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Baltic cod reproduction in the Gotland Basin: annual variability and possible causes

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Abstract

Baltic cod spawning takes place in the deep basins and reproduction success is mainly related to environmental conditions (salinity and oxygen regimes, i.e. the 'reproduction volume'). Due to the Baltic Sea heterogeneity, cod reproduction success in the Southern and Central Baltic spawning grounds can differ significantly. Recent oceanographic changes i.e. decrease of water exchange and stagnation, as well as a strong reduction of spawning stock caused the diminishing of the reproduction potential of the Gotland spawning grounds. The Gotland spawning grounds belong to four main cod spawning sites in the Baltic and historical analyses revealed that abundant generations of Baltic cod were produced when successful cod reproduction took place also in the Gotland Basin.

Analyses of revised reproduction volume estimates for the Gotland Basin taking into account the spatial structure of hydrology in the basin during stagnation and aeration periods reveals high seasonal and inter-annual variability. To describe changes of abundance and distribution of the spawning stock and the recruits in relation to hydrographic conditions, results from trawl surveys carried out in 1975-1998 in the Gotland Deep are analyzed. In this analysis, the reproduction volume is used as a proxy for the environmental conditions.

Introduction

Cod is a temperate marine fish that spawns in saline water layers of the continental shelf and produces pelagic eggs. Conditions in the Baltic, with a surface salinity of 7-8 psu and bottom salinity up to 10-17 psu, are marginal for marine species. This generally confines cod spawning to four deep areas: the Bornholm Basin, the Gdansk Deep, the Gotland Basin and to a less extent the Slupsk Furrow (Bagge *et al.*, 1984). As a result, cod eggs in the Baltic are concentrated in deep waters below a permanent halocline (Grauman, 1984; Wieland & Jarre-Teichman, 1997; Wlodarczyk & Horbowa, 1997; Makarchouk & Hinrichsen, 1998). Due to the irregularity of water exchange between the Kattegat and the Baltic Sea and to limited vertical mixing, the hydrological conditions in the spawning and egg concentration areas significantly varying. Periods between the inflows are characterized by oxygen depletion and decreasing of salinity. Therefore, the volume of water that provides minimum environmental conditions for spawning and successful egg development as well as for survival has been named as 'reproduction volume' (RV). Presently RV is determined by threshold values of salinity (>11psu) and oxygen (>2 ml/l). It has been demonstrated that the actual salinity regime is the primary factor determining the vertical distribution and fertilization of eggs, whereby critical oxygen levels have effects on egg survival (Wieland *et al.*, 1994; Nissling and Westin, 1997; Nissling & Vallin, 1996). However, the actual definition of the 'reproduction volume' has been criticized, as it does not account for the effects of critical temperature and actual oxygen 'inside' the volume. Experimental studies revealed that egg survival increases if oxygen increases from 2 to 5 ml/l (Wieland *et al.*, 1994). Nevertheless, the 'reproduction volume' or 'thickness of the spawning layer' contributes significantly to explaining the variability in recruitment success of Baltic cod (Lablaika *et al.*, 1984; Sparholt, 1996; Jarre-Teichman *et al.*, 1997). These analyses mainly were performed for the entire population of Central Baltic cod. However, the Baltic Sea is characterized by heterogeneity and critical environmental factors determining reproductive success and stock-recruitment relations can differ between spawning areas (Berner et al., 1989; Lablaika et al., 1989; Köster *et al.*, 1999).

Historical analyses have shown that production of abundant generations of cod in the Baltic is associated with successful reproduction in the Gotland Basin. Therefore, the main aim of the present investigation is to examine whether variations in reproduction volume, its quantitative measures and the hydrographic characteristics in the Gotland Basin can explain the fluctuations in cod recruitment.

Material and methods

The Gotland Basin is the most eastward located cod spawning area of Baltic cod (Figure 1). Presently the reproduction volume is defined by salinity below 11psu and oxygen above 2 ml/l and in comparison with the Bornholm Basin area it has been observed during the last decades only in some cases. This circumstance did not allow to use the quantitative estimate of RV in recruitment analyses for the Gotland Basin (majority of years has 0 values although the conditions in stagnation periods significantly vary by years).
The formation of the reproduction volume in the Gotland Deep mainly is related to strong or major Baltic inflows. A schematic of its formation is shown in Figure 2.

During periods of advection of saline and aerated water masses from the Kattegat into the Gotland Basin, salinity increases below the halocline while oxygen only increases in near bottom layers and decreases in intermediate layers. This is caused by the vertical displacement of less dense 'old' water masses. From such dynamical patterns it resulted that reproduction volume can be formed in two distinct layers.. In dependency on the amount of water masses penetrating into the Gotland Basin and on its density there may occur more or less expressed deviations from above presented patterns either in the particular areas or in the whole basin.
During stagnation periods, the isooxygen usually is located above the isohaline 11 psu. The thickness of this layer varies by years. depending on the duration of stagnation. Hence, the layer determined by salinity below 11psu and oxygen above 2ml/l, with both parameters being outside of the necessary requirements for successful cod egg development, we named as '*negative volume*'. Such assumption allowed us to construct time series of quantitative measures of environmental conditions.

1. Re-evaluation of 'reproduction volume' time series (1964-1998)

Extended data series of reproduction volume (RV) in different months of the year obtained by the Latvian Fisheries Research Institute (LATFRI) were calculated for Southern and Central Gotland Basin based on single point observations at 3 stations (Figure 1) – BY9A, BY15A and 43 (Plikshs *et al.*, 1993). The contouring software "Balthypsograph' (Wulff and Anderson, university of Stockholm) was used for the volume estimations by the hypsographic function for the Baltic Proper derived from a gridded 5' x 5' bathymetric database by Stigebrandt (1987) and Stigebrandt and Wulff (1987). This function quantifies the volumes of water below horizontal surfaces at given depth levels.
The RV data set was updated by recent hydrographic measurements performed during surveys in 1995-1999 made by the Institute of Marine Science (IFM) in Kiel, Germany and LATFRI. Then it was evaluated how hydrographic heterogeneity in the basin can influence the RV estimations.
The hydrographic data set consists of measurements from 11 cruises carried out in the Gotland Basin between February1969 and May 1999 on stations at two transects of the Central Gotland Basin: northern - stations 36, BY15A, 38 and 38A and southern – stations 42, 43, 44 enclosed by 80m isobath (Figure 1). On average, the spatial resolution was about 30 nm in latitude and 15 nm in longitude. The survey data were used to calculate the thickness of the reproduction layer of Baltic cod with respect to its classical definition ($S > 11$ psu; $O_2 > 2$ ml/l) as well as with regard to suboptimal oxygen and salinity conditions, the so called 'negative volume' ($O_2 < 2$ ml/ l and salinity < 11 psu).
The hydrographic data set was used to construct horizontal fields of the thickness of reproduction layers by a multi-dimensional linear function

$$F_{(x,y)} = \sum_{i=1}^{N}\sum_{j=1}^{N} A_{ij} \times x^{(i-1)} \times y^{(j-1)} \tag{1}$$

which is determined by a multiple regression analysis using the least square criteria.
For the present analysis of the fields of the reproduction layers it was assumed that a horizontal trend of the data could be approximated by (1) fitted to the data using a multiple regression scheme. Applying this method a unit array configuration with

dx=dy=5km was provided for depths >80 m, with each grid point being representative for the positive or negative layer thickness centered around it. The reproduction volumes of the Central Gotland Basin area were calculated for each of the different surveys by simply integrating the fields of reproduction layer thickness horizontally.
The new method allows to take into consideration the basin-wide trends in the depths of oxygen concentrations and in the haline stratification and thus, the method is able to include spatial variability. The hydrographic data used for the estimation derived by LATFRI were collected at only one site in the deepest part of the basin. This site was considered only for rough approximations of the conditions, but allowed estimates of reproduction volumes to be calculated for a long period because the station was frequently visited as part of various national and international monitoring programs.

Presentations of long term hydrological regime changes in the Southern and Central Gotland Basin are based on data from stations BY15A and BY9A (LATFRI hydrographic monitoring). Water density was calculated according to Millero and Kremling (1976).

2. Annual cod recruitment and female spawning stock index

Annual indices of cod recruitment and female spawning stock were calculated from LATFRI research surveys in the Southern and Central Gotland Basin during 1975-1999. Although the surveys were carried out with the same trawl, the area coverage varied. Because these single haul cpue data could not be combined directly a General Linear Model approach was applied based on area mean and log transformed cpue data (in numbers), weighted by depth strata. The number of hauls used in the model separated by years, areas and depth strata is shown in Table1.

To obtain the age 1 index the following model was used:

$$Age1 = Y + A + S + D + A*D + S*A + \varepsilon,$$

where Y is the year effect, A the sub-area effect (Southern Gotland and Central Gotland), S the season effect (January-February, March-April) and D is the depth strata effect (21-40m, 41-60m, 61-100m, 101-120m and 121-140m). A*D and S*A are interaction terms, and ε is the error term. The descriptive statistics for the model were: df = 285; Rsquare = 0.48; F =6.21; $p<0.0001$.

For obtaining the female spawning stock annual index, the single haul numbers of fish in each 5 cm length group were multiplied by the proportion of females and the proportion of mature females of corresponding size groups and in 10 m depth strata. The fishes were staged according to a 6-stage maturity scale (Kiselewich, 1923, cit. after Pravdin, 1966). According to Shirokova (1969), maturity stages 3-6 were assumed as the fishes spawn in the given year.
The following model was used:

$$F\_ssb = Y + A + D + A*D + \varepsilon,$$

where again Y is the year effect, A the sub-area effect (Southern Gotland and Central Gotland) and D is the depth strata effect (21-40m, 41-60m, 61-100m, 101-120m and 121-140m), A*D is an interaction terms, and ε is the error term. Only surveys carried out in March and April were used. The descriptive statistics for the model were: df = 176; Rsquare = 0.4861; F =7.25; $p<0.0001$.

Results

1. *Inter-comparison of 'reproduction volume' estimates by two methods for the Gotland Basin*

Hydrographic data sets allowed a comparison of 15 monthly estimates of positive or negative reproduction volumes. Regression analysis between two data series generally showed that there is a strong correspondence between estimates obtained from 2 single stations in the center of the basin and estimates obtained taking into account spatial heterogeneity of salinity and oxygen content (Figure 3). The regression is highly significant ($p<0.0001$) and explains 91% of variation. Largest deviations (15-23%) were observed during inflow months, when the dynamic of water mass transport was highest. Transects obtained during inflow periods show that in the eastern part of the basin, the isohaline 11 psu is located shallower and the isooxygen of 2ml/l more deeper then in the western part of the basin, i.e. the influence of the inflows was highest in the eastern part of the basin.
In stagnation periods, the differences are much smaller – from 1 to 8% and the isohalines as well as the isooxygens are more evenly distributed in west – east directions. Bagge and Thurow (1994) have observed a similar pattern of even distributions of salinity and oxygen during the stagnation period in 1991 across the Gotland basin. Although the present comparison covered only 15 monthly observations, we can conclude that single point estimates sufficiently quantify the reproduction volume conditions and thus similar to the Bornholm basin can be used for estimation of the RV (MacKenzie *et al.*, submitted).

2. *Vertical distribution of reproduction volume*

A historical overview of .the dynamic of positive as well as of negative reproduction volumes revealed different trends within different areas of the Gotland Basin (Figure 4). In the Southern Gotland Basin positive reproduction volumes were observed more frequent and for longer time periods. Usually it was ranging from 90 m depths to the bottom (120 m). Until the mid of the 80-ies this spatial pattern was maintained. The frequency of the occurrence of the RV was decreasing from the southern basin towards the north where it was registered very seldom. It clearly can be seen that periods of positive reproduction volume existences in the southern Gotland Basin coincide with Kattegat water advection into the Baltic (Matthäus and Franck, 1992). Only strong or major inflows (such as in 1964, 1970, 1976, 1977) were able to significantly improve the hydrological situation by providing favorable conditions for cod spawning in the Central Gotland. Basin. In the Southern Gotland Basin negative volumes develop mainly during stagnation periods, especially during time periods between inflows, while in the Central Gotland Basin it was observed almost during all the years. Usually negative volumes were recorded in depths from 65 to 110 m but an exceptionally long stagnation periods since the mid of the 80-ies lead to an extension of negative volume zones from 90 m to the deepest part of the basins in the early 90-ies.
The recent major inflow of 1993 (Matthäus and Lass, 1995), reached the Gotland Basin in 1994 and significantly influenced the hydrological regime. In the Central Gotland Basin an increased positive reproduction volume was generated from

approximately 130 m depth down to the bottom. Such situation was not observed during previous periods.

According to the conception of the reproduction volume, it describes the limiting oxygen and salinity values for egg survival. In this respect it is very important to understand how this volume can be utilized for egg development, i.e. in which layers the cod eggs really are floating. Available informations from the Gdansk and Gotland Basins (Makarchouk & Hinrichsen, 1998) show that highest abundances of cod eggs were observed in density ranges from1008.6 to 1008.9 kg/m^3. Density profiles in combination with observations of the distribution of negative and positive reproduction layers indicate that only in the Southern Gotland Basin vertical egg distribution coincides with sufficient salinity and oxygen conditions for their successful development (Figure 5). In the Central Gotland Basin, eggs usually were exposed to insufficient oxygen conditions with the exception of 1976 and 1977, partly also in 1985.
Analysis of the density profiles revealed:

- in general the density decreases in a given depth during cod spawning season (March-August). This is obviously related to the seasonality of inflows and water dynamic in the deep layers, i.e. it means that eggs in spring compared to summer months can be distributed more upwards.
- the density at the 11 psu isohaline, changes between aeration and stagnation periods from 1008.9 kg/ m^3 to1009.4 kg/ m^3.

It is generally assumed that wider positive volumes have higher oxygen contents then smaller ones or negative volumes. However, during periods of unstable and highly variable environmental conditions in the Gotland Basin it is necessary to take into account real oxygen conditions in a quantitative way. As it was shown, the egg survival significantly increases if oxygen contents increase from 2-5 ml/l (Wieland *et al.*, 1994). Although, temperature effects may have influence on egg survival for the area under consideration it has not to be taken into account. As an alternative approach we have chosen the oxygen and temperature values at specific salinity levels – 10 and 11 psu (Figure 6). Long-term oxygen and temperature changes in the Southern and in the Central Gotland Basin show similar trends. Additionally, similar trends of parameters are observed at salinity 10 and 11 psu.
Temperature at salinities of 11 psu ranges from 3 to 6 °C in Southern Gotland Basin and 4-6 °C in the Central Gotland Basin, but fluctuations of oxygen content are more pronounced. Strong increase of oxygen contents was observed during inflow periods 1976-1977, 1980-1981 and 1994 while during stagnation periods, oxygen decreased down to 0 ml/l. However, the oxygen increases during 1984-1986 is not explainable by major Baltic inflows. Obviously, this event can be interpreted by intensive vertical mixing (1) or inflows of less saline and aerated waters from the southern Baltic (2). More reliable seems to be the second option because a decrease of salinity in deep water layers was not encountered.

3. Stock recruitment relationships in the Gotland Basin

Stock recruitment relationships obtained for age group 1 and female spawning stock indices from Latvian surveys, are shown in figure 7. There appears to be a linear relationship between stock size and recruitment, however relatively high recruitment occurred in 1975 and 1976 at intermediate spawning female stock.

The environmental factors identified and described above, were incorporated into stock recruitment relationship analyses. The following factors were included in the analyses: positive reproduction volume (1) and negative volume (2) as average of May and August, temperature (3), as well as oxygen at salinity of 11 psu (4) and female spawning stock index from research surveys in March-April (5). The relation and factor significance was explored by multiple linear regression analysis. Temperature in all trial runs appeared to be insignificant and therefore was excluded from the model.

The diagnostics of the multiple linear regression analyse is given in Table 2. The statistical model for the whole time series (1975-1999) explains 31% of variability (adjusted for degree of freedom). The positive reproduction volume is the only significant factor ($p< 0.01$). The data time series was divided into two different periods: 1975-1985 and 1986-1998. The first period is characterized by relatively regular formations of reproduction volume and higher spawning stock abundance showing an increasing trend during the period 1975-1980 and a decreasing trend afterwards. In the second period, the reproduction volume was observed in some occasions only, with stagnation processes prevailing and the female spawning stock on very low level. As it can be seen from analyses for 1975-1985, the model results are significant ($p<0.09$) and explain 48% of variation. The highly significant were the environmental parameter: positive RV, negative volume and oxygen saturation at salinity of 11 psu. Female spawning stock was nearly significant ($p<0.13$). For the second period none of the factors was significant, with also the model being insignificant.

Discussion

The presented analyses revealed that the main factor determining the dynamics of water masses suitable for cod reproduction in the Gotland basin is the water advection from Kattegat. Major inflows into the Baltic usually start from August to April, in 60% of the cases from November to January (Franck *et al.*, 1987). The hydrological changes in the Gotland Basin usually take plase 6-9 months after an inflow was registered in the Bornholm Basin, respectivelly during May–August (Kaleis, 1977). Oxygen is mainly renewed by inflows and is depleted due to biochemical processes. (Kaleis, 1990). Our analyses taking into account the heterogeneity of the Gotland Basin similar to the Bornholm Basin (MacKenzie, *et al.*, in press), shows that hydrographic monitoring stations in the center of the basin can represent the entire regime and allow to quantify environmental conditions for successful cod reproduction, e.g. reproduction volume. The egg survival strongly decreases if temperature is below 2° C (Wieland *et al.*, 1994). As the cod reproduction in the Gotland Basin takes place in deep layers, where the ambient temperature regime shows no pronounced annual fluctuations, direct lethal effects on cod egg survival and on hatching rate are expected to be limited.

We have identified several environmental parameters (negative volume, reproduction volume, and oxygen at specific salinity) which can influence the reproduction success of cod. However, it appears to be too premature now to re-define the reproduction volume concept. Information on water densities where cod eggs have been distributed is variable between seasons, hydrographic regimes and spawning sites. They also differ between experimental and field observations (Makarchouk & Hinrichsen, 1998; Wlodarczyk & Horbowa, 1997; Köster *et al.*, 1999; Nissling & Vallin, 1996; Nissling

et al., 1994; Thoresen *et al.*, 1996 *al.*, 1999). More buoyant eggs have lower chances to be exposed into low oxygen conditions and therefore have higher chances to survive. Field samplings in the Bornholm Basin revealed a strong linear relationships between egg size and ambient water densities greater then 1008 kg/m^3 (Wlodarczyk & Horbowa, 1997). Therefore, egg size can be regarded as one of the most significant factors determining the vertical egg distribution. Grauman (1969a) found that the proportion of large eggs increases with increasing female size (from 42% for 36-40 cm females to 85-89% for > 66 cm). In the majority of females the egg size is also dependent from the batch number (Nissling *et al.*, 1994). Probably due to this, spawned egg sizes for all three areas (Bornholm, Gdansk and Gotland) show a seasonal trend – with the egg size gradually decreasing from April to August (Grauman, 1969b). This trend may, however also be explained by size/age specific timing of spawning with large females spawning earlier (Tomkiewicz and Köster, 1999).
Changes in the hydrographic situation in the Central Gotland Basin during 1994 when a high positive reproduction volume was observed at depths below 130 m, did not significantly influence cod recruitment. Although density profiles show that eggs could be exposed in this lower volume, the utilization of it was obviously be limited by the extremely low spawning stock size in this area.

The variability of the reproduction volume in different parts of the Gotland Basin suggests that the main spawning and the successful reproduction area during the last decades in general was located in the Southern Gotland Basin. This is also confirmed by distribution of juvenile fish in different parts of the basin. In Southern Gotland Basin the age group 1 cod shows more stable concentrations while in the central Gotland Basin high abundances were registered in specific periods (Lablaika and Uzars, 1983). Nevertheless, a significant correlation was found between juvenile abundance indices in the Southern and in the Central Gotland Basin but correlation with the neighboring Gdansk Deep was poor for both areas (Kondratowich and Lablaika, 1989). It is well known that spawning cod prefers higher salinity and oxygen regimes (Lablaika and Lishev, 1964; Tiews, 1976; Tomkiewicz *et al.*, 1998). During spawning mature cod can re-distribute from the Central to the Southern Gotland (Uzars *et al.*, 1991). Also spawning cod migrations from the Gotland to Bornholm Basin has been described during stagnation periods and in dependence of the stock size in the Gotland Basin (Lishev and Lablaika, 1989). Nevertheless, the environment where spawning of cod takes place does not always correspond to the conditions necessary for egg survival. Spawning cod has been observed at salinity of 9.5 psu and oxygen 1.5 ml/l (Plikshs and Kalejs, 1990).

Age group 1 abundance indices from Latvian surveys are significantly correlated with age group 1 estimates derived from the BITS database for the Gotland Basin (r=0.87) (Mackenzie *et al*, 1999). Correlation with age 1 estimates for subdivisions 28 and 26 (Sparholt & Tomkievizs, 1998; ICES, 1999) is lower but still highly significant (r=0.77 and r=0.59). Similarly, good agreement was found between female spawning stock indices from Latvian surveys and total spawning stock estimates from the BITS database. Although, the female spawning stock and the age group 1 estimates is in a good agreement with the BITS estimates, it should be mentioned that since beginning of 90-ies obtained female index may be overestimated. Changes in the timing of cod spawning and extended maturation in the 90-ies as well as higher possibilities of westward spawning migrations due to stagnation in the Gotland Basin suggest that surveys in March-April may not reflect adequately the distribution of the spawning stock (Wieland *et al.*, 1997; Baranova & Shics, 1999).

In view of the numerous factors that can influence cod recruitment including size of spawning stock, structure of parent stock, egg predation by sprat and herring and cannibalism it seems to be remarkable that a significant relationship was found between recruits and RV in the Gotland Basin. The significance of positive reproduction volumes for the whole period obviously is determined by extremely high recruitment and highest positive RV observed in 1976. Analyses of the period from end of the 70-ies to the beginning of the 80ies suggest that in variable environmental conditions cod recruitment in the Gotland Basin is mainly determined by environmental factors and only to a less extent by the spawning stock biomass. Oxygen and negative volume, which are characteristics of cod spawning habitat in stagnation periods, also seems to contribute significantly to the recruitment. Failure in the statistical analyses to identify significant factors for the most recent period suggests that in long stagnation periods without favourable environmental conditions spawning success is negligible. Obviously the stock and recruitment are maintained in the Gotland Basin by successful spawning in other areas of the Baltic.

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Table 1

Number of research trawl stations in the Gotland Basin

Year	January-February										March-April										Total
	Southern Gotland					Central Gotland					Southern Gotland					Central Gotland					
	21-40	41-60	61-80	81-100	100<	21-40	41-60	61-80	81-100	100<	21-40	41-60	61-80	81-100	100<	21-40	41-60	61-80	81-100	100<	
1975												1	5	6	3	1	3	3	3		25
1976							2	6				1	1	1	4	1	2	4	1		23
1977			3		2		5	2	2			1	2	3	13		3	6	5	10	57
1978		1		1		1	4	5	2			1	1	1	7		1	1		1	27
1979			1				4	2	3	2		1	1	1	4			2	1	1	23
1980											2	2	4	3	2	1	6	15	5	1	41
1981						2	5	4	1		1	1	6	2	3	1	1	9	3	2	41
1982	3		1	2	1	1	4	4	1		2	1	2	4	8	1	3	6	4	2	50
1983	1					3	3	7	1		1	1	1	1	11	4	6	8	5	1	54
1984	2	2				3	3	4	1		2	2	4	2	18	2	2	5	9	6	67
1985	4	3				2	1	5	3			5	1	2	20	1	1	3	3	11	65
1986						1	4	1		1		3	6	5	9		3	2	9	20	64
1987	1	2	1		3		2	3	1		1	2	2	5	17		3	10	8	5	66
1988	1	2	2	1	2	3	3	4	1	5		2	3	8	9	2	3	11	11	8	81
1989	1	1	1		1	2	2	6	2		2	2	2	5	9	1	4	4	9	14	68
1990	1	2	1	1		1	1	2			1	1	1	8	8		3	4	5	14	54
1991	1		1			3	4	2	4			1	2	2				1	5		26
1993												3	2	2	5	2	5	3	3	2	27
1994												2	5	7			2	5	3	4	28
1995														1			2	11	6	3	23
1996											1	9	6	15	3		2	9	5	4	54
1997												2	3	1	3		2	3		1	15
1998														1	1		3	6	3	2	16
1999													4	3	3		3	5	4	1	23
Total	15	13	11	5	9	22	47	57	22	8	13	44	64	89	160	17	63	136	110	113	1018

Table 2

Diagnostics of multiple factor regression analysis of stock recruitment relationship in the Gotland Basin

Period	Model				Factors	p<
	df	R^2 adjusted	F	*p*<		
1975-1998	21	0.47	3.3	0.03	Intercept	0.45
					Positive RV	0.01
					Negative volume	0.38
					Female spawning stock	0.92
					O_2 saturation	0.49
1975-1985	10	0.48	3.3	0.09	Intercept	0.05
					Positive RV	0.04
					Negative volume	0.03
					Female spawning stock	0.13
					O_2 saturation	0.01
1986-1998	11	0.0	0.6	0.65	Intercept	0.11
					Positive RV	0.81
					Negative volume	0.51
					Female spawning stock	0.53
					O_2 saturation	0.31

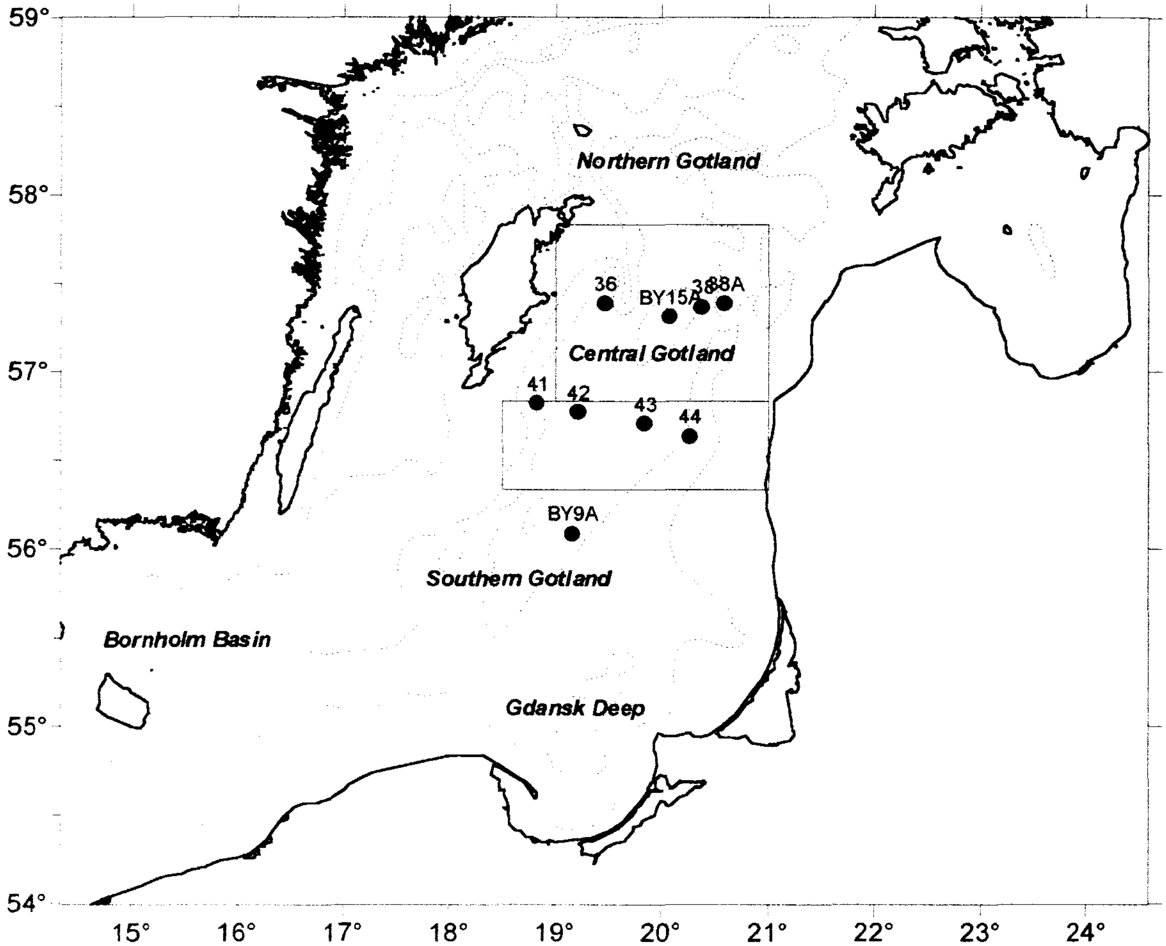


Figure 1. LATFRI hydrologycal monitoring stations in the Gotland Basin. Squares indicate 'reproduction volume' estimation area in the Central Gotland.

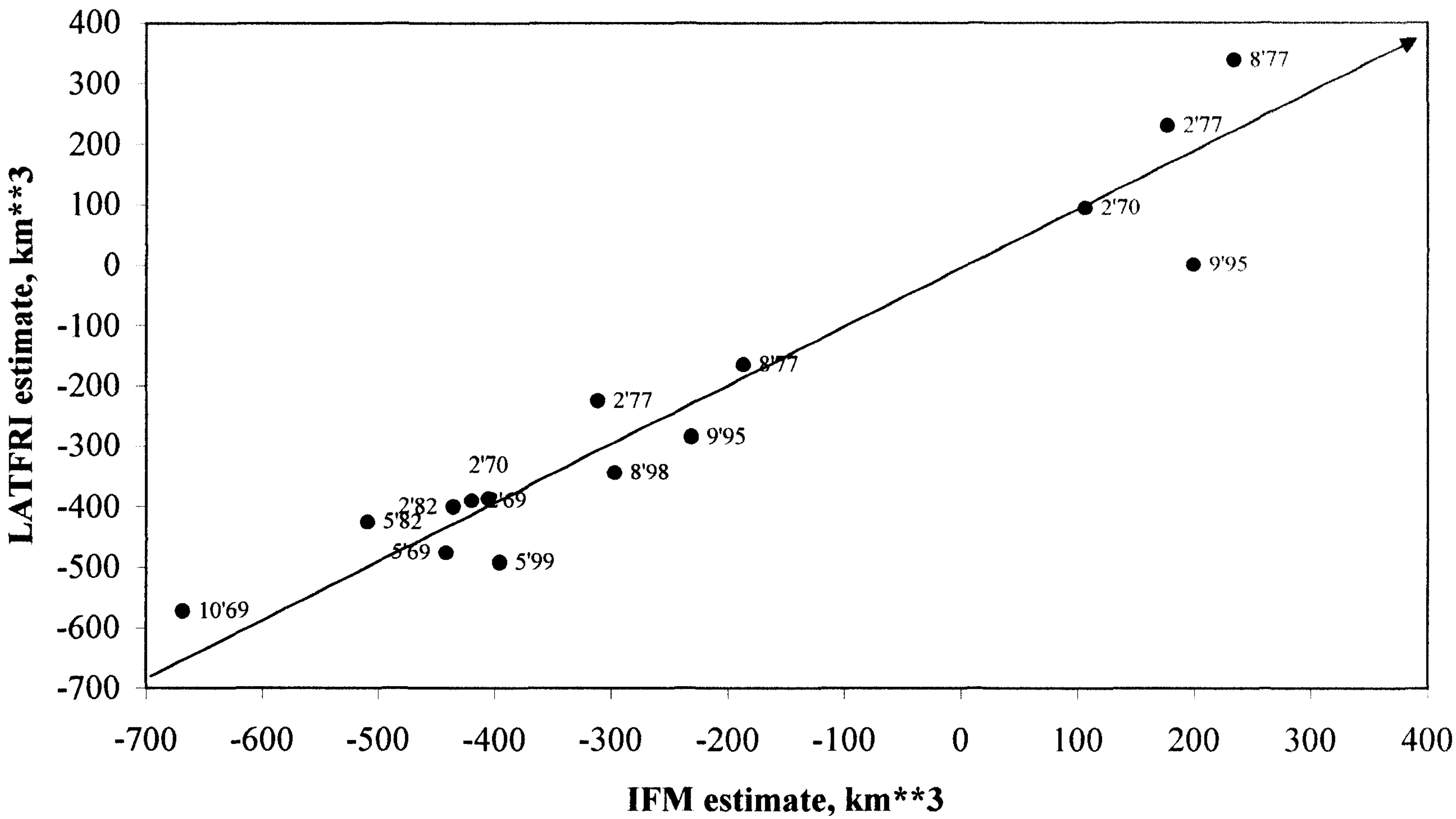


Figure 3 . Comparison of LATFRI and IFM estimates of positive and negative 'reproduction volume'

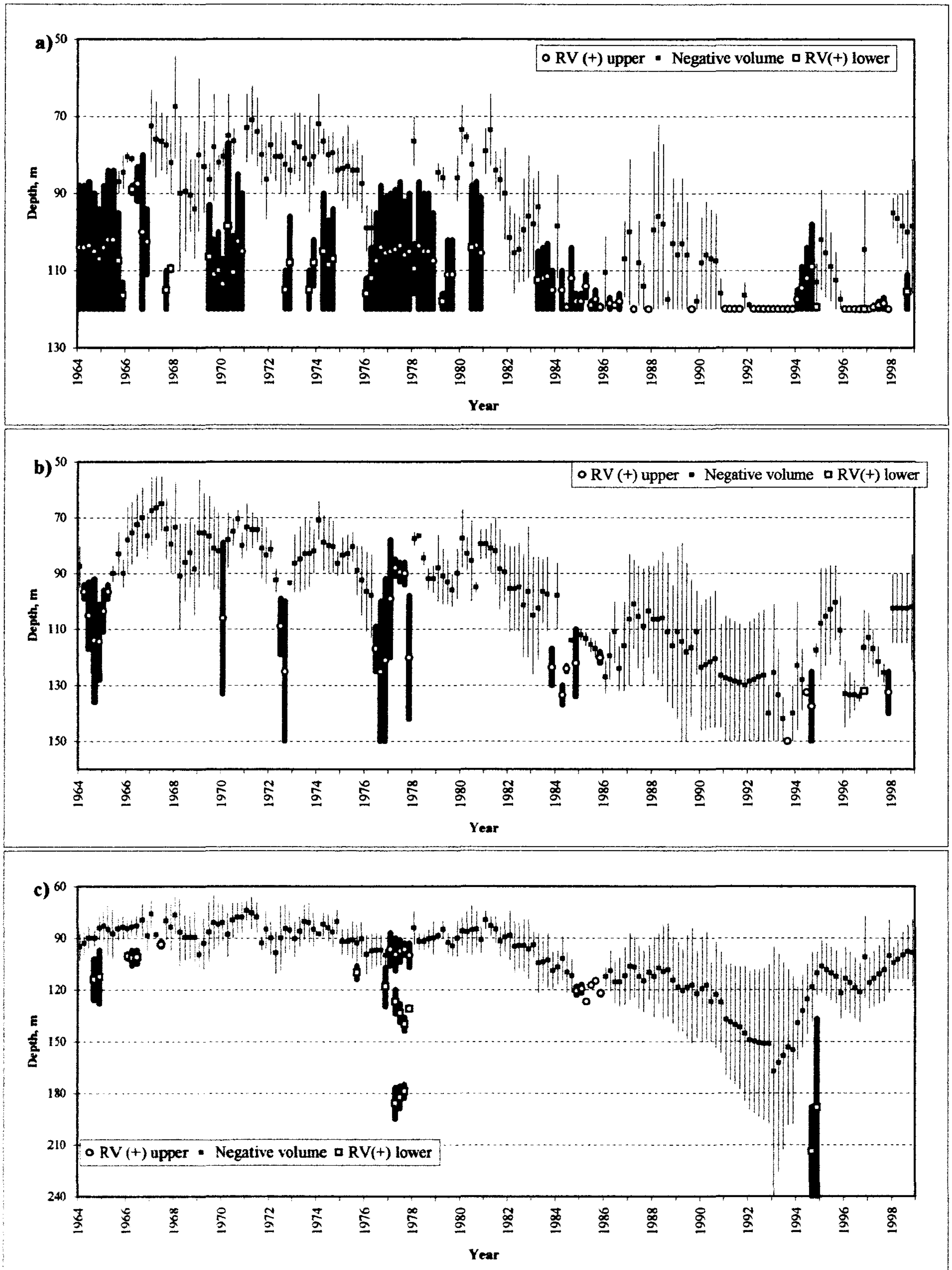
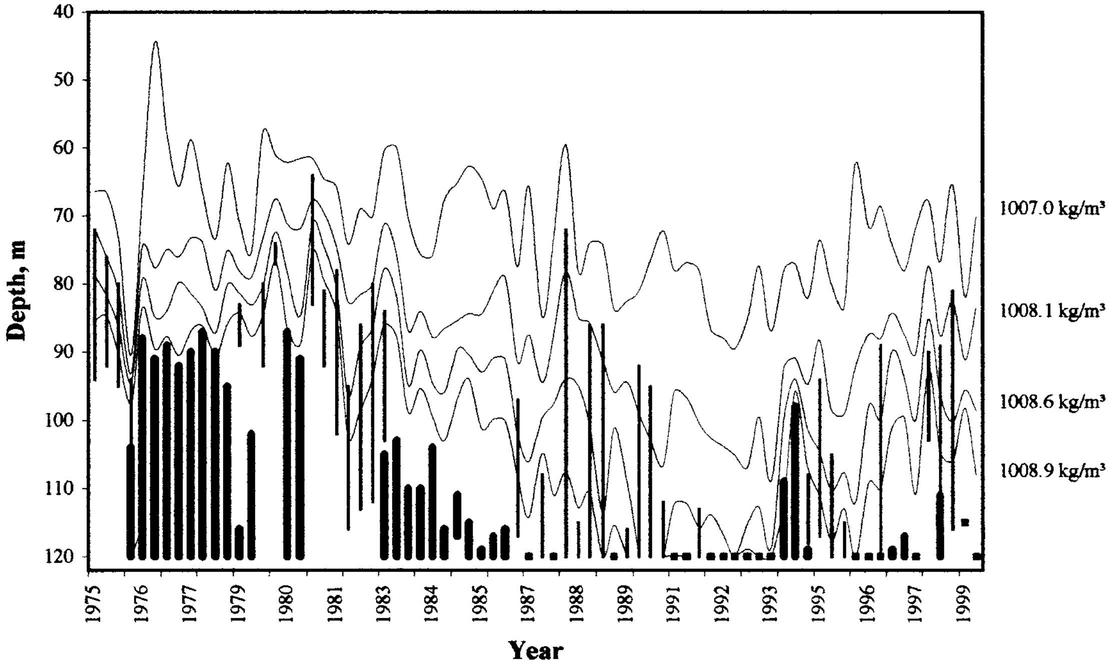


Figure 4. Vertical distribution of positive 'reproduction volume' and negative volumein the Gotland basin (February-August):
c) Southern Gotland - station BY9A
b) Central Gotland - station 43
a) Central Gotland - station BY-15A

——— negative volume ━━━ positive RV

Southern Gotland - station BY9A



Central Gotland - station BY15A

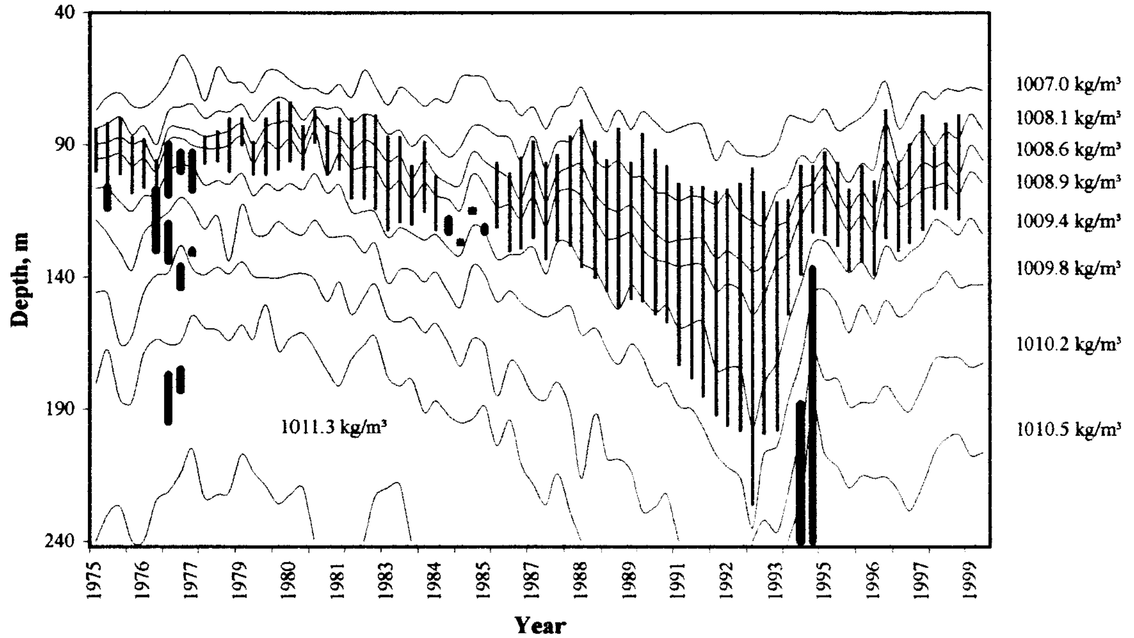


Figure 5 . Water densities and vertical distribution of Baltic cod 'reproduction' volume during March, May and August in the Gotland Basin.

Bars: ——— negative RV ▬▬▬ positive RV

Isolines - density in kg/m³