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Original article

The influence of biotic and abiotic factors on the growth of sprat (*Sprattus sprattus*) in the Baltic Sea

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Abstract

We analysed spatial and temporal patterns of condition factor (CF) of sprat (*Sprattus sprattus*) between 1986 and 2000 in different areas of the Baltic proper. Results showed a moderate increase in CF between 1986 and 1989. Afterwards, an abrupt decrease in CF, between 22% and 29%, occurred in all the areas of the Baltic proper. However, from 1998 and onwards, CF increased compared to the previous years. Weight-at-age and CF of Baltic herring showed a similar pattern in the same period. Several factors affecting variability of sprat CF were evaluated. Data showed that sprat CF was density-dependent and possibly related to the pelagic fish abundance and individual food intake. Temperature did not influence sprat CF while salinity seemed to affect variability of sprat CF in the northern Baltic proper. Changes in salinity levels may shape pelagic fish growth rates both indirectly changing the zooplankton community structure and abundance and/or directly via fish physiology and metabolisms. © 2002 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS. All rights reserved.

Résumé

Influence des facteurs biotiques et abiotiques sur la croissance du sprat (*Sprattus sprattus*) en mer Baltique. Nous analysons l'évolution dans le temps et dans l'espace du facteur de condition (CF) du sprat (*Sprattus sprattus*) entre 1986 et 2000 en différentes zones de la Baltique. Les résultats montrent une légère augmentation du CF entre 1986 et 1989. Par la suite, une baisse importante (de 22 à 29%) du CF est observée dans toutes les zones de la Baltique. Cependant, depuis 1998, le CF est en augmentation par rapport aux années précédentes. Le poids corrélé à l'âge et le CF du hareng de la Baltique présentent les même tendances à la même période. Plusieurs facteurs affectant la variabilité du CF du sprat sont évalués. Les données montrent que le CF du sprat est corrélé à la densité et probablement à l'abondance des poissons pélagiques et à leur prise de nourriture. La température n'a pas d'influence sur le CF du sprat tandis que la salinité semble affecter la variabilité du CF du sprat dans la partie Nord de la mer Baltique. Des changements de niveaux de salinité peuvent donner le profil de croissance, à la fois indirectement, en modifiant la structure et l'abondance de la communauté zooplanctonique, et/ou directement, via la physiologie et le métabolisme du poisson. © 2002 Ifremer/CNRS/Inra/IRD/Cemagref/Éditions scientifiques et médicales Elsevier SAS. Tous droits réservés.

Keywords: Clupeids; Condition factor; Density-dependent growth; Abiotic factors; Baltic Sea

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1. Introduction

Sprat (*Sprattus sprattus*) plays a significant role in the ecosystem of the Baltic Sea both as one of the principal prey for several piscivores and as one of the major zooplanktivores (Rudstam et al., 1992; Arrhenius and Hansson, 1993; Hansson et al., 1990; Karlsson et al., 1999). Unlike herring (*Clupea harengus*), the other principal pelagic species in the Baltic Sea, sprat is strictly zooplanktivorous. The primary preys of sprat consist of the calanoid copepods *Temora longicornis* and *Pseudocalanus elongatus* (Möllmann and Köster, 1999).

During the last decade the biomass of sprat has drastically increased (Cardinale and Arrhenius, 2000a), becoming the most abundant and commercially important fish species of the Baltic Sea (Karlsson et al., 1999). At the same time herring biomass decreased due to intense fishing and reduced growth rates (Cardinale and Arrhenius, 2000a). How-

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ever, as a whole, the total spawning biomass of pelagic fish stock (herring and sprat) has increased to reach a peak in 1996 (Cardinale and Arrhenius, 2000a) and decreased moderately thereafter (ICES, 2001). The stock of Baltic cod (*Gadus morhua*), the major predator of sprat in the Baltic Sea, decreased during this period to a very low population level owing to high fishing mortality and poor recruitment (Cardinale and Arrhenius, 2000b).

Due to high population level of pelagic fish, we could expect a density-dependent effect on sprat growth in the Baltic Sea. A decrease in sprat condition could be caused by reduced individual food intake and, thus, be directly connected with a decline in fish growth rate. A decreasing pattern in individual growth rates has been shown for Atlantic herring in the same area (Cardinale and Arrhenius, 2000a). It could be also assumed that the increase in the abundance of pelagic fish might have reduced zooplankton biomass in the Baltic proper (i.e., top-down effect) (Cardinale and Arrhenius, 2000a). On the other hand, due to lack of occasional inflow of oxygen-rich waters from the North Sea (MacKenzie et al., 2000), stressing environmental conditions (abnormal levels of temperature, oxygen and salinity content) occurred in the Baltic Sea in the last decade. Any abiotic factor that affects rates of food consumption and metabolism may be expected to have a profound influence on the growth of fish (Jobling, 1994). Temperature and salinity are known to influence both ingestion and metabolism. The metabolic costs of iono- and osmoregulation are lowest in environments where gradients between blood and water are minimal (Jobling, 1994). However, it is important to distinguish between the effect of temperature and salinity per se (Jobling, 1994) and their effect on fish growth induced by the interaction with the structure and abundance of zooplankton (Flinkman et al., 1998; Dippner et al., 2000; Möllmann et al., 2000).

Nevertheless, to our knowledge, a statistical analysis of changes in Baltic sprat growth rates and possible factors affecting them is lacking so far. To investigate the effects of biotic and abiotic factors that we considered critical for sprat growth rates, the following hypotheses were tested:

1. The increase in pelagic fish abundance negatively affects Baltic sprat growth rate possibly via a decrease of the individual food intake (density-dependent hypothesis) (DDH).
2. Temperature and salinity levels affect Baltic sprat growth rate either directly via metabolism or indirectly changing the structure and/or abundance of zooplankton community (environmental hypothesis) (EH).

2. Materials and methods

2.1. Biological sampling

Fish samples were taken in September–October in the Baltic proper (ICES subdivisions 25–29s) annually between 1986 and 1990 and for 1999 and biannually between 1990 and 2000 (Fig. 1), using pelagic mid-water trawls during the national acoustic survey carried out onboard the Swedish research vessel “Argos”. The sampling stratification in the Baltic Sea is based on ICES statistical rectangles (0.5° in latitude and 1° in longitude). Two trawl hauls were normally taken per statistical rectangles. Fishing operations were performed with two different pelagic trawls (14–17 m vertical opening; 21 mm stretched mesh size in the cod end) in the mid-water as well as near the bottom depending on the fish distribution detected by the hydroacoustic equipment. Both trawls used, Macro 4 and Fotö, have the same selectivity (Bethke et al., 1999). The hauls lasted 30 min with a trawling speed varied between 3 and 4.5 knots (for further details on fishing operations see Bethke et al., 1999).

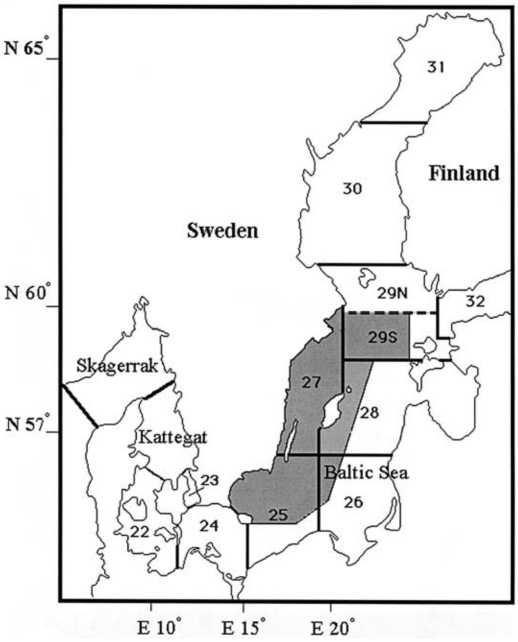

Fig. 1. Map of the Baltic Sea divided into ICES subdivisions (25–32). The shaded area (Baltic proper) was covered by the Swedish acoustic survey in September–October 1986–2000.

All sprat individuals were immediately frozen on board and successively analysed in laboratory. For all samples, total fish length measured to the nearest 0.5 cm and body weight to the nearest 1 g were recorded. Otoliths were removed from all individuals and analysed using a stereomicroscope. Age was determined using the otoliths illuminated from above against a dark background. The age was estimated as the number of hyaline rings. The same scientists, periodically intercalibrated, were involved in the age analysis for all the individuals sampled.

2.2. Time-series data

Data on clupeids number were available from annual stock assessment reports calculated with a multi-species virtual population analysis (MSVPA) (ICES, 2001) for the Baltic proper (subdiv. 25–29s). Catch-at-age data from commercial landings were tuned with index of abundance estimated from trawl survey. For details on mathematical calculations of VPA-type model see Hilborn and Walters (1992).

Data on zooplankton biomass were available for subdiv. 27 only (HELCOM, 1996). In this study we considered the biomass estimate of those species that constitute more than 90% of the diet of sprat, namely the copepods *Temora longicornis* and *Pseudocalanus elongatus* (Möllmann and Köster, 1999). The available data time-series covered the period 1986–1996. The estimate for 1998 was interpolated using the average value of the previous 3 years. For details on zooplankton sampling strategy see HELCOM (1996).

Data on temperature and salinity were collected in September–October in the Baltic proper (subdiv. 25–29s) during the national acoustic survey carried out onboard the Swedish research vessel "Argos". Profiles of water temperature (°C) and salinity (psu) were recorded at 0, 2.5, 5, 10, 15, 20, 30, 40, 50, 60, 70 and 80 m depth using a conductivity temperature depth probe (CTD). The data time-series covered the period 1986–1999. As an indicator of the environmental conditions during summer–autumn, we used the average temperature and salinity of the water column between 0 and 50 m where Baltic pelagic fish species are mainly distributed (Orlowski, 1998), due also to the occurrence of severe anoxic conditions below this depth range.[1] These values of temperature and salinity represent point estimates that obviously do not reflect the environment experienced by sprat throughout the entire year. However, they mirror the mean environmental conditions that sprat experiences during the period of maximum growth (summer-autumn) and therefore they may be useful for inter-annual comparisons of variation in sprat condition.

3. Statistical analysis

3.1. Estimate of sprat condition

For the analysis of sprat condition, we followed the procedure used by Winters and Wheeler (1994) and Tanasichuk (1997), where the (double natural logarithmic) length–weight regression is considered as the most reliable index of the condition of the fish (Bolger and Connolly, 1989; Patterson, 1992) and usually related to the feeding condition in the sea. It is particularly suitable in studies on pelagic fish (Winters and Wheeler, 1994; Tanasichuk, 1997; Cardinale and Arrhenius, 2000a). Therefore, condition is defined as the variation in the whole body weight (soma plus gonads) of fish of the same total length (i.e., common length) after testing for differences in slope among years and subdiv. (Winters and Wheeler, 1994). We restricted our analysis to adult fish, i.e. sprat 1–5 years old. The number of samples containing fish older than 5 years was not consistently large enough ($n < 10$) for the combination of different years and areas and was excluded from the analyses. Relationships were based on the natural logarithms of weight and length and modelled as:

$$\log_e(y) = a + b \log_e(x)$$

Where y represents the fish weight, x is the fish length and a and b are the parameters of the linear regression (Sokal and Rohlf, 1995). We used the Gabriel's approximate test (Sokal and Rohlf, 1995) to determine if the regression coefficients (slopes) estimated for the different years and subdiv. were statistically different. The slopes whose the 95% comparisons intervals, calculated by the GT2 method, do not overlap were considered significantly different (Sokal and Rohlf, 1995). The GT2 method employs the studentised maximum modulus distribution for estimating the critical value in means comparison (Sokal and Rohlf, 1995).

Sprat condition (i.e., total body weight in grams at the common length) was estimated at the total length of 120 mm that corresponded to the estimated mean length of the sprat population in the study area. Therefore, sprat condition factor (CF) was estimated (after logarithmic transformation) as:

$$\mathrm{CF}_{\mathrm{subdiv.,\,Y}} = 120(a_{\mathrm{subdiv.,\,Y}} + b_{\mathrm{subdiv.,\,Y}})$$

Comparison intervals (95%) of the CF estimates were calculated using the Tukey method for multiple comparisons based on unequal sample size (Sokal and Rohlf, 1995). Hereafter, condition factors and growth rates were used as synonymous in this study.

3.2. Non-linear regression analysis

Relationships between a dependent variable and one or more factors are in nature often non-linear (Maravelias, 1997; Maravelias and Reid, 1997). Therefore, linear models are inadequate for quantifying interactions between different variables and a more flexible non-linear technique is necessary (Maravelias and Reid, 1997; Cardinale and Arrhenius, 2000b). Particularly, the relationship between fish condition and different biotic and abiotic factors is biologically constrained between the minimum and the maximum weight at length possible for the species. This relationship should theoretically approach a sigmoidal curve:

$$y = \frac{a}{(1 + b^{(-kx)})}$$

Where y is the weight at the common length (response), x is the predictor and a (asymptote), b and k are parameters

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[1] Arrhenius, F., 1999. Hydroacoustic survey in the Baltic proper by R/V *Argos*, October 4–21, 1999. Working report from the Institute of Marine Research, Lysekil, Sweden.

Table 1
Data used in the analysis. See text for details

			Subdivision 25		Subdivision 27	
Year	Clupeid number (10^9)	Zoo/ind (μg m^{-3}) (ind^{-1})	Temperature 0–50 m (°C)	Salinity 0–50 m (psu)	Temperature 0–50 m (°C)	Salinity 0–50 m (psu)
1986	112.69	20.9	8.5	8.0	6.7	7.2
1987	138.18	94.5	8.4	7.6	7.4	6.8
1988	104.88	16.0	8.5	7.9	6.8	7.1
1989	131.73	30.3	10.9	7.9	8.9	7.1
1990	165.04	21.3	10.1	7.3	8.7	6.8
1992	255.34	14.0	11.0	7.9	9.4	6.9
1994	261.28	11.0	10.9	7.4	10.1	6.4
1996	387.10	7.2	10.7	7.8	9.6	6.6
1998	350.00	7.9	10.0	7.4	9.0	6.7
1999	278.94	–	8.8	7.6	9.5	6.8
2000	317.45	–	–	–	–	–

of the curve (Snedecor and Cochran, 1989). We assumed asymptotic values of sprat CF to be close to the minimum (8 g) and the maximum (14 g) weight at 120 mm observed during our study period. Successively, we fitted the sigmoidal curve using available data for the different factors. The biotic factors used in the analysis were the total number of clupeid fish (herring and sprat) and the zooplankton biomass (μg m^{-3}) available per individual pelagic fish. The abiotic factors used were temperature and salinity, averaged between 0 and 50 m depth. The survey carried out by the Swedish research vessel Argos investigated primarily the western part of the Baltic proper (subdiv. 25 and 27), while the eastern part (subdiv. 26 and 28) was covered only partly (Cardinale and Arrhenius, 2000a). Thus, relationships between sprat condition and abiotic factors were estimated for subdiv. 25 and 27 only. Data used in the analysis are presented in Table 1.

Residuals of fitted relationships were analysed to test for deviation from the model assumptions or other anomalies in the data or in the model fit using analytical methods (Kitadinis, 1997). Q_1 statistic was used to verify the general unbiased conditions of the model. We tested if the residuals were normally distributed using the Shapiro and Wilk's test (Shapiro et al., 1968). Residuals were also plotted against the predicted values to test for their homogeneity. We also tested for inter-correlation between factors (Pearson correlation method) (Sokal and Rohlf, 1995) and for auto-correlation of the time-series (Chatfield, 1997). Auto-correlation (r_k) measures the correlation between observations at different distances (k) apart and provides insight into the probability model, which generated the data. If a time-series is random, all values of r_k should lie between $\pm 2/\sqrt{N}$. On the other hand, short-term correlation series show often a large value of r_1 followed by further coefficients that tend to approach 0 (see Chatfield, 1997 for details on auto-correlation). In order to assess the effect of removing auto-correlation from each time-series, we used smoothing time-series with a two-points running mean as suggested by Pyper and Peterman (1998).

3.3. Correlation analysis

Correlation analysis between adult sprat condition and herring condition for each subdiv. (25–29s) was performed. Data for herring condition (1986–2000) for the different subdiv., estimated with the same method as in this study, were available from Cardinale and Arrhenius (2000a). Correlation analysis was performed using the Pearson correlation method (Sokal and Rohlf, 1995). However, trends and autocorrelation particularly in short time-series violate the assumption of statistical independence used in estimating standard significance level. As a result the significance levels calculated are inflated compared to true significance levels. One way to deal with this is to transform the raw data. This usually reduces trends and autocorrelation problems associated with short time-series.

The level of significance was set at 5% for all the statistical tests used in this study. Statistical analysis was performed with Statistica (1995) computer software.

4. Results

4.1. Statistical analysis

4.1.1. Estimate of sprat condition

Between 18 and 43 hauls were carried out each year (Table 2). A total of 21 497 sprats were collected in the Baltic proper (subdiv. 25–29s; Fig. 1) between 1986 and 2000. The age in the catches ranged from 0 to 8 years. The most common age classes were 1 to 5 years old, constituting around 80% of the total catch. To avoid the use of age classes constituted by few individuals (i.e., less than 10), only 1–5 year old fish were used in the analysis. However, at least 727 individuals per year sample were used (Table 2).

The results of regression analysis between length and weight of sprat are presented in Table 2. We found no statistical difference between the slopes estimated for each year and between different subdiv., except for 5 of them

Table 2
Number of hauls (in brackets for each year) and individuals of Baltic sprat (n) used in the regression analysis between $\log_e$ of fish length (x variable) in mm and $\log_e$ of fish weight (y variable) in g; mean ± 95% confidence intervals

Subdiv.		Year										
		1986 (23)	1987 (33)	1988 (30)	1989 (20)	1990 (24)	1992 (18)	1994 (40)	1996 (43)	1998 (37)	1999 (33)	2000 (30)
25	*a*	–8.49 ± 0.14	–9.00 ± 0.14	–9.88 ± 0.14	–9.15 ± 0.10	–8.35 ± 0.21	–8.57 ± 0.10	–9.15 ± 0.23	–9.19 ± 0.14	–9.62 ± 0.10	–9.47 ± 0.19	–8.86 ± 0.15
	b	2.31 ± 0.03	2.39 ± 0.03	2.59 ± 0.03	2.45 ± 0.02	2.28 ± 0.04	2.32 ± 0.02	2.43 ± 0.05	2.41 ± 0.03	2.49 ± 0.02	2.48 ± 0.03	2.37 ± 0.03
	r	0.98	0.97	0.96	0.98	0.93	0.98	0.95	0.97	0.97	0.95	0.96
	P	***	***	***	***	***	***	***	***	***		***
	n	209	424	645	611	419	581	300	451	814	368	386
26	*a*	–9.15 ± 0.17	–8.74 ± 0.15	–9.64 ± 0.18	–9.49 ± 0.32	–6.42 ± 0.25	–7.52 ± 0.13	–6.26 ± 0.42	–8.88 ± 0.22	–8.34 ± 0.26	–	–10.15 ± 0.40
	b	2.44 ± 0.03	2.33 ± 0.03	2.54 ± 0.04	2.52 ± 0.07	1.87 ± 0.05	2.08 ± 0.03	1.82 ± 0.09	2.32 ± 0.05	3.21 ± 0.05	–	2.61 ± 0.08
	r	0.94	0.96	0.97	0.96	0.98	0.97	0.95	0.97	0.98	–	0.96
	P	***	***	***	***	***	***	***	***	***	***	***
	n	307	512	350	115	59	311	47	155	72	–	18
27	*a*	–9.44 ± 0.14	–9.42 ± 0.12	–9.69 ± 0.17	–9.56 ± 0.10	–8.48 ± 0.11	–7.34 ± 0.20	–8.02 ± 0.18	–9.81 ± 0.10	–8.59 ± 0.08	–9.12 ± 0.22	–7.85 ± 0.28
	b	2.50 ± 0.03	2.48 ± 0.02	2.56 ± 0.03	–2.53 ± 0.02	2.30 ± 0.02	2.06 ± 0.04	2.18 ± 0.04	2.52 ± 0.02	2.26 ± 0.02	2.39 ± 0.04	2.13 ± 0.05
	r	0.98	0.98	0.97	0.99	0.97	0.97	0.96	0.98	0.97	0.96	0.96
	P	***	***	***	***	***	***	***	***	***	***	***
	n	312	402	368	454	543	164	287	538	869	288	190
28	*a*	–10.65 ± 0.27	–9.48 ± 0.10	–9.17 ± 0.11	–8.92 ± 0.18	–7.85 ± 0.22	–7.35 ± 0.19	–7.35 ± 0.18	–8.91 ± 0.28	–8.38 ± 0.10	–7.80 ± 0.44	–9.29 ± 0.49
	b	2.75 ± 0.06	2.49 ± 0.02	2.45 ± 0.02	2.40 ± 0.04	2.16 ± 0.04	2.06 ± 0.04	2.12 ± 0.04	2.33 ± 0.06	2.22 ± 0.02	2.11 ± 0.09	2.44 ± 0.09
	r	0.96	0.98	0.98	0.98	0.95	0.99	0.99	0.96	0.98	–	–
	P	***	***	***	***	***	***	***	***	***	***	***
	n	219	565	433	178	250	72	58	119	508	85	59
29S	*a*	–9.84 ± 0.19	–8.45 ± 0.11	–9.85 ± 0.23	–10.21 ± 0.54	–7.86 ± 0.13	–8.14 ± 0.17	–8.24 ± 0.16	–9.29 ± 0.11	–8.27 ± 0.09	–6.67 ± 0.21	–7.70 ± 0.42
	b	2.58 ± 0.04	2.28 ± 0.02	2.58 ± 0.05	2.65 ± 0.11	2.17 ± 0.03	2.22 ± 0.03	2.22 ± 0.03	2.40 ± 0.02	2.19 ± 0.02	1.87 ± 0.04	2.09 ± 0.08
	r	0.93	0.99	0.99	0.94	0.98	0.98	0.97	0.98	0.98	0.95	0.96
	P	***	***	***	***	***	***	***	***	***	***	***
	n	299	258	65	81	269	141	272	446	534	222	74

*** $P < 0.01$.

(5/55 = 0.09) that we considered being comparable with a result that would occur by chance.

Changes of sprat condition (CF) at the common length (120 mm) showed a similar pattern in all the subdiv. analysed (Fig. 2). During the period 1986–1989, CF was constant or slightly increasing, except for 1987 when a decrease occurred in most of the subdiv. Afterwards, CF suffered an evident decrease reaching the minimum values in 1996 (subdiv. 28 and 29s) or in 1998 (subdiv. 25–27). This decrease was between 22 to 29% of sprat CF, for the different subdiv. During the latest period (1996–2000), an increase of CF occurred in all the subdiv. There were spatial differences in sprat CF between subdiv. with a slight decrease from the south-west (subdiv. 25) to the north-east (subdiv. 29s) part of the Baltic proper in most of the years observed (Fig. 2). However, those differences were not statistically significant (Gabriel's test, data not shown).

4.1.2. Non-linear regression analysis

Clupeids number in subdiv. 25 and 27 significantly affected sprat condition (Fig. 3). The fitted curves explained 52 and 71% of the observed variation of sprat condition, for subdiv. 25 and 27, respectively (Table 3). The estimated curves showed a value around 14.5 g at the hypothetical clupeid numbers of 0 (Fig. 3). We found also a significant effect of zooplankton biomass (μg m^{-3}) per individual fish, estimated for subdiv. 27, which explained around 67% of the variation in sprat condition (Table 3). The value of sprat condition, estimated at the zooplankton biomass per individual fish close to 0, was 7.3 g (Fig. 3).

Concerning abiotic factors, we did not find a significant effect (explained variance between 5 and 10%) of temperature averaged between 0 and 50 m on condition of Baltic sprat. However, salinity averaged between 0 and 50 m in subdiv. 27 explained around 42% of the variation in sprat CF (Table 3). The estimated curve for salinity showed a value of 8.2 g at the value of 6 psu that was assumed as the lowest possible values for this area of the Baltic Sea (Fig. 3). No effect of salinity on sprat CF was found in subdiv. 25 (explained variance around 15%). All the estimated values (intercepts) of the curves were close to the minimum and the maximum (8 and 14 g, respectively) sprat weight at 120 mm observed in the Baltic proper during the study period. Residuals were normally distributed and the standardised residuals (Q_1 statistic) had a mean close to 0 for all the models fitted (data not shown). Estimated parameters of fitted relationships were always different from 0 (t-test; $p < 0.05$). Concerning inter-correlated factors, temperature between 0 and 50 m was significantly positively correlated ($r = 0.68$) with clupeids number while inter-correlation between the remaining factors was not significant (data not shown). All time-series showed a stationary process characterised by short-term correlation (1-year lag), with r_1 always larger than successive coefficients, followed by r_k non-significantly different from 0. No significant difference was found when re-estimating the relationships between

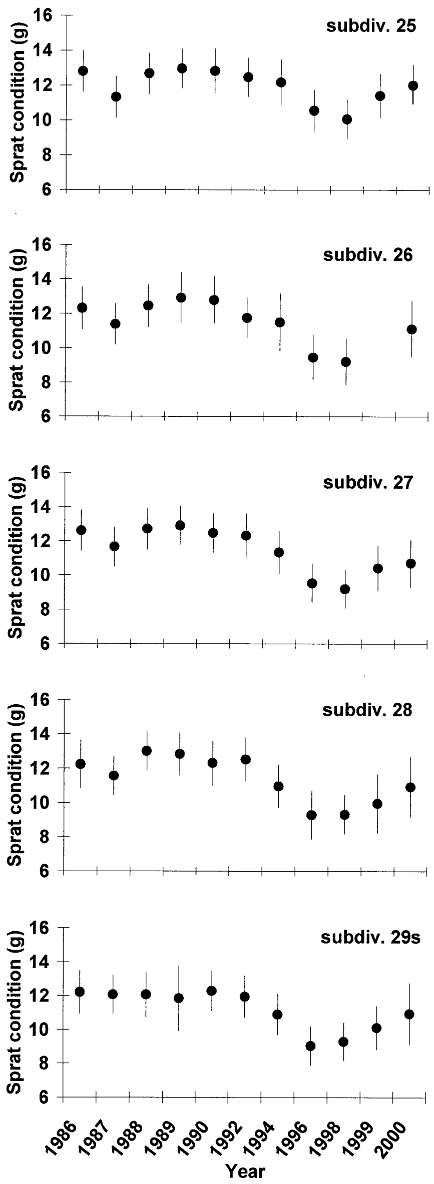

Fig. 2. Condition of the sprat at the common length (120 mm) by ICES subdivision between 1986 and 2000. Error bars show the 95% comparison intervals.

sprat condition and considered factors using smoothing time-series with a two-points running mean (data not shown).

Herring condition was positively significantly correlated with sprat condition for all the subdiv. analysed (*r* between 0.80 and 0.95 for the different subdiv.) (Fig. 4). Moreover, there was no substantial difference between correlation coefficients estimated using the raw dataset and transformed data. Thus, only the analysis using raw data is shown here.

5. Discussion

Our data showed that the condition factor (CF) of Baltic adult sprat decreased significantly during the period 1986–1996 in all the ICES subdiv. analysed (subdiv. 25–29s). However, between 1986 and 1990, sprat growth rates were constant or slightly increased compared with the 1990s while, from 1996 and onwards, an interruption of the negative trend and a noteworthy increase occurred. Weight-at-age (WAA) and condition of Baltic herring showed a similar pattern during the same period (Cardinale and Arrhenius, 2000a). Sprat and herring CF were significantly correlated in all the Baltic subdiv. analysed (this study). Sprat and herring dominate the pelagic zone in the Baltic Sea, both of them feeding on zooplankton. Therefore, we should discuss the observed decrease in sprat growth taking also in account studies on herring (see Cardinale and Arrhenius, 2000a for a recent review).

Data from this study showed a significant effect of the pelagic fish abundance (sprat and herring) on growth rates of sprat, this phenomenon strongly supporting the DDH. Moreover, the significant positive correlation between sprat and herring CF during the period analysed indicates that common factors affect sprat and herring growth rates in the Baltic Sea. For herring, several authors suggested that growth is food limited (e.g., Blaxter and Hunter, 1982; Arrhenius and Hansson, 1993, 1999) and condition (properly estimated) inversely related to stock abundance (DDH) (e.g., Winters and Wheeler, 1994; Tanasichuk, 1997; Cardinale and Arrhenius, 2000a).

Sprat and herring are both zooplanktivorous and may compete for the same available resources in the pelagic zone. Therefore, the increase in the number of pelagic fish that occurred during the period 1986–1996 could have caused a density-dependent reduction of individual food intake. Aps (1989) noticed that an extremely high increase in sprat abundance in the second half of the 1950s in the Northern Baltic coincided with a noticeable decrease of the asymptotic values of length and weight. In 1960–1980 the asymptotic length and weight of sprat considerably increased in correspondence with an extremely low abundance in the 1980s. The author assumed that sprat growth is closely related to its feeding condition, which, in turn, is influenced by both sprat stock abundance and the abundance dynamics of planktonic food (Aps, 1985). Horbowy and Swinder (1989) found a linear relationship between the reciprocal of length increment and stock density as well as between the reciprocal of length increment and the ratio of stock density to food biomass. Nevertheless, all these studies focusing on length as a measure of adult growth should be considered with caution (see Winters and Wheeler, 1994 for a useful discussion). Growth in length is a trait controlled by temperature-dependent chemical processes (Beverton, 1987) that measures only a marginal fraction of the annual production. On the contrary, condition factor (length-specific weight) (CF) is a compensatory trait, which reflects the seasonal accumulation and depletion of energy and therefore can provide a reliable index of total annual production (Winters and Wheeler, 1994). As shown by Winters and Wheeler (1994), Tanasichuk (1997) and

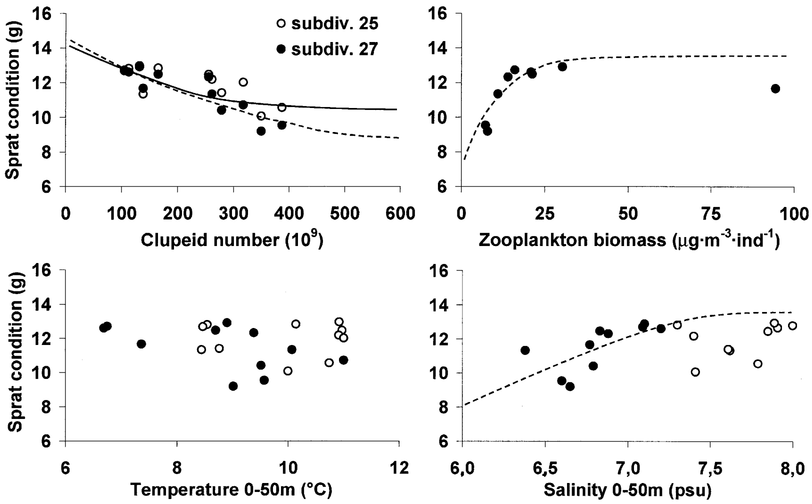

Fig. 3. Relationships between condition of sprat and the biotic and abiotic factors analysed between 1986 and 2000 for ICES subdivisions 25 and 27. Only significant relationships are shown.

Cardinale and Arrhenius (2000a), the length-weight relationship (CF) is the only reliable index of growth in pelagic fish.

In our study, we found a significant effect of zooplankton biomass per individual clupeid fish on sprat CF. At the same time, there is evidence of a decrease in abundance of copepods, especially *Pseudocalanus elongatus* and *Temora longicornis*, in different areas of the Baltic proper (Dippner et al., 2000; Möllmann et al., 2000). *Pseudocalanus elongatus* and *Temora longicornis* are the main food items of both sprat and herring in the central and southern Baltic Sea (Möllmann and Köster, 1999; Cardinale et al., in press). Thus, the decrease of such prey species could partly be a consequence of the increased zooplanktivory by the clupeid fish (i.e., top-down effect) (Szypula et al., 1997; Cardinale and Arrhenius, 2000a) and at the same time the cause of the contemporary reduction in sprat and herring condition (DDH).

On the other hand, the structure of the zooplankton community is also regulated by the environment through changes in the hydrography and stratification (Johansson, 1992; Viitasalo et al., 1995; Flinkman et al., 1998). This implies that abiotic factors may affect sprat growth rates directly via fish metabolisms or indirectly regulating the structure and abundance of zooplankton community (EH). We did not find any significant effect of temperature on sprat CF. On the other hand, the variation in salinity explained 42% of the variability of sprat CF in the northern part of our study area where salinity level are lower than in the southern Baltic. This could be explained by the fact that under a certain value, the effect of changes in salinity on sprat growth begins to be significant. In the central Baltic, salinity is the most important factor regulating zooplankton community structure (Dippner et al., 2000; Möllmann et al., 2000) and the decrease of *Pseudocalanus elongatus* has been attributed to a reduced salinity in the Baltic Sea. Thus, variations in salinity may mirror in changes of zooplanktivorous fish growth rates via altering the zooplankton community structure (Möllmann et al., 2000) by a bottom-up process (Flinkman et al., 1998; Möllmann et al., 2000). As stated above, *Pseudocalanus elongatus* is one of the main preys of sprat and herring. Moreover, as shown by Cardinale et al. (in press), the selection process depends not only on the profitability of the prey but also on the prey's relative abundance. Thus, a decrease of the preferred prey items, caused by a reduced salinity, could have had the effect to shift to some extent the feeding habits of sprat and herring to other less profitable prey items, thus affecting

Table 3

Results of the non-linear regression analysis. Only parameters for those factors explaining more than 25% of sprat condition factor (CF) variance were presented; *a* is the asymptote, *b* and *k* are the parameters of the sigmoidal curve. All parameters were significantly different from zero (*t*-test). For details on the fitted model see text

	Response	Factors	% Variance explained	*b*	*k*	*a*
Subdiv. 25						
	CF	Clupeid number	52	–0.43 ± 0.03	$1.2 \times 10^{-3} \pm 0.4 \times 10^{-3}$	8
		Temperature	–	–	–	–
		Salinity	–	–	–	–
Subdiv. 27						
	CF	Clupeid number	71	–0.45 ± 0.01	$1.9 \times 10^{-3} \pm 0.2 \times 10^{-3}$	8
		Zoo. Biomass × ind^{-1}	67	0.93 ± 0.38	0.12 ± 0.04	14
		Temperature	–	–	–	–
		Salinity	42	$10.1 \times 10^{-3} \pm 1.6 \times 10^{-3}$	1.58 ± 0.04	14

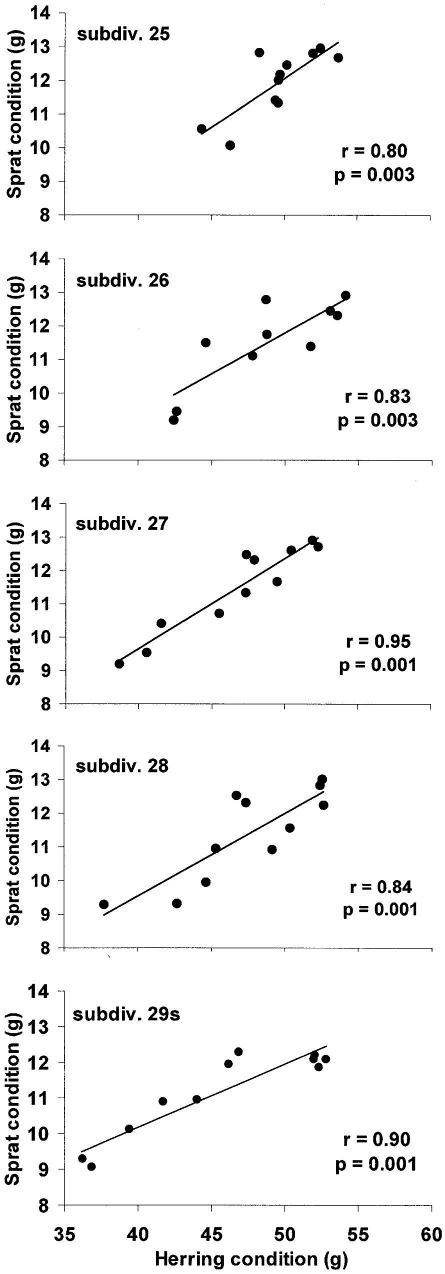

Fig. 4. Relationship between condition of sprat and condition of herring per each ICES subdivision between 1986 and 2000.

both sprat and herring condition. However, salinity not only influences the composition of the clupeid preys but also fish physiology. An increase in salinity should reduce the metabolic cost of iono- and osmoregulation due to the decreased difference between the internal iono-concentration of fish and that of the seawater (Jobling, 1994). This may contribute to explain the observed effect of salinity on growth performances of sprat (this study). Nevertheless, the two hypotheses (EH) are not mutually exclusive.

We would also stress the fact that the choice of a non-linear regression analysis was based on the assumption that CF of a fish at a certain length is constrained between the minimum and the maximum weight possible at that fish length. Considering this as a necessary and realistic assumption, we chose a non-linear model instead of a traditional linear one. Moreover, all the estimated intercepts of the fitted curves (Fig. 3) were close to the expected minimum and maximum values (8 and 14 g, respectively) for sprat CF at 120 mm in the Baltic proper, this further justifying our assumptions.

In the last decade, the Baltic cod population decreased by almost an order of magnitude due to an intensive fishery and reduced recruitment caused by unfavourable environmental conditions (Hansson and Rudstam, 1990; Larsson et al., 1985; Sparholt, 1996) and changes in stock structure (Cardinale and Arrhenius, 2000b). Consequently, the Baltic Sea fish community changed between 1980 and 1990 switching to a clupeid dominated system (Rudstam et al., 1994; Köster and Möllmann, 1997) with a plausible increase of the predation pressure on the zooplankton community. We have shown in this paper as growth rates of Baltic sprat and herring decreased simultaneously during the study period. It is, therefore, conceivable that the variability of pelagic fish growth rates in the Baltic Sea has two main highly interconnected causes. A density-dependent factor (herring and sprat competing for the same feeding resources) probably connected to a decline in the individual food intake caused by an increased fish biomass (density dependent hypothesis [DDH]). A modification of the environmental conditions (i.e., salinity levels) that regulates pelagic fish growth rates both indirectly via zooplankton community structure (Flinkman et al., 1998; Dippner et al., 2000; Möllmann et al., 2000) and/or directly via fish physiology and metabolisms (environmental hypothesis [EH]). Data from this study indicated that a combination of both causes might constitute the most plausible explanation.

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