International Council for
the Exploration of the Sea

C.M. 1999/Y:25
Theme Session on Cod and
Haddock Recruitment Processes

Maturation process and spawning time of cod in the Bornholm Basin of the Baltic Sea: Preliminary results

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Abstract

A series of trawl surveys during the spawning period of Baltic cod (*Gadus morhua* L.) were carried out in the Bornholm Basin during the years 1995-97 as part of the Baltic CORE project. The gonadal maturation process was found to differ between the sexes. Males reached spawning condition earlier than females and entered the spawning area earlier resulting in a high proportion of males in the spawning area during the early spawning period. The sex composition of the spawning components changed over time with the proportion of females exceeding that of males late in the spawning period. Maturation was also observed to vary relative to size. Large sized females commenced spawning earlier and spawn over a greater length of time than smaller sized females. The timing of peak spawning of females, however, did not differ substantially relative to size. The onset of spawning and spawning duration differed between male size groups in a similar way, but less pronounced than for females.

These preliminary results indicate that the duration of the spawning period of the stock depends on its size and sex composition, whereas the timing of peak spawning does not. The earlier start and also longer duration of the male spawning period in combination with earlier sexual maturation suggest that male mortality exceeds that of the females due to increased natural mortality as well as prolonged exposure to fisheries activities. This behaviour potentially explains the decreasing proportion of males with increasing size/age observed in the stock.

Introduction

The Baltic Sea is effectively a large stratified estuary with a low salinity surface layer and a deep saline layer. Outside the spawning season, the main distribution area of eastern Baltic cod is in the bottom depth range from about 40 to 80m (Sparholt et al., 1991) with highest abundance in the saline layer near the bottom. In relation to spawning, the adult cod migrate into the deep basins (Aro, 1989; Bagge et al., 1994), where they aggregate and spawn in an intermediate water layer just below the halocline but avoid the deep oxygen poor water (Tomkiewicz et al., 1998). Three deep basins in the Baltic Sea provide salinity levels required for neutral egg bouyancy, i.e. the Bornholm Basin, the Gdansk Deep and the Gotland Basin. However, the water volume suitable for successful egg survival and development, i.e. the reproductive volume, also depends on the oxygen conditions in the water layer, where the eggs float. The reproductive volume in the Baltic varies considerably between years and seasons depending on the frequency and intensity of intrusions of saline, oxygenated water and the oxygen consumption rate within and below the permanent halocline (Plikshs, 1993; MacKenzie et al., 1996; Plikshs et al., 1999). Due to a long period with only limited intrusion of saline water, the Bornholm Basin is presently the main spawning area of Baltic cod owing to unfavourable oxygen conditions in the Gdansk Deep and Gotland Basin (e.g. Plikshs et al., 1993; Köster et al., 1999).

The eastern Baltic cod stock has a considerably longer spawning period than other cod stocks in the North Atlantic, i.e. spawning in the Bornholm Basin starts in February and ends in August (Brander, 1994). This behavioural pattern is generally explained as an adaptation to the variable and sometimes critical environmental conditions in the Baltic Sea. The time of peak spawning based on egg abundance estimates in the Bornholm Basin occurred between the end of April and mid June in the 1970' s and 1980's. From the early 90's and onwards the time of peak egg production has gradually changed from the end of June to the end of July (Wieland et al., in press). The key-factors determining the time of peak egg abundance was found to relate to changes in ambient temperature during the period of ovary development and to stock size. The composition of the spawning stock was suggested also to have an effect, with the progressive delay of spawning in 1990's being caused by a high proportion of first time spawners in combination with decreasing water temperatures (Wieland et al., in press).

Inter-annual variability or trends in spawning time have previously been associated with changes in ambient temperature (e.g. Hutchings & Myers, 1994; Kjesbu, 1994), low growth rates caused by high population density relative to food availability (e.g. Kosior & Skolski, 1992; Baranova, 1995;) and age structure (e.g. Hutchings & Myers, 1993; Kjesbu et al., 1996; Thorsteinsson & Marteinsdottir, 1998). Experimental results have shown that a drop in temperature of 1°C during vitellogenesis delayed the onset of spawning of individual Atlantic cod by about 8-10 days (Kjesbu, 1994). Baranova (1995) found that gonadal development of Baltic cod occurred earlier in years with good feeding and hydrographic conditions than in years with limited food availability and stagnation conditions. A relation between size/age and the duration of spawning has been described for different cod stocks in the North Atlantic for both females and males. In a study of Hutchings and Myers (1993), older individuals of both sexes were found to initiate and complete spawning later and to spawn for a greater length of time than younger individuals. Within regions, males were also found to be in spawning condition longer than females. The finding that older individuals start spawning later in this stock differ from results of studies of cod in Icelandic waters (e.g. Thorsteinsson & Marteinsdottir, 1998) and in the Baltic Sea (e.g. Baranova, 1995; Berner 1985; Bleil & Oeberst, 1997), where larger females are reported to start spawning earlier than smaller ones. A longer duration of the spawning period of larger females has been reported also by Kjesbu et al. (1996) for captive Atlantic cod and by Marteinsdottir and Steinarsson (1996) for Icelandic cod. The time of arrival to the spawning sites has been found also to differ between of males and females. For cod on the Grand Bank and the Scotian Shelf (Morgan and Trippel 1996) as well as in the Baltic (e.g. Thurow 1970, Berner 1985; Tomkiewicz et al., 1998) males are reported to arrive earlier in the spawning areas than females.

An understanding of the processes involved in the timing of gonadal maturation and spawning of different stock components may be valuable for the understanding of spawning stock recruitment relations and recruitment success. If there is an association between the stock structure and the time and duration of spawning this might represent important sources of variability in the reproductive success of the stock due to seasonal changes in environmental parameters. The results of Hutchings & Myers (1993) indicated that the observed increase the proportional abundance of younger individuals was concomitant with a decline in the duration of the spawning time, reducing the probability that larval emergence will match peak abundance of zooplankton. The aim of the present study is in this context to investigate (i) the timing and duration of the Baltic cod spawning period in relation to sex and size and (ii) the composition of the adult population structure in main spawning area, the Bornholm Basin, during the spawning season. Data were collected as part of the Baltic CORE project in 1995-97 through a series of surveys conducted in the spawning area as well as on surveys outside the spawning period with a representative sampling of the entire stock. Sampling has continued in the proceeding STORE project in 1998 and 1999 and the inclusion of these data in database in later analyses is expected to improve the results of the study especially regarding the late spawning period. The results presented in this paper should therefore be perceived as preliminary.

Materials and methods

Data on sex, maturation stage, length distributions and catch per unit effort were collected onboard German, Danish and Swedish research vessels during the years 1995-97 (Table 1). The cruises during the periods January-March and late August-October mainly applied bottom trawl hauls and covered the depth range from 30-90 m in Sub-division 25. The cruises in April to August applied pelagic as well as bottom trawl hauls and covered the area in the Bornholm Basin deeper than 60 m including the spawning area (e.g.Bagge, 1994; Brander 1994). The coverage, gear and trawl time differed between cruises and hauls, and catches were therefore standardised to the average catch rate per trawl hour for each survey.

From each trawl haul, all cod or a representative sub-sample of the catch was length measured (total length). For the determination of sex and maturity stage at size a sample size of at minimum 3 specimen per cm group larger than 14 cm was aimed at for each haul or sub-area. Sub-areas of varying size were applied during non-spawning area surveys in 1995. The data were raised to population level by the length frequency according to the sampling design (haul/sub-area) to calculate the CPUE per sex and maturity stage. Around 50.000 cod were length measured and around 15.000 cod sex and staged during the period in total, but the sampling intensity and size varied between surveys (Table 1). The maturity was staged visually according to a 10-level index scale, which represents a modification of the scale suggested by Maier (1908). The stages are defined: Stage I: Early immature, II: late immature with early signs of gonadal development, III-IV: maturing stages, V: early spawning phase, VI: main spawning phase, VII: late spawning phase, VIII: spent condition, IX: adults in resting condition and X: individuals with diseased gonads. In the beginning of the sampling period and in the data analysis, specimens in Stage X were omitted, as they may not show normal behaviour, while stages II and IX were combined, because the two stages could not be separated accurately by macroscopic characters (Tybjerg & Tomkiewicz, 1999).

The data on individuals in maturation stage I were omitted in the analysis of the maturation process, because the main part of specimen in this stage belongs to the size group below 15 cm, which were not sexed and staged). In the analysis of the maturation process, the relative CPUE per maturation stage or phase (maturing: III+IV, spawning: V-VII, spent: III, and late immature and resting (II+IX) was calculated for each sex (and size group: 15-39 cm, 40-59 cm and > 60 cm) following the methodology described by Iles (1964). Applying this procedure, the progression of the relative proportion in particular stages in the population over time indicates the duration, peak occurrence and timing of the stages in the population during a specific period. The median day of the particular cruises was applied to reference the time of sampling.

The proportion per sex and maturity stage/phase from cruises conducted at the same time of the year was averaged over the range of years using 2 weeks periods as time intervals. The average proportions were related to the median day of the combined cruises. In the analysis of the proportions by length group, however, all cruises conducted in April were combined. This was necessary due to low catch rates and limited coverage of the survey in April 1995, which did not include enough specimens to separate data by length group, sex and maturity stage.

In the analyses of sex ratios all cod larger than 15 cm were included independent of their maturity stage, because the earlier sexual maturation of males compared with females (Tomkiewicz et al., 1997) otherwise would influence the sex ratio and obscure the results. The estimated sex ratio per survey were based on CPUE data as in above analyses.

Results

The estimated proportions per maturation stage within surveys are illustrated for males and females in Figure 1A and 1B. The coverage in time varied between years, but the inter-annual variability in the timing of the maturation stages appeared to be relatively low, except that spawning tended to commence slightly later in 1997 than in 1995 and 1996, especially for females. A large proportion of males had entered maturing stages in January and no males in spawning condition were observed independent of the year. The proportion of males in spawning condition increased rapidly from March though April. From May through July, males were almost exclusively in spawning condition with the proportion in spent stage increasing from August. In all years, the females were observed to be in maturing stages from January through March without any observations of females in spawning condition. Females commenced spawning in April with a high proportion in spawning condition from late May through July. Spent specimens were not observed until late July, where also the proportion of females in late spawning phase was high independent of the year.

The proportion in different stages and phases in Figure 2 illustrates the average progression of the reproductive cycle for males and females during the sampling period. The proportion of males leaving Stage II and IX to enter the maturing stages ceased from January through March. The proportion of males in stage III decreased from January and almost all males had completed the Stage IV by the end of May. The timing of the maturating stages of females was later than for males and the proportion in stage III did not decline until April. Females in Stage IV were observed until July, but the duration of this stage was quite similar for both sexes. The males accordingly entered the spawning phase earlier than females and the duration of the different stages was longer resulting in a longer spawning period extending from April to October. The female spawning period extended from mid May to September. The cease of the spawning illustrated by the decrease in the proportion in late spawning condition and the increase in the proportion of spent specimens was concurrent for males and females and occured in August. A low proportion in early maturing stage was observed in September.

The average proportion in the maturing, spawning and spent stages and the duration of the phases is shown in Figure 3. The average duration of the maturing phase indicated by the length of time with the proportion of stages III+IV being above 50 %, was about 2.5 months with a time lag of about 1.5 months between males and females. The average duration of the male spawning period was about 4 months and around 2.5 months for females with the difference owing to a lag in the time at which 50% had reached spawning condition. The proportion of spawning males peaked in June and July, while the spawning female proportion peaked in July.

The timing of spawning of different size groups of males and females is illustrated in Figure 4. The proportion of males in spawning condition for the different size groups indicated that larger males in general start spawning earlier and spawn longer, but the time of peak spawning was similar for all size groups i.e. in June-July. Around 25 % of the large males (>60 cm) were observed to be in spawning condition already in early March and spawning in this size group continued into September with around 25 % being in spawning condition at the beginning of this month. Spawning males in the smallest size group (<40 cm) were mainly observed from April to August with only a negligible proportion in spawning condition by the end of August. The medium sized males (40-59 cm) exhibited an intermediate pattern through out the season. The overall length of the spawning season covered 8 months for the largest size groups of males and about 6 months for the smallest male size group. The large sized females similarly were in spawning condition for longer periods than smaller sized females, but as for males the time of peak spawning tended to be similar for all size groups, i.e. in July. The proportion of large females in spawning condition increased from a few percent in

March to more than 25% in mid April and a low proportion tended to continue into September. The smallest female size group (<40 cm) showed a pronounced delay in the onset of spawning and spawning ended earlier. Only around 10 % had reached spawning condition in mid May and hardly any were spawning by mid August. As for males, the intermediate female size group (40-59 cm) showed an intermediate pattern with respect to the onset and ending of spawning. The overall spawning season of small females was considerably shorter, i.e. less around 4 months, than for the largest size group i.e. around 6 months.

Earlier arrival in the spawning area due to the earlier progress of the male maturation was evidenced by the observed sex ratio (Fig. 5). The male proportion dominated the female on the spawning ground in the early spawning period (April/May) reaching a maximum of two thirds being males, while the proportion of female exceeded male in late spawning season (July/August) reaching a maximum of almost three quarters being female. In contrast, the sex ratios derived from trawl surveys in January-March and August-September assumed to cover the entire population in Sub-division showed a relatively even sex ratio.

The change in sex ratio seemed to concomitant with a redistribution of the population in relation to the spawning season (Fig. 6). The relative CPUE of the smallest size groups was substantially lower than in the entire population, while the CPUE of the intermediate and especially the largest size group was substantially higher. The decline in proportion of males on the spawning grounds was mainly caused by a decrease in the relative CPUE of the intermediate sized and also most abundant length group as the spawning season progressed. The relative CPUE of the intermediate and large sized females increased concurrently throughout the spawning season. The relative CPUE of the smallest size group of males was considerably lower than for the intermediate size group during the spawning season, however an increase to a higher level was observed from mid May to mid July. The relative CPUE of small females remained at a very low level through out the spawning season. The proportion of the large size group is the population is clearly very low, especially for males, although the relative CPUE increased during the spawning season.

Discussion

The scale applied for grading the maturation status of the cod in very fine graded, which adds to the variation in the observations of the individual stages, since the judgement of the macroscopic characters is subjective. However, the accuracy increases, when data are aggregated into reproductive phases. The scale for females has been evaluated by histological methods to increase its accuracy and has a major point brought about a redefinition of Stage 5. This stage was graded as a maturing stage in the original scale of Maier (1908), but is in fact an early spawning stage (Tybjerg & Tomkiewicz, 1999). The fine grading of the scale has been fortunate in this respect, as it has not affected the applicability of existing data. The redefinition of this stage has also led to a higher degree of agreement between the timing of spawning in the population and the observed seasonal egg abundance's (Wieland et al., in press). This stage has also been reclassified in the present analysis, since the duration of Stage IV is quite similar for males and females, but it needs evaluation. If Stage V appear to be a maturing stage it will delay the onset of male spawning, but not change the timing of peak spawning considerable.

The timing of gonadal maturation differed between the sexes with the male maturation in general being more progressed than that of females in relation to time, except in the late spawning period. The months in which the early maturation process is initiated were not covered in the present study, but the process is assumed to start mainly in November-December, though some specimens in maturing stages were observed in October. These specimens, which mainly originated from the area close to Bornholm might belong to the adjacent stock in the western Baltic, which is spawning earlier, i.e. February-April (Brander, 1994; Bleil and Oeberst, 1997) and thus not reflect the general maturation pattern of the eastern Baltic stock. Further information about this period will be provided by data from 1998 and 1999. However, the rapid transition from the early to late maturing stage in February-March for males and April-May for females indicates that the maturation process should be initiated latest by the end of February for males and by the end of March for females, if spawning shall take place. The disappearance of specimens in the late immature stage from April to August should not be perceived as an indication of that all specimens in this stage enter maturing stages. This stage may occur throughout the year in the more shallow areas outside the spawning area, which were not covered during the April to August surveys.

The males in general reached spawning condition earlier than females and spawned over a greater length of time, which agree with previous investigations of this stock (Berner,1985; Bleil & Oeberst, 1997) and the observed pattern in other cod stocks (e.g. Hutchings & Myers, 1993; Kjesbu et al., 1996; Thorsteinsson & Marteinsdottir, 1998). The onset of male spawning in March and females in mid May was, however, later than usually reported for the stock (Brander, 1994; Berner, 1985; Bleil & Oeberst, 1997). Peak spawning time of males was observed in June-July and in July for females, which agrees with peak spawning dates in the Bornholm Basin that has been derived from cod egg abundance estimates obtained from ichthyoplankton sampling (Wieland et al., in press). Spawning ceased concurrently for both sexes in the early part of August. However, the abrupt decline of spawning might to some extent be due to the unbalanced data with the late spawning season only being covered in 1995. A slightly later timing of spawning in 1996 and 1997 as indicated by the proportion in spawning phase suggests a more gradual decrease than the average proportions imply.

The time of the onset and the duration of the spawning phase differed between length groups of females and to a lesser extend also between males, with the larger fish maturing earlier and having a more extended spawning season. This size dependence is likely to reflect that the amount of energy required for gonadal development is not only sex, but also size dependent. The amount of energy and protein needed for development of gonads relative to the size of the fish decreases with size in cod (Shapiro 1988). This may explain the earlier onset of spawning of larger females compared with smaller as well as the earlier maturation of males in general and in relation to size. The increased fecundity with size and larger number of egg batches to be spawned by females might explain the longer duration of the spawning period. The time of peak spawning, however, did not differ substantially within size groups independent of sex. These preliminary results tend not to support the hypothesis that a change in the stock structure towards a higher proportion of younger females should contribute significantly to the change in time of peak spawning to later in the year during the last decade (Wieland et al., in press). However, adverse conditions might affect smaller females more than larger, which could cause a more pronounced shift in time of peak spawning of small females than of larger.

The average individual spawning periods of females ranged between app. 1.7 to 2.7 months, which appears to be rather long compared with individual spawning times for other cod stocks (Hutchings and Myers, 1993; Thorsteinsson and Marteinsdottir, 1998). However, the limited overlap between the maturing and spent stages indicates that the duration of the main spawning period to a large degree reflect the average spawning time of an individual in the population. This is supported by the finding that all size groups have very similar peak spawning times except being more extended for males and by the change in sex ratio as well as in the relative CPUE of different size groups during the spawning period.

The observed increase in the proportion of males early in the spawning period agree with their more progressed maturation and with previous findings for the stock (e.g. Berner). The increase in the female proportion in the late spawning season agrees with the increasing proportion of especially intermediate sized females. On the contrary, the sex ratio within the population as observed in January-March and in late August-October seemed to be rather equal. The redistribution of the stock during spawning is also indicated by the relative CPUE of different sized females and males during the spawning period. The CPUE of the intermediate size group decreased during the spawning period concurrent with an increase in the relative CPUE of intermediate and large sized females, which in accordance with the spawning time of these size groups. The relative CPUE of smaller males in the spawning area that is considerably higher than for similar sized females agree with their earlier sexual maturation (e.g. Berner, 1985; Tomkiewicz et al. 1997), while the relative CPUE of large sized males clearly indicate shorter longevity of males in the population.

The size dependent spawning duration found in this study supports the hypothesis by Hutchings and Myers (1993) that the stock structure influences the duration of the spawning period. Their results indicated that the observed increase the proportional abundance of younger individuals was concomitant with a decline in the duration of the spawning time, reducing the probability that larval emergence will match peak abundance of zooplankton. This might also apply to the Baltic Sea where the reproductive volume generally declines from spring to summer (MacKenzie et al., 1996), and the availability of zooplankton as prey of cod larvae and pelagic juveniles (e,g. Krajewska-Soltys & Linkowski, 1994; Zuzarte et al., 1996) as well as predation on cod eggs by clupeids (Köster & Schnack, 1994, Köster & Möllmann, 1997) varies seasonally. Also the quality of eggs produced by different sized females differs, i.e. large females produce larger eggs and larvae (Nissling et al., 1998) that may have a higher probability survival, which might further influence recruitment the variability. An improved understanding of the processes involved in the timing of the gonadal maturation and spawning may thus prove to be valuable in fisheries management, e.g. regarding stock-recruitment relations and minimum acceptable spawning stock levels or in evaluation of different management strategies e.g. season or area closures (ICES 1999/ACFM:15).

In summary:

The average spawning period was observed to extend from April into September in 1995-97 confirming the long duration of the eastern Baltic cod spawning time. The preliminary results of our study suggest that the duration of the spawning period of this stock depends on both its sex and size composition, whereas the timing of peak spawning seems not to be influenced by size. These findings tend to confirm the hypotheses that a high proportion of larger sized cod tends to extend the spawning period which might enhance the probability of eggs and larvae emerging at a time with favourable environmental conditions for development and growth thereby decreasing the risk of recruitment failure. This might be especially important under unfavourable environmental conditions, which might influence also the adult stock and the timing and quality of spawning in general. The difference in the observed reproduction pattern with males reaching spawning condition earlier, completing spawning later and a longer duration of the main spawning time results in a complete overlap in spawning time between females and males. Such a strategy might ensure a high fertilisation probability of all eggs produced during the spawning season, which would make sense from an evolutionary point of view. However, the cost of the strategy in combination with the earlier sexual maturation males seems to be an decreased male longevity either caused by fishery on especially early spawning aggregations or from an increased natural mortality due to physiological stress or a combination of both factors.

Acknowledgements

We wish to express our thanks to the scientific personnel participating in the various surveys and the crew of the research vessels for their assistance in sampling the data. We especially thank Barbara Johnson for giving us the opportunity to sample onboard R/V Argos. We thank Norbert Rohlf and Gerd Kraus for assistance with the data preparation. The sampling was performed as part of the Baltic CORE project (AIR2 94 1226) and data analysis has been continued within the frame of the Baltic STORE project (FAIR 98 3959). The European Commission has funded both projects.

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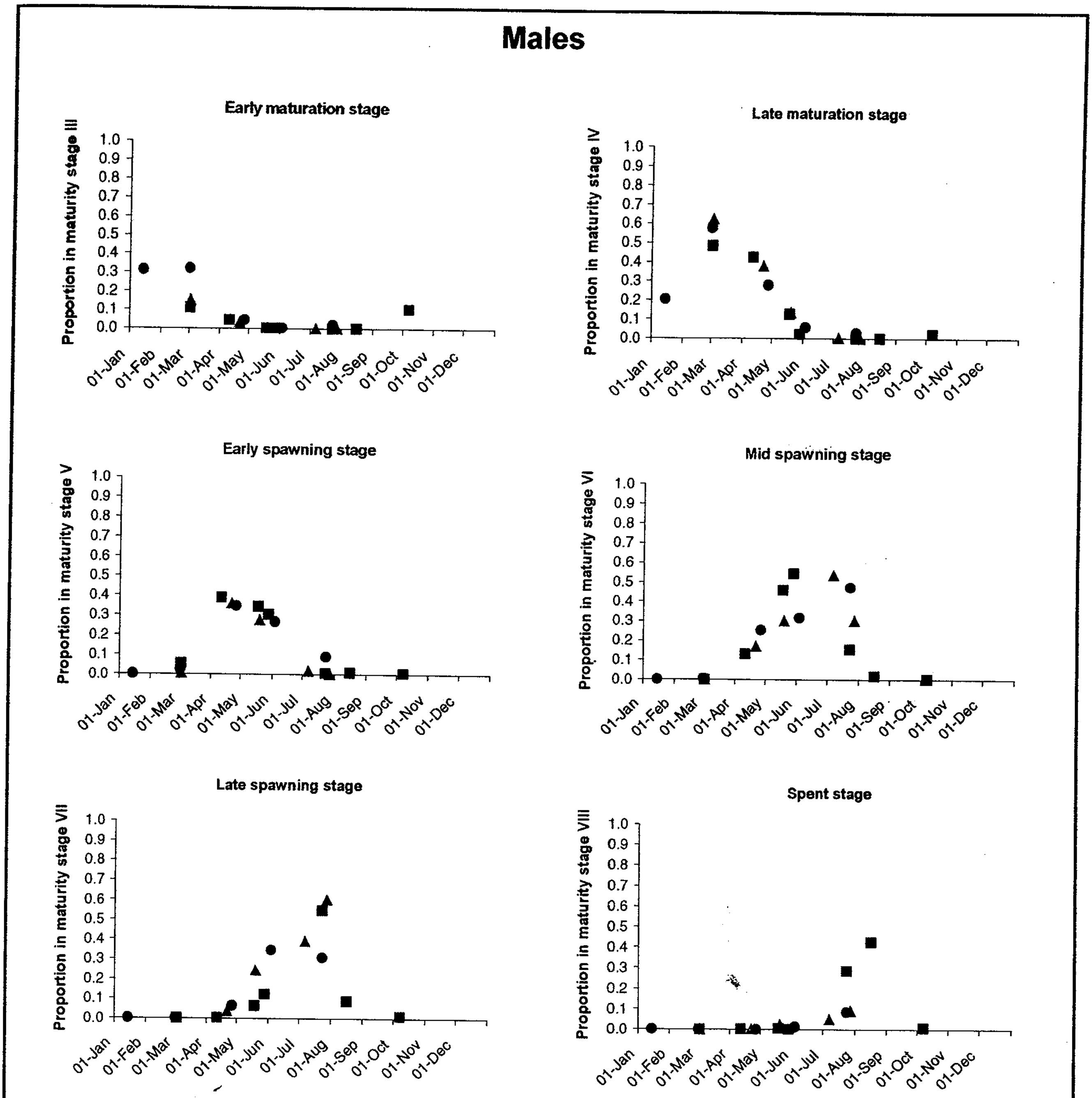
Table 1: Cod directed trawl surveys conducted in the Bornholm Basin (ICES Sub-Division 25) during the years 1995-1997 by the German R/V Alkor, the Danish R/V Dana and the Swedish R/V Argos. The time period refers to the exact period in which sampling was conducted.

Year	Time period	Research vessel	Number of hauls	Numbers length measured	Number of specimens sexed and staged
1995	24-Feb - 08-Mar	Dana	35	7196	608
1995	10-Apr - 12-Apr	Alkor	10	489	473
1995	16-May - 21-May	Alkor	18	1376	1365
1995	26-May - 30-May	Dana	18	13478	3236
1995	20-Jul - 27-Jul	Alkor	21	3130	1655
1995	14-Aug - 18-Aug	Argos	10	2507	698
1995	06-Oct - 09-Oct	Dana	15	1868	304
1996	25-Feb - 09-Mar	Dana	25	8349	688
1996	19-Apr - 23-Apr	Alkor	26	577	577
1996	18-May - 20-May	Alkor	15	653	488
1996	02-Jul - 10-Jul	Dana	25	4398	1286
1996	24-Jul - 30-Jul	Alkor	19	1890	1237
1997	10-Jan - 18-Jan	Dana	28	857	295
1997	20-Feb - 10-Mar	Dana	28	2511	868
1997	24-Apr - 29-Apr	Alkor	22	253	253
1997	30-May - 08-Jun	Alkor	21	745	745
1997	20-Jul - 27-Jul	Alkor	15	550	500
Total:			351	50827	15276



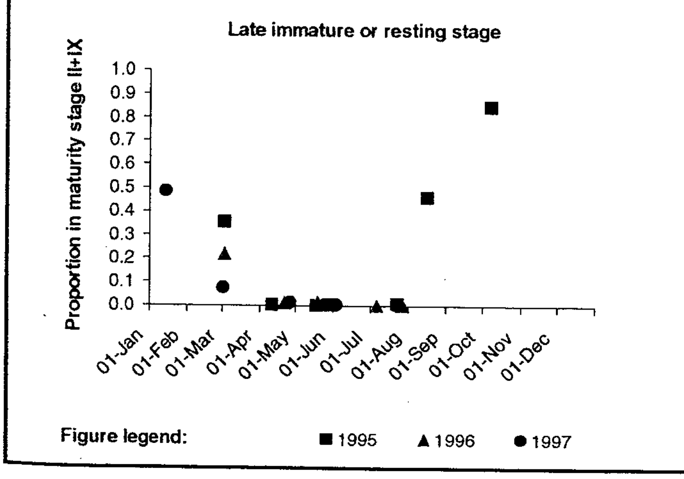


Figure 1A. Relative proportion of males in different stages of the reproductive cycle based on CPUE of males in stages II-IX at different times of the year in 1995-97.

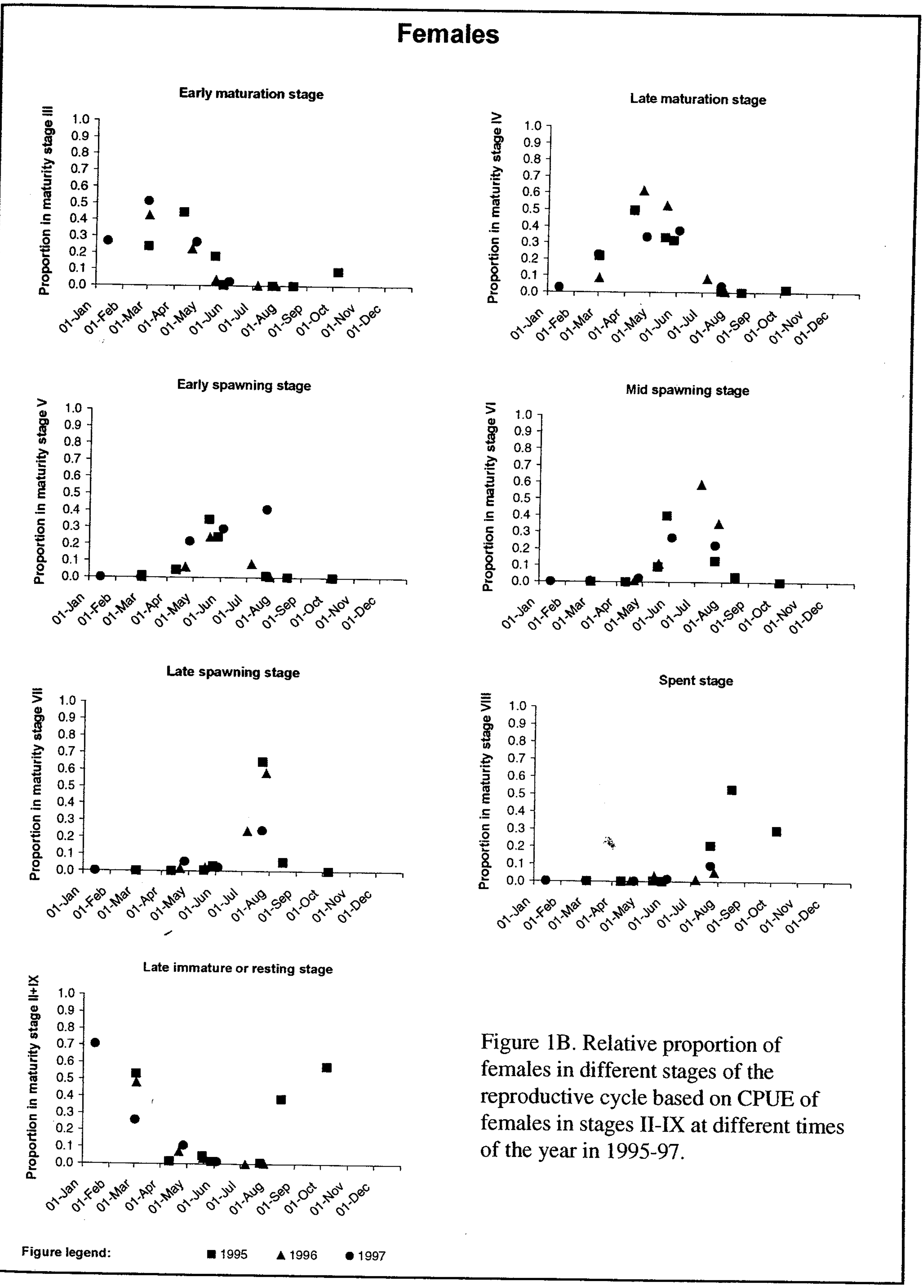


Figure 1B. Relative proportion of females in different stages of the reproductive cycle based on CPUE of females in stages II-IX at different times of the year in 1995-97.

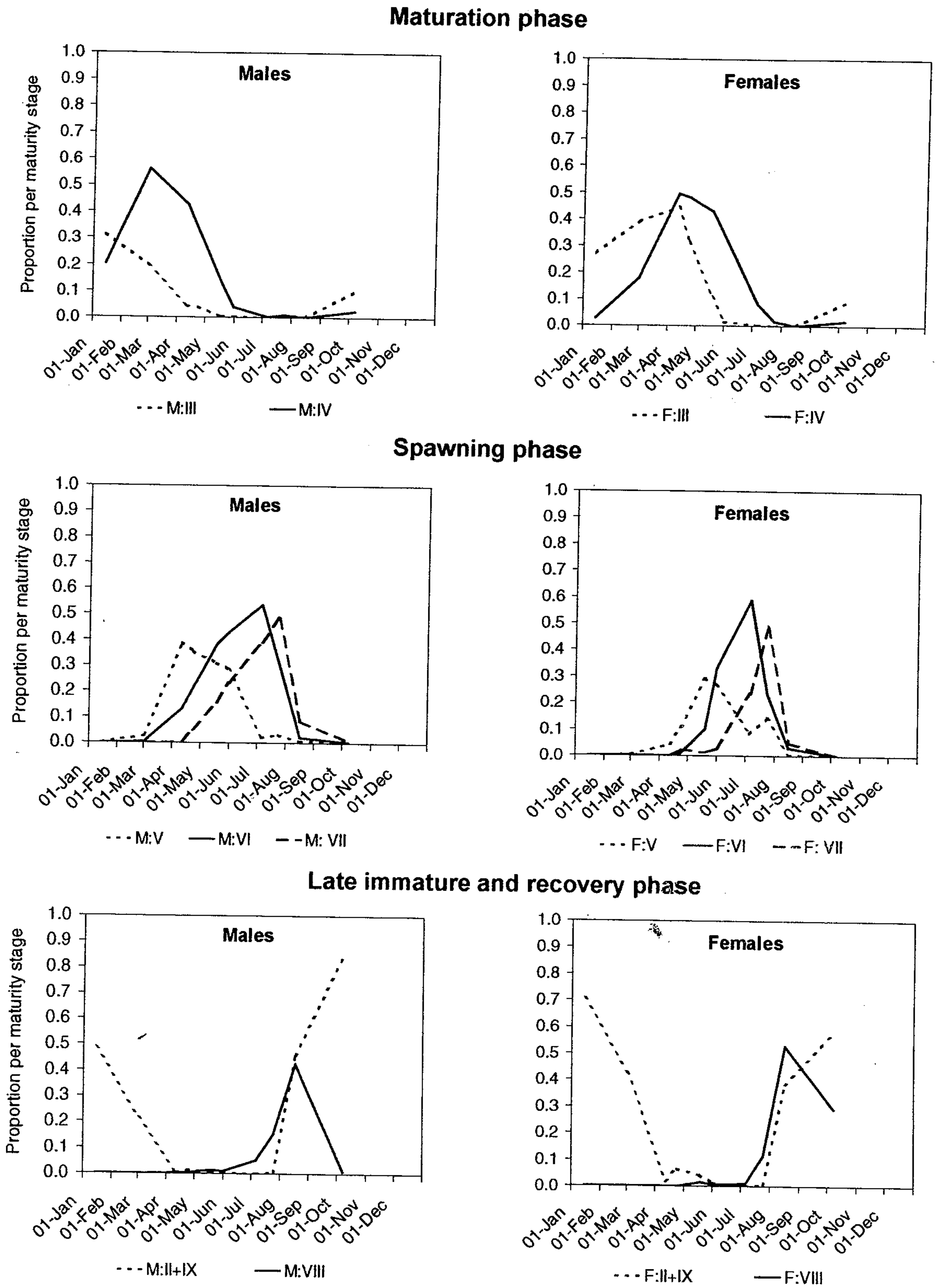


Figure 2. Average male and female proportions in different stages and phases of the reproductive cycle based on the CPUE of stages II-IX during the years 1995-97.

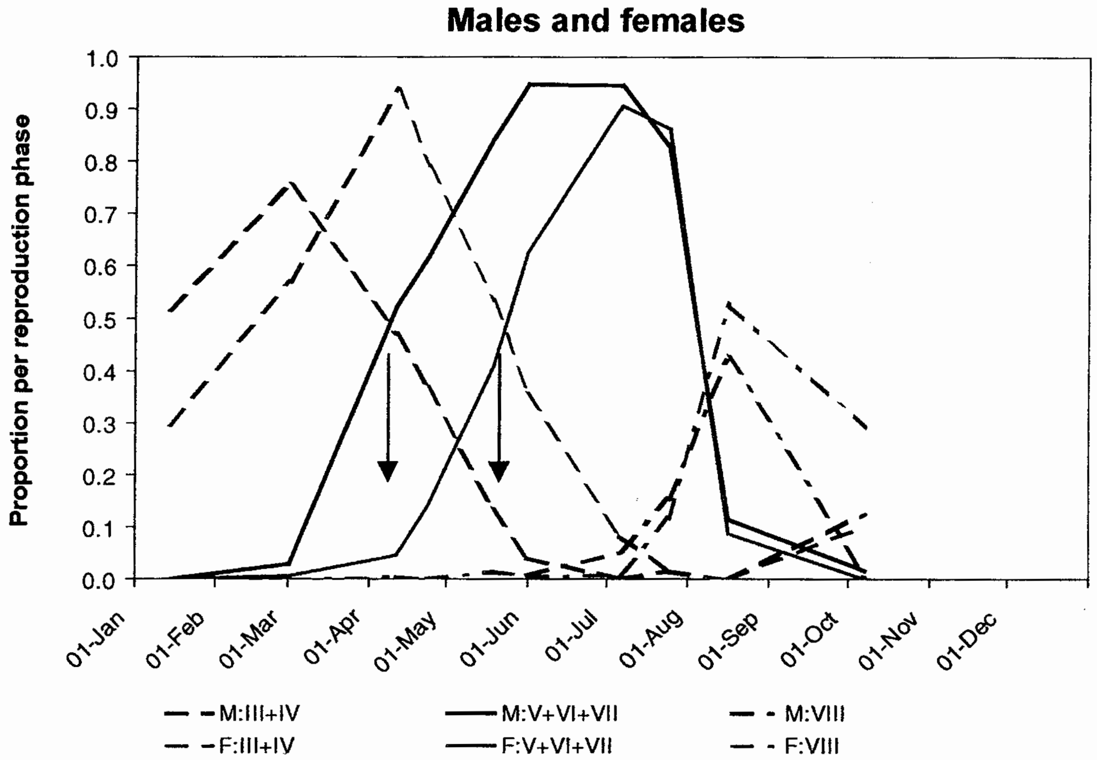


Figure 3. Average proportion and timing of the maturing stages (III-IV), spawning stages (V-VII) and spent stage (VIII) for males and females during the years 1995-97. Late immature and resting stages (II and IX) are included in the calculation of the proportions, but not illustrated in the figure. The arrows indicate the time when 50% of the female or male cod have entered spawning condition, respectively.

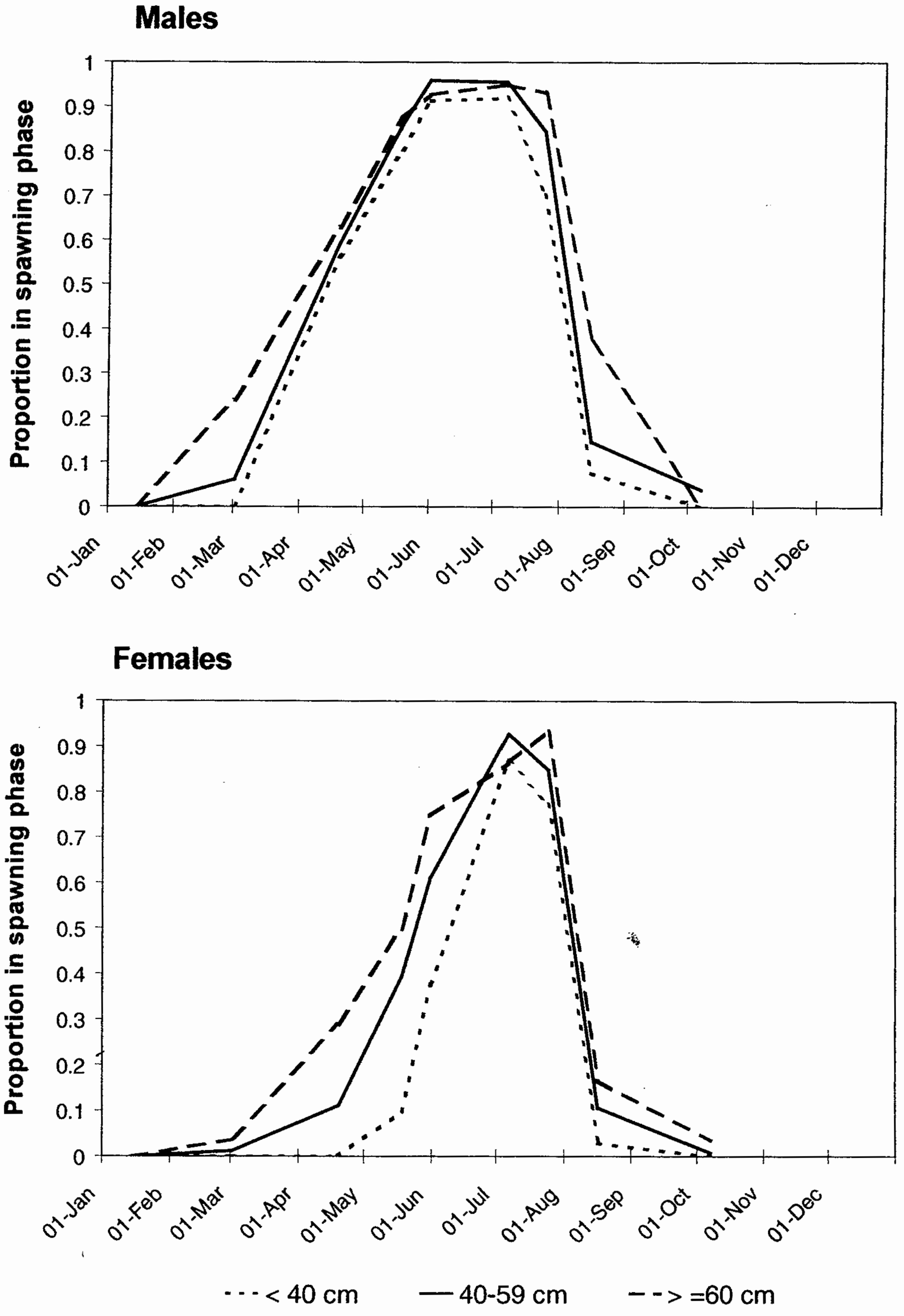


Figure 4. Average proportion of female and male cod in spawning phase (stages V-VII) for different size groups during the years 1995 and 1997. The proportions relate to the CPUE of stage II-IX.

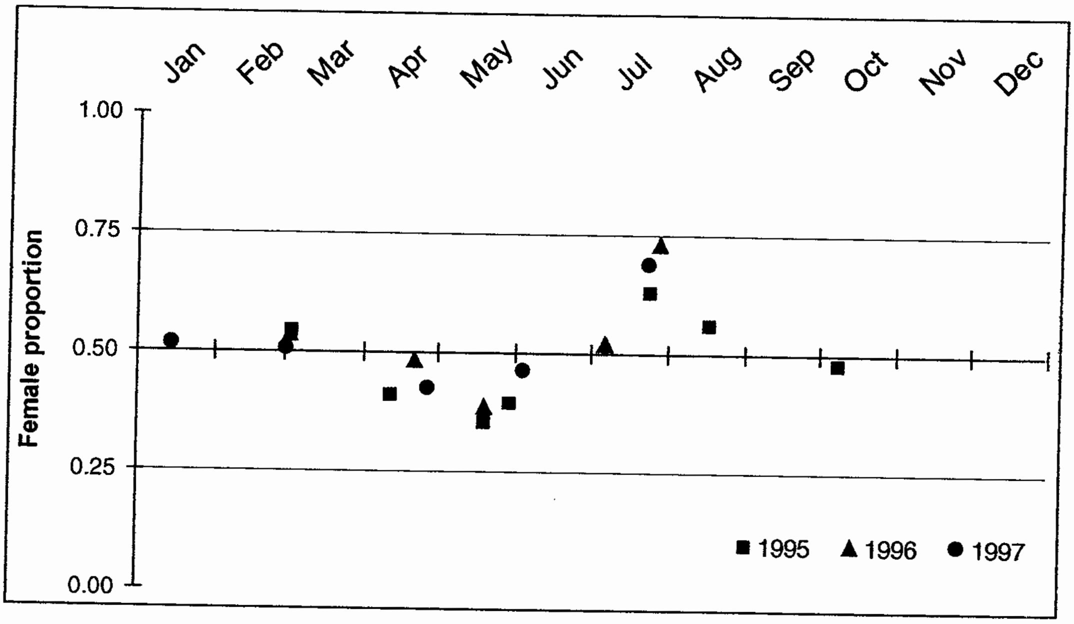


Figure 5. Proportion of females in the catches based on the average CPUE of cod larger than 15 cm during surveys in 1995-1997.

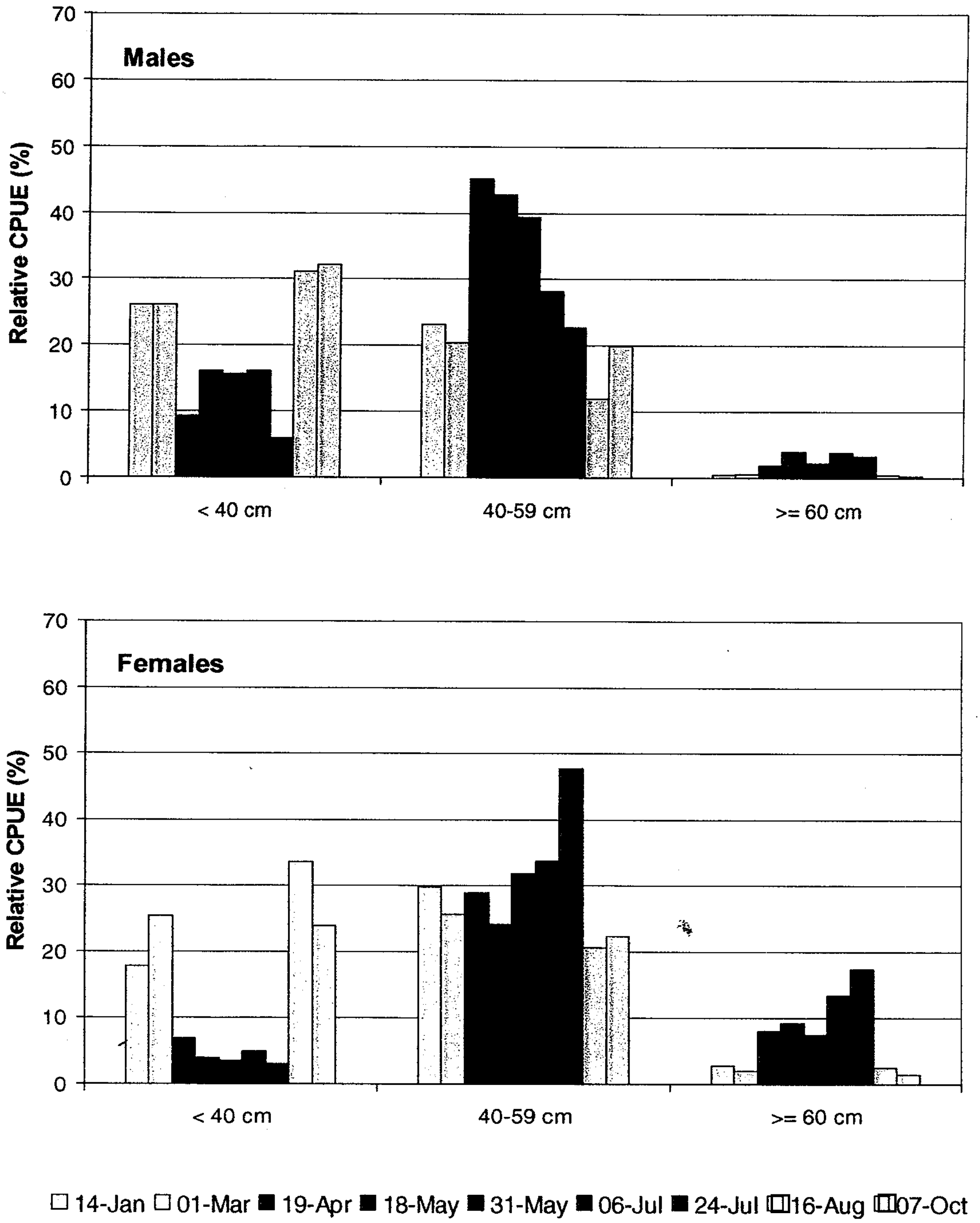


Figure 6. Relative CPUE per sex and size groups based on the average CPUE of cod larger than 15 cm during surveys in 1995-97.