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Duration, frequency and timing of sprat spawning in the Central Baltic: An analysis based on gonadal maturity.

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ABSTRACT

The duration, frequency and peak of sprat spawning in the 1999 spawning season are described. Spatial and year to year variations in the timing of spawning were analysed utilising maturity data obtained in June 1999 in ICES Sub-divisions 25, 26 and 27 / 28, respectively in April 1995, 1996, 1998 and 1999 in Sub-division 25. All analysis were based on gonadal maturity inspections of catches obtained from hydro acoustic- and trawl surveys as well as commercial fisheries. The sprat spawning season in 1999 lasted from February to July peaking in June with an average spawning frequency of 27% during main spawning time. The course of the 1999 season was validated against egg abundance data obtained from ichthyoplankton surveys conducted in parallel. Marked differences in the timing of spawning were found between the Bornholm Basin / Gdansk Deep and the Gotland Basin with delayed spawning activities of sprat in the latter. Both areas encounter pronounced differences in the temperature regime, whereas the Gotland Basin is characterised by the colder water temperatures. Furthermore, a consistent trend towards later spawning in most recent years has been observed. This trend was negatively related to the recently declining total biomass concurrent with increasing landings, but not to winter water temperatures.

Keywords: Baltic sprat, gonadal maturity, spawning, timing of spawning, spawning interval, spawning frequency.

INTRODUCTION

The timing and duration of the spawning season of temperate fish stocks is generally believed to be well adjusted to the prevailing environment so that the eggs and larvae emerge into favourable conditions (Cushing, 1969). However, temporal and spatial variability in environmental conditions (MacKenzie et al. 2000) as well in the timing and duration of the spawning season (Wieland et al. 2000) exists, whereas the latter might be positively or negatively coupled to the previous. Among the abiotic environmental factors water temperature has been identified to affect the timing of spawning of sprat (Elwertowski 1964; Johnson 1970; Wahl & Alheit 1988), focussing on internal factors the stock structure revealed to be of great importance in cod (Trippel et al 1997; Tomkiewicz & Köster, 1999). Especially in the Central Baltic, where the environment has a distinct seasonality, successful egg and larval development crucially depends on the timing of spawning (e.g. cod: MacKenzie et al 1996).

Stock sizes of Baltic sprat reached highest levels on record in the mid 1990ties exceeding a biomass of 3.1 million tons in 1995 concurrent with increasing catch rates due to a rising attraction for the fish meal industry (Anon. 2000; ICES C.M. 2000:ACFM 16). The years 1995 to 2000 included in this study covered the historic peak in stock size in 1995 / 1996, a 25% decline in SSB until 1999 and a predicted further downward trend (Anon. 2000). So far, for Baltic sprat no attempt has been undertaken to evaluate the temporal and spatial variability of the spawning time by means of gonadal maturity staging. Relating the timing of spawning to stock structure and size or hydrographic conditions could lead towards an enhanced understanding of variations in recruitment.

Within the EU funded Baltic CORE and STORE projects (AIR2 CT94-1226 and FAIR CT 983959) a length stratified maturity sampling scheme has been implemented. In order to enable the determination of timing and duration of the spawning season as well as spawning frequency of Baltic sprat a modified version of the maturity scale introduced by Alekseejev & Alekseejeva (1996) was applied. In particular, we addressed within our study the determination of peak spawning, the duration of the spawning season, the spawning frequency and individual interval as well as spatial variability in the timing of the season between ICES Sub-divisions in 1999. Sprat egg abundance data from Ichthyoplankton surveys conducted in parallel were used to validate the analysis. Additionally, inter-annual variations in the timing of spawning of Baltic sprat in the years 1995, 1996, 1998, 1999 have been investigated and related to stock size and winter water temperatures assuming that they were representative for the annual maturation period.

MATERIAL AND METHODS

Spawning frequency, peak spawning time and duration of the spawning season 1999

Sampling was carried out on hydro-acoustic and regular trawl survey cruises covering the entire spawning and post-spawning period in ICES Sub-division 25. Samples from commercial fisheries covering the pre-spawning period were suspected to be biased towards larger individuals and were, therefore, only included to estimate the starting point of the spawning season. For the type of sampling and samples sizes see Table1. A length stratified sampling scheme (10 individuals per 1 cm length class per station) was chosen to estimate sex ratio and maturity stage using a modified version of the macroscopic visual maturity scale introduced by Alekseejev & Alekseejeva (1996) (Table 2). In addition to the original scale females containing hydrated eggs were split into two groups according to whether they going to spawn the first batch or have already entered the spawning process.

Length frequency distributions were established for each station measuring approx. 200 randomly chosen individuals. An average length frequency distribution was compiled for each cruise by weighting the haul specific length frequency distributions for catch rates. Cruise specific proportions of females per length class were applied establishing cruise specific female length frequency distributions. Proportions of mature females in spawning condition (**pfs**; maturity stages 4-5; 5; 6-3; 6-4; 6-4h) were averaged by weighting length specific proportions for the cruise specific female length frequency distributions. To estimate the duration and peak of the spawning season, the **pfs** were related to the sampling time and a Gauss curve was fitted to survey data only. To validate the analysis of peak spawning time the data were contrasted with sprat egg abundances of the youngest egg stage determined from concurrent ichthyoplankton surveys again fitting a Gauss curve. To estimate the spawning frequency the above calculation scheme was applied again with **pfs** being substituted by the portion of **pfs** containing hydrated eggs (**pfh**; maturity stages 4-5; 5; 6-4h), assuming that these individuals will spawn within the next 24 hours.

Spatial variation in timing of spawning

Sampling was carried out on a hydro-acoustic survey at peak spawning time in June 1999 covering Sub-divisions 25 to 28 (see Table 1 for sample sizes). Samples from Sub-divisions 27 and 28 were grouped to achieve a sufficient sample size in the southern Gotland Basin. Proportions of adult females in the various maturity stages have been grouped into spawning (**pfs**) and pre-spawning condition (**p-pfs**), proportions in post spawning condition were nearly or equal to zero (< 0.01) in all Sub-divisions and not considered. In contrast to the above calculation scheme, Sub-division specific length frequency distributions were compiled and used to calculate average proportions. The further estimation procedure closely followed the scheme described above, whereas maturity stages 3 and 4 were used to estimate **p-pfs** and stages 4-5, 5, 6-3, 6-4, 6-4h represented **pfs**. To detect spatial differences in the timing of spawning **p-pfs** and **pfs** per area have been compared.

Inter - annual variation in timing of spawning

Sampling for this analysis was carried out on trawl survey cruises in April / May 1995, 1996 and 1999 completed by data from commercial fisheries in April 1998, no data is available for 1997 (Table 1). The calculation of average **p-pfs** and **pfs** followed the above described scheme with cruise specific length frequency distributions. A different methodology had to be applied for the commercial samples because of a possible bias in their corresponding length frequency distribution (see above). Instead of using the length frequency distribution the inverse variance was applied as weights for the data set to account for differences in sample sizes (Tomkiewicz et al. 1997; appendix 1). Again **p-pfs** were contrasted with **pfs** for every year. Additionally, first quarter water temperatures (ICES hydrographic database; plain averages over Sub-division 25, 26 and 28, all depth strata) as well as sprat total biomass in the assessment area (Sub-divisions 25-32; calculated for the start of the year; ICES 2000) have been used as independent variables in linear regressions of **p-pfs.**

RESULTS

Spawning frequency, peak spawning time and duration of the spawning season 1999

In 1999 spawning of sprat in Subdivision 25 started between January and February with a relatively low increase of the **pfs** until end of April (Fig.1; note that the data for Jan. to March is from commercial fisheries and only used as a reference to estimate the beginning of the season). May, June and early July displayed the highest spawning intensity, while the **pfs** sharply dropped from July to August with spawning activity having stopped on the 13th of August. Our analysis of the gonadal maturation process showed a peak spawning time at early June with 78 % of the mature females in spawning condition (Fig. 1). For the validation of this analysis the maturation data was contrasted with abundance data of the youngest egg stage (IA) of sprat from concurrent ichthyoplankton surveys. The peak spawning time was corresponding in both analysis, whereas the increase / decrease rates were differing, i.e. the major increase in the **pfs** was observed between April and May, while the major increase in the egg abundance was delayed and observed between May and June. A complementary trend was observed towards the end of the spawning season, egg abundance descended earlier than the **pfs** (Fig.1).

The cruise specific average spawning frequencies were estimated via the proportions **pfh** of **pfs**. The highest spawning frequency was observed during the April cruise with 85 %. May, June and July samples showed a low variability in spawning frequency with values between 26% (July) and 30% (May) (Fig.2). The extraordinary high value of **pfh** in April (85 %) was excluded from the calculation of the spawning interval as a regular spawning pattern had not established (**pfs**: 21%) by that time. Commercial data from the first quarter of the year was also not included in the analysis due to the same reason. Utilising data for May, June, July, i.e. the main spawning time, resulted in an average spawning frequency of 27 % indicating an average spawning interval of approximately four days for Baltic sprat.

Spatial variation in timing of spawning

To detect spatial variations in the timing of spawning samples had to be obtained quasi simultaneously in all Sub-divisions to be comparable. Data on gonadal maturation used within this analysis was obtained on a hydro-acoustic survey during peak spawning time in June 1999 within the time frame of one week in Sub-division 25, 26 and 27+28. Small scale temporal differences were not considered in this exercise. **Pfs** were generally high in all areas varying between 0.72 in Sub-division 27+28 and 0.85 in Sub-division 25 (Fig. 3), whereas the **p-pfs** varied between 0.04 in Sub-division 25 and 0.11 in Sub-division 27+28 (Fig. 3). Similar conditions were observed in Sub-divisions 25 and 26, whereas spawning seemed to be delayed in Sub-divisions 27+28, with the proportion in pre-spawning condition being 36% higher and the proportions in spawning condition being 25% lower (setting the highest value 100%) than in Subdivision 25 (Fig. 3).

Inter - annual variation in timing of spawning

A clear temporal trend was observed in the timing of spawning from 1995 to 1999. In April 1995 **pfs** added up to 92 % showing a sharp almost linear decrease to 1999 with only 37% being in spawning condition in April (Fig. 4). As proportions in post-spawning condition were neglectable for all sampling years (< 1 %), a complementary trend was observed in the **p-pfs**, showing that the timing of the sprat spawning season in Sub-division 25 shifted towards summer in most recent years (Fig. 4). The extremely high **pfs** values in April 1995 and 1996 of 92 and 82 % respectively, indicated that April was peak spawning time in these years (see also determination of peak spawning time 1999, above). A significant negative correlation of **p-pfs** with total biomass of sprat in Sub-divisions 25-32 ($r^2 = 0.98$; $p < 0.01$) while the first quarter water temperatures were not related to **p-pfs** ($r^2 = 0.22$; $p > 0.05$).

DISCUSSION / CONCLUSIONS

The investigation of the reproductive biology of sprat including the annual maturation cycle has been the subject of research since many years and various stocks of the North East Atlantic and adjacent areas have been investigated (Heidrich, 1925, Petrova, 1960, De Silva, 1973, Alheit, 1988, Torstensen, 1998). Studies focussing on the temporal patterns of the spawning season most often utilised egg abundance data to describe the course of spawning. Within the present study we were able to show that also the easy to obtain data on gonadal maturity can be utilised not only to describe variations in the onset of spawning, but furthermore the duration, peak and frequency as well as the individual interval of sprat spawning.

In the analysis of the course of the 1999 spawning season consistent survey data were only available for the major spawning period from April to August. Nevertheless, to determine the starting point of the season first quarter samples from commercial fisheries were included. A further incorporation of these data seemed to be unwise as it did not fit to the expected distribution of **pfs** from survey data, the latter indicating a faster increase of **pfs**. It is suspected that the commercial data is biased towards larger individuals (e.g. differences in gear selectivity). As larger sprat mature earlier than smaller ones (Torstensen 1998), this would explain the earlier increase of **pfs** determined from commercial data.

The determination of the spawning frequency and, hence, spawning interval revealed that this type of analysis should only be performed during the main spawning season, when spawning aggregations showing a regular spawning pattern have established. The spawning frequency of 85 % in April concurrent with only 21 % of the females being in spawning condition was unreliable and excluded from the analysis. Sampling months May, June and July, all characterised by more than 60 % of the females in spawning condition, revealed stable values for spawning frequency. The average of 27 % led to an estimate of an approximate spawning interval of four days for Baltic sprat.

A prolonged spawning season lasting from early spring to mid summer has been described for many sprat stocks including Baltic (Heidrich, 1925, Graumann, 1980, Müller et el. 1990), North Sea (Wahl & Alheit, 1988, George & Alheit 1987) and west of Scotland (De Silva, 1973) stocks. Most investigations on variations in timing and duration of the spawning season were based on abundance estimates of eggs and larvae (Wahl & Alheit, 1988, Graumann, 1980). The combination of both analysis within this study revealed a similar peak spawning time. The minor differences in the slopes of the rising and falling legs did not corrupt the validity of either method. They may be attributed to the time lag between ripeness and spawning or temporal variations in egg quality aspects as e.g. fertilisation rate.

For multiple batch spawners the duration of the individual spawning period increases with fish size (Hunter & Macewicz 1985) due to, inter alia, an increase in the number of batches and time interval between batches (Trippel et al. 1997). Larger sprat tend to spawn earlier (Torstensen 1998) and, furthermore, the time between batches as well as the onset of spawning (Elwertowski 1964; Johnson 1970; Wahl & Alheit 1988) are positively correlated with water temperature. This implies that environmental conditions as well as the stock structure may have a severe impact on the reproductive potential of the stock and, hence, on recruitment.

No investigations of the duration and intensity of spawning could be performed within the spatial and inter-annual analysis. All three Subdivisions were only covered on one cruise in 1999 and historic data was restricted to April. Nevertheless, these analysis were, firstly, able to show marked differences in the timing of spawning between the Bornholm / Gdansk Basin and the Gotland Basin with delayed spawning activities of sprat in the latter. Both areas encounter pronounced differences in the temperature regime (ICES 1999), whereas the Gotland Basin is characterised by the colder water temperatures. Another explanation could be stock specific differences in the spawning time, as especially the Bornholm Basin is still a mixing area of sprat from western and eastern neighbouring areas (Parmanne et al. 1994) while the Gotland Basin is considered to be solemnly inhabited by Baltic proper sprat. Secondly, a consistent trend towards later spawning in most recent years has been observed. We have included the 1998 data from commercial fisheries into this analysis, as it seemed that the above discussed bias, though significant on the intra-annual level, was obviously overwhelmed by the strong year effect. Nevertheless, the reliability of the 1998 data should be treated with caution. The annual trend in spawning time was not related to differences in winter water temperatures, which might due to the low temperature variation in the time period covered (min.: 3.67°C; max.: 5.15 °C), but negatively correlated with estimates of stock size. Sprat biomass in the assessment area was in 1995 at the highest level on record since 1974, whereas landings in 1998 and 1999 were considerably higher than in 1995 (ICES 2000), indicating a rise fishing pressure concurrent with an increasing likelihood of alterations in the stock structure. Though direct relationships between alterations in the stock structure and the timing and duration of the spawning season could not be shown in this study, the relationship between stock size, fishing mortality and alterations in the stock structure as e.g. described by Taggart et. al. (1994) for cod could be one reason for the recent delay in the sprat spawning season. The methods we utilised to describe the course of spawning of sprat could, furthermore, in combination with environmental and stock structure data be a useful tool for explorative analysis of the stock recruitment relationships when applied on a larger time scale.

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REFERENCES

Alekseejev F.E. & Alekseejeva E.I., 1996. Identification of gonads, maturity stages and study of sex cycles, fecundity, eggs production and maturation rate of marine commercial fishes. Methodical manual. Kaliningrad, AtlantNIRO, 75 p. (in Russian).

Alheit, J. 1988. Reproductive biology of sprat (*Sprattus sprattus*): Factors determining annual egg production. Journal du Conseil International pour l´Exploration de la Mer, 44: 162-168.

Cushing, D.H. 1969. The regularity of the spawning season of some fishes. Journal du Conseil International pour l´Exploration de la Mer, 33: 81-97.

De Silva, S.S. 1973. Aspects of the reproductive biology of sprat, Sprattus sprattus (L.) in inshore waters of the west coast of Scotland. Journal of Fish Biology, 5: 689-705.

Elwertowski, J. 1964. The influence of the 1956 and 1963 winter seasons on the life of the southern Baltic sprat. ICES C.M. 1964, Sardine Comm., Doc. No. 75 (mimeo), 5pp.

George, M.R., Alheit, J. 1987. Ovarian maturation cycle of sprat, *Sprattus sprattus.* ICES C.M. 1987 / H:47.

Graumann, G.B. 1980. Ecological peculiarities of main pelagophillous fishes reproduction in the Baltic Sea. Fischerei-Forschung 18 (2): 77-82.

Heidrich, H. 1925. Über die Fortpflanzung von *Clupea sprattus* in der Kieler Bucht. Wiss. Meeresunters., Neue Folge, Abt. Kiel, 20: 1-47.

Hunter J.R., Macewicz, B.J. 1985. Rates of atresia in the ovary of captive and wild northern anchovy, Engraulis mordax. Fishery Bulletin, 83: 119-136.

ICES 1999. Report of the Study Group on Multispecies Model Implementation in the Baltic. ICES C.M. 1999 / H:5.

ICES 2000. Report of the Baltic Fisheries Assesment Working Group. ICES C.M. 2000 / ACFM:14.

Johnson, P.O. 1970. The Wash Sprat Fishery. Fishery Investigations, Ser. II, Vol. 26, No. 4: 64-77.

MacKenzie B.R., St. John M., Wieland, K. 1996. Eastern Baltic cod: perspectives from existing data on processes affecting growth and survival of eggs and larvae. Marine Ecology Progress Series, 134:265-281.

MacKenzie, B.R., Hinrichsen, H.H., Pliksh, M., Zezera, A.S. 2000. Quantifying environmental heterogenity: habitat size necessary for successful development of cod *Gadus morhua* eggs in the Baltic Sea. Marine Ecology Progress Series, 193: 143-156.

Müller, A. Muhsin, K., Köster,F.W. 1990. Ovarian maturation and batch fecundity in Baltic sprat from the Bornholm Basin. ICES C.M. 1990 / J:30.

Parmanne; R., Rechlin, O., Sjöstrand, B. 1994. Status and future of herring and sprat stocks in the Baltic Sea. Dana, 10: 29-59.

Petrova, E.G. 1960. On the fecundity and the maturation of the Baltic sprat. Trudy Vsesojuznyj naucno issledovatelskij. Institut Morskogo Rybnogo Xozjajstva i Okeanografii, 42: 99-108 (in Russian).

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, G., Lilly, G., Morgan, J., Murphy,E., Myers, R., Rose, G., Shelton, P. 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on Northern cod. ICES Marine Science Symposia, 198: 140-157.

Tomkiewicz, J., Eriksson, M., Baranova,T., Feldman, V. and Müller H. 1997. Maturity ogives and sex ratios for Baltic cod: establishment of a database andtime series. ICES CM. 1997/CC:20.

Tomkiewicz, J., Köster, F.W. 1999. Maturation processes and spawning time of cod in the Bornholm Basin of the Baltic Sea: Preliminary results. ICES C.M. 1999 / Y:25.

Torstensen, E. 1998. Growth and maturity of sprat in Norwegian coastal waters. ICES C.M. 1998 / CC:19.

Trippel, E.A., Kjesbu, O.S., Solemdal, P. 1997. Effects of adult age and size structure on reproductive output in marine fishes. In *Early Life History and Recruitment in Fish Populations* (eds. R.C. Chambers and E.A. Trippel) Chapman & Hall, London: 31-62.

Wahl; E., Alheit, J. 1988. Changes in the distribution and abundance of sprat eggs during spawning season. ICES C.M. 1988 / H:45.

Wieland, K., Jarre-Teichmann, A., Horbowa, K. 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. ICES Journal of Marine Science, 57: 452-464.

TABLES & FIGURES

Tab. 1: Sprat maturity sample sizes and sources by year, month and ICES Sub-division.

Year	Month	Sub-div. 25	Sub-div. 26	Sub-div. 27-28	Sampling type	Total
1995	**April**	230			trawl survey	230
1996	**April**	755			trawl survey	755
1998	**April**	114			commercial	114
1999	**April**	1178			trawl survey	1178
	May	1738			trawl survey	1738
	June	2083	270	211	hydro-acou.	2564
	July	4223			trawl survey	4223
	August	1788			trawl survey	1788
	Sum	12109	270	211		12590

Tab. 2: Maturity stages for female Baltic sprat (modified after Alekseejev F.E. & Alekseejeva E.I., 1996)

Stage	**State**	**Females**
I	Juvenile	Gonads are thin, thread-like, colorless and transparent. Sex of fish is not distinguishable by naked eye.
II	Immature (non-mature)	Ovaries are small, tubular, slender, **yellow-orange**. Oocytes are **not visible by eye**. If the color is dark violett: stage **VI-II**!!!
III	Ripening	Ovaries increasing the size and at the end of the stage **occupy up to 2/3 of body cavity**. In the beginning of stage oocytes are half-transparent, but at the end of stage non-transparent, yellow. Only at the caudal end there might be some reddish area. Non-transparent and yellow oocytes are **seen by naked eye** through the membrane of ovary. Diameter of oocytes is 0.2 mm in the beginning of stage and 0.5 mm at the end of the stage. (Sub-stages of stage III (differentiation of the ripening females from those who are close to the mature stage) are no longer separated.) To distinguish between stage III and IV use the **size** of the oocytes. Oocytes in stage IV are slightly bigger! III is separated from VI-III with the help of the **color** of the ovary (VI-III: reddish violet).
IV	Mature (ripe)	Ovaries occupy all empty space in body cavity. Non-transparent oocyte diameter is 0.5-0.6 mm, so oocytes are **slightly bigger than in III**. The color of the ovary is **light yellow**, not reddish!
IV-V	Pre-spawning	Ovaries occupy all empty space in ventral cavity firmly pressing on all other organs. Through the membrane of the ovary **large** (diameter 0.7-1.0 mm) and transparent (**hydrated) oocytes** can be seen. In the ovary they are evenly distributed between different sized ripening, non-transparent oocytes. There are no eggs available in ovaries cavity. It is **important** to distinguish between IV-V and **VI-IVh** (modification!) to separate between first batch and repeat spawners. IV-V is mostly yellow in contrast to VI-IVh which is red-violet at the caudal end.
V (VI-V)	Spawning	Slight pressure upon the belly extrudes eggs from the genital opening (press before cutting the fish!). Hydrated eggs in the ovary cavity. **Running** during daytime is really seldom!
VI-III	Partly spawned - ripening	Ovaries are similar to the stage III, but have **reddish-violet** color. Ovaries are soft on touch. In cross-sectionsof the ovary separate, not spent eggs can be distinguished. Use the **size** of oocytes to differenciate between VI-III and VI-IV
VI-IV	Partly spawned - mature	Ovaries are similar to stage IV but reddish-violet. In the ovary cavity separate, not spent eggs can be seen. Do not judge by the size of the ovary but again by the size of the oocytes!
VI-IVh	(modification)	**New invention** to separate between first batch spawners (IV-V) and those which are entering from VI-IV: Similar to IV-V (see above) but the color is **red-violet**!!!
VI	Spent (Spawned)	Like an early stage III, but Ovaries are **very flabby** (and small), mainly **dark red**, half-transparent. **Small number** of remaining yellow oocytes can be seen through membrane of ovaries. The ovary cavity has a large opening in which separate, not spent or remaining eggs can be seen.
VI-II	Post-spawning (Resting)	**Similar to stage II**: Ovaries are small and half-transparent but the color is **still dark red**. No oocytes can be seen by naked eye.

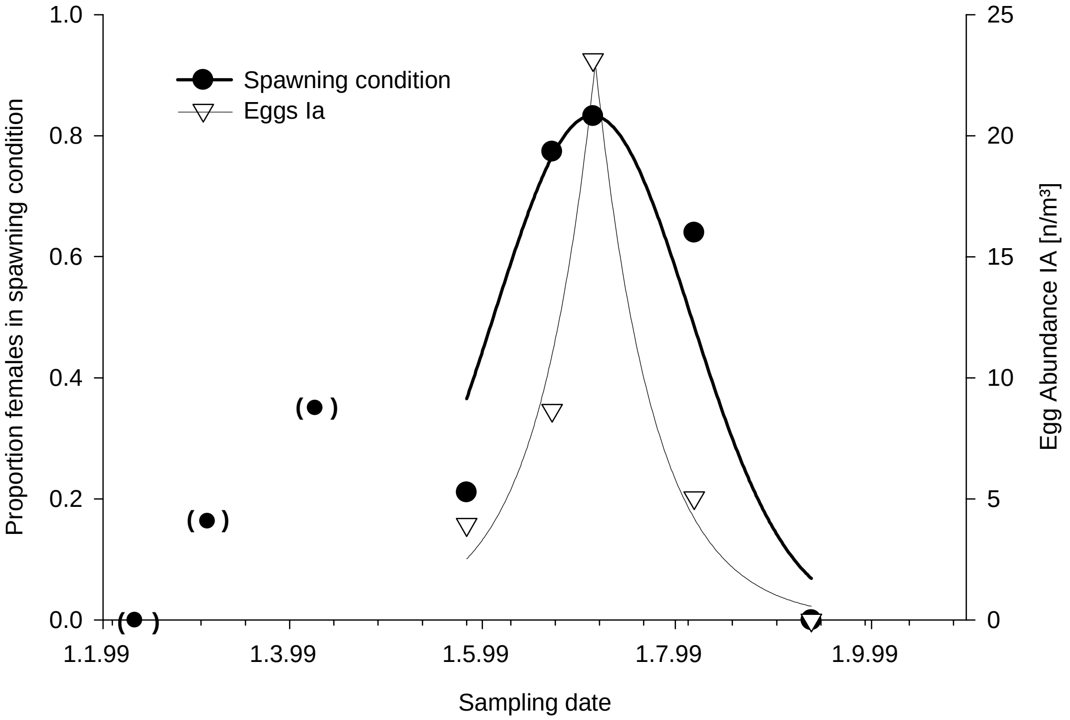

Fig. 1: Average proportions of mature females in spawning condition and corresponding egg abundance of the youngest egg stage [IA] per sampling date. Three respectively four parameter Gaussian curve fit; commercial data for the first quarter (in brackets) not included.

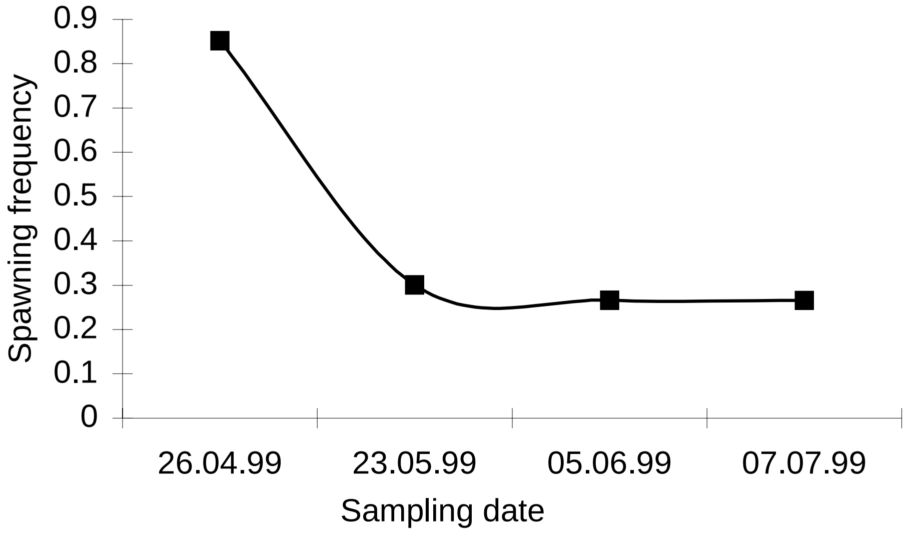

Fig. 2.: Female spawning frequency (average proportions of **pfh** from **pfs**) in the 1999 spawning season.

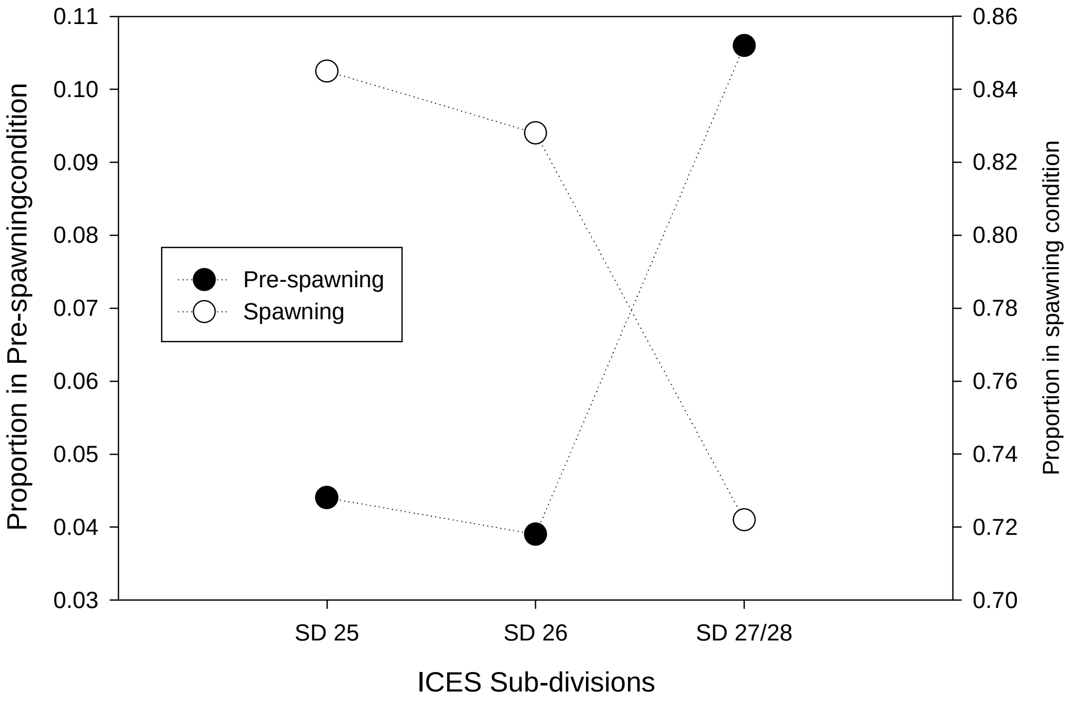

Fig. 3: Proportions of females in pre-spawning and spawning condition at peak spawning time in June 1999 according to ICES Sub-divisions. Proportions are calculated from mature females.

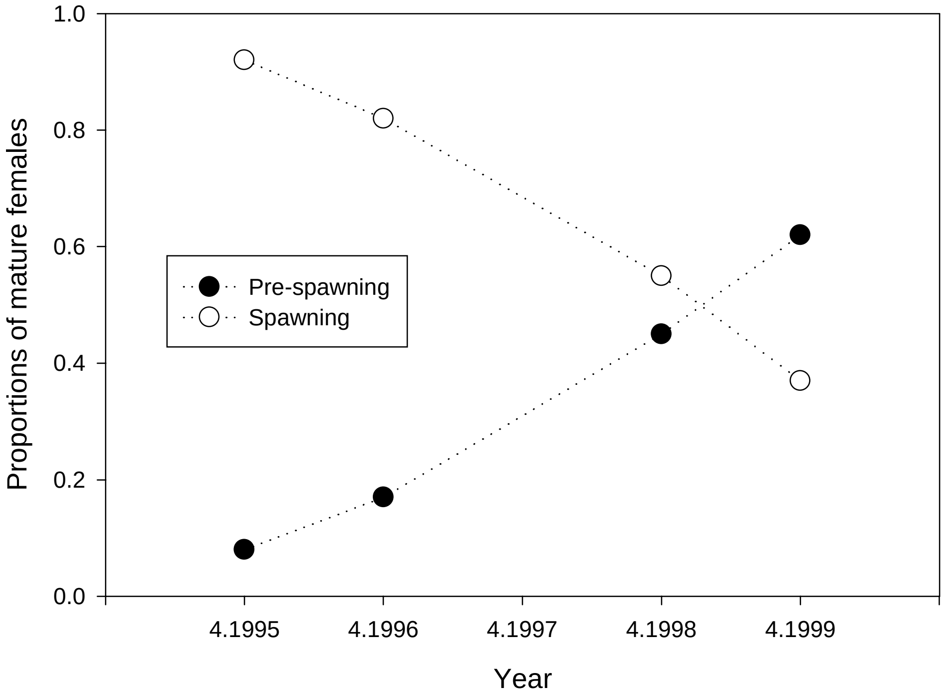

Fig. 4: Proportions of females in pre-spawning and spawning condition in April in ICES Sub-division 25. Proportions are calculated as proportions from mature females. No data was available for 1997.

APPENDIX1:

Calculation of inverse sample variance as weighting factors (Tomkiewicz et al. 1997) for averages of **pfs** and **p-pfs** for commercial data:

Equation 1

$$\delta^2{}_k = p_k * (1 - p_k) / n_k$$

$\delta^2 = Variance$

$p = proportion$

$n = sample \cdot size$

$k = length \cdot class \cdot (cm)$

The weighted average over all length classes was than computed as followed:

Equation 2

$$\overline{p} = \sum_{i=1}^{k} p_i * (1/\delta^2{}_i) / \sum_{i=1}^{k} 1/\delta^2{}_i$$