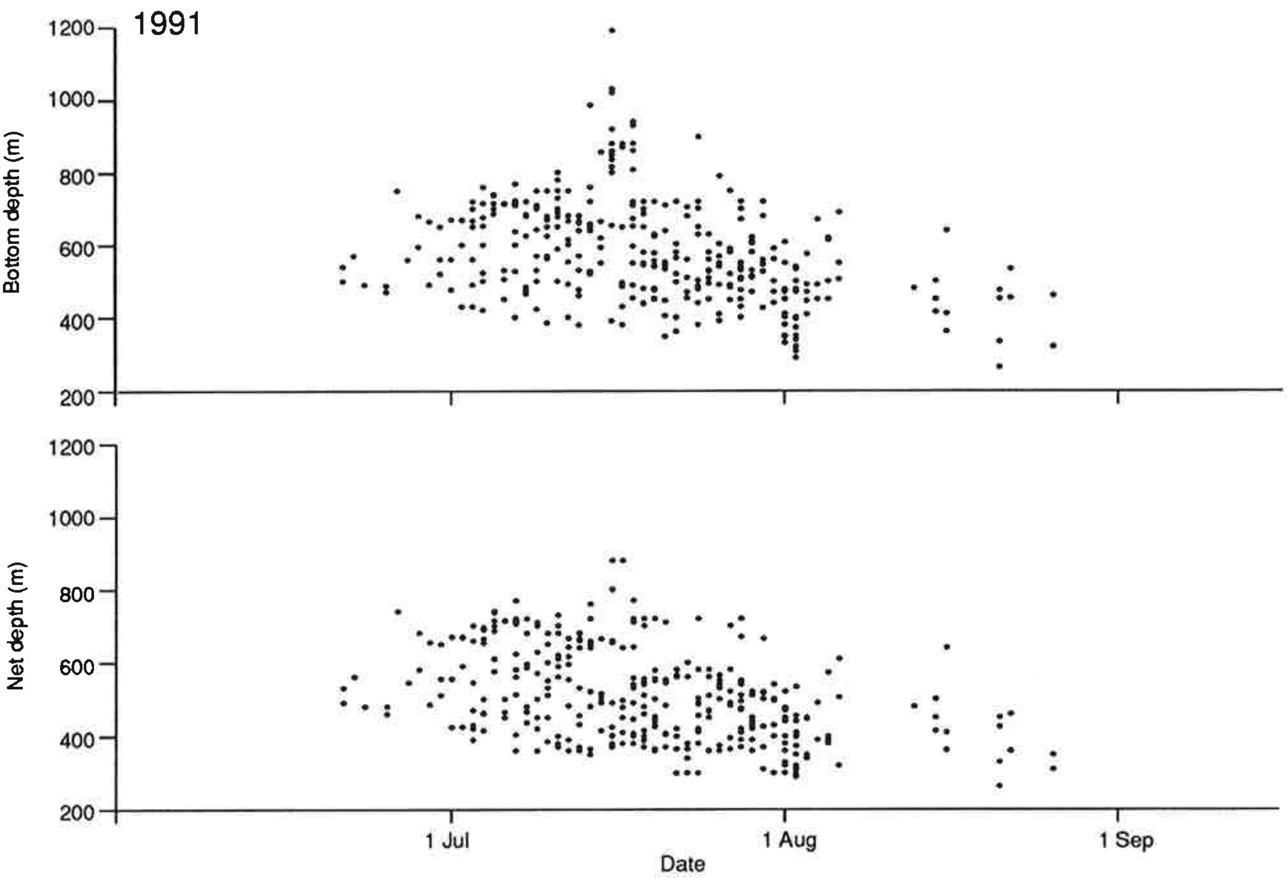

Figure 7 — *continued.*

Spawning dynamics

Spawning biomass

The immigration of maturing fish and their subsequent spawning do not appear to occur as a single continuous event. The daily percentage of maturing female fish caught from the Hokitika Canyon during the 1989, 1990, and 1991 seasons is shown in Figure 9. The percentage of fish fluctuates greatly during the season. Conversion of staging data to estimates of the relative number of fish caught at each stage better depicts seasonal trends in the spawning population (Figure 10). Each seasonal estimate of relative numbers at each stage is comparable within and between years. However, annual variation in the total number of fish caught depends on the total catch and the distribution of the commercial fleet.

The large peaks of stage 2 fish early in the season suggest that fish enter the fishery as several units or "spawning groups". These peaks are thought to represent the arrival of new fish because the total number of fish at other ovarian developmental stages is maintained, whereas the proportion and number of maturing fish increases.

An interpretation of these data is that each spawning group of fish arrives over 5–7 days, at a frequency of one new group entering the fishery about every 10 days. Four major spawning groups arrived in each of the 1989, 1990, and 1991 seasons. However, the pattern is complicated by the fact that hoki are batch spawners which revert to stage 2 between the spawning of individual batches. Consequently, during the mid season, stage 2 hoki will include both prespawning fish and fish which have previously spawned. However, the appearance of stage 5 fish in peaks at the end of the season supports the theory of spawning groups. The assumed relationships between groups of maturing and spent fish are shown in Figure 10.

Regular spawning events during the season could also be responsible for the observed fluctuations in the number of stage 2 fish. The relative number of stage 2 fish appears to be related to the relative number at stage 3. When the relative number of stage 2 fish decreases during the spawning season, the relative number of stage 3 fish increases, and vice versa. This may be an artefact of the scaling of calculated daily percentages to the catch, but it could also reflect the occurrence of major spawning events. Even if such events occurred, hoki could still

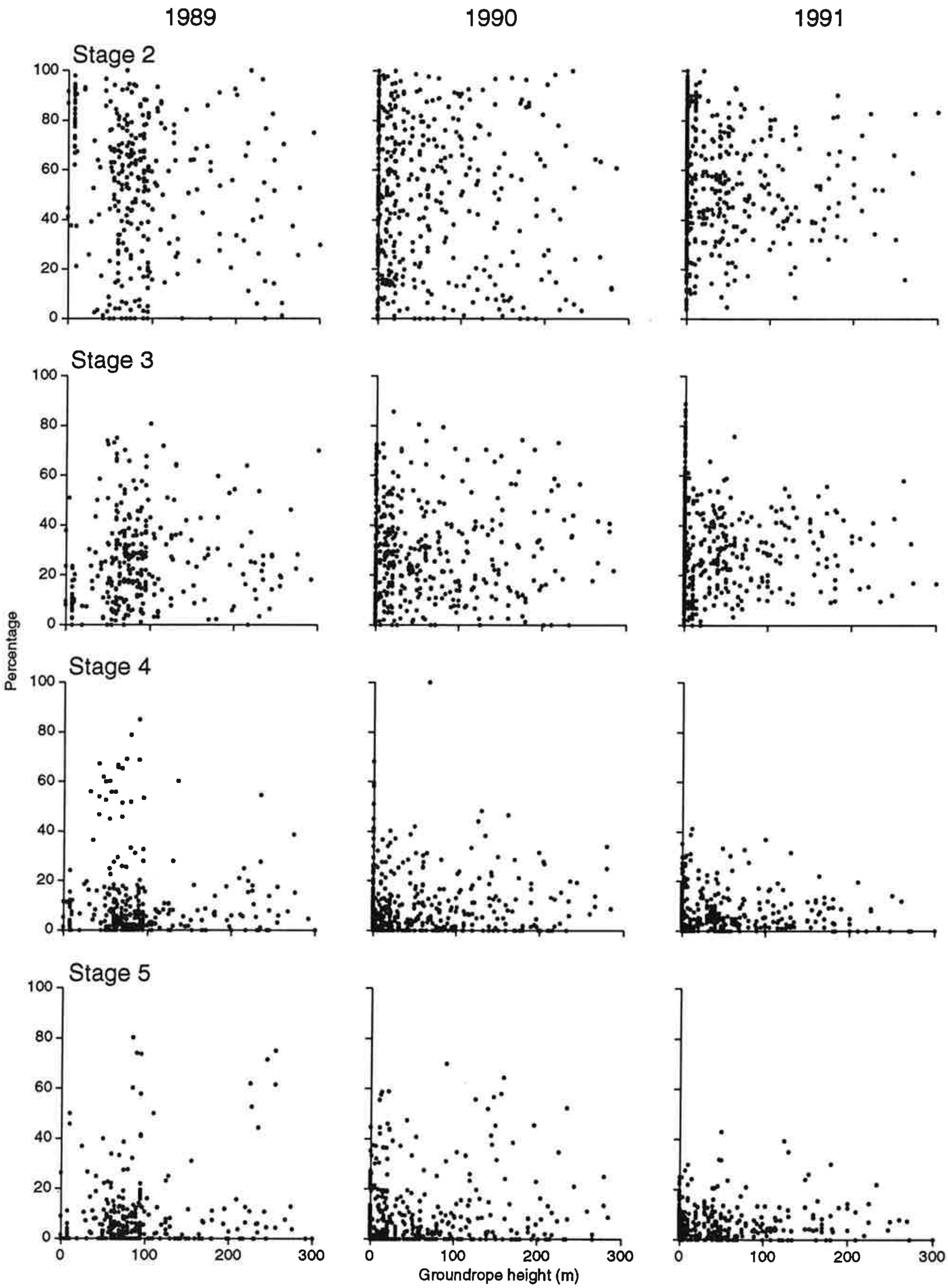

Figure 8: Percentage of each ovarian stage against groundrope height (above the bottom) for the 1989, 1990, and 1991 hoki spawning seasons.

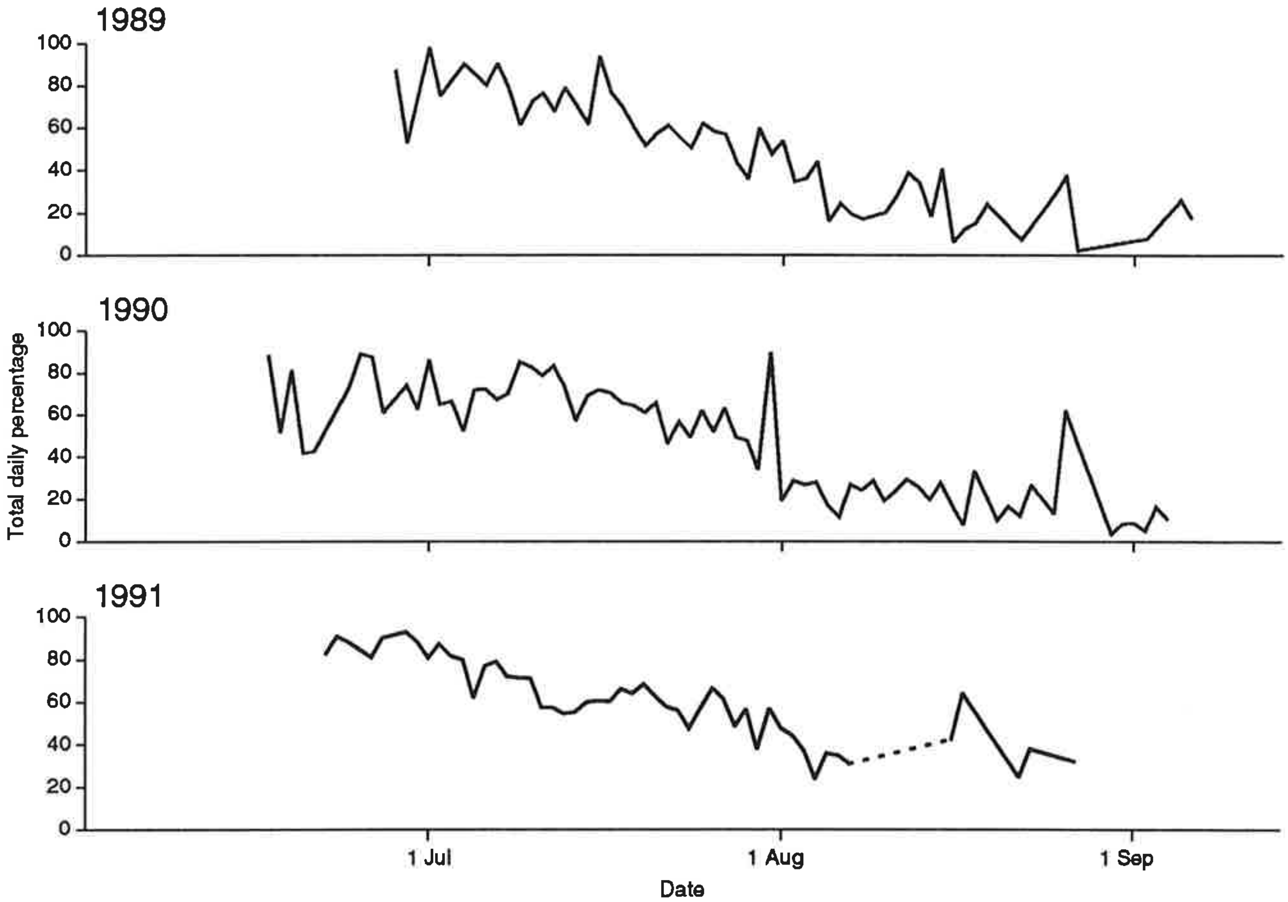

Figure 9: Total daily percentage of stage 2 (maturing) fish from ovarian samples collected in the Hokitika Canyon for the 1989, 1990, and 1991 hoki spawning seasons.

arrive in spawning groups. It is possible that both factors could be determining the seasonal spawning dynamics observed in the Hokitika Canyon.

The inherent variability between samples, due to the stratification of fish aggregations, imposes broad confidence intervals on the estimates of numbers at stage at this level of sampling intensity. This between-sample variability may also produce extreme peaks in the data when daily proportions are determined from only a few samples.

Estimation of spawning time

Length frequency data. A decline in mean length of female hoki during the spawning season is apparent for each ovarian development stage. The daily mean length of stage 2 and stage 5 fish from the Hokitika Canyon declined during the 1990 and 1991 spawning seasons (Figure 11). At a given time the mean length of spent hoki is generally larger than that of maturing fish.

There is a good linear relationship between mean length of fish at a particular ovarian stage and day of the spawning season for data from both years. The annual sets of regression lines are approximately parallel and have significantly different intercepts (Table 1). These results show that the decline in mean length of stage 2 fish is

Table 1: Parameters (and standard errors) of the regression of mean length of stage 2 and stage 5 female hoki from the Hokitika Canyon by day for the 1990 and 1991 seasons

	Slope	Intercept	Multiple R^2
1990			
Stage 2	–0.200	95.89	0.767
	(0.015)	(0.86)	
Stage 5	–0.233	102.00	0.757
	(0.019)	(1.30)	
1991			
Stage 2	–0.175	95.77	0.523
	(0.025)	(1.25)	
Stage 5	–0.164	99.59	0.521
	(0.024)	(1.26)	

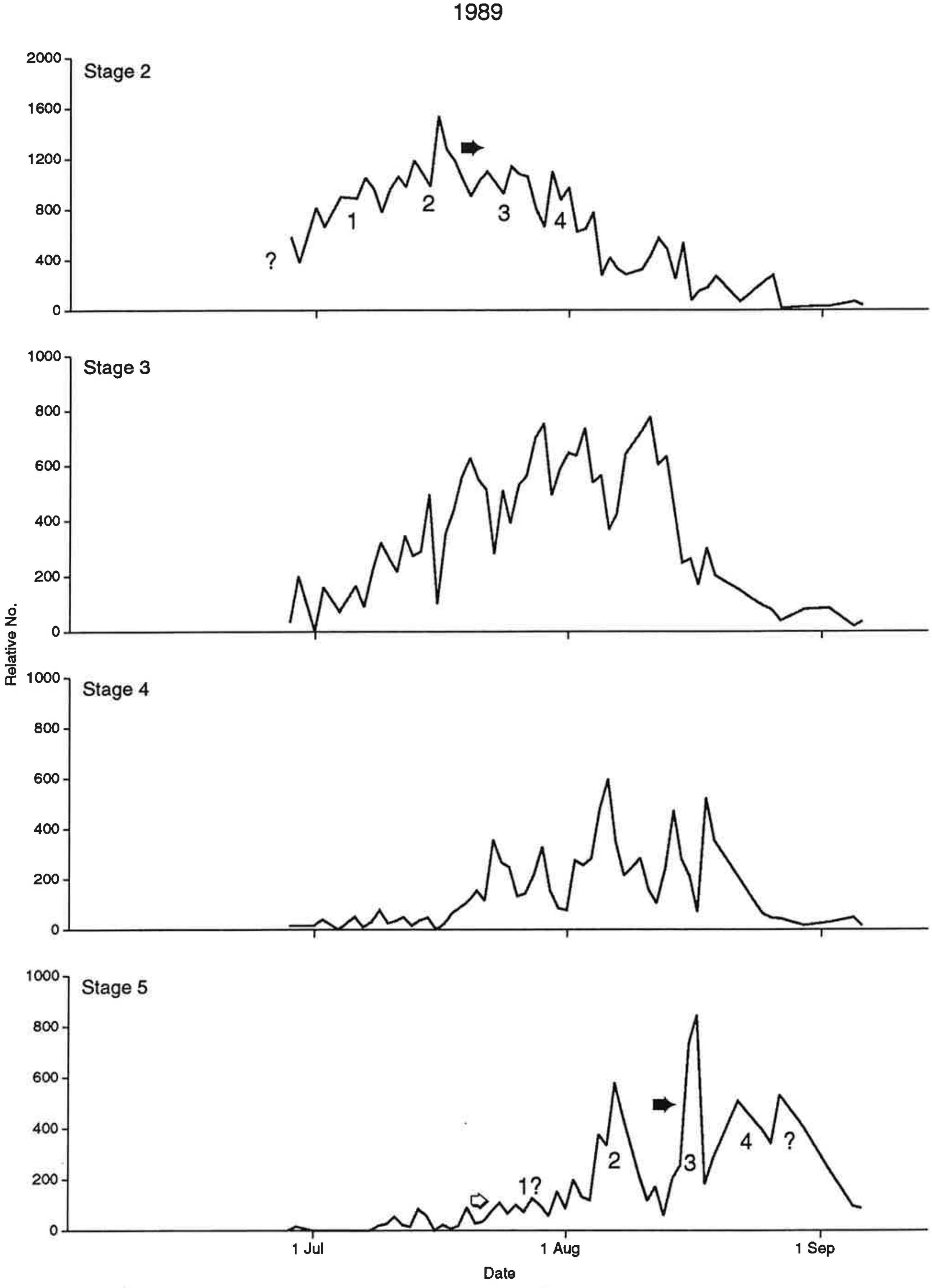

Figure 10: Daily estimates of relative numbers of ovarian stage 2, 3, 4, and 5 fish caught from the Hokitika Canyon during the 1989, 1990, and 1991 hoki spawning seasons. (Numeric labels show suggested spawning groups of stage 2 and stage 5 fish; solid arrows denote median days for relative numbers of stage 2 and stage 5 fish; open arrows indicate events during the spawning season referred to in the text.)

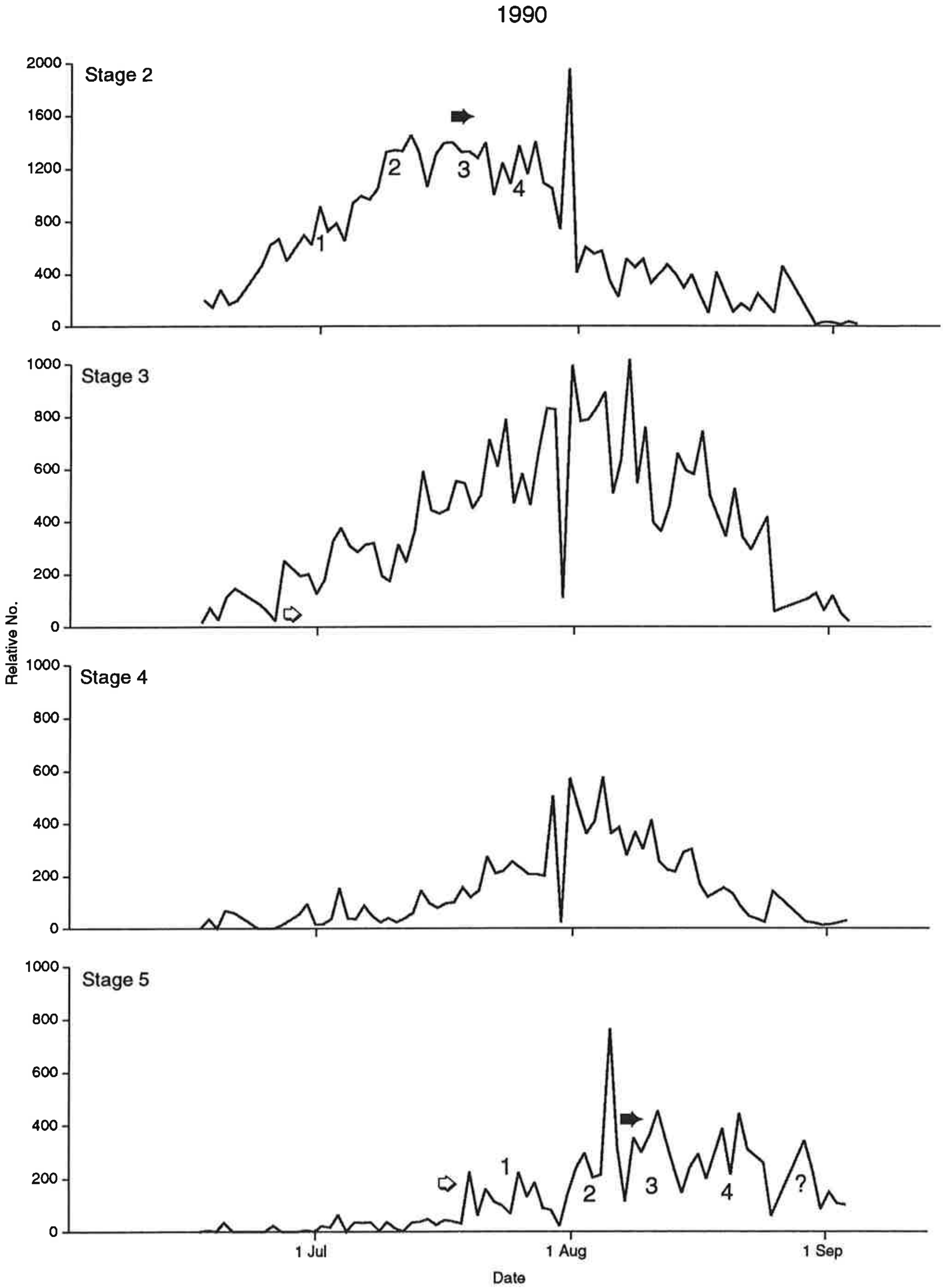

Figure 10 — *continued.*

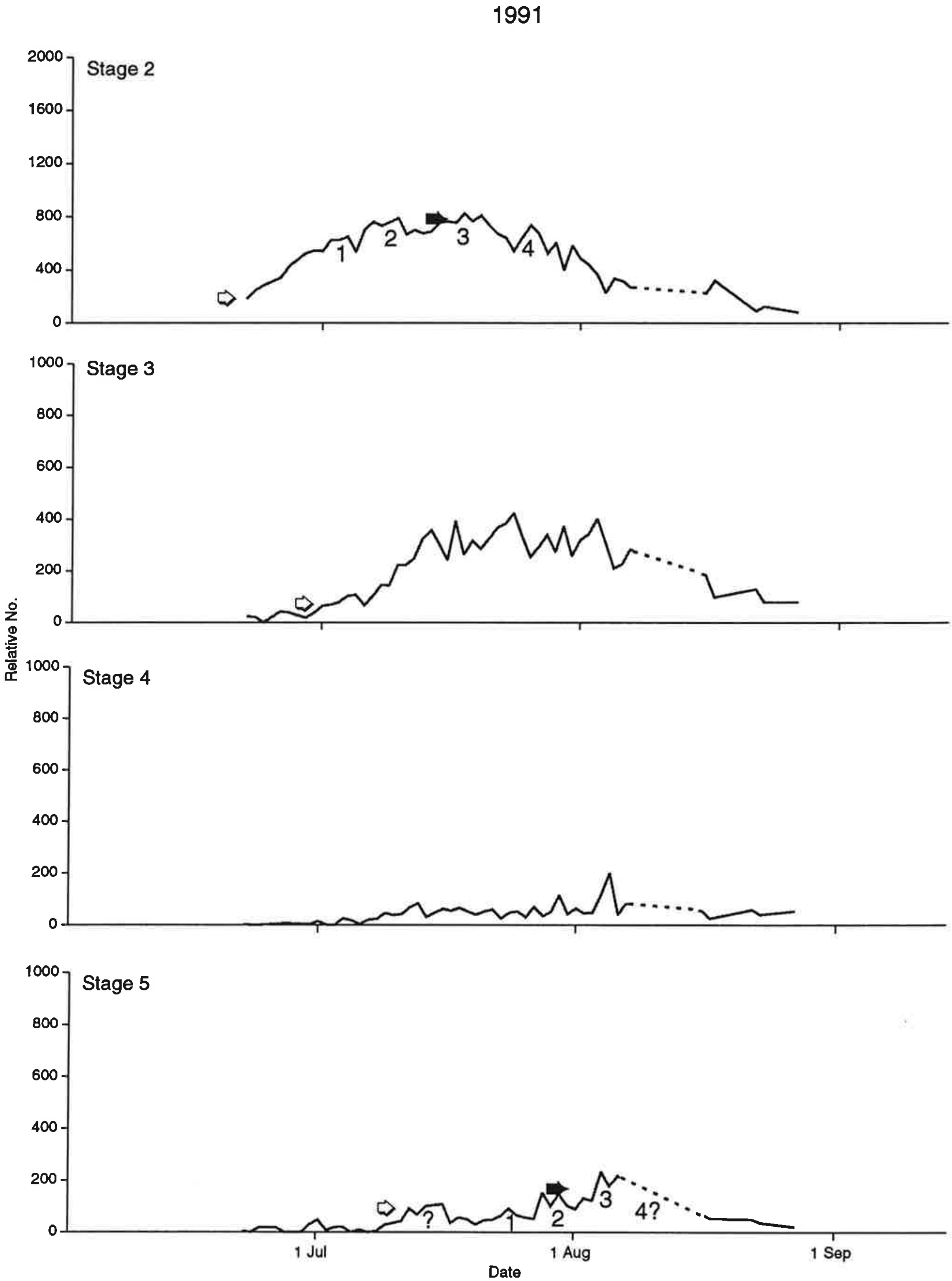

Figure 10 — ***continued.***

closely tracked by the mean length of stage 5 fish. One interpretation of the data is that there is a large delay between the arrival of stage 2 fish of a given mean size and the emergence of fish of same mean size in the population of stage 5 fish. This time difference is assumed to provide an estimate of the minimum residence time that hoki spend on the spawning grounds. This interpretation assumes that the length frequencies of stage 2 and stage 5 fish with the same mean lengths have similar distributions around the mean. The mean season spawning times calculated from length-based data were 19.3 days (standard error 7.2) and 26.4 days (10.4) for 1990 and 1991 respectively.

The fecundity of female hoki increases exponentially with length (MAF Fisheries Greta Point unpublished data). Consequently, larger hoki will spawn larger batches of eggs and/or produce more batches during a spawning season. The time required for these events could increase the spawning time of larger fish on the grounds. A linear regression fitted to the mean length ovarian data assumes a linear relationship exists between spawning time and fish length. The validity of this assumption is unknown.

Early in the 1990 and 1991 seasons some very large spent hoki were caught (*see* Figure 11). However, no maturing hoki of a corresponding size were sampled in the catch. This is probably because the largest maturing hoki arrive early on the spawning grounds, when insufficient samples are taken. Consequently, these fish may not be represented in the daily length frequencies of stage 2 fish, but may be sampled later in the catch as stage 5 fish.

Seasonal ovarian development

In 1990, large numbers of stage 2 fish arrived from about 25 June (*see* Figure 10). There was a time lag of about 5 days before many stage 3 fish appeared in the catches. This probably represents the development time for the initial stage 2 fish to ripen to stage 3. Early in the season the time lag was maintained because numbers of stage 3 fish appeared to closely track numbers of stage 2 fish. Numbers of stage 4 fish followed a similar pattern, behind the numbers at stage 3. This suggests that maturing fish undergo vitellogenesis of the first batch of eggs in about 5–6 days, which is followed by rapid ovulation and spawning. Stage 5 fish were caught 20 days later, which suggests a minimum spawning time of 25 days.

Similar trends were also apparent in the 1989 and 1991 data, though estimates of the time for spawning differed from the 1990 value. In 1989 the numbers of stage 5 fish built up slowly during late July, whereas in 1991 more were first caught in mid July. The appearance of spent fish related to the arrival of maturing fish suggests spawning time estimates of about 20 days and 15 days for the 1989 and 1991 seasons respectively (*see* Figure 10).

Table 2: Median day and day interquartile range (IQR) for relative numbers of stage 2 and stage 5 fish, and calculated spawning times from Hokitika Canyon for the 1989, 1990, and 1991 fishing seasons. (Days are numbered consecutively from 1 June.)

	Stage 2		Stage 5		
	Median day	Day IQR	Median day	Day IQR	Spawning time (days)
1989	49	18	76	16	27
1990	47	19	70	17	23
1991	45	19	59	18	14

The relationship between relative numbers of stage 2 and stage 3 fish was also less clear during 1989 and 1991. Early in the 1991 season there was a 5–6 day delay between the arrival of stage 2 fish and the apperance of large numbers of stage 3 fish. This was consistent with the 1990 data. However, the developmental period could not be defined for 1989 because insufficient ovarian samples were collected from early in the season.

The seasonal median days and the day interquartile ranges for relative numbers of stage 2 and stage 5 fish were used to quantify gross trends in the spawning time. Annual estimates of spawning time were calculated as the difference between the median day for stage 2 and stage 5 fish, and they were similar to those determined qualitatively above (except for 1989, possibly because of the reasons discussed above) (Table 2). The spawning time calculated for the 1991 season was much shorter than those for the 1989 and 1990 seasons. This can be explained by the appearance of a peak in the relative numbers of stage 5 fish early in the season, which was not seen in the previous seasons. The relative numbers at each stage are also poorly known towards the end of the 1991 season because no samples were collected from the Hokitika Canyon during 6–15 August (*see* Figure 10). In previous seasons, many spent fish were caught during this period, and the absence of data has probably resulted in an underestimation of both the median season day for spent fish and the estimated spawning period.

Estimation of spawning frequency

Quantitative estimation of the number of batches and frequency of spawning can be made by the use of seasonal spawning data. The delay between the arrival of fish on to the grounds and the time of first spawning suggests a development time of about 5–6 days. If the time required for a fish to ripen and spawn each batch of eggs is constant, a mean spawning time of 20–30 days would allow female hoki time to spawn 3–5 batches of eggs.

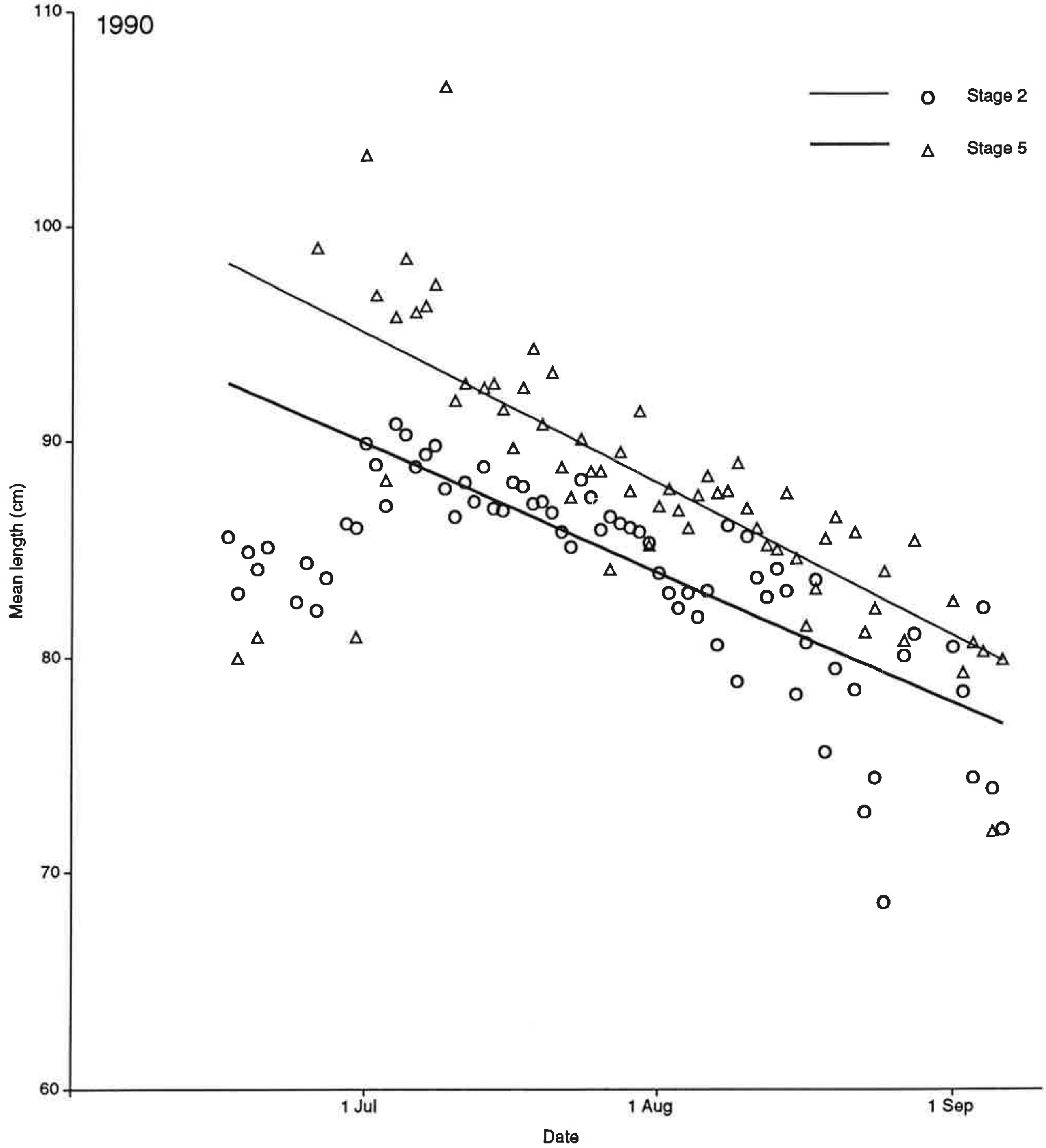

Figure 11: Daily mean length of stage 2 (maturing) and stage 5 (spent) fish from samples collected within the Hokitika Canyon in the 1990 and 1991 hoki spawning seasons. (Plotted lines are linear regression fits to the data.)

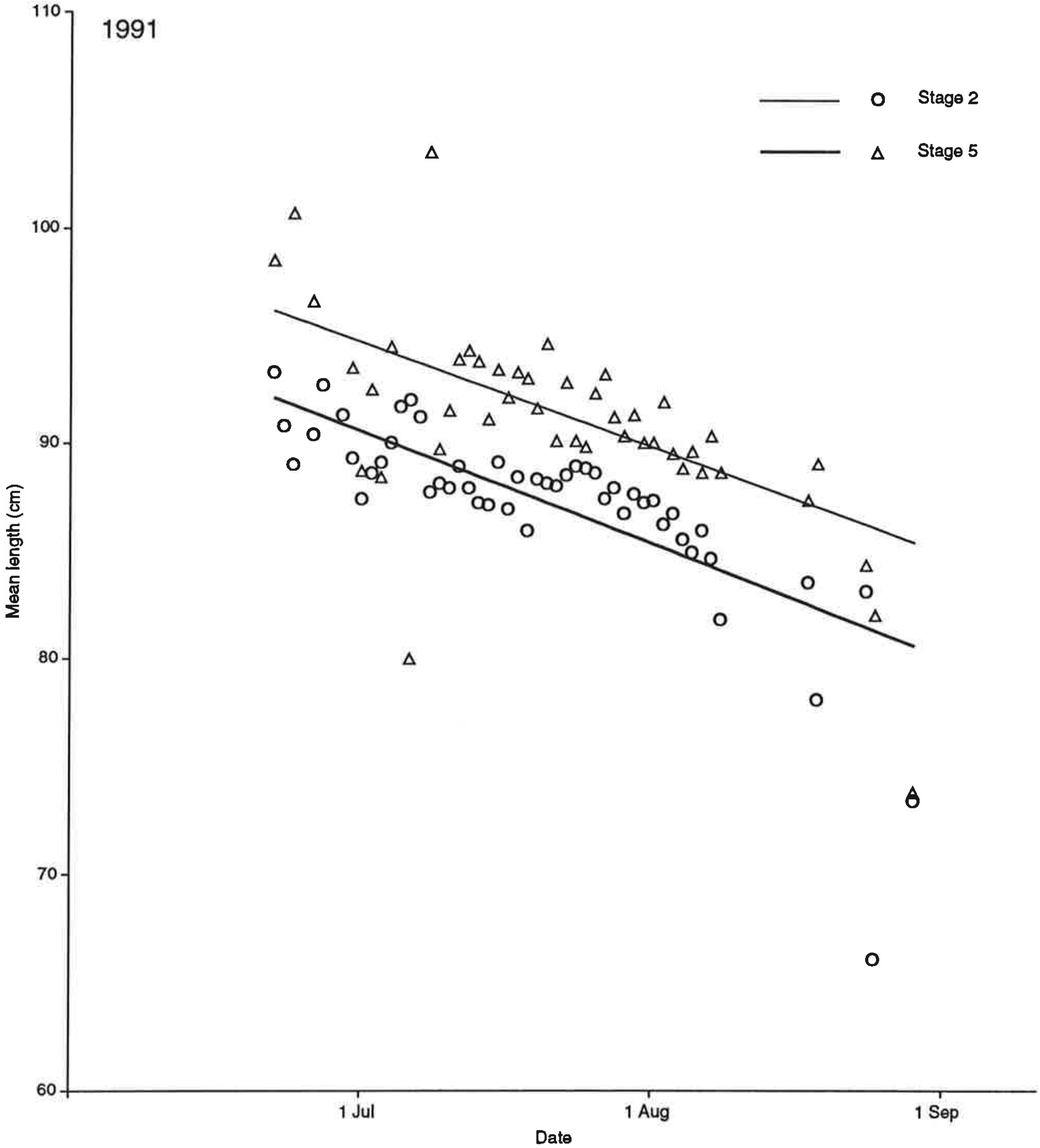

Figure 11 — *continued.*

General discussion

Potential biases in the data

The ovarian development stages collected should not be considered representative of the entire WCSI hoki spawning stock. Catch sampling was restricted by the activity of the fishing fleet, which concentrated effort on large aggregations of fish outside the 25 n. mile exclusion zone. However, acoustic surveys have shown that this area has a substantial hoki biomass (Cordue 1991). The ovarian condition of fish in the aggregations sampled may vary from that of the total population (sampling effort cannot be considered random across all ovary stages) which potentially biases estimates of relative abundance at each stage. However, the gross trends observed in spawning behaviour through the season are still valid for the fished aggregations.

The ability to determine any diurnal and areal trends in spawning behaviour may be impaired by the fishing pattern of the fleet. Because commercial trawls are of long duration and occur around canyon features, accurate time and depth data cannot be collected at each station. Consequently, the relationship between these variables, and the proportion at each stage, is obscured by the quality of data collected. More precise sampling could be carried out by research trawls.

Population sex ratio

During the 1986 and 1987 fishing seasons, when exploitation of the WCSI hoki fishery was increasing, the sex ratio of the sampled catch was about 50 : 50 (author's unpublished data). The decline in the annual percentage of male fish caught from 1989 to 1991 can be attributed to differential maturity ogives for male and female hoki. Male hoki generally recruit into the fishery at a younger age than female hoki (Sullivan & Cordue 1990) and consequently may be exposed to greater fishing mortality. In 1991, the annual decline in the proportion of male fish was maintained, despite the recruitment of a strong year class which dominated the seasonal catch of male hoki (Sullivan 1992).

Spawning behaviour

Observer data suggest that spawning occurs mainly in 400–600 m. Samples taken from research trawls suggest that spawning also occurs in the shallower water inside the 25 n. mile exclusion zone. In a sample of 20 fish from a single trawl at the head of the Hokitika Canyon in August 1989, 50% of female fish staged were running ripe (MAF Fisheries Greta Point unpublished data).

Hoki in spawning aggregations undergo diurnal vertical migrations. On the WCSI aggregations of fish are closely associated with the bottom during the day, but may occur as midwater aggregations at night. These aggregations may be several hundred metres thick and as shallow as 250 m (Patchell 1982). At dawn the fish return to the bottom.

Vertical migration is assumed to be related to diurnal changes in the spawning behaviour of hoki. Early stage eggs occur in the plankton at night, which suggests that spawning occurs nightly over 6–8 h centred at about 0200 h (Zeldis in press). This daily spawning rhythm is supported by the ovarian development staging data. Although good numbers of hydrated fish were caught at all times of the day, a daily maximum of hydrated females was more likely between 1800 and 2400 h. The decline in the percentage of ovulated fish during early morning may indicate that spawning had occurred. This result is consistent with macroscopic ovarian staging data collected from the Hokitika Canyon by the commercial trawler *Ohtori Maru* in 1987 (N. W. Bagley, MAF Fisheries pers. comm.). Ovulated fish were caught throughout the day, though the proportion of ovulated females appeared to reach a minimum early in the morning, which suggests spawning occurred at night (Zeldis in press, D. A. Robertson, MAF Fisheries unpublished data). The data suggest also that female hoki may ovulate at all times of the day and/or may remain in the ovulated state for more than 1 day. Zeldis (in press) considered that the high proportion of ovulated fish in catches supported the latter interpretation.

Estimation of spawning time

Independent calculations of spawning time from the seasonal progression of ovarian development and from length-based staging data produce estimates of a similar magnitude. The estimates of the time taken for fish to spawn should be considered as minimum estimates. Both estimation techniques will underestimate mean spawning times because they are calculated from the assumed delay in the emergence of stage 5 fish from stage 2 fish. This does not allow prespawning stage 2 fish arriving in the Hokitika Canyon to be distinguished from the stage 2 fish that have already spawned at least one batch of eggs.

Spawning duration for the three seasons ranged from 14 to 27 days, though estimates of 20–27 days were probably most reliable. The inconsistency between these seasonal estimates questions the reliability of these techniques. In 1991 the spawning time estimated from the length-based analysis was 26.4 days, whereas that for seasonal changes in ovarian development was 14 days. The length-based method is probably the most feasible of the two techniques proposed to estimate spawning and minimum residence times. It has the potential to estimate a mean spawning time over the entire season and does not depend on accurate definition of the time that prespawning fish enter the spawning grounds and spent fish appear. However, assumptions are still required for the length distributions of prespawning and spent fish and the relationship between spawning time and the size of female hoki. These assumptions can only be validated from extensive random length frequency sampling of fish.

Spawning time estimates suggest the minimum mean duration that fish reside on the spawning grounds. More realistic estimates require data on the migration of hoki into the Hokitika Canyon and the time spent on the grounds after spawning. The rapid decline of the "peaks" of spent fish and the low numbers of these fish caught during a season show that spent fish either depart soon after spawning or become unavailable to the fishing gear. If the prespawning and postspawning behaviour of hoki remains constant between years, the annual estimates of spawning time could be considered as relative indices of residence time. This would enable the monitoring of annual fluctuations in the time that hoki remain on the spawning grounds.

The estimates of spawning time, derived from the length-based technique, have large standard errors, and the estimates calculated for 1990 and 1991 are not significantly different. It is not known whether the variation between seasons is due to variability in the mean spawning period of hoki or to sampling error.

Estimates of spawning time from ovarian development stages can also be extrapolated to estimate spawning time for male fish. The mean length in the commercial catch declines during the spawning season (Sullivan 1991). In general, the magnitude and rate of the decline is similar for both sexes (Figure 12). There was a larger decline in the mean length of male fish in 1991, and this was attributed to the emergence of a strong year class and differences in recruitment ogives between sexes (Sullivan & Cordue 1992). Similar proportions of male and female hoki are present on the spawning grounds during the season, so the observed decline in the mean length of male fish would occur only under similar rates of turnover to that of female fish. Therefore, spawning and residence time are probably similar between sexes.

Seasonal spawning dynamics

Ovarian developmental data collected from the fishery suggest that prespawning hoki may migrate into the spawning grounds in groups. During 1989, 1990, and 1991 four possible major spawning groups were detected entering the Hokitika Canyon each season, over 40 days. The arrival of fish in prespawning groups is also consistent with the movements of large masses of hoki into the Hokitika Canyon seen during acoustic surveys (P. L. Cordue, MAF Fisheries pers. comm.).

If hoki arrive in prespawning groups, the biomass in the Hokitika Canyon could be expected to increase with the arrival of each successive group of spawning fish and possibly peak with the arrival of the last group. Therefore, spawning of the total population could be considered to occur as a series of spawning groups which are undergoing synchronous maturation and spawning. The biomass would decline as each group completed spawning and departed. Each proposed spawning group probably remains in the Hokitika Canyon for 20–30 days. The seasonal trends in ovarian data show that this time could enable female hoki to spawn 3–5 batches of eggs. Similar estimates of batch production have been obtained from examination of egg production and batch fecundity. Patchell (1982) estimated that a 90 cm female hoki would spawn 4–5 batches of eggs per season.

Implications for hoki stock assessment

To enable annual comparisons between hoki biomass estimates, the acoustics model assumes that residence time is constant between years. However, annual variations in residence time would directly affect estimates of relative biomass.

The analysis of ovarian development stages provides two alternative techniques for the estimation of hoki mean spawning time. The time that fish reside on the spawning grounds will probably be directly related to the time required for fish to spawn. Estimates of spawning duration from the 1990 and 1991 spawning seasons, calculated from length-based staging data, were 19.3 days and 26.4 days respectively. The variability between these estimates may show possible annual variability in residence time. Yearly estimates are not necessarily comparable because they are derived from datasets which are potentially biased by the activity of the commercial fleet, and fishing activity is assumed to be similar between years.

The acoustics programme requires further research to validate the current assumptions of constant annual residence time. Reliable estimates of residence time from successive hoki spawning seasons could indicate the constancy of residence time between years. Estimation of residence time

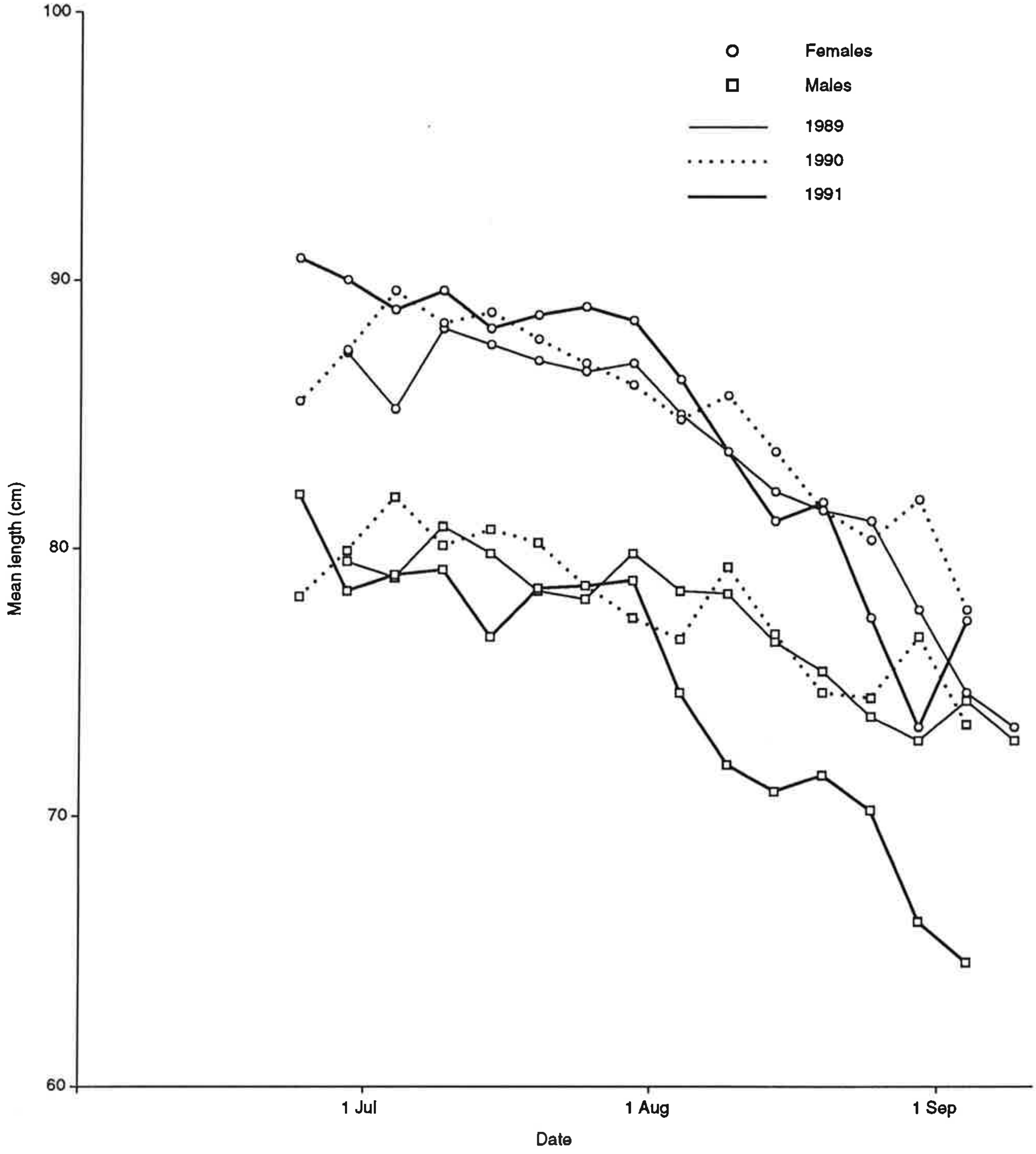

Figure 12: Mean length of male and female hoki for the 1989, 1990, and 1991 WCSI hoki spawning seasons (modified from Sullivan 1991).

could also allow the results of acoustic surveys to be quantified, once the acoustic target strength of hoki was determined. The acoustic survey results could then be interpreted to provide estimates of the absolute spawning biomass.

A targeted sampling programme could provide an estimate of annual residence time. It would require intensive sampling of the spawning population within a restricted area, such as the Hokitika Canyon, over the whole spawning season. Both techniques used in this report provided estimates of spawning time from the delay between the arrival of prespawning fish and the emergence of spent fish. The values of spawning time obtained were underestimates because the ovarian development staging scheme classified prespawning fish and fish which had previously spawned as maturing fish. However, comments from scientific observers suggest that prespawning hoki are clearly distinguishable from those which have already spawned at least one batch of eggs. A more detailed macroscopic staging scheme could result in more accurate estimates of hoki spawning and residence times. The prespawning and spent fish populations in the area surveyed would have to be regularly sampled and this would mean targeting aggregations of fish throughout the depth range that hoki occupy in the spawning grounds.

The collection and analysis of ovarian development stage data has also provided useful background information required for the design of hoki egg production surveys. The data defined the likely period of maximum egg production and the time of the hoki spawning season over which surveys should be conducted. They also helped with the design of a sampling programme that would be needed to provide an estimate of the batch and annual fecundity of female hoki and the sex ratio of the spawning population.

Consequently, further study of hoki reproductive biology is necessary before this model could be used for stock assessment purposes. This research could be conducted in association with a sampling programme designed to estimate residence time. Intensive macroscopic and microscopic ovarian development staging of the spawning population may also enable definition of the diurnal spawning cycle of hoki. This could allow determination of the fraction of the population which spawned on a given day. Examination of hoki ovarian samples would also enable the batch and total fecundity of female hoki to be quantified for application to an egg production model.

Understanding the spawning dynamics of hoki is crucial to any assessment of hoki spawning biomass. The ongoing data collection by the MAF Fisheries Scientific Observer Programme will enable more targeted research into hoki spawning dynamics. Data from subsequent spawning seasons may provide further evidence to support the hypotheses proposed in this paper.

Acknowledgments

I would like to thank all MAF Fisheries scientific observers for the collection of data and the Stock Monitoring Group for coordination of the data collection. Marianne Vignaux and Stuart Hanchet provided valuable analytical and statistical assistance. Constructive comments on the manuscript were provided by Stuart Hanchet, Don Robertson, Peter Horn, John Zeldis, Patrick Cordue, Marianne Vignaux, Mary Livingston, and Kevin Sullivan.

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Appendix 1

The criteria used for the determination of maturity stages in female hoki

Stage 1	Immature or Resting	Ovary 1–2 cm long, 3 mm diameter in juvenile fish; resting ovary translucent, longer, and lightly speckled (primary oocytes) in larger fish
Stage 2	Ripening or Maturing	Fish usually ⩾55 cm total length; ovary swollen with opaque eggs, either creamy white and tightly packed or pink-grey with more blood and loosely packed (residual hyaline eggs may be present in central lumen from previous spawning)
Stage 3	Ripe	Ovary very swollen (up to 5–6 cm diameter); hyaline eggs present and adhered to ovary wall
Stage 4	Running ripe (ovulated)	Ovary very swollen; hyaline eggs flow freely in central lumen
Stage 5	Spent	Ovary less swollen, flaccid, and bloody (dark purple-red); some residual hyaline and resorbing opaque eggs may remain

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