

# Climate, zooplankton, and pelagic fish growth in the central Baltic Sea

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Oceanographic conditions in the brackish central Baltic Sea are strongly linked to atmospheric forcing and the unusual period of persistently strong westerlies that, since the late 1980s, have resulted in an increase in average water temperatures and decreasing salinity. These changes in temperature and salinity resulted in a change in the dominance of the mesozooplankton community from *Pseudocalanus* sp. to *Temora longicornis* and *Acartia* spp. Similar to the copepod community, the central Baltic fish community shifted from cod (*Gadus morhua*), dominant during the 1980s, to sprat (*Sprattus sprattus*), dominant during the 1990s. Further, the commercially important pelagic fish species herring (*Clupea harengus*) and sprat exhibited reductions in growth. Using Principal Component and Correlation Analyses we investigated the temporal variability in the importance of the food supply as well as competition on condition of central Baltic pelagic fish species. Our results indicate that herring condition results from a combined effect of changes in the food environment and increased competition with sprat, while sprat condition appeared to be primarily determined by intra-specific competition.

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## Introduction

Oceanographic conditions in the brackish Baltic Sea are strongly linked to atmospheric forcing. The unusual period of a persistently high North Atlantic Oscillation (NAO) index since the late 1980s, with a dominance of westerly weather, resulted in an increase in average spring water temperatures and decreasing salinities (Hänninen *et al.*, 2000; Fonselius and Valderrama, 2003). Changes in temperature and salinity have resulted in a dominance change in the mesozooplankton community (Möllmann *et al.*, 2000). While in the late 1970s/early 1980s *Pseudocalanus* sp.<sup>1</sup> dominated the copepod community,

the population size decreased afterwards in association with decreasing salinity (Möllmann *et al.*, 2003b). In parallel, the other two important copepod species, *T. longicornis* and *Acartia* spp., increased because of the higher temperatures (Möllmann *et al.*, 2003b).

Similar to the copepod community, a climate-induced dominance shift occurred in the central Baltic fish community. While the central Baltic cod (*Gadus morhua*) stock collapsed through overfishing and unfavourable environmental conditions, the stock of sprat (*Sprattus sprattus*) increased during the 1990s to approximately three times the stock size of the 1980s (Köster *et al.*, 2003). This increase was partly due to a release in predation pressure by the collapsed cod stock but, to a large degree, was also due to high recruitment success. The latter was coupled to the direct effect of warmer temperature on sprat egg survival, and also to the increased *Acartia* spp. population, the major food of sprat larvae (Köster *et al.*, 2003; Voss *et al.*, 2003).

<sup>1</sup> Recent studies indicate that *Pseudocalanus* in the central Baltic, hitherto named as *P. elongatus*, might be the sibling *P. acuspes* (Bucklin *et al.*, 2002). Until the final evaluation, we name the copepod *Pseudocalanus* sp.

The commercially important pelagic fish species in the central Baltic Sea, i.e. herring (*Clupea harengus*) and sprat, exhibited drastic fluctuations in growth (Parmanne *et al.*, 1994). The weight-at-age (WAA) of herring decreased to almost half of that observed in the 1980s, with dramatic effects on the biomass and catches of herring (e.g. Parmanne *et al.*, 1994; Cardinale and Arrhenius, 2000).

Historically, three different hypotheses have been tested to explain the decrease in WAA of Baltic herring, involving (i) selective predation of cod on herring (Sparholt and Jensen, 1992; Beyer and Lassen, 1994), (ii) mixing of sub-stocks with different growth rates (ICES, 1997), and (iii) a real decrease in growth rates caused by changes in the biotic environment. Recently, increased evidence supported the latter hypothesis. For example Rönkkönen *et al.* (2004) showed the growth rates of herring in the northern Baltic to be explicitly dependent on the abundance of the copepod *Pseudocalanus* sp. Also for the central Baltic Sea, the condition of herring is dependent on the population size of this calanoid copepod (Möllmann *et al.*, 2003a). Food availability, especially *Pseudocalanus* sp. population size, also has been hypothesized to be crucial for the growth of sprat (Cardinale *et al.*, 2002; Möllmann *et al.*, 2004a). Sprat age-specific weights declined in the central Baltic, but later than herring, i.e. during the early 1990s (Cardinale *et al.*, 2002).

Besides changes in the food environment, density-dependence may have affected clupeid fish growth in the central Baltic (Cardinale and Arrhenius, 2000; Cardinale *et al.*, 2002). For example, the increase of the sprat stock may have increased intra- and interspecific competition among the clupeid stocks.

As described above, we demonstrated in earlier publications (i) the link between hydrography and mesozooplankton (Möllmann *et al.*, 2000, 2002, 2003b), (ii) general herring and sprat feeding ecology (Möllmann *et al.*, 2004a), as well as (iii) the influence of *Pseudocalanus* sp. on herring growth (Möllmann *et al.*, 2003a). In this study, we conduct a comprehensive analysis of climate-induced ecosystem effects on growth of both herring and sprat in the central Baltic. First, we demonstrate the link between climate, hydrography, and the abundance of main mesozooplankton species using updated time-series. Second, using condition as an indicator of growth, we test for the effect of mesozooplankton abundance as well as sprat stock size on the growth of herring and sprat. Our results indicate a combined effect of changes in the feeding environment and increased competition on condition of herring, while sprat condition appears to be primarily determined by intra-specific competition.

## Material and methods

### Climate and hydrography

To investigate climate effects on hydrography we used the Baltic Sea Index (BSI), which is closely related to the NAO

index but directly reflects the impact of climate variability on local oceanographic processes in the central Baltic Sea. The BSI is defined as the difference of normalized sea level pressure anomalies between the positions 53°30'N, 14°30'E (Szcecin, Poland) and 59°30'N, 10°30'E (Oslo, Norway). Positive values of the index correspond to approximately westerly winds over the Baltic, whereas a negative index corresponds more to easterly winds (Lehmann *et al.*, 2002). Here, we used the averages of the BSI for December, January, and February.

Temperature and salinity data for 1977–2003 were obtained from a database at the Latvian Fisheries Research Agency (LATFRA) in Riga. Measurements were performed on regular surveys covering eight stations in the Gdańsk Deep and the central Gotland Basin, using a water sampler (Nansen type; 1 l bottle capacity) in 5 or 10 m steps. Salinity was measured either by the Knudsen Method (until 1992) or with an Inductivity Salinometer (since 1993).

Only spring salinity and temperature data were used in the analysis since earlier studies demonstrated that hydrographic conditions in this season determine the annual development of mesozooplankton populations (Möllmann *et al.*, 2000, 2003b). We used salinity at 80 m, which is typically situated in the permanent halocline, and is the preferred location of fully marine species in the area, e.g. *Pseudocalanus* sp. adults (Möllmann and Köster, 2002; Schmidt *et al.*, 2003). Temperature at 30 m was used since it characterizes the environment of surface-orientated mesozooplankton species, e.g. *T. longicornis*, *Acartia* spp., and cladocerans (Möllmann and Köster, 2002).

### Mesozooplankton

Mesozooplankton abundance data for all seasons during 1977–2003 were obtained from a database at the LATFRA (in total 585 stations). Sampling was conducted in the Gdańsk Deep and the Gotland Basin of the central Baltic Sea (Figure 1), mainly in February (winter), May (spring), August (summer), and November (autumn) using a Juday Net (UNESCO Press, 1968). The gear, having a mesh size of 160 µm and an opening diameter of 0.36 m, is operated vertically and considered quantitatively to catch all copepodite stages as well as adult copepods, whereas nauplii may be underestimated (Anon., 1979). Individual hauls were carried out in vertical steps, resulting in a full coverage of the water column to a depth of 100 m on every station. Here, we used a subset of data from stations in the Gdańsk Deep and the central Gotland Basin provided in Möllmann *et al.* (2003b). For information on sample processing, see Möllmann *et al.* (2000).

### Fish diet and condition

Herring and sprat were sampled by pelagic trawling in different months during 1977–2003 by LATFRA (in total 18 321 herring and 19 345 sprat; for details see Möllmann

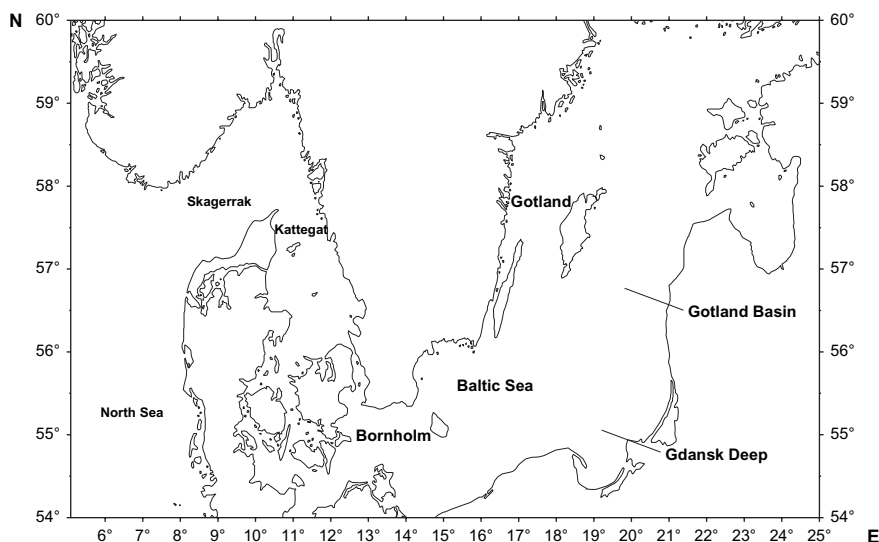


Figure 1. Map of the central Baltic Sea with the area of investigation, i.e. the Gdansk Deep and the Gotland Basin, shown.

*et al.*, 2004a). Sampling was performed during daytime, which corresponds to the diurnal feeding time of clupeids in the area (Köster and Schnack, 1994). A fixed number of stomachs was taken randomly from each sampled station, so no weighting according to the length frequency distribution of the herring stock was necessary. Total length and weight of individual fish were recorded and stomachs extracted.

From the very detailed stomach content data, we collected details of the quantities of the dominant copepods *Pseudocalanus* sp., *T. longicornis*, and *Acartia* spp. (including *A. bifilosa*, *A. longiremis*, and *A. tonsa*), as well as cladocerans (including *Bosmina coregoni maritima*, *Evadne nordmanni*, *Podon polyphemoides*, *Podon leuckarti*, and *Podon intermedius*). As fish condition is regarded as the best descriptor of growth (Winters and Wheeler, 1994), we adopted the approach of using a (double logarithmic) length–weight regression as an index of condition (Winters and Wheeler, 1994; Tanasichuk, 1997; Cardinale and Arrhenius, 2000). Regressions were performed on a seasonal basis, and condition was calculated as the weight at the overall mean length for the data sets, i.e. 18 cm for herring and 12 cm for sprat. Poorly represented fish sizes < 10 cm and > 25 cm for herring and < 6 cm and > 15 cm for sprat were excluded from the analysis.

#### Fish stock sizes

Stock sizes of herring and sprat (ages 1+) were derived from Extended Survivor Analyses (XSA) performed during the regular assessment of the ICES Baltic Fisheries Assessment Working Group. Herring in the central Baltic Sea are assessed for ICES Subdivisions 25–32, while sprat stock sizes are calculated for the whole Baltic Sea

(Subdivisions 22–32). More detailed information on the assessment can be found in ICES (2004).

#### Numerical analyses

All time-series, except the BSI, were log-transformed to stabilize the variance. Missing values in the original time-series were interpolated using a linear trend regression (StatSoft, 1996). Anomaly time-series of seasonal abundances were calculated by subtracting the average of the time-series from the original values.

A Principal Component Analysis (PCA) was conducted to extract the main time-trends from the seasonal abundance time-series of the main mesozooplankton species. Simple correlation analyses were performed for investigating relationships between different variables. To account for autocorrelation in the data, the degrees of freedom (d.f.) in the statistical tests were adjusted using an equation by Chelton (1984), modified by Pyper and Peterman (1998). t-Tests were used to test for differences in variables between different time-periods (i.e. 1977–1988 vs. 1989–2003).

## Results

### Climate, hydrography, and mesozooplankton

The climate over the central Baltic Sea, as described by the winter BSI, showed two significantly distinct periods during the study period (Figure 2). Until 1988, mainly low and negative air pressure gradients were found. Afterwards mainly high positive BSI values were observed, with the exception of 1996. The means of the two periods were statistically different (t-test 1977–1988 vs. 1989–2003:  $p < 0.05$ ).

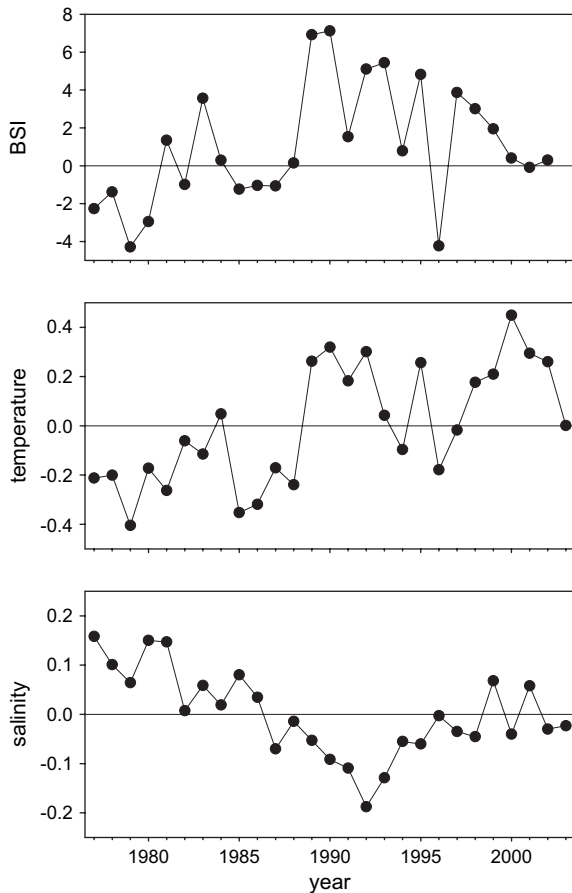


Figure 2. Time-series of the Baltic Sea Index (BSI), as well as anomalies of spring temperature ( $^{\circ}\text{C}$ ) at 30-m depth and spring salinity at 80-m depth.

A similar time-trend with two different periods as observed for the BSI is visible for the spring water temperature anomalies at 30-m depth (Figure 2; t-test 1977–1988 vs. 1989–2003:  $p < 0.01$ ). Consequently, both variables were closely correlated ( $r = 0.65$ ,  $p < 0.01$ ). For spring salinity anomalies at 80 m, a continuous downward trend was recorded until the early 1990s, slightly increasing thereafter. Salinity and the BSI were also significantly, but negatively, correlated ( $r = -0.60$ ,  $p < 0.01$ ).

The population size of *Pseudocalanus* sp. decreased continuously until the early 1990s, and increased again in recent years (Figure 3). In contrast, *T. longicornis* and *Acartia* spp., having low abundances during the 1980s, increased stepwise in stock size during the 1990s, especially in spring (t-test 1977–1988 vs. 1989–2003:  $p < 0.01$ ). Generally, time-trends were similar in all seasons, but with higher amplitude changes in the first half year. Cladocerans showed a similar stepwise increase in abundance as observed for *T. longicornis* and *Acartia* spp. in spring (t-test 1977–1988 vs. 1989–2003:  $p < 0.05$ ), while in summer variability was decadal.

Using a PCA, we extracted principal components (PC1 and PC2), reflecting the main time-trends in the most important mesozooplankton species in the central Baltic Sea (Figure 4). PC1 (explaining 35% of the overall variance) shows a continuous upward trend throughout the investigation period, while PC2 (explaining 16% of the overall variance) declines until 1990, increasing afterwards.

Factor loadings demonstrate the negative association of *Pseudocalanus* sp. abundance with the PC1, showing the highest negative loadings in winter (Table 1). PC2 was positively related to *Pseudocalanus* sp. abundance, with highest loadings in the second half of the year. Loadings of *T. longicornis* and *Acartia* spp. with the PC1 were very high in all seasons, with the exception of *T. longicornis* in autumn. Low factor loadings were encountered for both calanoids and PC2. For cladocerans, loadings were positive with PC1 and negative with PC2, however only relatively high with PC1 in spring.

In summary, PC1 reflects the temperature-driven increase in abundance of *T. longicornis* and *Acartia* spp. as well as cladocerans, and the salinity-driven decrease of *Pseudocalanus* sp. The first trend is demonstrated by the significant positive relationships with the water temperature ( $r = 0.76$ ,  $p < 0.01$ ), the second trend by the negative relationship with salinity ( $r = -0.55$ ,  $p < 0.01$ ). PC2 reflects more directly the trend in *Pseudocalanus* sp. abundance, which is positively related to salinity ( $r = 0.47$ ,  $p < 0.05$ ).

### Fish diet, condition, and mesozooplankton

The observed trends in dominant mesozooplankton are clearly reflected in the diet of herring (Figure 5a). The amount of *Pseudocalanus* sp. in the diet declined continuously throughout the study period, increasing slightly in spring during recent years. The increase in *Acartia* spp., and especially *T. longicornis* abundance, is clear in the summer diet composition. An additional food source for herring, mainly in winter and autumn, was mysids. While the amount of mysids in the herring stomachs was relatively constant from winter to summer, the trend was clearly negative in autumn (Figure 5a).

Similar to herring, the amount of *Pseudocalanus* sp. in the winter and spring diet of sprat decreased in parallel with the copepod abundance (Figure 5b). In contrast to herring, the increase of *T. longicornis* and *Acartia* spp., as well as cladoceran abundance since the 1990s, is not reflected in the sprat diet composition. Rather, negative anomalies in stomach contents of these food items were observed during that period.

Herring condition declined continuously until the early 1990s and increased slightly since the late 1990s (Figure 6). Sprat condition was high during the 1980s and significantly lower during the 1990s (t-test 1977–1988 vs. 1989–2003:  $p < 0.01$ ). Time-trends were similar in all seasons.

Correlation analyses among the PCs of mesozooplankton time-series and herring as well as sprat condition were

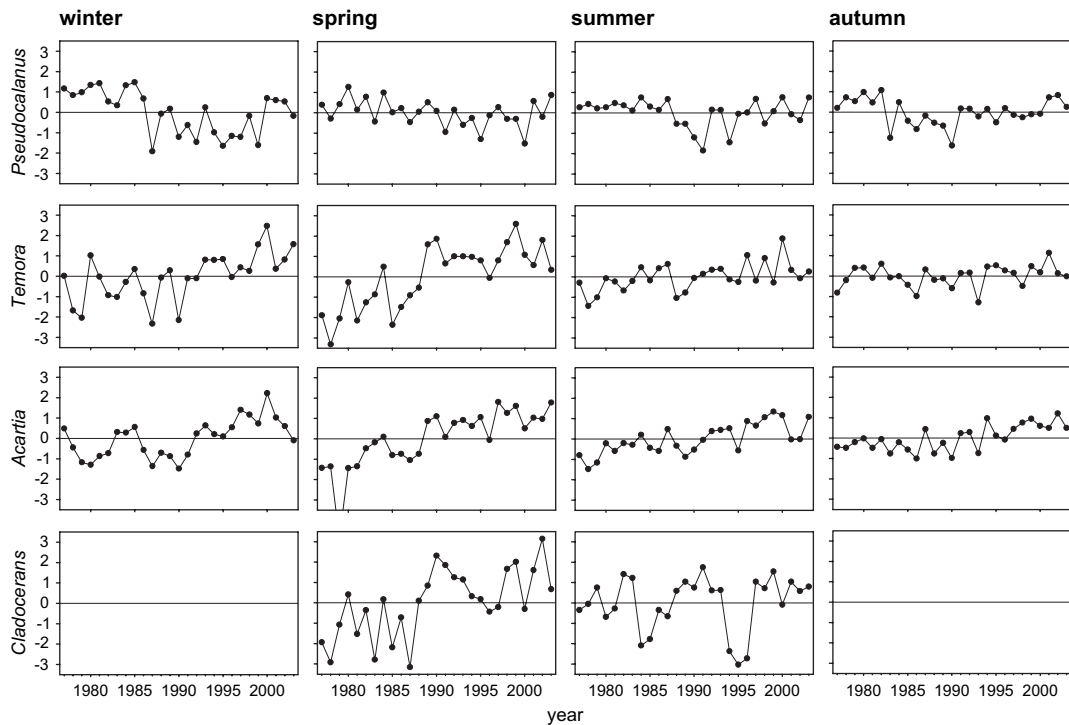


Figure 3. Anomaly time-series of seasonal abundance (numbers  $m^{-2}$ ) of *Pseudocalanus* sp., *Temora longicornis*, *Acartia* spp., and cladocerans.

performed to identify the effect of the zooplankton community on pelagic fish growth. The seasonal and annual conditions of both herring and sprat were negatively correlated to PC1. Correlations with herring condition were not statistically significant for summer and autumn, however (Table 2). While herring condition was mainly positively related to PC2, sprat condition correlated negatively to PC2. However, no significant relationship could be found.

#### Fish stock size and condition

The stock size of herring declined continuously during the study period (Figure 7). The sprat stock size was low until

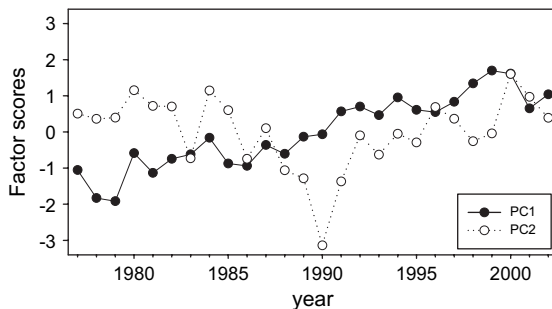


Figure 4. Time-trends of mesozooplankton abundance summarized by PCA: factor scores of PC1 and PC2.

the end of the 1980s, with an intermediate peak in 1983. During the 1990s, the sprat population increased drastically, peaking in 1996 and remained high (t-test 1977–1988 vs. 1989–2003:  $p < 0.01$ ).

Correlation analyses yielded significant relationships of herring winter and spring conditions as well as sprat winter and annual conditions with sprat stock size (Table 3).

Table 1. Factor loadings of mesozooplankton seasonal abundance and principal components 1 and 2 (PC1 and PC2).

Biomass	PC1	PC2
<i>Pseudocalanus</i> sp. (winter)	-0.54	0.42
<i>Pseudocalanus</i> sp. (spring)	-0.44	0.18
<i>Pseudocalanus</i> sp. (summer)	-0.26	0.68
<i>Pseudocalanus</i> sp. (autumn)	-0.09	0.74
<i>Temora longicornis</i> (winter)	0.67	0.37
<i>Temora longicornis</i> (spring)	0.88	-0.30
<i>Temora longicornis</i> (summer)	0.60	0.24
<i>Temora longicornis</i> (autumn)	0.24	0.41
<i>Acartia</i> spp. (winter)	0.64	0.43
<i>Acartia</i> spp. (spring)	0.82	-0.24
<i>Acartia</i> spp. (summer)	0.84	0.21
<i>Acartia</i> spp. (autumn)	0.71	0.38
Cladocerans (spring)	0.67	-0.30
Cladocerans (summer)	0.05	-0.32

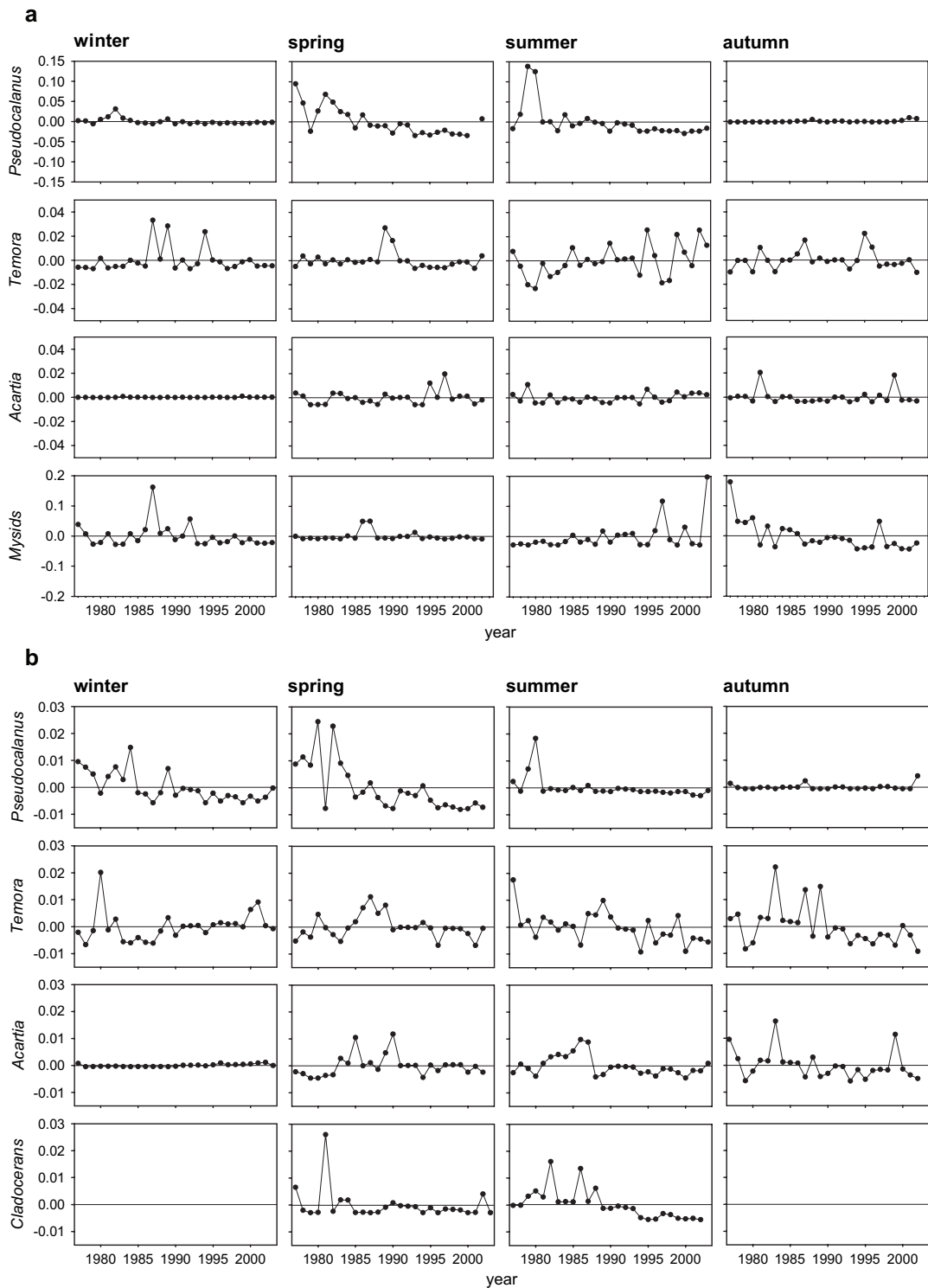


Figure 5. (a) Anomaly time-series of the seasonal mean herring stomach content (g wet weight) of *Pseudocalanus* sp., *Temora longicornis*, *Acartia* spp., and mysids. (b) Anomaly time-series of the seasonal mean sprat stomach content (g wet weight) of *Pseudocalanus* sp., *Temora longicornis*, *Acartia* spp., and cladocerans.



## Discussion

### Climate, hydrography, and mesozooplankton

The physical conditions in the Baltic Sea respond to climate change through (i) direct air–sea interaction, (ii) the magnitude of freshwater run-off, and (iii) interactions with the ocean at the open boundary (Stigebrandt and Gustafsson, 2003). Surface temperatures are determined by the dominance of either westerly winds with mild Atlantic air (high BSI), or easterly winds with cold continental air (low BSI). Increased river run-off, a result of increased zonal atmospheric circulation, affects salinity in the Baltic by directly freshening surface waters, and by preventing inflows of saline and oxygenated water from the Kattegat and North Sea, and the renewal of the bottom water in the deep Baltic basins (Matthäus and Schinke, 1999).

The period of high BSI values since the late 1980s resulted in a stepwise increase in average water temperatures. This change in the thermal state of the ecosystem has recently been identified as a “regime shift” and occurred in parallel with an event in the North Sea (Alheit et al., 2005). The dominance of westerly weather further increased the amount of run-off with the consequence of considerably decreasing salinities (Hänninen et al., 2000; Fonselius and Valderrama, 2003).

Our analyses confirmed time-trends of the main calanoid copepod species in the central Baltic Sea, e.g. decreasing *Pseudocalanus* sp. abundance with a slight increase in recent years, and increased *T. longicornis*, *Acartia* spp., and cladoceran populations (Möllmann et al., 2002, 2003b). A first PC, extracted using a PCA on mesozooplankton time-series, reflected the increase in *T. longicornis* and *Acartia* spp. in parallel to temperature, while reductions of *Pseudocalanus* sp. and salinity resulted in a negative relationship with PC1 and a positive one with PC2.

Recent investigations on the processes driving population dynamics of Baltic copepods indicate that the process behind the spring salinity–*Pseudocalanus* sp. relationship is probably a heavy mortality of eggs and nauplii during stagnation periods, i.e. periods without inflows characterized by low salinity and oxygen. Females (C6-f) of this calanoid reproduce during spring in the permanent halocline of the central Baltic basins, where they encounter maximum salinities, but during periods of low inflow to the Baltic Sea, very low oxygen levels develop, frequently down to  $0.7 \text{ ml l}^{-1}$  (Schmidt et al., 2003). Comparing inflow and non-inflow situations yielded a higher abundance of N per observed C6-f after an inflow of saline and oxygenated North Sea waters, indicating higher survival of eggs and nauplii (GLOBEC-GERMANY, unpublished data). In the last two decades only two major Baltic inflows have been observed (1993 and 2003), and this stagnation period resulted in decreasing salinity and low oxygen conditions, detrimental to *Pseudocalanus* sp. in the deep Baltic basins.

A recent study on processes driving *Acartia* spp. population dynamics in the Baltic showed that spring

recruitment of this copepod depends heavily on hatching of nauplii from resting eggs in the sediment, which is steered mainly by temperature (Dutz et al., 2004). This might be the process behind the positive relationship among spring temperature and *Acartia* spp. Further, the same process might also be true for *T. longicornis* and cladocerans, which produce resting eggs (Viitasalo and Katajisto, 1994; Katajisto et al., 1998).

Another climate-related process negatively affecting *Pseudocalanus* sp. dynamics is probably high predation pressure by the currently large sprat stock (Möllmann and Köster, 2002). Sprat stock size burgeoned through good recruitment, most probably related to higher temperatures and increased *Acartia* spp. abundance (Köster et al., 2003). During spring, adult sprat prey upon the reproducing *Pseudocalanus* sp. in the permanent halocline of the deep Baltic basins, removing a large proportion of the copepod production (Möllmann et al., 2004b). An important predation impact was also found for *T. longicornis*, but, not as strong as for *Pseudocalanus* sp., while predation pressure seems not to influence *Acartia* spp. dynamics (Möllmann and Köster, 2002; Möllmann et al., 2004b).

### Mesozooplankton, sprat stock size, and fish condition

We found trends in the dynamics of mesozooplankton species clearly reflected in the diet of herring, with the amount of *Pseudocalanus* sp. decreasing in spring and *Acartia* spp., as well as *T. longicornis* increasing in summer. The decrease in *Pseudocalanus* sp. in the diet has been described previously and hypothesized to be responsible for the decrease in herring growth (Möllmann et al., 2004a).

Supporting this, we found the mean annual condition of herring, as well as their winter and spring conditions, like *Pseudocalanus* sp. abundance, significantly negatively related to PC1. The significant correlations in winter and spring support the importance of *Pseudocalanus* sp. for the growth of herring, described previously (Möllmann et al., 2003a; Rönkkönen et al., 2004). In the first half of the year, *Pseudocalanus* sp. reproduces in the permanent halocline of the deep Baltic basins (Möllmann et al., 2003b). At that time of the year, late copepodite stages and adults of this copepod form the main food source of herring (Möllmann et al., 2004a). Further, as is common for spring-spawning herring, their condition is lowest in spring after spawning (McGurk et al., 1980), and the food supply encountered is important in refuelling the energy requirements of the fish (Möllmann et al., 2003a).

Another important food source for herring, especially in winter and spring, was mysids (Möllmann et al., 2004a). The availability of mysids is considered to be a determining factor for herring growth (Horbowy, 1997; Szypula et al., 1997). Unfortunately, no time-series of mysid abundance was available, which could be related to herring condition.

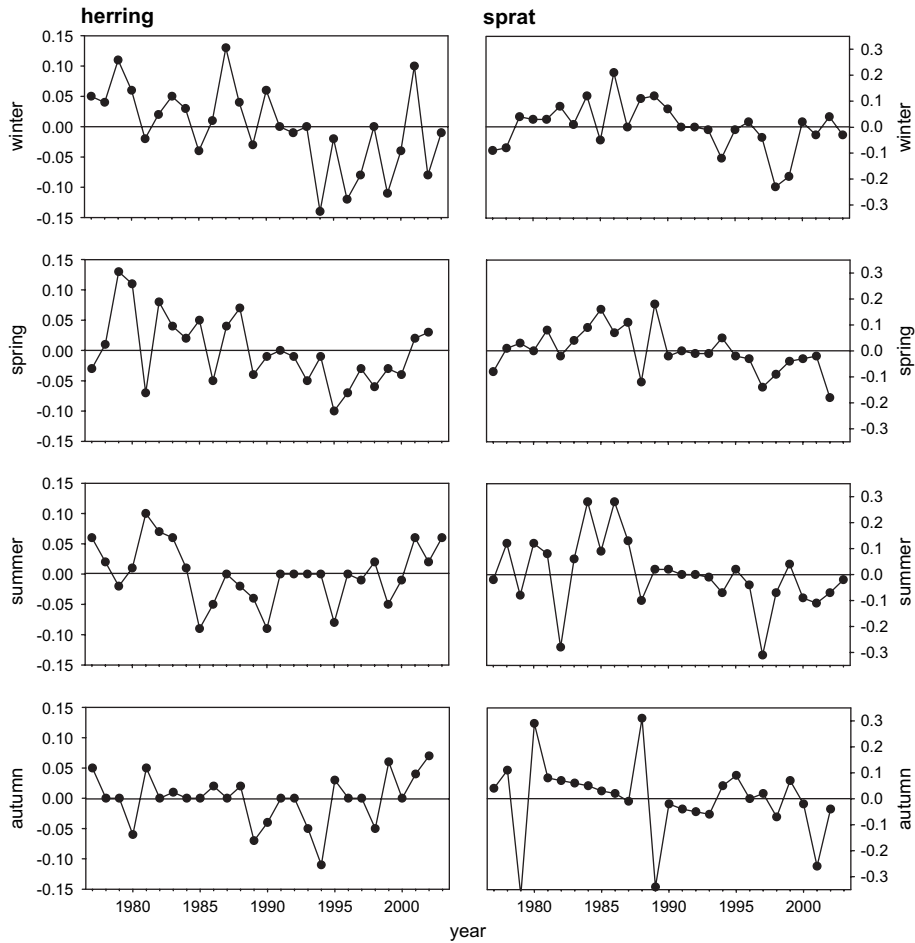


Figure 6. Anomaly time-series of the seasonal condition (g at the grand mean length) of herring and sprat.

Table 2. Correlation tests between the seasonal and annual conditions of herring and sprat, and principal components 1 and 2 (PC1 and PC2) of the mesozooplankton abundance time-series.  $N^{\text{eff}}$  = “effective” number of degrees of freedom,  $r$  = Pearson correlation coefficient,  $p$  = associated probability ( $\alpha$ ).

Condition	PC1			PC2		
	$r$	$p$	$N^{\text{eff}}$	$r$	$p$	$N^{\text{eff}}$
Herring (winter)	-0.58*	0.002	12	-0.09	0.675	17
Herring (spring)	-0.49*	0.017	14	0.18	0.381	17
Herring (summer)	-0.16	0.448	13	0.45	0.022	17
Herring (autumn)	-0.07	0.724	18	0.25	0.224	22
Herring (annual)	-0.57*	0.002	10	0.25	0.210	13
Sprat (winter)	-0.40	0.045	12	-0.16	0.423	17
Sprat (spring)	-0.39	0.047	12	-0.02	0.910	18
Sprat (summer)	-0.32	0.113	14	-0.08	0.701	19
Sprat (autumn)	-0.07	0.746	15	0.09	0.656	19
Sprat (annual)	-0.47	0.015	8	-0.06	0.757	13

\*Significant at 0.05.



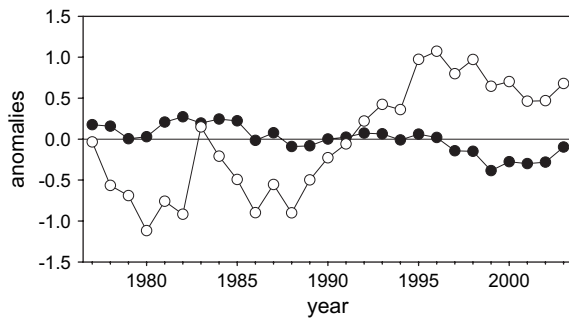


Figure 7. Anomaly time-series of herring (black dots) and sprat (white dots) stock size (numbers).

However, additional correlation analyses relating the quantity of mysids in the diet of herring to condition did not exhibit a significant relationship, suggesting that mysids had no influence on herring growth.

In contrast to herring, we found the trends in mesozooplankton abundance not fully reflected in sprat diets. While the decrease in *Pseudocalanus* sp. abundance is visible in the spring diet, the increase of *T. longicornis* and *Acartia* spp. as well as cladocerans during the 1990s was not observed. Consequently, we found no significant relationship among sprat condition with PC1, although relatively strong with winter and spring, as well as annual conditions. This indicates that although *Pseudocalanus* sp. is the main food source also for sprat at the beginning of the year, it is not as important as for herring over the whole season (Möllmann et al., 2004a). In summer after spawning, sprat move into shallower water (Köster and Schnack, 1994), where they feed mainly on *T. longicornis* (Möllmann et al., 2004a). The increase in abundance of

*T. longicornis*, therefore probably compensated for the decreased availability of *Pseudocalanus* sp.

Density-dependence was hypothesized to regulate growth of Baltic clupeids (Cardinale and Arrhenius, 2000; Cardinale et al., 2002). We found the strongest correlations among annual and winter and spring sprat stock sizes with herring and sprat conditions, indicating the importance of competition with the sprat stock for the growth of both fish species. The competition may, however, work mainly through the availability of mesozooplankton species (Cardinale et al., 2002). In winter, and especially in spring, when the diet overlap between both species is most pronounced, both species compete for *Pseudocalanus* sp. (Möllmann et al., 2004a). This may have resulted in reduced herring growth when *Pseudocalanus* sp. abundance decreased during the 1980s. During the early 1990s when competition was highest due to the small *Pseudocalanus* sp. stock and the large sprat stock, sprat growth also decreased. The importance of density-dependence for sprat condition is displayed by the relatively low stomach contents on the main food sources during the 1990s, although zooplankton availability increased, i.e. of *T. longicornis*, *Acartia* spp., and cladocerans. This occurred in parallel with the drastic increase in sprat stock size during the 1990s, suggesting strong density-dependent growth. This is supported also by the negative correlation of sprat condition and stock size.

The hypothesis of density-dependence is usually assumed to be accompanied by a depletion of the food resource over the whole area. Our analysis of mesozooplankton time-series showed that this might be true for *Pseudocalanus* sp., but not for *T. longicornis*, *Acartia* spp., and cladocerans. It is thus likely that patterns on smaller scales, such as the relative sizes of fish schools and patches of copepods, may determine the food availability, and eventually growth and condition of the fish.

Earlier studies also identified a direct relationship among salinity, and herring and sprat growth (Cardinale and Arrhenius, 2000; Cardinale et al., 2002; Rönkkönen et al., 2004). This relationship, most probably reflecting the change in mesozooplankton community structure, could not be shown by correlation analyses with our data. However, our analyses confirmed the lack of a relationship among temperature and growth/condition of Baltic clupeid fish (e.g. Cardinale et al., 2002).

#### Schematic description of relationships among climate, copepods, and pelagic fish growth

Our study demonstrates a tight coupling among climate effects on hydrography and further on mesozooplankton abundance, affecting growth of Baltic pelagic fish species (Figure 8). Two different climate-induced developments can be identified: (i) a stepwise increase in water temperature at the end of the 1980s, and (ii) a continuously decreasing salinity since the late 1970s. The increase in temperature had an abrupt and positive effect on the development of the

Table 3. Correlation tests between the seasonal and annual conditions of herring and sprat, and sprat stock size.  $N^{\text{eff}}$  = "effective" number of degrees of freedom,  $r$  = Pearson correlation coefficient,  $p$  = associated probability ( $\alpha$ ).

Condition	Sprat stock size		$N^{\text{eff}}$
	$r$	$p$	
Herring (winter)	-0.53*	0.006	12
Herring (spring)	-0.60*	0.001	12
Herring (summer)	-0.07	0.731	13
Herring (autumn)	0.07	0.721	18
Herring (annual)	-0.52	0.007	9
Sprat (winter)	-0.54*	0.004	12
Sprat (spring)	-0.45	0.021	12
Sprat (summer)	-0.35	0.083	14
Sprat (autumn)	-0.19	0.357	15
Sprat (annual)	-0.63*	0.001	8

\*Significant at 0.05 level.

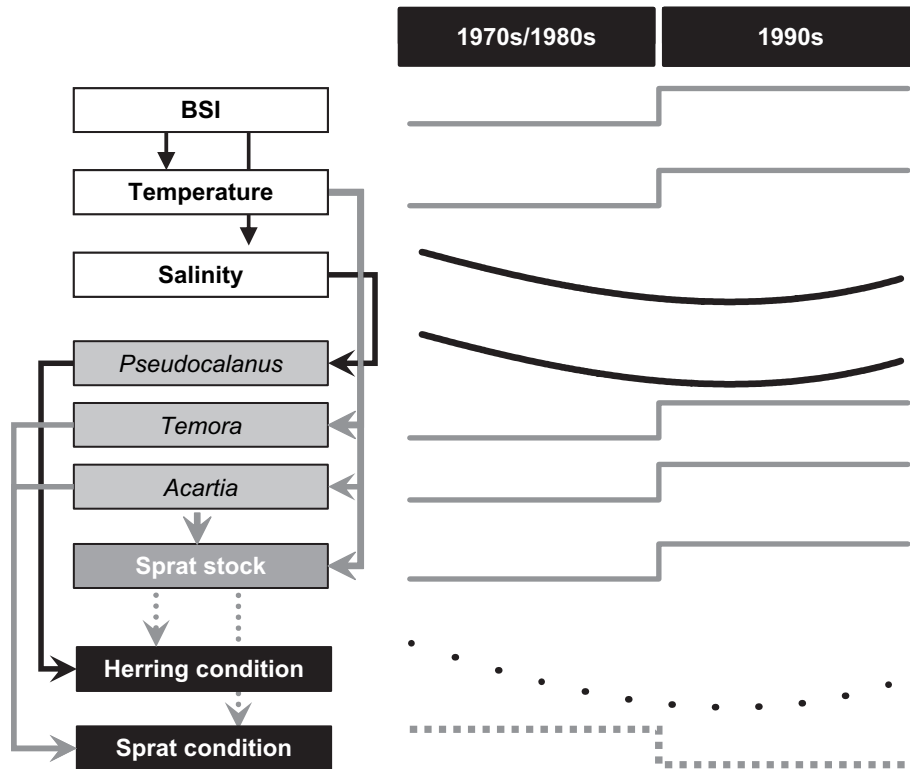


Figure 8. Schematic description of relationships among climate, copepods, and pelagic fish growth: left – relationships among variables; right – resulting idealized time-trends; grey lines and arrows represent temperature-driven processes, black lines and arrows represent salinity-driven processes.

copepods *T. longicornis* and *Acartia* spp. during the 1990s. Further, sprat recruitment benefited from higher temperatures leading to a large sprat stock in the 1990s (Köster *et al.*, 2003). As a result of decreasing salinity, however, population size of the copepod *Pseudocalanus* sp. declined continuously.

We found reduced herring condition to be mainly caused by the decline of *Pseudocalanus* sp., an effect amplified during the 1990s by strong competition with the large sprat stock. Although also relying on *Pseudocalanus* sp., sprat could obviously compensate for the decline of this copepod during the 1980s by feeding on the increasing populations of *T. longicornis* and *Acartia* spp. However, during the 1990s, strong intra-specific competition resulted in a decrease in sprat growth.

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