

Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment

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Interannual variations in spawning time, defined as the peak in egg abundance, of cod (*Gadus morhua*) in the Bornholm Basin, Baltic Sea, were analysed. Effects of water temperature, size and age structure of the spawning stock, abundance of food, and timing of spawning in preceding years were studied as possible determinants of annual spawning time. During the 1970s and late 1980s, peak spawning took place between the end of April and mid-June. A remarkable shift in the timing of spawning to the end of July was observed in the 1990s. The key factors governing the timing of spawning are water temperature during the period of gonadal maturation, density-dependent processes related to the size of the spawning stock, and food availability. The age structure of the spawning stock is suggested to have an additional effect. A high proportion of first-time spawners and decreasing water temperature have caused progressively delayed spawning since the early 1990s. Late spawning involves several processes that are detrimental to the survival of the early life stages. Recruitment in the mid-1990s was below what could be expected from spawning stock biomass and favourable hydrographic conditions. It is therefore suggested that the rebuilding of the Baltic cod stock could be improved by reduced fishing pressure in spring on early spawners.

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Key words: age structure, Baltic cod, recruitment, spawning stock biomass, timing of spawning, water temperature.

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Introduction

Spawning times of temperate fish species are generally believed to have evolved so that the early life stages emerge into an environmental regime which is suitable for their survival (Cushing, 1969). However, the environmental conditions at the time of egg development and larval hatch may differ from year to year due to variation in the environmental characteristics, changes in the timing of emergence of eggs and larvae, or a combination of both (Page and Frank, 1989). In most North Atlantic cod stocks, the eggs are released over a period of a few weeks in spring (Brander, 1994a). The median spawning date of Arcto-Norwegian cod has been remarkably consistent from year to year (Pedersen, 1984), while Northwest Atlantic cod stocks

show significant interannual variations in the timing (Hutchings and Myers, 1994). Hence, the assumption that spawning times are constant is not always appropriate.

Spawning is followed by an extensive feeding period, which is necessary to restart the gonadal maturation cycle. Gonadal maturation in Baltic cod begins in winter and lasts for about 4 months (Baranova, 1989, 1995; Bleil and Oeberst, 1997). Presumably, this represents essentially an annual cycle, where the underlying biogenic rhythm is adjusted by prevailing environmental conditions. Baltic cod has a later and much more prolonged spawning period than other cod stocks (Brander, 1994a). Surveys carried out since the beginning of this century show that cod eggs can be found in the central Baltic Sea from March to October (Kändler,

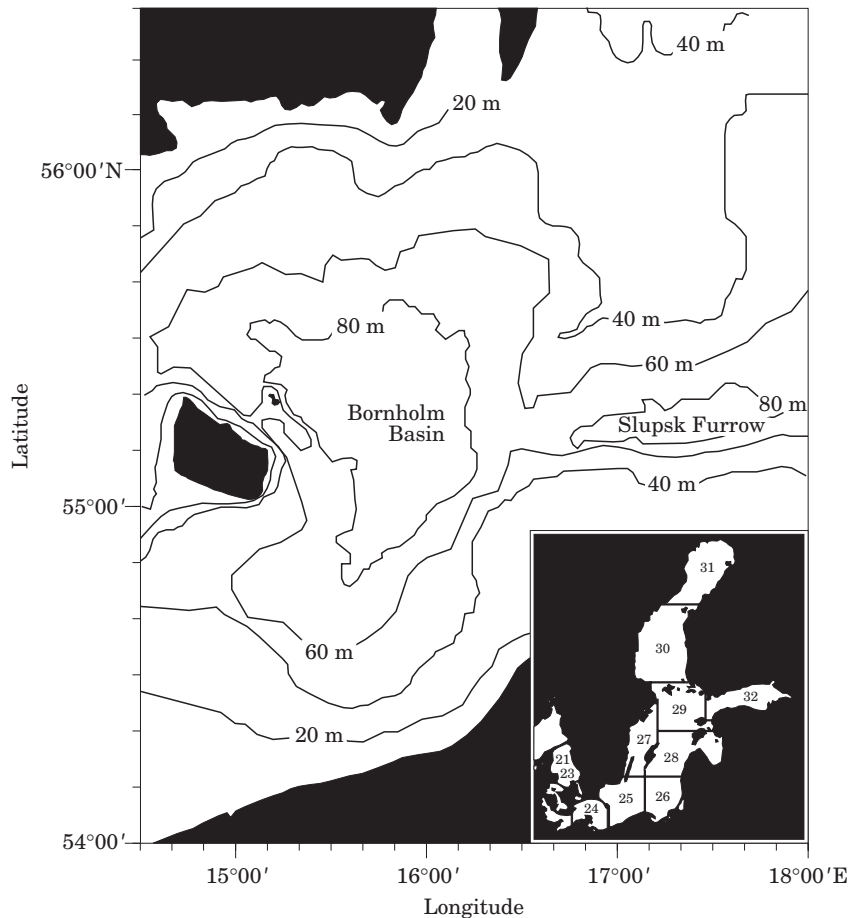


Figure 1. The study area and ICES Subdivisions of the Baltic Sea.

1949), but with considerable changes in the annual peak spawning date (MacKenzie *et al.*, 1996a). The environmental conditions determining successful egg and larval development in the main spawning areas show pronounced seasonal components (MacKenzie *et al.*, 1996a). Thus, the identification of mechanisms causing variations in the timing of spawning appears to be essential for understanding the recruitment dynamics of this stock.

We first describe changes in the timing of spawning of cod in the Bornholm Basin (Fig. 1), which has been by far the most important spawning area during the past decade (Bagge *et al.*, 1994). Secondly, we aim at identifying possible causes of these changes, considering variables that have previously been found to influence peak spawning time of cod stocks in different areas. Finally, we discuss the potential implications for the reproductive success of Baltic cod.

Material and methods

Annual peak spawning dates were estimated from cod egg surveys in the Bornholm Basin. To estimate the

mean spawning date in each year, the abundance of eggs was assumed to be normally distributed over time. Logarithmic transformation converted the normal distributions into parabolas of which the parameters were estimated by quadratic regression (Daan, 1981). The single survey observations were weighted for untransformed egg abundance in order to avoid an inappropriate strong effect of low egg numbers recorded at the beginning and end of the spawning season (Brander, 1994b).

Historical data on mean cod egg abundance by survey date were available for the period 1969 to 1978 from Grauman (1974, 1975, unpubl.), Krenkel (1981), Müller and Bagge (1984), and for 1985 from Müller (unpubl.). Because of insufficient information, no attempts were made to adjust the estimates for differences in sampling effort (i.e. number of stations) or area coverage.

During 1986–1996 a total of 67 ichthyoplankton surveys to the Bornholm Basin were carried out, involving various research vessels from different institutes (Table 1). The gear used was a Bongo net (60 cm diameter), which was towed obliquely from the surface

Table 1. Summary information on cod egg surveys conducted in the Bornholm Basin, 1986–1996.

	Sampling period	Research vessel	No. of stations			Sampling period	Research vessel	No. of stations	
			Total	Depth ≥ 75 m				Total	Depth ≥ 75 m
1986	14/05–15/05	Alkor	20	17	1992	16/03–17/03	Dana	13	10
	29/05–30/05	Alkor	20	18		07/04–08/04	Alkor	32	15
	17/06–19/06	Havfisken	20	16		19/05–21/05	Alkor	35	13
	02/08–03/08	Littorina	20	16		07/07–09/07	Poseidon	35	12
1987	20/03–21/03	Dana	10	8	1993	12/07–14/07	Poseidon	36	12
	23/04–25/04	Alkor	28	15		13/03–14/03	Dana	12	10
	29/04–30/04	Alkor	28	15		21/04–23/04	Alkor	36	18
	31/05–01/06	Littorina	20	12		22/05–26/05	Alkor	36	18
1988	03/07–04/07	Alkor	28	18	1994	06/07–08/07	Alkor	36	20
	08/07–09/07	Alkor	28	18		24/07–05/08	Baltica	39	26
	17/08–18/08	Poseidon	24	14		04/08/08/08	Dana	17	7
	08/09–10/09	Alkor	28	19		21/03–26/03	Dana	20	17
	21/03–22/03	Dana	19	16		28/04–30/04	Alkor	45	18
	06/04–07/04	Alkor	30	15		30/05–04/06	Alkor	45	20
	18/05–19/05	Littorina	30	13		07/07–11/07	Alkor	45	21
	24/05–25/05	Littorina	28	13		03/08–08/08	Dana	23	8
	28/06–30/06	Poseidon	30	17		21/08–25/08	Baltica	14	12
	30/07–02/08	Littorina	30	15		06/09–07/09	Baltica	5	4
	06/09–07/09	Alkor	30	15		30/09–05/10	Dana	24	11
	11/10–13/10	Poseidon	30	14	1995	03/03–06/03	Dana	20	13
1989	14/03–16/03	Dana	19	16		08/04–12/04	Alkor	45	22
	22/04–23/04	Alkor	23	16		12/05–17/05	Alkor/ A.v.Humboldt	45	19
	25/05–27/05	Alkor	30	13		22/06–25/06	Baltica	11	10
1990	24/06–26/06	Alkor	30	19	1996	17/07–23/07	Alkor	45	15
	20/03–22/03	Dana	21	11		07/09–10/09	Baltica	12	10
	21/04–25/04	Littorina	30	17		16/04–19/04	Alkor	45	18
	26/05–31/05	Alkor	30	20		16/05–20/05	Alkor	44	14
1991	05/07–08/07	Littorina	26	14		02/07–10/07	Dana	26	17
	17/03–19/03	Dana	21	12		20/07–28/07	Alkor	44	14
	17/04–19/04	Littorina	31	17		22/08–25/08	Baltica	12	12
	24/05–25/05	Littorina	29	15		19/09–21/09	Alkor	17	11
	06/07–07/07	Alkor	36	13		23/10–26/10	Alkor	20	11
	15/07–18/07	Alkor	36	13					
	10/08–12/08	Poseidon	36	15					
	16/08–18/08	Poseidon	36	14					

down to 2–3 m above the bottom at a constant towing speed of 3 kn. A mechanical flowmeter was mounted in the centre of the net opening, and catches were corrected for flowmeter readings and maximum towing depth. Samples were preserved in 4% buffered formalin/seawater solution and later transferred into a formaldehyde-free storage solution consisting of 0.5% propylene phenoxetol, 5% propylene glycol (1,2 propanediol) and 94.5% fresh water (Steedman, 1976) for further analysis. Cod eggs were sorted and staged using a five-stage classification (IA, IB II, III, and IV) based on morphological criteria given by Westernhagen (1970) and Thompson and Riley (1981), adapted for Baltic cod (Wieland, 1988; Wieland and Köster, 1996). In the present study, however, the data were pooled over all developmental stages to allow comparison with the historical data set. The number of stations, and hence the area covered, varied considerably between surveys

(Table 1). However, the central part of the Bornholm Basin was almost always covered adequately. Mean egg abundance was calculated including only stations in water depths ≥ 75 m, because these estimates were found to be representative for the entire spawning area (Wieland and Horbowa, 1996).

Monthly mean water temperatures in the 40–60 m depth range in the area bounded by 54°20' to 56°10'N and 14°30' to 18°00'E were obtained from the ICES oceanographic database for the period prior to 1996, complemented by own observations for 1995 and 1996. The area selected corresponds approximately to ICES Subdivision 25, including the Bornholm Basin and Slupsk Furrow (Fig. 1). The depth range selected reflects the temperature conditions also in the shallower areas, which are inhabited by cod during the pre-spawning period. The period January to April is critical for gonadal maturation of Baltic cod (Baranova,

1989), and, assuming that gonad development is affected by cumulative temperature encountered, the monthly mean temperatures during these 4 months were summed.

Stock size estimates of cod and sprat were derived from recent single species Virtual Population Analysis (ICES, 1997) covering the years 1966–1996 for cod and 1974–1996 for sprat. The time series for sprat was extended backwards to 1970 using VPA estimates from Thurow (1997), which were adjusted by means of the correlation between the two data sets for the overlapping period 1974–1991 (Jarre-Teichmann *et al.*, 2000). Estimates of cod distribution in the central Baltic (ICES Subdivisions 25, 26, and 28), as well as new maturity ogives and sex ratios, were provided by ICES (1997) for the periods 1980–1984, 1985–1989, 1990–1994, and 1995 to the present. For years prior to 1980, the conditions during 1980–1984 were assumed to apply according to ICES (1997).

Using the spatial distribution, the total spawning stock biomass estimates for Baltic cod (ICES, 1997) were adjusted to obtain estimates representative for ICES Subdivision 25 in order to match the egg survey data. The age-specific fraction of mature females in this area was computed from the spatial distribution and corresponding sex ratios and maturity ogives, and combined with the age-specific total stock numbers to derive an estimate of the mean age of spawning female cod. Age-specific fractions of first time (“recruit”) spawners in the stock were calculated from the female maturity ogives for each period from the difference between two consecutive age groups. However, we assumed that no recruit spawners were older than 5 years, except for the period 1985–1989 when first-time spawners were also recorded at age 6 due to bad condition (e.g., Baranova, 1989), and that variations in the maturity ogives for older age groups reflected resting cycles. Age-specific fractions of recruit spawners were then computed as the ratio of the fractions of recruit spawners and mature females by age group for each period. Finally, the fractions of recruit spawners were combined with the age-specific numbers of mature females and summed across age groups for an estimate of the fraction of recruit spawners in the total female spawning stock in Subdivision 25. A normalizing arcsine – square root transformation (Sokal and Rohlf, 1995) was applied to the fraction of female recruit spawners and the fraction of mature (ages 5+ or 6+) females prior to further statistical analysis.

Results

Date of peak spawning

Although temporal resolution varied considerably, estimates of cod egg abundance by sampling date for 1969–1996 in general fitted normal distributions

adequately (Fig. 2), identifying clear spawning peaks. In about 10 out of 22 years studied the observations were restricted to the main spawning period. In particular, for 6 years data were missing either at the beginning of the spawning season (1985, 1986) or at the end (1976, 1989, 1990, 1992). For three of these years a reasonable fit of the normal distributions with the onset of spawning around the beginning of March and the end of the spawning period in the fall could only be achieved when one (1976, 1986) or two (1992) observations were excluded. Hence, for 1986 and 1992 as well as for 1985 only three observations were available for curve fitting. For 1990, no realistic estimate could be obtained at all. For the remaining years the parabolic regressions yielded significant correlation coefficients ($p < 0.05$) in 14 cases, and the results obtained for years in which the entire spawning season was covered (e.g., 1994 and 1996) supported the underlying assumption that egg abundance is normally distributed over time.

Despite data deficiencies, a substantial change in the timing of spawning was identified (Fig. 3a). During 1969–1978, peak spawning time was between the end of April (1973; day 112) and the beginning of June (1974; day 161). Spawning dates were less variable during the late 1980s when they ranged between mid-May (1989, mean day of year 142) and mid-June (1985; day 171). In the early 1990s, peak spawning occurred progressively later, shifting from the end of June (1992; day 174) to the end of July (1996; day 210).

Effect of temperature and spawning stock size

Monthly mean temperatures in the 40–60 m depth range (Fig. 3, middle) ranged between 0.4°C (February 1987) and 11.3°C (October 1976). The size of the spawning stock varied substantially throughout the last three decades, with low levels in the late 1960s and early 1970s as well as in the early 1990s, and high values in the early 1980s (Fig. 3, bottom). In the late 1980s, the stock decreased due to poor recruitment and an increase in fishing mortality (ICES, 1997). At present, the stock is rebuilding from the historically low level in 1992.

Based on trends of water temperature (as indicated by 12-month moving average) and cod spawning stock biomass, the observed trajectory of spawning dates can conceptionally be described as follows (Fig. 3):

1970–1973: Spawning occurred successively earlier at increasing water temperatures

1974–1978: No pronounced temperature trend, late spawning relative to 1973 was accompanied by increasing spawning stock biomass (>40 000 t)

1985–1987: Spawning occurred earlier again at strongly declining spawning stock biomass, which may have superimposed a potential effect of decreasing temperatures

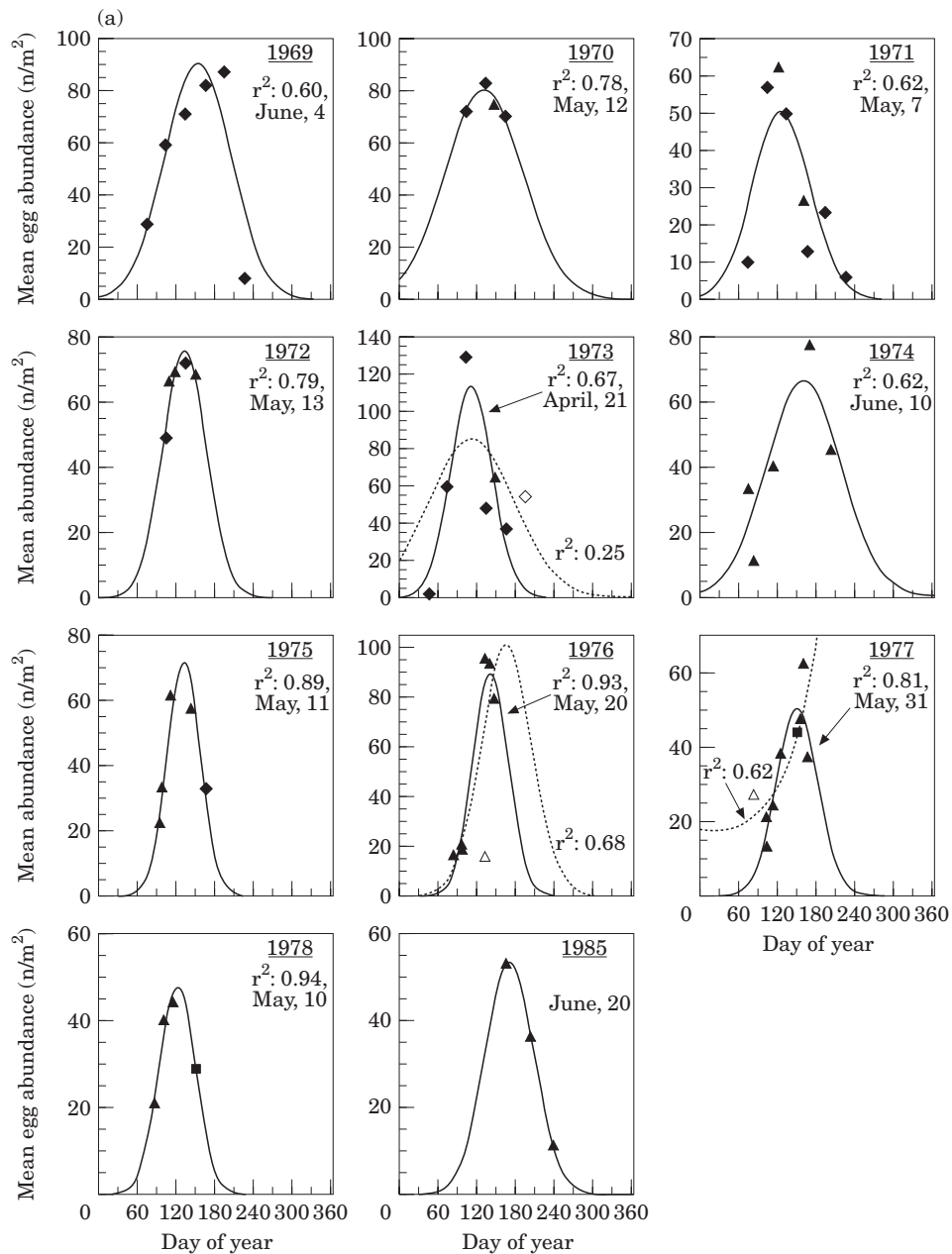


Figure 2. (a)

Figure 2. Estimates of cod egg abundance in the Bornholm Basin by survey, fitted normal distributions in relation to day of year and estimated date of peak abundance (r² values refer to parabolic regressions of untransformed data; open symbols were excluded from final curve fit; dotted lines are based on all data). (a) 1969–1978 and 1985 (◆: data from Grauman, 1974, 1975, unpubl.; ▲: data from Müller and Bagge, 1984, and Müller, unpubl.; ■: data from Krenkel, 1991).

1988–1989: Increasing temperatures had no substantial effect on the timing of spawning, whereas spawning stock biomass declined further

1991–1996: Spawning progressively delayed since 1992 at decreasing temperatures.

1969 was not considered here nor in any further analysis because of an exceptional temperature regime observed during spring (Fig. 4): water temperature in January exceeded values observed in all other years, but decreased to below average values in March and April.

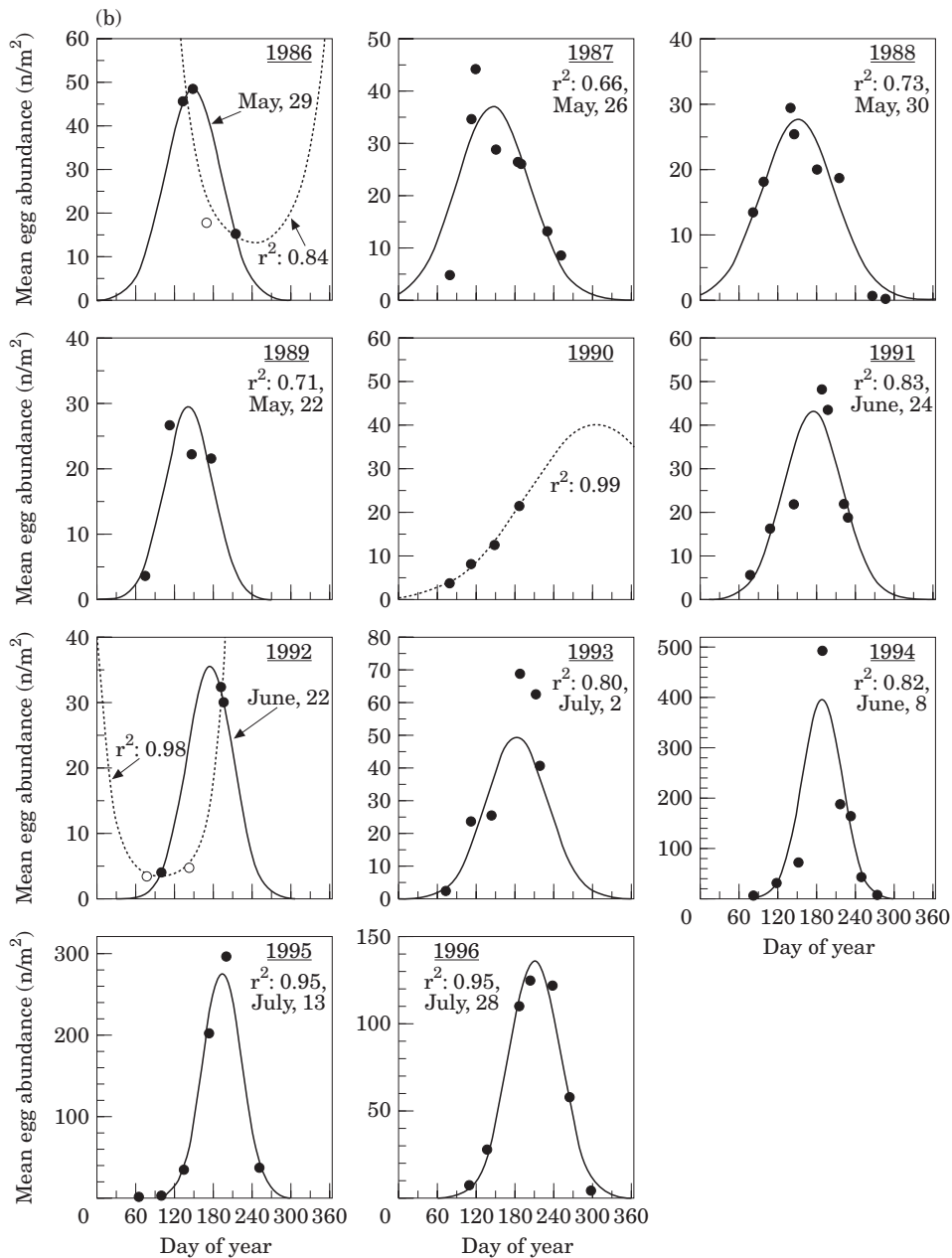


Figure 2. (b)

Figure 2. Estimates of cod egg abundance in the Bornholm Basin by survey, fitted normal distributions in relation to day of year and estimated date of peak abundance (r^2 values refer to parabolic regressions of untransformed data; open symbols were excluded from final curve fit; dotted lines are based on all data).

Although low temperatures during early spring were also recorded in other years (e.g. 1985–1987; Fig. 3, middle), such a marked drop in temperature during the period of gonadal maturation was never observed.

Spawning stock structure

Along with the change in cod biomass, considerable fluctuations in the age structure of the spawning stock

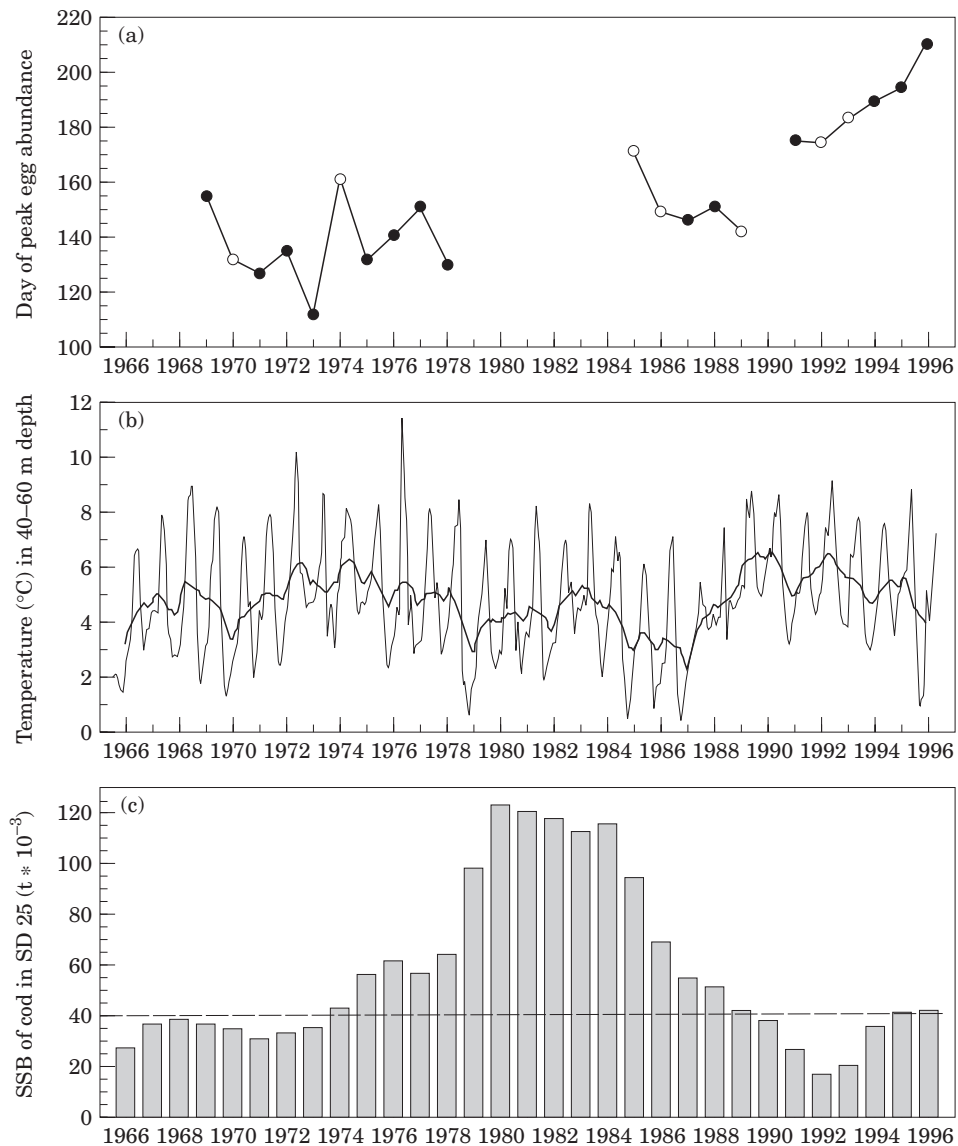


Figure 3. Time series 1966–1996 (labels x-axis refer to mid-year) of: (a) Day of peak egg abundance (open symbols: based on non-significant regressions or three observations only). (b) Monthly mean temperature in the 40–60 m depth range in the area bounded by 54°20′–56°10′N and 14°30′–18°00′E (heavy line represents 12-month moving average). (c) Spawning stock biomass of cod in ICES Subdivision 25 at January 1st (dashed line represents threshold level to distinguish between years of low and high SSB; see also text).

were observed (Fig. 5). The mean age of the female spawners ranged between about 3.5 and 4.3 years, with highest ages in the mid-1980s. In that period, the fraction of old (age 6+) females showed a pronounced maximum of 23% in 1986. A high proportion of recruit spawners of 71% was observed in 1993, when the mean age of female spawners was at the lowest level on record. The age structure, however, showed no consistent association with annual spawning time.

Conditions at different levels of spawning stock biomass

In the mid-1970s, when spawning stock biomass increased dramatically, intraspecific concurrence for food resulted in poor condition (Baranova, 1989, 1995) affecting the timing of spawning. Thus, for further analysis a threshold level of about 40 000 t (Fig. 3, bottom) was applied to distinguish situations of a low

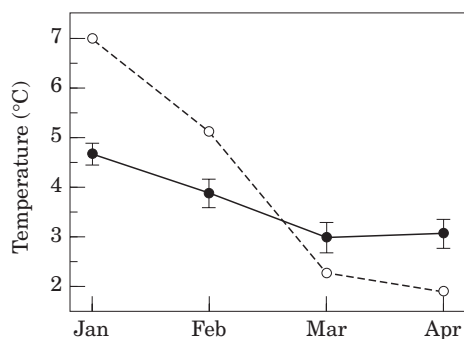


Figure 4. Monthly mean temperature (see Fig. 3b), January–April, in 1969 (open symbols) compared to average conditions during 1970–1979 and 1985–1996 (solid symbols; error bars refer to ± 1 standard error).

(1970–1973 and 1990–1996) and a high spawning stock biomass in Subdivision 25 (1974–1989). During the early 1990s, the biomass of sprat, an important prey for Baltic cod (Uzars, 1993), increased substantially (Fig. 6), and therefore the years 1995 and 1996, in which cod spawning stock biomass was close to the threshold level, were assigned to the first group.

At low levels of cod spawning stock biomass, peak spawning time was negatively associated with temperature. The relationships for early (1970–1973) and late (1991–1996) years were on different levels but had similar slopes (Fig. 7). For consecutive years the difference in timing was significantly correlated ($r^2=0.69$, $p<0.01$) with the corresponding difference in temperature in such a way that a drop in the sum of monthly mean temperatures encountered during the period of gonadal maturation of only 1°C would cause a delay in peak spawning of about 4 days. Multiple regression analysis of the effect of the fraction of recruit female spawners (R), in addition to the sum of the mean monthly temperature (January to April) in the 40–60 m depth range during the preceding winter (T), yielded an increase in the portion of explained variance in date of peak spawning (D), where both variables contributed significantly to the model ($r^2=0.75$, $n=8$, $p=0.03$):

$$D_y - D_{y-1} = -2.76 \cdot T_y + 3.11 \cdot \arcsin \sqrt{R_y} - 119.1,$$

where the subscript y refers to years (1971–1973 and 1992–1996). Other variables, i.e., mean age of female spawners, the fraction of old females as well as the stock

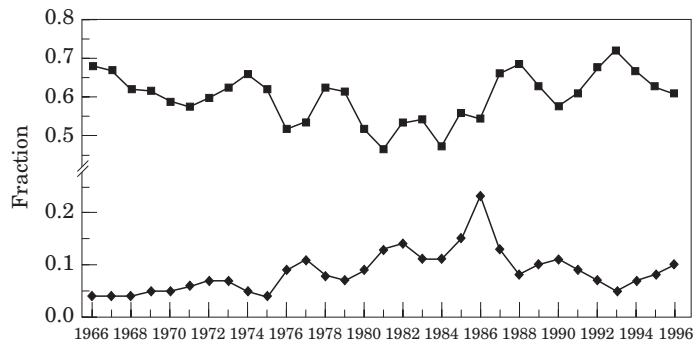


Figure 5. Fraction of recruit female spawners (■) and age 6+ females (◆) of cod in ICES Subdivision 25 at January 1st, 1966–1996 (based on ICES, 1997).

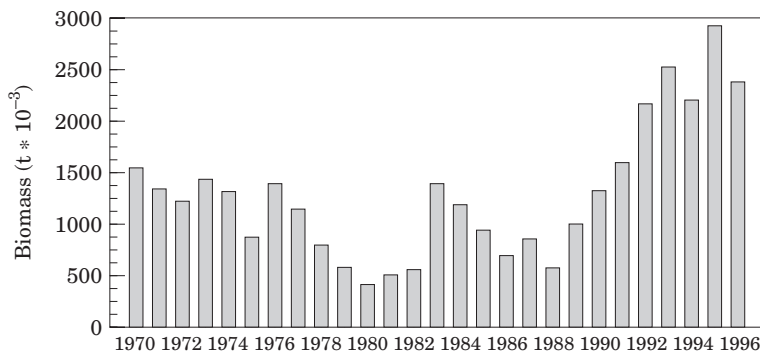


Figure 6. Stock size of sprat in ICES Subdivisions 22–32 at January 1st, 1970–1996 (based on ICES, 1997, and Thurow, 1997).

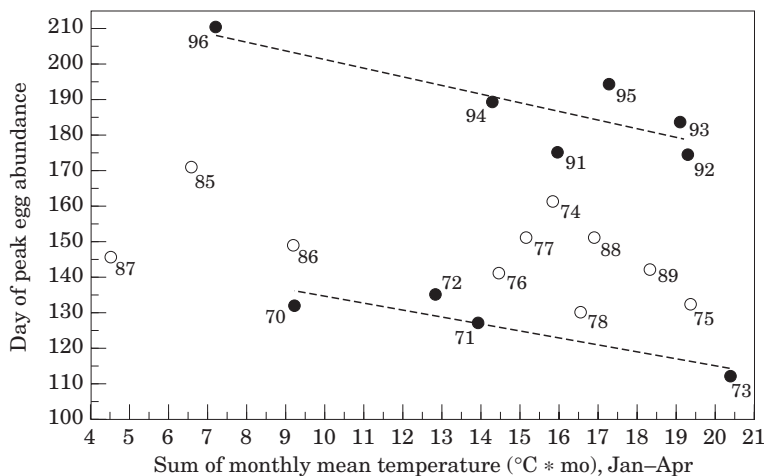


Figure 7. Day of peak abundance of cod egg abundance in the Bornholm Basin vs sum of mean monthly temperature (see Fig. 3b), January–April, during the preceding winter (solid symbols refer to year of low, and open symbols to years of high spawning stock biomass; dashed lines reflect estimated regressions for the two periods of low SSB).

sizes of cod and sprat did not contribute significantly to the model.

At high levels of cod spawning stock biomass, peak spawning date was not significantly influenced by water temperature (Fig. 7; $r^2=0.25$, $n=10$). Opposite trends were observed concerning the effect of stock size on peak spawning time (Fig. 3). A negative association is suggested for 1974–1978 ($r = -0.82$, n.s.), while a significant positive correlation was found for 1985–1989 ($r=0.92$, $p<0.05$), and hence no consistent relationship could be established for both periods combined. Multiple regression analyses including age structure of the spawning stock or biomass of sprat yielded no satisfactory results either, regardless of whether additive or multiplicative effects were considered. Note, however, that observations on peak spawning time are missing for 1979–1984, when spawning stock biomass was at its highest level on record (Fig. 3, bottom).

Situation at present

For the years since 1988, during which the most remarkable change in annual spawning time occurred (Fig. 3, top), multiple regression analysis revealed that water temperature and the fraction of 6+ year old females (F_{6+}) contributed significantly to the difference in peak spawning time between consecutive years. Other factors, such as stock sizes of cod and sprat, had no substantial effects and the following model was obtained by stepwise backward variable selection (symbols as before; $r^2=0.86$, $n=7$, $p=0.02$):

$$D_y - D_{y-1} = -1.96 \cdot T_y - 2.94 \cdot \arcsin \sqrt{F_{6+}_y} + 83.63,$$

where the subscript y refers to years (1988–1989 and 1992–1996). It is noteworthy that in this

model the fraction of age 6+ females ($p=0.03$) was selected, while the fraction of age 5+ females ($p=0.07$) and, in contrast to the previous model for periods characterized by low cod spawning stock biomass, the fraction of recruit female spawners ($p=0.11$) were not significant. This may indicate that old females are able to shorten the reproductive cycle under favourable food or temperature conditions, and that the presence of a high proportion of old females in the stock might result in earlier spawning even if spawning was late in the year before.

Discussion

Normal distributions could not be fitted satisfactorily to the observations on the seasonal occurrence of cod eggs in all years. This may have resulted from differences in sampling effort for which no corrections could be applied for years prior to 1986, insufficient numbers of surveys per season, and incomplete coverage of the spawning area in some years. Despite some doubts regarding data integrity, distinct changes in the timing of peak spawning during the past three decades were demonstrated.

Periods during which spawning of cod in the Bornholm Basin was timed either in spring or in late summer have been found in previous investigations, as reviewed recently by MacKenzie *et al.* (1996a). In summarizing information since the beginning of this century, Bagge *et al.* (1994) reported highest egg abundance in July and August during the early part of this century (1905–1938), whereas peak spawning was found on average in May during the period 1969–1978. However, a gradual regime shift from early to late spawning was

documented for the first time during the 1990s (Wieland and Horbowa, 1996).

A close negative correlation between spawning time and water temperature was detected for periods of low Baltic cod stock biomass. This is in agreement with experimental results for Atlantic cod from Kjesbu (1994), who reported that a drop in temperature of 1°C during vitellogenesis delays spawning by about 8–10 days, and confirms that gonadal maturation is in principle a temperature-dependent process. Moreover, a negative correlation would represent an adaptive response in so far as the production cycle of larval food is also coupled with temperature.

The influence of water temperature on the timing of cod reproduction off Newfoundland differed between regions, which has been attributed to regional differences in the thermal gradients between shelf and slope waters acting as a barrier to spawning migrations (Hutchings and Myers, 1994). Such a thermal barrier is to date not known to exist in the central Baltic Sea.

The depth layer of 40–60 m used as an indicator of the temperature conditions during maturation includes the so-called “winter water” located between the summer thermocline and the oxygen-poor bottom water. It is characterized by vertical mixing across the upper part of the halocline in winter. In cold years low temperatures are retained until mid-summer (Matthäus, 1984), while warm water is frequently advected from the Arkona Basin located west from Bornholm island during late summer and autumn (Wojewodzki and Grelowski, 1995).

Immature cod are predominantly found in shallower areas, i.e., in coastal zones and along the edges of the basins (Baranova, 1995), while only spawning individuals aggregate in the central Bornholm Basin at depths below 60 m (Tomkiewicz *et al.*, 1997), where temperature conditions are less influenced by winter cooling. It should be noted, however, that no fixed water depth interval could fully account for the environmental conditions encountered by cod in the prespawning period.

In the central Baltic, sprat tend to avoid the cold surface and intermediate water during severe winters and concentrate in the deeper water layers (Uzars, 1975), which may lead to an increase in the availability of food for cod. However, our results provide no evidence that this has implications for the timing of spawning, not even for years in which cod stock biomass was relatively high.

Indications were found that beyond a certain level of cod stock biomass, density-dependent processes (such as food competition) superimposed temperature effects on peak spawning time. This is supported by experimental studies in which Atlantic cod held at low ratios for 4–8 months before spawning began to spawn later than individuals that were fed moderately (Kjesbu, 1994). Furthermore, field observations on cod in the eastern

Baltic Sea revealed that in years with good feeding conditions (1972–1973, 1976) spawning was early (March to April), while at large stock sizes and poor feeding conditions (1980–1982) slow maturation prolonged and delayed the spawning season until April to June (Baranova, 1989, 1995). Bagge *et al.* (1994) suggested that age-specific spawning times may partly explain the prolonged spawning period of cod in the Baltic. In the central Baltic Sea, age at first maturity is about 3 years (Weber, 1989; ICES, 1997) and females spawn for the first time at a mean length of 37 cm (Berner and Vaske, 1981). However, in contrast to findings with Atlantic cod (Hutchings and Myers, 1993; Kjesbu, 1994), large females of Baltic cod spawn earlier than smaller ones (Berner, 1960; Baranova, 1995; Bleil and Oeberst, 1997). Hence, the decreasing fraction of early spawning old females is likely to have contributed to the delay in spawning in the early 1990s.

After a stagnation period lasting about 10 years, the hydrographic conditions in the Bornholm Basin became more favourable for successful cod reproduction in the early 1990s (Hinrichsen and Wieland, 1996), and more abundant year classes occurred (ICES, 1997). Larsson and Eriksson (1995) reported that the 1991 and 1992 year classes had a significantly lower size at age than usual, while no change in growth rate was observed. In general, fish must reach a critical size close to average size at first maturity before they perceive the environmental stimuli that trigger gonadal maturation (Pauly, 1984). Therefore, it is likely that these year classes attained maturity late in the year. Consequently, the high fraction of recruit spawners, in addition to decreasing water temperature, appears to have caused progressively late spawning in the mid-1990s. Although the fraction of recruit spawners has been declining since 1994, persisting low temperatures have so far prohibited a reversal of the delay in spawning.

Late spawning has consequences for several processes influencing survival of early life stages:

- In the central Baltic, cod eggs are predominantly found in the deeper water layers because their specific gravity does not allow them to float in the low saline surface layer (Nissling and Vallin, 1996; Wieland and Jarre-Teichmann, 1997). In general, oxygen content below the halocline decreases from spring to summer (MacKenzie *et al.*, 1996b, 2000), and hence egg mortality due to oxygen deficiency is assumed to be higher in years of late spawning (MacKenzie *et al.*, 1996a). Furthermore, eggs may be exposed to temperatures above the preferred range in late summer due to the advection of warm water from the Arkona Basin (Subdivision 24), as has been frequently observed during recent years (Wieland, 1995; Włodarczyk and Horbowa, 1997).
- Large females produce on average larger and more buoyant eggs than smaller ones (Nissling and Vallin,

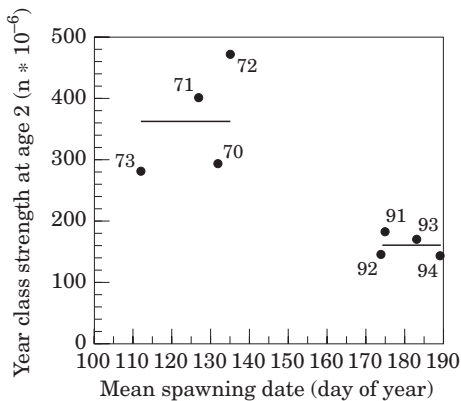


Figure 8. Year-class strength of cod at age 2 in ICES Subdivisions 25–32 (ICES, 1997) in relation to peak spawning date in 1970–1973 and in 1993–1994, two periods with comparable levels of spawning stock biomass (see Fig. 3, bottom; lines represent mean values).

1996). These eggs may have a higher probability to survive, as (1) they float at lower salinities, which reduces risks of exposure to oxygen-deficient water, and (2) they develop on average at more favourable hydrographic conditions prevailing earlier in the year.

- Predation by herring and sprat has been identified as an important source of egg mortality in Baltic cod (Köster and Schnack, 1994). In the early 1990s, egg predation by sprat was much larger in spring than in summer. Predation by herring was lower than by sprat, but increased from spring to summer. In the mid-1990s, egg consumption by sprat generally declined, whereas predation by herring increased dramatically (Köster and Möllmann, 2000). Besides, the presence of jellyfish (*Cyanea capillata*) as a potential predator on fish eggs in summer (Margonski and Horbowa, 1995, 1996) may have contributed to a high egg predation mortality during the past years of late spawning.
- Baltic cod larvae feed mainly on nauplii in spring and switch to copepodites and adult copepods during summer (Zuzarte *et al.*, 1996). Consequently, the life cycle of important prey might be out of phase with the food requirements of late hatching larvae.

At present, no quantitative information is available on how these processes affect the reproductive success of Baltic cod. However, it should be noted that early spawning corresponded to high recruitment in the 1970s, whereas year-class strength was considerably lower in the 1990s, when spawning was late (Fig. 8) and did not reach the level expected from the size of the spawning stock and the favourable hydrographic conditions (Larsson, 1995).

The Baltic cod fishery employs different gears – gill nets as well as bottom and pelagic trawls. The effort of

most fleets has been directed to the spawning grounds between January and July (Weber, 1989; Bagge *et al.*, 1994) and the major portion of the annual catch was usually taken during the first quarter of the year (ICES, 1997). In the mid-1990s, however, fishing mortality on older fish in particular (age groups 5 to 7) was higher during the second quarter than during the first (ICES, 1997). This probably reflects the change in spawning time, as the fish aggregate in the spawning areas later in the year and it can be assumed that the cod fishery still selects for early spawners.

Fishing mortality has been substantially reduced since the mid-1980s (ICES, 1997) and biomass as well as the proportion of old females in the stock increased slightly (Figs 3, 5). Although water temperature turned out to be the most important factor determining the timing of cod spawning in the Bornholm Basin at the present biomass level, the structure of the spawning stock contributes significantly to shifts in peak spawning date. Since the offspring of repeated spawners are likely to have a better chance of survival, our results suggest that a ban on the pelagic cod fishery during spring would promote a recovery of the stock, as it would specifically reduce the removal of repeat spawners at the onset of the spawning season.

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