International Council for the
Exploration of the Sea

ICES CM 1999/Y:34
Cod and Haddock Recruitment
Processes - Integrating Stock and
Environmental Effects

# TIME AND DURATION OF SPAWNING OF COD IN ICELANDIC WATERS.

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Time and duration of spawning among cod on the main spawning grounds southwest of Iceland, varies from one year to another, as well as within spawning seasons between different size/age groups of spawning females. In 1994 - 1997, onset and duration of spawning was found to be related to size and age of females where larger and older females started spawning earlier and over a longer time period than the smaller and younger females. A similar, however, less distinct trend is seen in 1998 and 1999, where larger females started spawning later than during the years1994-1997. The influence of stock and environmental factors, including the effects of changing stock structure, female condition, temperature, feeding conditions and the distribution of capelin on the time and duration of spawning is discussed.

## INTRODUCTION

Protracted spawning over prolonged periods is thought to present beneficial adaptations to uncertain spawning conditions (Nicholsky, 1962), faciliating the match of larval emergence and optimal feeding conditions (Cushing, 1990). Supporting evidence have shown that the timing and location of spawning of Atlantic cod (*Gadus morhua*) on the Scotian Shelf matched the peak abundance of *Calanus finmarchius* (Brander and Hurley, 1992). Furthermore, a significant relationship between the width of the spawning window and recruitment variability among the major cod stocks of the North Atlantic was demonstrated by Mertz and Myers (1994). Protracted spawning may also influence the survival of eggs and larvae by spreading the risk of predation over a longer time period (Lambert and Ware, 1984) and by offering greater variability with respect to hydrographic conditions influencing transport and entrainment of eggs and larvae (Myers and Drinkwater, 1988; McEvoy and McEvoy, 1992).

Although protracted spawning is achieved by multiple spawning of individual fish (Kjesbu, 1989; Chambers and Waiwood, 1996), the duration of spawning may also be extended by asynchronicity of spawning among age or size classes of cod. The influence of age and size on the duration of spawning has been demonstrated for cod on both the eastern and western side of the Atlantic. Kjesbu et al. (1996) showed that the size of captive females was positively related to the number of batches and the length of the spawning period in Norwegian Coastal cod. Hutchings and Myers (1993) demonstrated that older cod spawned over a longer time period than younger cod in the northwest Atlantic. Furthermore, the time of spawning may also be influenced by the size or age of spawners. Hutchings and Myers (1993) demonstrated that younger cod in the northwest Atlantic initiated and completed spawning earlier than older cod. This is in contrast to observations of cod in Icelandic waters, where larger females initiated spawning earlier than smaller females (Marteinsdottir and Steinarsson, 1996; Thorsteinsson and Marteinsdottir, 1998)

As spatial and temporal variation in timing and duration of spawning may be a significant source of recruitment variability, documentation of the physical and biological parameters that influence this variation is important. The main objective of this study is to determine the influence of age, size and condition of females on time and duration of spawning in cod as well as to document any annual variation that may exist with respect to the timing of spawning.

## MATERIAL AND METHODS

Sexually mature cod were sampled on the main spawning grounds of cod, at Selvogsbanki and nearby coastal areas, with a bottom trawl during several cruises conducted in the 1994-1999 spawning seasons. A total of three cruises were conducted in 1994, four in 1995, four in 1996, three in 1997, one in 1998 and two in 1999. Additional samples (1-6/week) were obtained from gill nets starting in late February, and continuing until early May each year. Collections from gillnets were obtained from commercial sources in 1994-1997 by sampling the landed catch from different mesh size and locations. In 1998 and 1999, weekly samples were obtained from experimental gill net series, each composed of four different mesh sizes (6, 7, 8 and 9") positioned at different locations at the main spawning areas. For each sample, information was collected on sex, maturity stage, length (±1 cm), weight (gutted/ungutted (±1 g), weight of livers and gonads (±1 g). Sampling onboard the research vessels was conducted so that the first 25 cod sampled were measured, sexed, weighed and operated for otoliths. The following specimens (up to 50 fish per tow) were only sexed (including maturity stages) and length measured. In the commercial samples, usually all measurements were obtained from the first 50-100 randomly selected specimen after which additional recording was preformed for females only (up to 75 females per sample). Total numbers sampled are provided in Table 1.

*Table 1. Number of cod sampled during the spawning season (March-May) in 1994-1999. All cod sampled for length measurements were also sexed and assigned to sex maturity stages.*

| Year | Numbers length measured | Total number of mature females length measured | Total number of aged females |
|---|---|---|---|
| 1994 | 6669 | 1527 | 1527 |
| 1995 | 7236 | 2655 | 1735 |
| 1996 | 9308 | 4269 | 2857 |
| 1997 | 4716 | 1980 | 941 |
| 1998 | 9713 | 2965 | *Not completed* |
| 1999 | 9224 | 3279 | *Not completed* |

All measured cod were assigned a maturity stage of reproductive development. Females were classified into four stages (stage 1, 3-4, 5 and 6 in Kjesbu *et al*, 1991); e.g. immature; maturing (opaque oocytes and rich in yolk), spawning (large easily seen hyaline oocytes present in the ovary), and spent. Males were also classified according to four maturity stages: immature, maturing, spawning (freely running milt), and spent. Cod that could not be assigned to one of these stages were recorded as unidentified. Female condition was estimated as:

$$K = (\text{Eviscerated body weight} * \text{Length}^{-3}) * 100 \qquad (1)$$

$$HSI = (\text{Liver weight} * \text{Eviscerated body weight}^{-1}) * 100 \qquad (2)$$

In order to forecast the first day of spawning, by individual females of different length, the diameter of the 10 most advanced vitellogenic (G1) oocytes were measured in samples collected from commercial sources in late January or early February in 1997. Similar data from 1998 and 1999 has not yet been analyzed. Oocytes were stored in ovarian fluid and measured within 24 hours of capture. The time to start of spawning (Y) was estimated by the equation (for 5° C) of Kjesbu (1994):

$$Y\ (\text{days}) = 4.41 * 10^6 * X^{-1.817} \qquad (3)$$

where, X = mean G1 oocyte diameter (µm).

The influence of female size or age on the timing of a given maturation stage were analyzed using maximum likelihood probit analysis (see Hutchings and Myers, 1993; Wright *et al.*, 1999). As the number of females in the largest size classes were low in some years, females larger than 115 cm were pooled. All females whose ovaries were in a maturity stage preceding the stage of interest (either spawning or spent) were classified as 0 and all remaining individuals were classified as 1. The Binary probit analysis preformed in S-plus, Version 3.4, as demonstrated in Venable and Ripley (1994), was used to analyze the effects of length and age on the timing of two maturity stages, spawning and spent. The probability, *p*, of an individual maturing at length (or age) on day of year *t* was assumed to be:

$$p = \Phi(\beta_0+\beta_1 t+\beta_2 a) \qquad (4)$$

where $\Phi$ is the cumulative distribution function for the standard normal distribution and $\beta_0$, $\beta_1$, $\beta_2$ are the probit regression parameters where $t$ = calendar day, $a$ = length or age. The times of initiation and cessation of spawning of individuals of length l , on which 50% of the fish were respectively expected to be spawning or spent were determined from $t = (-\beta_0-\beta_2 a)/\beta_1$, given that $\Phi(0) = 0.5$ (Hutchings and Myers, 1993). Duration of spawning was defined as the difference between the time of 50% spawning and spent. Further statistical analysis examining the inter-annual variation on the timing of a given maturity stage (as done by Hutchings and Myers, 1994) will follow age determination of cod collected in 1998 and 1999.

In order to look at the possible influence of prey distribution and availability on condition and time of spawning of cod, the distribution of capelin in February and March (during the spawning migration of capelin) was recorded, based on locations of capture by the capelin fishing fleet and the abuncance of capelin in cod stomachs sampled in the ground fish survey in March

## RESULTS

Time (start or cessation) of spawning varied between years and between different size classes of female cod (Fig. 1). Although larger females did not always initiate spawning earlier than smaller females (Fig. 1), the level of 50% spawning was, in all years, attained at an earlier date by the larger females than by the smaller females (Fig. 2, Table 2). The influence of age, as well as length on the initiation of spawning was significant in all years, with older and larger females spawning earlier than younger and smaller females (Figs. 2 & 3, Table 2).

Time to spawning, predicted from the size of the most advanced oocytes present in the ovary 2-3 weeks before spawning started, varied distinctly between females of different sizes (Fig. 4), thus confirming the results based on the visual observation of ovarian maturity stages

*Table 2 . Probit regression coefficients ($\beta_2$ in equation 2) of the effects of age and length on the timing of reproduction in female cod (standard error in parentheses).*

| Year | Variable | Spawning | Spent |
|---|---|---|---|
| 1994 | Length | 0.041 (0.002)*** | 0.006 (0.004) |
| | Age | 0.261 (0.02) *** | 0.053 (0.03) |
| 1995 | Length | 0.042 (0.002)*** | 0.021 (0.003)*** |
| | Age | 0.244 (0.02) *** | 0.091 (0.03)** |
| 1996 | Length | 0.056 (0.002)*** | 0.023 (0.002)*** |
| | Age | 0.302 (0.02) *** | 0.111 (0.03) ** |
| 1997 | Length | 0.049 (0.002)*** | 0.018 (0.003)*** |
| | Age | 0.246 (0.04)*** | 0.204 (0.11) |
| 1998 | Length | 0.035 (0.003)*** | -0.002 (0.002) |
| | Age | *Not completed* | *Not completed* |
| 1999 | Length | 0.024 (0.002)*** | 0.01 (0.005) ** |
| | Age | *Not completed* | *Not completed* |

*$p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

*Table 3. Comparisons of mean condition indices (Fulton's K and Hepatosomatic indices, HIS, based on eviscerated body weight) between females, classified into three size groups, that had initiated spawning and those that had not initiated spawning during the first weeks of the spawning periods.*

| | | Females < 75 cm | | Females 75 – 100 cm | | Females > 100 cm | |
|---|---|---|---|---|---|---|---|
| Year | Maturity stages | K | HSI | K | HSI | K | HSI |
| 1994 | Pre-spawning | 0.74 ± 0.1 | 8.25 ± 3.1 | 0.78 ± 0.1* | 9.7 ± 3.1** | 0.89 ± 0.2 | 10.3 ± 2.5 |
| | spawning | 0.74 ± 0.1 | 7.2 ± 3.1 | 0.81 ± 0.1* | 8.7 ± 2.2** | 0.90 ± 0.1 | 10.0 ± 2.5 |
| 1995 | Pre-spawning | 0.76 ± 0.1 | 9.11 ± 3.1 | 0.81 ± 0.1** | 9.3 ± 3.2 | 0.89 ± 0.1* | 9.4 ± 2.1 |
| | spawning | 0.78 ± 0.1 | 7.21 ± 4.5 | 0.89 ± 0.1** | 7.7 ± 2.1 | 0.93 ± 0.1* | 10.35 ± 0.1 |
| 1996 | Pre-spawning | 0.74 ± 0.1 | 6.9 ± 3.2 | 0.78 ± 0.1 | 8.9 ± 2.6** | 0.89 ± 0.1 | 9.3 ± 2.3 |
| | spawning | 0.74 ± 0.1 | 6.7 ± 3.2 | 0.84 ± 0.1 | 8.1 ± 2.6** | 0.89 ± 0.1 | 9.1 ± 2.5 |
| 1997 | Pre-spawning | 0.77 ± 0.1* | 7.9 ± 2.4 | 0.80 ± 0.1** | 8.8 ± 2.3** | 0.91 ± 0.1 | 9.8 ± 2.1** |
| | spawning | 0.92 ± 0.3* | 7.2 ± 2.7 | 0.85 ± 0.1** | 8.1 ± 2.3** | 0.93 ± 0.1 | 8.9 ± 2.0** |
| 1998 | Pre-spawning | 0.73 ± 0.1 | 7.4 ± 2.6 | 0.81 ± 0.1 | 8.6 ± 2.9** | 0.85 ± 0.1 | 8.7 ± 2.4** |
| | spawning | 0.80 ± 0.05 | 6.8 ± 2.7 | 0.83 ± 0.1 | 7.7 ± 2.6** | 0.86 ± 0.11 | 7.8 ± 2.6** |
| 1999 | Pre-spawning | 0.73 ± 0.1 | 7.7 ± 2.5* | 0.79 ±0.1* | 8.2 ± 2.3** | 0.83 ± 0.1* | 8.86 ± 2.1** |
| | spawning | 0.79 ± 0.1 | 8.2 ± 2.3* | 0.77 ± 0.1* | 7.6 ± 2.3** | 0.80 ± 0.1* | 7.8 ± 1.2** |

*$p < 0.05$; ** $p < 0.01$

The influence of female condition on the time of spawning was not conclusive. In some cases, especially among females in the mid-sized range (75 -100 cm), condition (K) of females that had initiated spawning was significantly higher than condition of females that had not initiated spawning (e.g. in the years 1994, 1995, 1997 and 1999, respectively; Table 3). In contrast, female condition based on relative weight of livers (HSI) was frequently lower among those females that had initiated spawning compared to those that had not initiated spawning (Table 3). A probable explanation may be due to rapid decline in HIS after spawning has been initiated.

Spawning duration, the difference between spawning initiation and cessation, was extended over a longer period, in all years, for larger and older females than for smaller and younger females (Figs. 2 & 3, Table 3). In some years (1994, 1996 and 1997) the divergence of the slopes of the probit regressions was more evident among females of different size classes than among females of different ages (Figs. 2 & 3).

*Table 3. Day of year at which 50% of large (120 cm) and small (70 cm) female cod had entered into spawning or spent maturity stages. Duration is defined as the difference between these times.*

| Year | 50% Spawn 70 cm | 50% Spent 70 cm | Duration 70 cm | 50% Spawn 120 cm | 50% Spent 120 cm | Duration 120 cm |
|---|---|---|---|---|---|---|
| 1994 | 108 | 129 | 21 | 65 | 128 | 62 |
| 1995 | 113 | 139 | 23 | 79 | 125 | 46 |
| 1996 | 113 | 121 | 9 | 72 | 112 | 39 |
| 1997 | 108 | 124 | 16 | 72 | 117 | 44 |
| 1998 | 105 | 117 | 12 | 87 | 118 | 31 |
| 1999 | 99 | 122 | 23 | 83 | 117 | 34 |

Both time and duration of spawning varied from one year to another (Table 3). Earliest start of spawning was estimated for 120 cm females in 1994 when 50% spawning was attained on day 65. In the following years, large females started to spawn at a later time and 50% spawning was not attained until on day 87 and 83 in 1998 and 1999 respectively. The cessation of spawning varied in an opposite way, with large females terminating spawning at a later time in 1994 and 1995 compared to 1996-1999. Consequently, duration of spawning decreased gradually from 1994 – 1999. The time and duration of spawning did not vary in the same way among the smaller females. Earliest time of 50% spawning of 70 cm females was estimated as day 99 in 1999 (Table 3). Latest time of 50% spawning was estimated as day 113 in 1995 and 1996. Duration of spawning of 70 cm females ranged from little more than one week in 1996 to more than three weeks 1995 and 1999.

Size or age composition of the samples used to determine the time and duration of spawning (Figs 5 & 6) appeared to have some effects on the duration of spawning but no significant effects on the time of spawning (Table 4). Significant positive correlations were obtained between the duration of spawning among the large females and the proportion of cod greater than 105 cm long ($r = 0.96$). Duration of spawning among the smaller females was also significantly correlated with proportion of young cod (5 years old or younger) in the samples. In contrast, the relationship between the proportion of small fish (< 76 cm) in the samples and the duration of spawning among smaller females was not significant ($r = 0.11$), as well as the relationship between proportion of old cod (10+) and duration of spawning among large females($r = 0.75$).

*Table 4. Correlation between parameters describing the stock structure and time and duration of spawning of large (120 cm) and small (70 cm) cod (*$p < 0.05$). Correlation between age structure and spawning time and duration may change when aging of cod from 1998 and 1999 is completed.*

| | 50% Spawn 70 cm | Duration 70 cm | 50% Spawn 120 cm | Duration 120 cm |
|---|---|---|---|---|
| Proportion of cod ≥ 105 cm | 0.19 | 0.80 | -0.77 | 0.96* |
| Proportion of cod < 76 cm | 0.75 | 0.11 | -0.77 | 0.57 |
| Proportion of cod ≥ 10 years | 0.38 | 0.41 | -0.58 | 0.75 |
| Proportion of cod < 6 years | -0.08 | 0.88* | -0.41 | 0.85 |

Analysis on the relationship between temperature and the time and duration of spawning are not completed. However, first attempts examining winter temperatures and time of spawning have not given any conclusive results (Table 5).

Table 5. Correlation between time of spawning and temperatures in February at 200 m or bottom depth (South Coast) at stations located off the South (63°29'00 N, 20°54'00 V), West (67°30'00N, 13°16'00V), North (66°44'00 N, 18°50'00 V) and East coast (65°00'00, 11°17'00 V)

| | Temperature °C | | | | | | 50% spawn 70 cm | 50% spawn 120 cm |
|---|---|---|---|---|---|---|---|---|
| Years | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | Pearson's r | Pearson's r |
| South Coast | 5.3 | NA | 6.47 | 5.72 | 6.09 | 5.27 | 0.79 | -0.15 |
| West Coast | 4.83 | 3.59 | 5.78 | 4.12 | 6.11 | 6.15 | -0.29 | 0.54 |
| North Coast | 2.43 | 0.89 | 3.64 | 2.34 | 2.94 | 3.65 | -0.20 | 0.68 |
| East Coast | 0.36 | 1.95 | 0.54 | 0.71 | 1.32 | 0.28 | -0.62 | 0.31 |

Annual variation in time and duration of spawning may be related to condition of female cod which in turn may depend on the availability and distribution of capelin during late winter or early spring as capelin is one of the major dietary component of cod (Pálsson and Björnsson, 1993; Marshall *et al.*, 1998; Yaragine and Marshall, 1999). Condition of large (> 100 cm) and mid-sized female cod (75-100 cm) based on the relative weight of livers (HSI) decreased significantly ($p < 0.01$) from 1994-1999 (Table 2). Lowest values were obtained in 1998 and 1999. A decline in the somatic condition factor (K) was also observed among the largest females in 1998 and 1999. This decline in condition may be related to the availability and condition of the capelin during the weeks prior to spawning. Distribution and migration of capelin, was different in 1998 and 1999 compared to the earlier years of 1993-1997 (Fig 7). The spawning migration of capelin is described in detail by Vilhjálmsson (1994). In summary, the spawning capelin migrate south along the east coast appearing at the southeast coast in early February. From there the capelin follows the south coast, migrating around Reykjanes peninsula into the Faxafloa Bay and north along the West coast. In 1993-1997, capelin followed this pattern (Vilhjalmsson, 1994). The capelin appeared in the coastal waters off the southeast coast in early February (Fig. 7). In late February and early March, the capelin followed the southern coast during their migration towards the west coast. By the end of March the fishing fleet had followed the capelin into Faxafloa Bay and around the Snaefellsnes Peninsula on the west coast. In 1998 and 1999 the capelin followed a different pattern (Fig. 7). The capelin appeared later at the southeast coast and the migration stopped before they reached the waters of the West coast. In 1999, no capelin was detected west of Westmanna Islands while in 1998 some capelin was found in cod stomachs at Selvogsbanki, however at a later time during the season than in 1993-1997 when consumption of capelin at Selvogsbanki started, most likely, 2-3 weeks earlier than in 1998 (Fig. 8).

## DISCUSSION

Both size and age of female cod had significant effects on time of spawning on the main spawning grounds, southwest of Iceland. In all years, older and larger females started to spawn earlier than younger and smaller females. This is concordant with previous reports by Jonsson (1961) and Jonsson (1982) that first time spawners start spawning later in the season than repeat spawners. Size related onset of spawning has been reported for many species (see reviews in DeMartini and Fountain, 1981; Hutching and Myers, 1993; Kjesbu, 1994). In cod, earlier spawning by larger females has been either observed or indicated based on length frequency distributions, gonadosomatic indices, and/or earlier arrival of large spawners on the spawning grounds in Iceland by Jónsson (1961) and Jónsson (1982), at Lofoten, Norway by Sund (1938), in the Oslo fjord by Ruud, 1939 and in the Baltic by Berner (1985). A positive size related onset of spawning has also been reported for haddock (Wright, et al, 1999), herring (Lambert, 1987), capelin (Carscadden et al., 1997), queenfish (DeMartini and Fountain, 1981) and several other species listed by DeMartini and Fountain (1981) and Kjesbu (1994). Other studies on cod have reported contrasting observations. For example, in the Newfoundland/Laboratory Region, younger cod started spawning earlier than older cod (Hutchings and Myers, 1993). In Lofoten, there has not yet been found any size-related effect on the time of spawning (Kjesbu, 1994). However, Kjesbu (1994) concluded that more comprehensive studies have to be undertaken in this geographical area before any firm conclusions could be reached because of major problems in terms of representative sampling.

Duration of spawning was also influenced by size and age of female cod. Larger and older females spawned over a longer time period in all of the years with completed age records. This is in concordance with other studies on cod (Hutchings and Myers, 1993; Kjesbu *et al.*, 1996), and haddock (Wright *et al.*, 1999). Such protracted spawning periods may be achieved by individual fish spawning repeatedly, and/or by a partitioning of the parental stock into asynchronously spawning groups. Hislop et al. (1978) and Kjesbu et al. (1990) reported that cod and haddock are deterministic serial spawners, indicating that their protracted spawning period is at least in part due to individual fish spawning repeatedly. For example, Kjesbu, et al. (1996) showed that female Norwegian

Coastal cod were able to produce 4-21 batches over a 6-48 day period. Protracted spawning is believed to be a behavioral trait that reduces the risk of reproductive failure due to short-term variations in egg and larval mortality (Giesel, 1974). There can be considerable selective advantages to spreading reproduction over time to reduce temporal variation in offspring production (Gillespie, 1977). By spawning over a wider seasonal window an individual reduces the probability of having all its offspring experience suboptimal conditions for growth and survival (Mertz and Myers, 1994). The potential significance of demographic changes to spawning duration has been recognized in a number of marine fishes (Parrish et al., 1986; Hutchings and Myers, 1993; Mertz and Myers, 1994; Trippel et al., 1997). Changes in the number of age-classes in populations with asynchronous spawning and its affect on the duration of spawning have been implicated in recruitment variability (see Lambert, 1987, 1990; Marteinsdottir and Thorarinsson, 1998). For example, in Icelandic cod, the probability of obtaining above average recruitment seems higher when the diversity of the age distribution is also above average (Marteinsdottir and Thorarinsson, 1998).

Considerable annual variation in the initation of spawning were reported for cod in Icelandic waters during 1953-1981 (Jonsson, 1982). This study provides strong evidence that such variation may depend, at least partially, on the size and age structure of the spawning population. Interannual differences in the start and completion of spawning ranged from 2-3 weeks, depending on the size or age of females. Duration of spawning among different size groups was significantly and positively related to either the proportion of large fish or the proportion of young fish in the stock.

Inter-annual variation in time of spawning of cod was shown to be significantly influenced by temperature prior to spawning (Hutchings and Myers, 1994). Lower water temperatures during vitellogenesis have been shown to delay spawning in both cod (Kjesbu, 1994; Hutchings and Myers, 1994) and herring (Lambert, 1987; Ware and Tanasichuk, 1989). The influence of temperature on time of spawning of cod in Icelandic waters may be as complicated as in the Newfoundland regions (Hutchings and Myers, 1994), where it may be attributed to regional differences in temperature influencing both the distribution and migration of cod, as well as the rate of gonad development. Previous observations of cod in Icelandic waters (Jónsson, 1982) have shown both positive and negative relationships between temperature and start of spawning in individual years. The influence of temperature through regional differences was indicated by the occurrence of prolonged and relatively late spawning during years of large spawning migrations arriving from Greenland (Jónsson, 1982). As Iceland is located in the middle of the North Atlantic, where northern currents meet water masses from the south, hydrographic conditions including temperature vary extensively from one region to another. Results from data storage tags (DST's) have shown extreme differences in ambient temperatures experienced by cod during winter and early spring, before the cod enter the spawning grounds (Thorsteinsson, pers comm.). Some cod appear to reside at relatively stable temperatures throughout out the winter months, while others exhibit frequent vertical migrations between temperature ranges of several degrees each day. More work is needed, including the accumulation of existing temperature data from hydrographichal recordings and data capture tags obtained from spawners, in order to resolve the influence of temperature on time of spawning of cod in Icelandic waters.

Condition has also been shown to influence spawning time in cod. Kjesbu (1994) demonstrated that spawning could be delayed up to 2 weeks if females were reared on low ration compared to moderate ration. In this study, a decline in condition, especially the liver condition index (HSI) was detected among the larger spawning cod from 1994 to 1999, with lowest values in 1998 and 1999. The Somatic condition index (K) of the largest cod was also lowest in 1998 and 1999. At the same time, large fish started spawning later in 1998 and 1999, and the duration of spawning was 1-4 weeks shorter compared to the other years. Some of this variation may be due to behavioral differences of spawning cod, that may in turn be related to the capelin migrations during these two years. In contrast to observations in other areas (Kjesbu, 1994), spawning cod in Icelandic water are known to actively feed throughout the spawning period (Marteindsottir, unpublished data). One of the main food source during this period is capelin, which migrate through the main spawning areas of cod in February and March (Vilhjálmsson, 1994). A significant relationship has been reported for the liver condition index of Northeast Arctic cod and the abundance and biomass of capelin (Yaragina and Marshall, 1999). Similarily, the relatively low liver condition index of cod on the main spawning grounds in 1998 and 1999 may result from a limited access to capelin. Distribution of capelin based on commerical catches in 1994-1999, showed clearly the capelin did not migrate as far west in 1998 and 1999 compared to the years before. In these years, none or few capelin appeared to enter the main spawning grounds of cod on Selvogsbanki and none migrated into the waters west of the country. One of the main reasons for the termination of the westward migration of the capelin is thought to be the presence of an unusually strong eastward flowing current in this area during the spawning season (Vilhjalmsson, pers. comm). For cod, the spawning capelin is one of the most easily captured prey available. This is confirmed by the large amount of capelin in cod stomach, sampled in the areas south and west of Iceland in March. The weight of capelin in the cod stomacs in this area was frequently more than 10-15% of the cod total body weight, which is considerably more than recorded for any other prey captured during the rest of the year (Pálsson and Björnsson, 1993). Observations during the sampling of spawning cod have shown that the cod are usually stuffed with capelin during the first few weeks of the spawning seasons (Marteinsdottir, unpubl. data). This easy meal, may play an important role for the physical condition of the spawning cod providing more energy that can be used for reproduction. It is therefore quite possible that those cod that are most dependet on this energy supply (the large cod ?) may follow the capelin and stop on their route to the main spawning areas and delay their spawning if the food supply, or the capelin migrations are delayed or cut short in other areas on the way. The possibility that the spawning cod (i.e. the large cod) may have stopped on its route to along the south coast in the areas east of the main spawning grounds (where the capelin migration stopped), is supported by information from the annual gill net survey. This survey showed significant decrese in the abundance of large cod in 1999 on the main spawning grounds, while a significant increase was recorded in the abundance of large cod in the southeast areas (unpublished data from the annual gill net survey).

The results presented here demonstrate that age, length and possibly condition of spawners, in combination with other physiological and behavioral factors, influence the spawning time of cod. The data presented were collected in just a few of the many spawning areas of cod in Icelandic waters, and may not represent the reproductive pattern of cod in other areas. For example, recent recordings of spawning time and behavior of cod in fjords west and north of the country have not demonstrated such distinct relationships between size of spawners and spawning time (Marteinsdottir *et al.*, unpubl). Other studies have shown that the surviving population of 0-group individuals originate from many spawning areas and that the total egg production or the contribution of different spawning areas towards recruitment varies both spatially and temporally (Marteinsdottir et al., 1998, 1999; Begg and Marteinsdottir, 1999). The completion of this work, as well as future analysis on spawning time and behavior in different areas may increase our understanding of how spatially and temporally variable stock composition, in combination with biological, physiological, environmental factors, influences recruitment processes.

## ACKNOWLEDGEMENTS

We thank all those that conducted the sampling of cod, especially Groa Petursdottir, Adalbjorg Jonsdottir and Kristin Hardardottir who directed the sampling process during the field season of 1996-1997, 1998 and 1999 as well as Bjorn Gunnarsson, Carolin Gillis, Asgeir Gunnarsson and all the others who helped in the field and in the laboratory. We thank Þordur Viðarsson and Groa Petursdottir for the aging of cod otoliths and Hrefna Einarsdottir for assistance with data entering. We thank G. Bjarnasson and G. Thordarsson of the r/v Árni Fridriksson and I. Lárussonand G. Gunnarsson of r/v Bjarni Saemundsson and threir crew.

This study was supported by the Ministry of Fisheries as well as being a part of the Eu funded projects FAIR-PL95-84, "Recruitment processes in cod and haddock: Developing new approaches" and FAIR-PL98-4122, "An operational model of the effects of stock structure and spatio-temporal factors on recruitment (STEREO) and a project funded by the Icelandic Research Council, "Samverkandi áhrif stofns og umhverfis á nýliðun þorsks".

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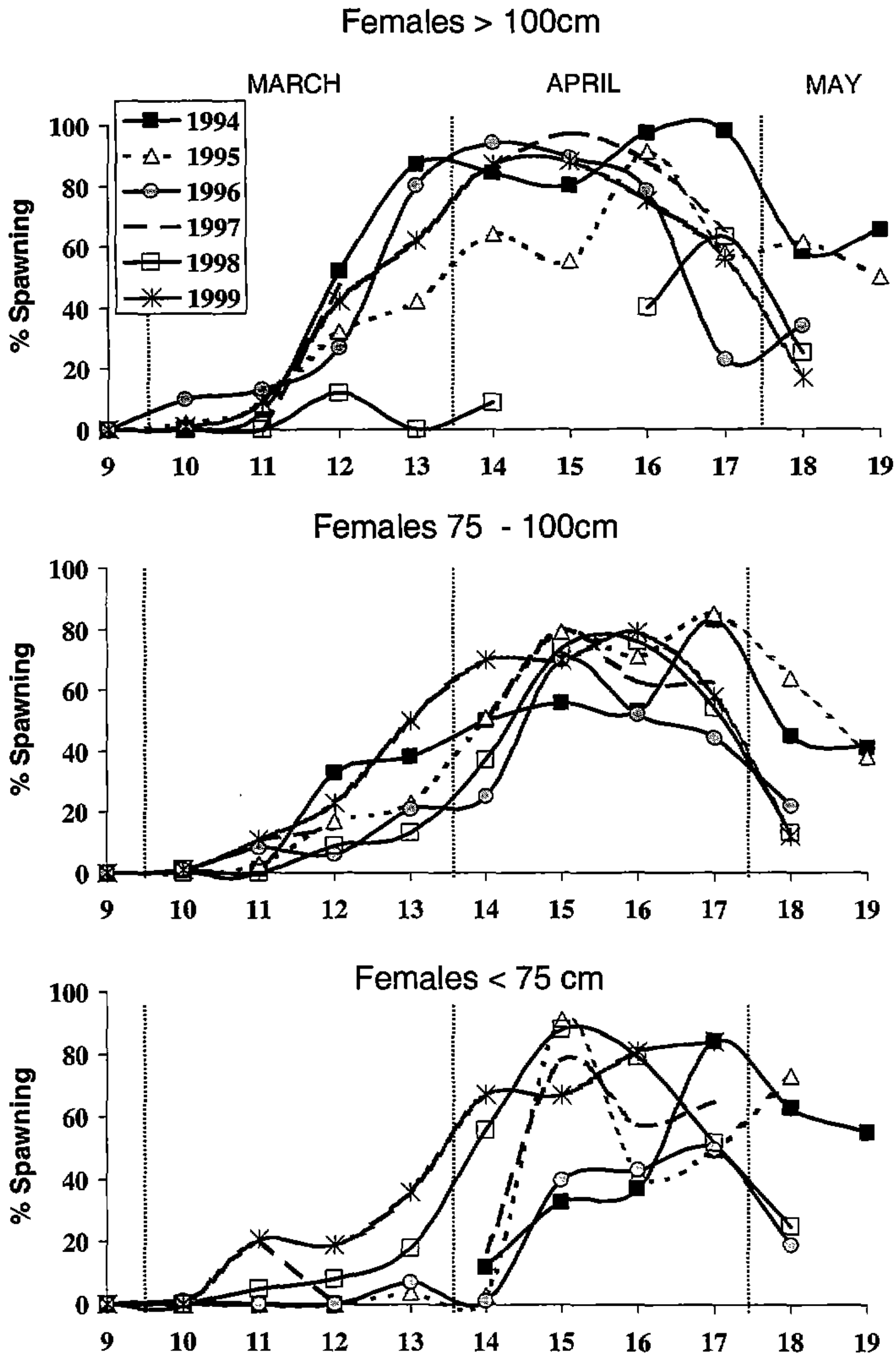

Figure 1. Frequency of spawning females (stage 3) during each week of the year in 1994-1999. Females are grouped into three length classes.

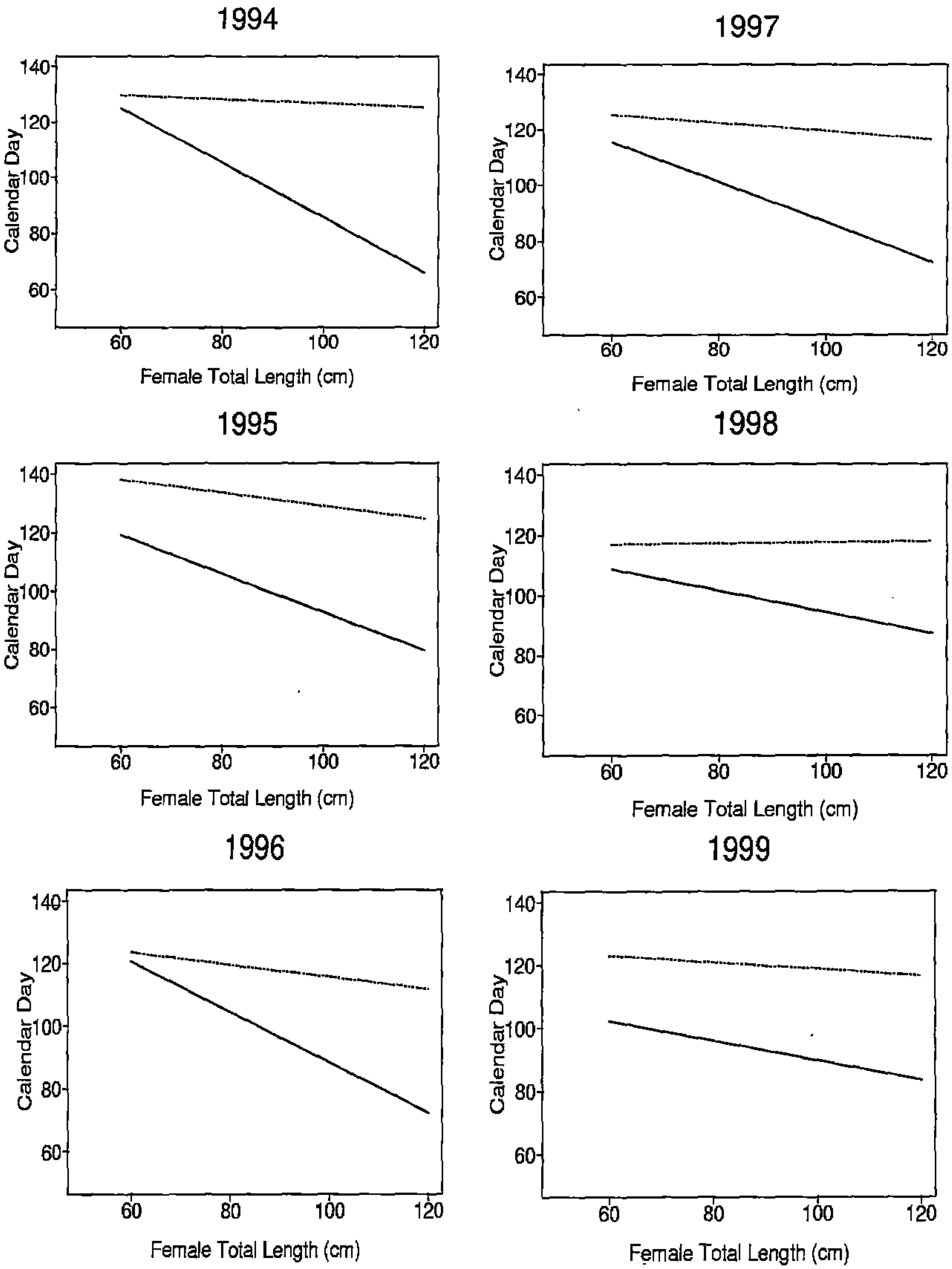

Figure 2. The relationship between female length and the estimated mean day at which 50% of the females were classified as spawning (solid line) or spent (dashed line).

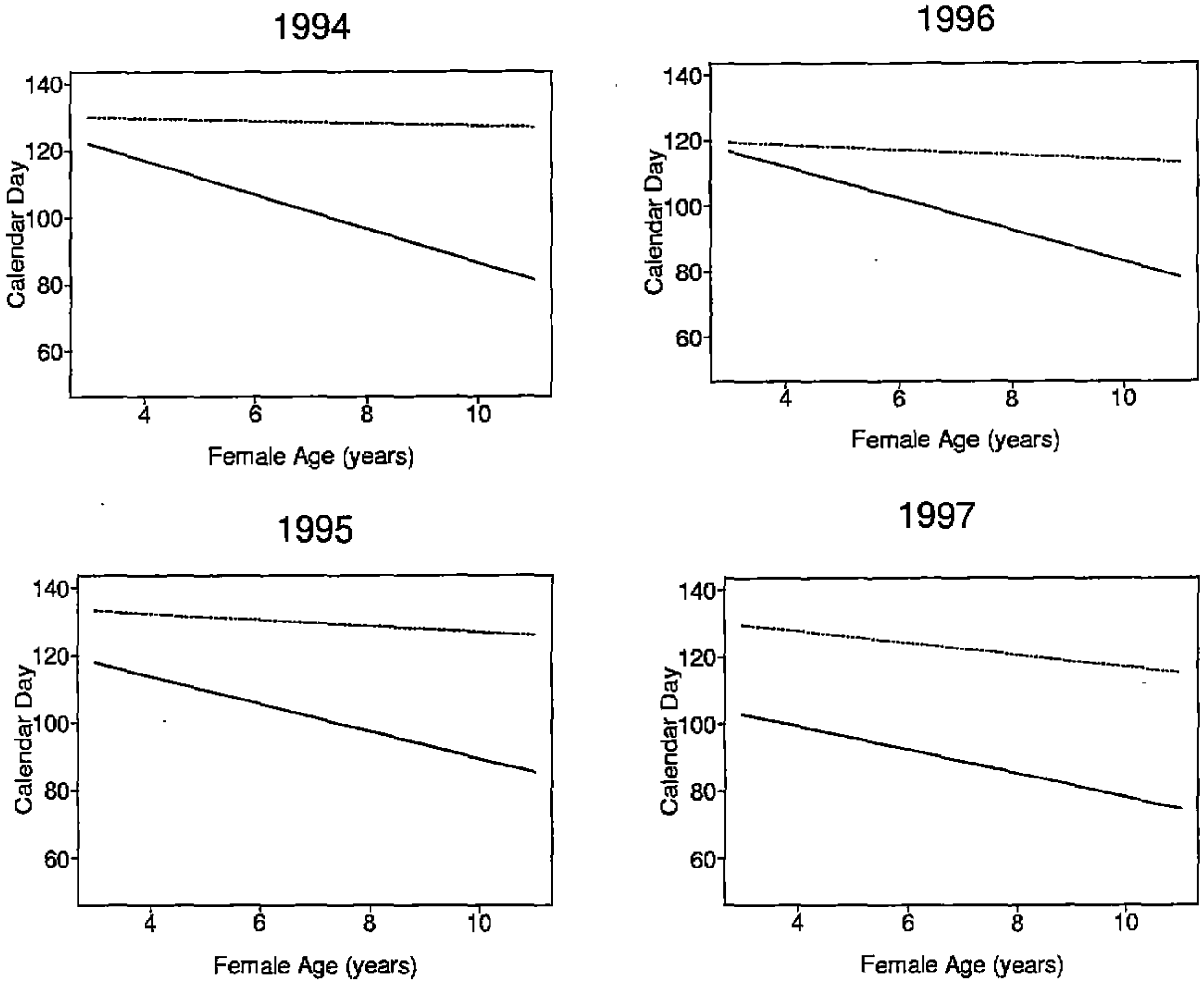

Figure 3. The relationship between female age and the estimated mean day at which 50% of the females were classified as spawning (solid line) or spent (dashed line).

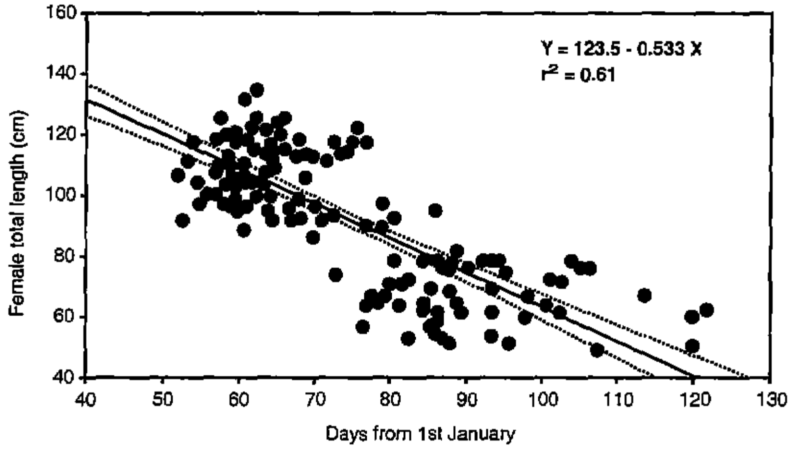

Figure 4. Estimated time to start of spawning (days) in relation to the size of female cod prior to the 1997 spawning season. Each estimate was based on the size of the largest oocytes (according to Kjesbu, 1994) present in the ovary 4-6 weeks before start of spawning.

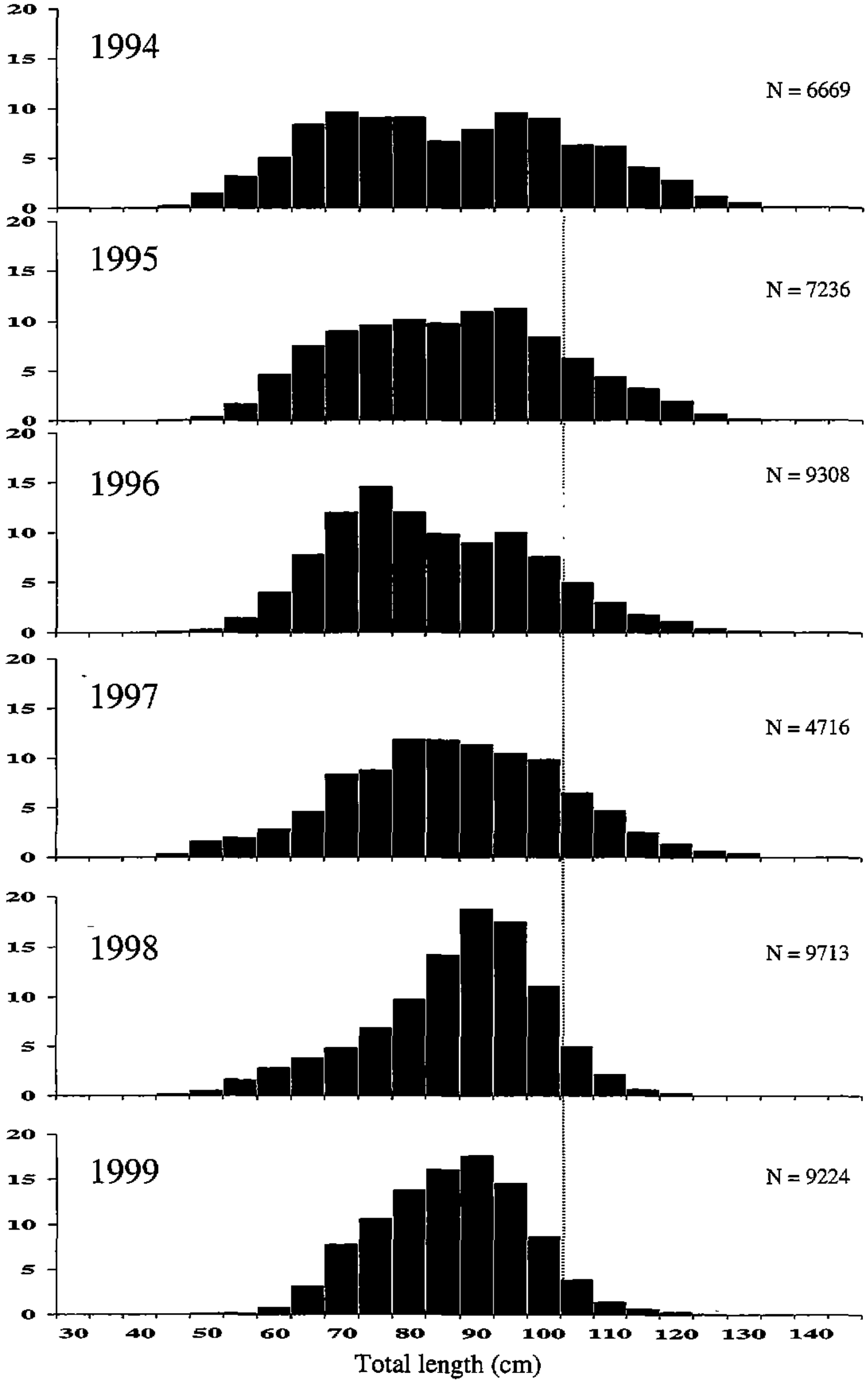

Figure 5. Length distribution of cod sampled with bottom trawl and gill nets on the main spawning grounds during the spawning periods in 1994-1999. A reference line is drawn at 105 cm.

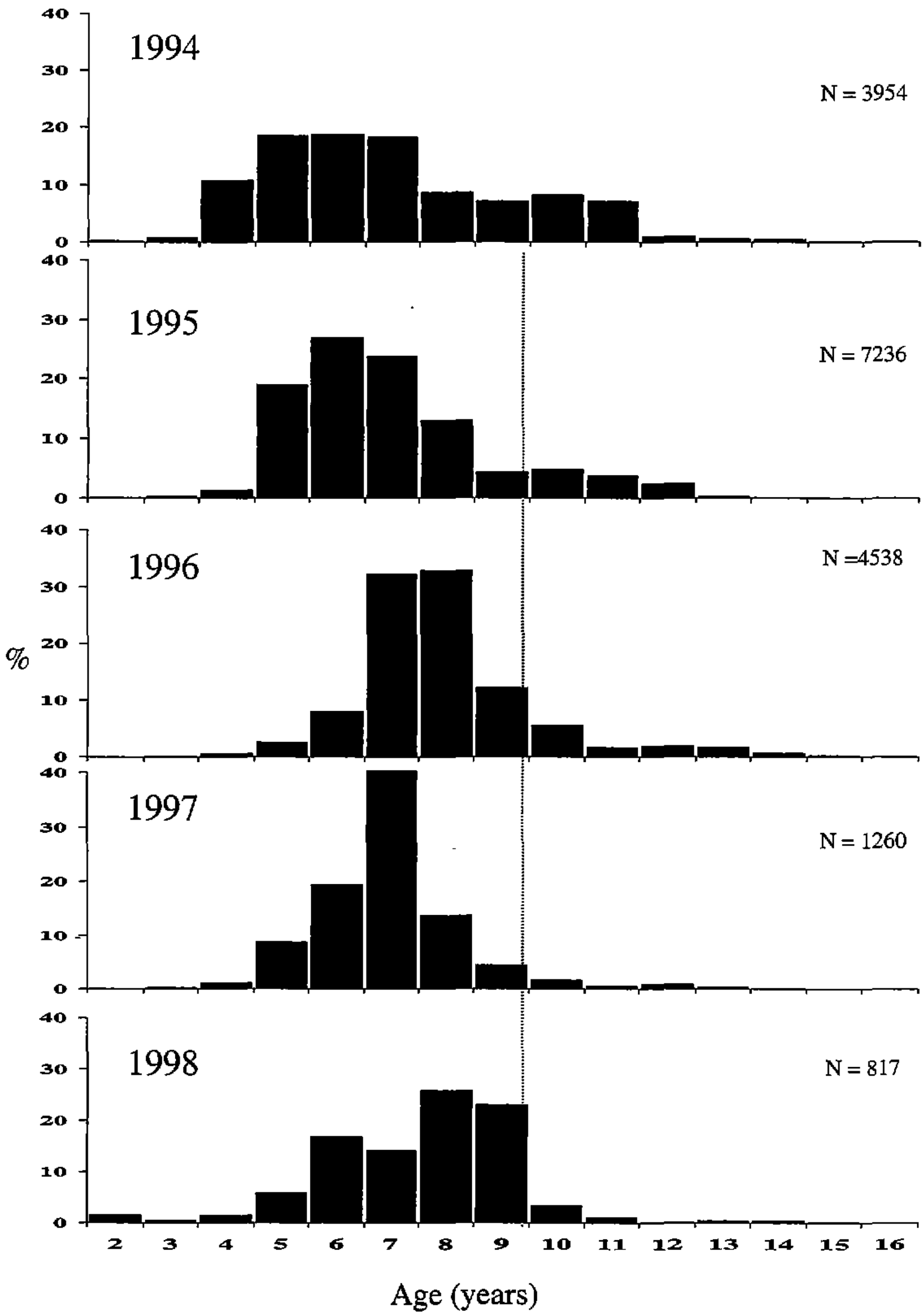

Figure 6. Age distribution of cod sampled with bottom trawl and gill nets on the main spawning grounds during the spawning periods in 1994-1999. A reference line is drawn at the age of 10 years.

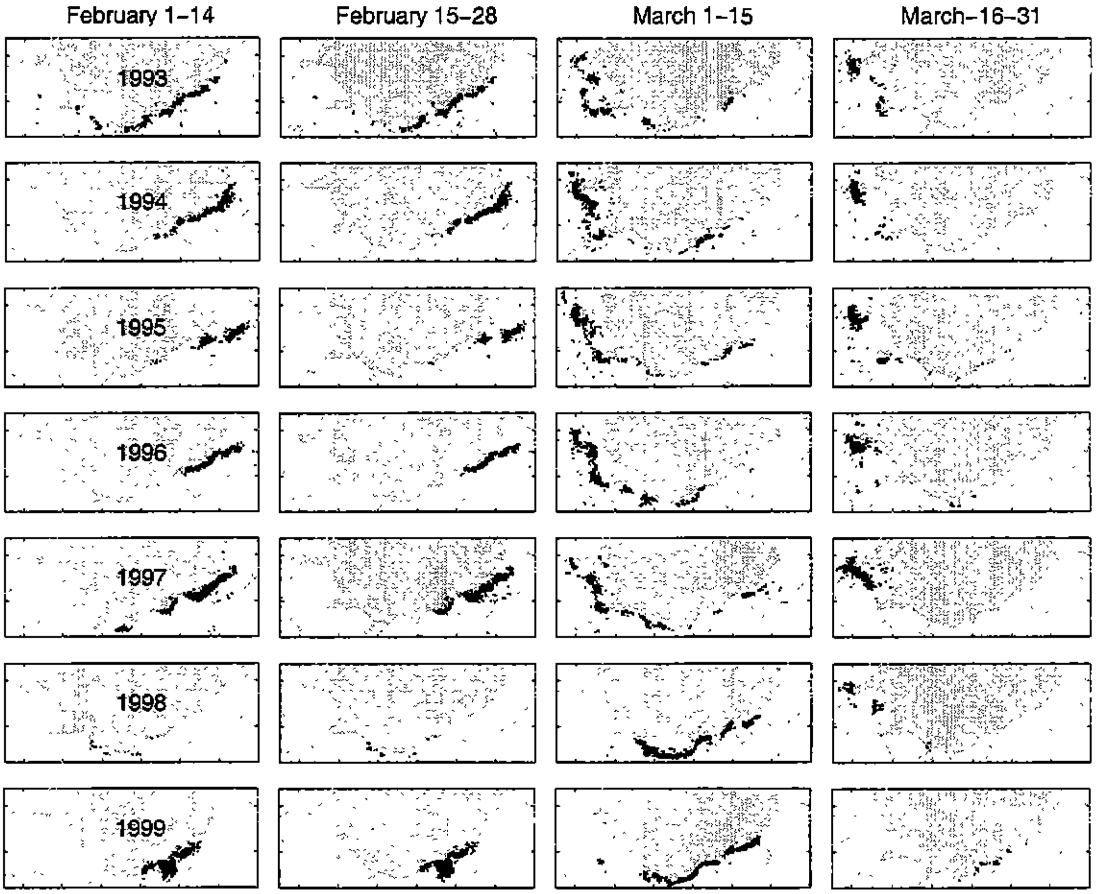

Figure 7. Location of purse seine casts in the capelin winter fishery 1993 to 1999.

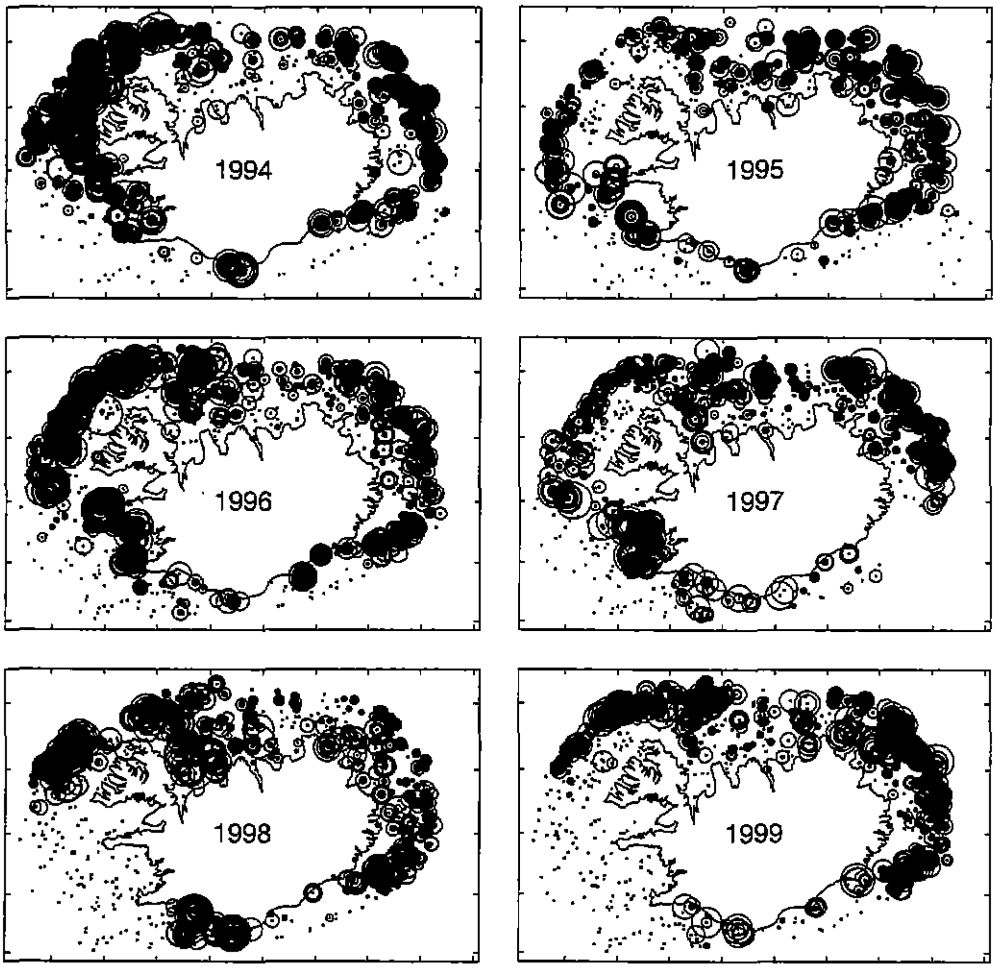

Figure 8. Amount of capelin in cod stomachs in the March groundfish survey. The area of the circles are proportional to the amount as % of bodyweight.