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Herring and sprat growth changes in the Central Baltic Sea

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Abstract

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

Keywords: Climate, competition, condition, Herring, mesozooplankton, salinity, Sprat, temperature.

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Introduction

Oceanographic conditions in the brackish Baltic Sea are strongly linked to the atmospheric forcing. The unusual period of persistently high NAO-index values since the late 1980s with a dominance of westerly weather, resulted in an increase in average spring water temperatures and decreasing salinities (Dippner et al., 2000; Hänninen et al., 2000; Fonselius and Valderrama, 2003). Changes in temperature and salinity have resulted in a dominance change in the mesozooplankton community

(Dippner et al., 2000; Möllmann et al., 2000). While in the late 1970s/early 1980s *Pseudocalanus* sp.¹ dominated the copepod community, afterwards the population size decreased coupled to decreasing salinities (Möllmann et al., 2003a). In parallel, the other two important copepod species, *T. longicornis* and *Acartia* spp., increased due to the on average warmer water temperature (Möllmann et al., 2003a).

Similar to the copepod community, a climate-induced dominance shift occurred also in the Central Baltic fish community. While the Central Baltic cod (*Gadus morhua*) stock collapsed due to overfishing and unfavourable environmental conditions, the stock of sprat (*Sprattus sprattus*) increased drastically during the 1990s (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 also due high recruitment success. The latter was coupled to the direct effect of warmer temperature on sprat egg survival, but also due to the increased *Acartia* spp. population, the major food of sprat larvae (Köster et al., 2003; Voss et al., 2003).

The commercially important pelagic fish species herring (*Clupea harengus*) and sprat exhibited in the Central Baltic Sea drastic fluctuations in growth (Parmanne et al., 1994). Especially the drastic decrease in the weight-at-age (WAA) of herring, observed since the 1980s and with dramatic effects on the biomass and catches of herring, has been extensively discussed (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, 1997a), and (iii) a real decrease in growth rates due to changes in the biotic environment. Recently, increased evidence supported the latter hypothesis, as e.g. Flinkman et al. (1998) showed changes in WAA in the Northern Baltic to be related to the mesozooplankton species composition. Rönkkönen et al. (2004) showed the growth rates in the same area to be explicitly dependent on the abundance of the copepod *Pseudocalanus* sp. Also for the Central Baltic Sea, a number of studies indicate the outstanding importance of *Pseudocalanus* sp. for nutrition of Baltic herring (Davidyuk et al., 1992; Naglis and Sidrevics, 1993; Davidyuka, 1996; Möllmann et al. submitted). Consequently Möllmann et al. (2003b) showed the condition of herring to be dependent on the population size of this calanoid copepod in Central Baltic deep basins. Food availability and especially *Pseudocalanus* sp. population size, has been hypothesized to be crucial for growth of sprat (Cardinale et al., 2002; Möllmann et al., submitted). Sprat age-specific weights declined also in the Central Baltic, but later as herring during the early 1990s (Cardinale et al., 2002).

Beside changes in the feeding environment, density-dependence may have affected clupeid fish growth in the Central Baltic (Cardinale and Arrhenius, 2000; Cardinale and Arrhenius, 2002). Especially the increase of the sprat stock may have increased intra- and interspecific competition among the clupeid stocks.

Here we first demonstrate the link between climate, hydrography and the abundance of main mesozooplankton species. Using condition as an indicator of growth, we afterwards test the effect of mesozooplankton as well as sprat stock size on growth of Central Baltic herring and sprat. Our results

¹ 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.

indicate a combined effect of changes in the feeding environment and increased competition on condition of herring, while sprat condition appeared to be primarily determined by intra-specific competition.

Materials and methods

Climate and hydrography. To investigate climate effects on hydrography we used the Baltic Sea Index (BSI) as an index which reflects directly the impact of climate variability on local oceanographic processes in the Central Baltic Sea (Lehmann et al., 2002; Möllmann et al., 2003b). The BSI is defined as the difference of normalized sea level pressure anomalies between the positions 53°N30', 14°E30' (Szcecin, Poland) and 59°N30', 10°E30' (Oslo, Norway) (Lehmann et al., 2002). Positive values of the index correspond to westerly winds over the Baltic, whereas a negative index corresponds 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 years 1977-2003 were derived from a database setup by the Latvian Fisheries Research Institute (LATFRI) in Riga. Measurements were performed on regular surveys covering 8 stations in the Gdansk Deep and the central Gotland Basin using a water sampler (Nansen type; 1l capacity) in 5 or 10m steps. Salinity was measured either by the Knudsen Method (until 1992) or with an Inductivity Salinometer (since 1993).

Mesozooplankton. Earlier studies have demonstrated the dependence of dominating mesozooplankton species on the prevailing hydrographic situation. While *Pseudocalanus* sp. was mainly related to salinity, *T. longicornis*, *Acartia* spp. and the taxonomic group of cladocerans was mainly depending on the ambient thermal conditions (Möllmann et al., 2000). Here we summarize these relationships in the light of climate change using updated datasets. We related *Pseudocalanus* sp. to the salinity in 80m depth, which resembles the situation in the permanent halocline, being the preferred habitat of *Pseudocalanus* sp. adults (Hansen et al., submitted; Schmidt et al., 2003). *T. longicornis*, *Acartia* spp. and cladocerans were related to the temperature in 30m, according to their average vertical distribution (Hansen et al., submitted).

Mesozooplankton abundance data for all seasons of years 1977-2003 were also derived from a database of LATFRI. Sampling was conducted in the Gdansk Deep and the Gotland Basin of the Central Baltic Sea (Fig. 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 160µm and an opening diameter of 0.36m, is operated vertically and considered to quantitatively catch all copepodite stages as well as adult copepods, whereas nauplii may be underestimated (Anonymous, 1979). Individual hauls were carried out in vertical steps, resulting in a full coverage of the water column to a depth of 100m on every station. Here we used a subset of data from stations in the Gdansk Deep and the central Gotland Basin provided in Möllmann et al. (2003a). For information on sample processing see Dippner et al. (2000) and Möllmann et al. (2000).

Fish diet and condition. Herring and sprat were sampled by pelagic trawling in different months during the period 1977 to 2003 by LATFRI. 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 randomly taken from each sampled station, thus 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 extracted the amounts of the dominant copepods *Pseudocalanus* sp., *T. longicornis* and *Acartia* spp. (including *A. biflosa*, *A. longiremis* and *A. tonsa*), as well as the taxonomic group of cladocerans (including *Bosmina coregoni maritima*, *Evadne nordmanni*, *Podon polyphemoides*, *Podon leuckarti* and *Podon intermedius*)

As condition of fish is regarded as the best descriptor of growth (Winters and Wheeler, 1994) we adopted the approach to use a (double logarithmic) length-weight regression as an index of condition (Cardinale and Arrhenius, 2000; Winters and Wheeler, 1994, Tanasichuk, 1997). Regressions were performed on a seasonal basis and condition was calculated as the weight at the grand mean length of the data set, i.e. 18cm for herring and 12cm for sprat. Poorly represented fish sizes < 10cm and > 25cm for herring and < 6cm and > 15cm 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 is assessed for ICES Subdivisions 25-32, while sprat stock sizes are calculated for the whole Baltic Sea (Subdivisions 22-32). Stock estimates of the Baltic International Acoustic Survey were used for tuning the XSA. More detailed information on the assessment can be found in ICES (2004).

Numerical analyses. Data were log-transformed to stabilize the variance. Missing values in the original time-series were interpolated using a linear trend regression (Statsoft, 1996). Seasonal anomaly time-series were calculated by subtracting the average of the time-series from the annual values.

A Principal component analyses (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 time-series, we adjusted the degrees of freedom (d.f.) in the statistical tests (Pyper and Peterman, 1998; Möllmann et al., 2003a).

Results

Climate, hydrography and mesozooplankton. The climate over the Central Baltic Sea as described by the BSI showed two distinct periods during the study period (Fig. 2). Until 1989 mainly low and negative airpressure anomalies were found. Afterwards mainly high positive BSI-values were observed, with the exception of 1996, declining in recent years.

A similar time-trend as observed for the BSI is visible for the water temperature in 30m depth (Fig. 2). Consequently both variables are closely and significantly correlated ($r=0.65$, $p<0.01$). For salinity in 80m depth, representing the conditions in the permanent halocline, a continuous downward trend was recorded until the early 1990s, slightly increasing afterwards. Salinity and the BSI were also significantly, but negatively correlated ($r=-0.60$, $p<0.01$).

Population sizes of the main calanoid copepod species in the Central Baltic showed pronounced time-trends (Fig. 3). *Pseudocalanus* sp. abundance decreased continuously until the early 1990s, and increased again in recent years. In contrast, *T. longicornis* and *Acartia* spp., having low abundances during the 1980s, drastically increased in stock size during the 1990s. Especially in spring, a drastic stepwise increase is visible in the end of the 1980s. Generally, time-trends were similar in all seasons, however with a higher amplitude of the changes in the first half year.

The taxonomic group of cladocerans showed the same interannual time-trend as observed for *T. longicornis* and *Acartia* spp. in spring, with low abundances during the 1980s and mainly drastically higher population sizes afterwards. In summer, an undulating time-trend in cladoceran abundance was observed.

Using a PCA we extracted principal components (PC1 and PC2), reflecting the main time-trends in main mesozooplankton species in the Central Baltic Sea (Fig. 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 the beginning of the year (Table 1). Consequently 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 shows the opposition of 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, the second trend by the negative relationship with salinity (Table 2). PC2 reflects more directly the trend in *Pseudocalanus* sp. abundance, which is positively related to salinity and negatively to the BSI.

Fish diet, condition and mesozooplankton. The observed trends in dominating mesozooplankton species are clearly reflected in the diet of herring (Fig. 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 clearly observable in the summer diet composition of herring. An additional food source for herring, mainly in winter and autumn, were mysids. While the amount of mysids in the herring stomachs was relatively constant from winter to summer, while a clear negative trend was observed in autumn (Fig. 5a).

Similar to herring, the amount of *Pseudocalanus* sp. in the winter and spring diet of sprat decreased in parallel to the decrease of the copepod's abundance (Fig. 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 of stomach content of these food items were observed during this time-period.

The time-series of condition of herring and sprat showed clear interannual time-trends (Fig. 6). Herring condition declined until the early 1990s and increased slightly since the late 1990s. Sprat condition was high during the 1980s and declined during the early 1990s. The decline appeared later as observed for herring. Time-trends were similar in all seasons.

Correlation analyses among the PCs of mesozooplankton time-series and herring as well as sprat condition were performed to identify the effect of the zooplankton community on Baltic pelagic fish growth. Both herring and sprat seasonal as well as annual condition was negatively correlated to PC1, being statistically significant for herring annual as well as winter and spring condition (Table 3). 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 (Fig. 7). The sprat stock size was low until the end of the 1980s with an intermediate peak in 1983. After 1990 the sprat population increased drastically peaking in 1996 and remaining further on a very high level.

Correlation analyses yielded in significant relationships of herring winter and spring condition, as well as sprat winter and annual condition with sprat stock size (Table 4).

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 runoff, 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 NAO) or easterly winds with cold continental air (low NAO). River runoff affects salinity in the Baltic by directly freshening surface waters. Indirectly, inflows of saline and oxygenated water from the Kattegat and North Sea, renewing the bottom water of the deep Baltic basins below the permanent halocline, are prevented by increased freshwater input as a result of increased zonal atmospheric circulation (Matthäus and Schinke, 1999).

The period of high NAO(BSI)-index values since the late 1980s, probably at least partially due to the anthropogenic greenhouse effect (Ulbrich and Christoph, 1999), resulted thus in a stepwise increase in average water temperatures (Dippner et al., 2000; Fonselius and Valderrama, 2003). This change in the thermal state of the ecosystem has recently been identified as a “regime shift” and occurred in parallel to an event in the North Sea (Alheit et al., submitted). The dominance of westerly weather increased further the amount of runoff with the consequence of drastically 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: decreasing *Pseudocalanus* sp. abundance with a slight increase in recent years, and increased *T. longicornis*, *Acartia* spp. and cladocerans populations (Möllmann et al., 2002; Möllmann et al., 2003a). Using PCA we summarized the main trends in seasonal abundance of the dominating mesozooplankton species and related them to the climate index and hydrography. Clearly PC1 reflected the increase in *T. longicornis* and *Acartia* spp. in parallel to temperature, while the negative

development of *Pseudocalanus* sp. and salinity was displayed by the negative relationship to PC1 and a positive one to PC2.

Recent investigations on the processes driving population dynamics of Baltic copepods indicate, that the process behind the salinity/*Pseudocalanus* sp.-relationship is probably a high egg and nauplii (N) mortality during stagnation periods. Females (C6-f) of this calanoid live in the permanent halocline of the Central Baltic basins, where they encounter maximum salinities, but during periods of low inflow frequency very low oxygen conditions down to $0.7 \text{ ml} \cdot \text{l}^{-1}$ (Schmidt et al., 2003). Comparing inflow and non-inflow situations yielded in a higher ratio of N/C6-f after an inflow of saline and oxygenated North Sea waters, indicating higher survival of eggs and N (GLOBEC-GERMANY, unpublished data). In the recent 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 for *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 N 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 temperature and *Acartia* spp. Further the same process might be true also for *T. longicornis* and cladocerans, which also produce resting eggs (Viitasalo and Katajisto, 1994; Katajisto et al., 1998).

Another climate-related process negatively affecting *Pseudocalanus* sp. dynamics is probably a high predation pressure by the presently large sprat stock (Möllmann and Köster, 2002). Sprat stock size increased to a large degree due to a high recruitment success, 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's production (Möllmann et al., 2004). An important predation impact was also found for *T. longicornis*, however not as strong as for *Pseudocalanus* sp., while predation pressure seems not to influence *Acartia* spp. dynamics (Möllmann and Köster, 2002; Möllmann et al., 2004).

Mesozooplankton, sprat stock size and fish condition. We found the trends in 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 *T. longicornis* increasing in summer. The decrease in *Pseudocalanus* sp. in the diet was described before and hypothesized to be responsible for the decrease in herring growth (Davidyuk et al., 1992; Naglis and Sidrevics, 1993; Davidyuka, 1996; Möllmann et al., submitted).

Supporting this, we found herring annual as well as winter and spring condition, 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 before (Möllmann et al., 2003b; Rönkkönen et al., 2004). In the first half of the year *Pseudocalanus* sp. reproduces in the permanent halocline of the deep Baltic basins, with peak reproduction in spring (Möllmann et al., 2003a). At this time of the year, late copepodite stages and adults of this copepod form the main food source of herring (Möllmann and Köster, 2002; Möllmann et al., submitted). Further, as common for

spring-spawning herring, condition of herring is lowest in spring after spawning (McGurk et al., 1980; Ojaveer, 1987), and the food supply encountered is important for refilling the energy requirements of the fish (Möllmann et al., 2003b). Additionally, *Pseudocalanus* sp. seems to be in spring the most energetically valuable copepod in terms of lipid content, when compared to *T. longicornis* and *Acartia* spp. (Peters et al., 2003).

Another important food source for herring, especially in winter and spring, were mysids (Möllmann and Köster, 1999; Möllmann et al., submitted). The availability of mysids was considered to be a determining factor for herring growth (Horbowy, 1997; Szygula et al., 1997). Unfortunately no time-series of mysid abundance was available which could be related to herring condition. However, additional correlation analyses relating the amount of mysids in the diet of herring to condition could not display a significant relationship. Thus we could not find an important influence of mysids on herring growth.

Contrary 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 spring, 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 condition. This may indicate that although *Pseudocalanus* sp. is the main food source also for sprat in the beginning of the year, it is over whole season not as important as for herring (Möllmann and Köster, 1999; Möllmann et al., submitted). Sprat move in summer after spawning in shallower water layers (Köster and Schnack, 1994) feeding mainly on *T. longicornis* (Möllmann and Köster, 1999), which increased in abundance, thus 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 as well as winter and spring sprat stock size with herring and sprat condition, 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 spring, when the diet overlap between both species is most pronounced, both species compete on *Pseudocalanus* sp. (Möllmann et al., submitted). 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, also sprat growth 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 their availability increased, i.e. *T. longicornis*, *Acartia* spp. and cladocerans. This occurred in parallel to the drastic increase in sprat stock size during the 1990s, suggesting strong density-dependence. This is supported also by the negative correlation of sprat condition and stock size.

Earlier studies identified also 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 could confirm 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 mesozooplankton abundance, affecting growth of Baltic pelagic fish species (Fig. 8). Thereby 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 positive effect on the development of the copepods *T. longicornis* and *Acartia* spp. during the 1990s. Further sprat recruitment profited 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 herring condition mainly influenced by the decline of *Pseudocalanus* sp., an effect amplified during the 1990s by a strong competition with the large sprat stock. Although also relying on *Pseudocalanus* sp., sprat could obviously compensate 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 intraspecific competition has resulted in the drastic decrease in sprat growth

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Figure captions

- Fig. 1. Map of the Central Baltic Sea with the area of investigation, i.e. the Gdansk Deep and the Gotland Basin.
- Fig. 2. Time-series on the Baltic Sea Index (BSI), as well as anomalies of spring temperature (°C) in 30m depth and spring salinity (psu) in 80m depth. Solid lines represent a fitted cubic polynomial.
- Fig. 3. Time-series on anomalies of seasonal abundance ($n \cdot m^{-2}$) of *Pseudocalanus* sp., *Temora longicornis*, *Acartia* spp., and cladocerans. Solid lines represent a fitted cubic polynomial.
- Fig. 4. Time-trends of mesozooplankton abundance summarized by PCA: Factor scores of PC1 and PC2.
- Fig. 5a. Time-series on anomalies of the seasonal mean herring stomach content (g wet weight) on *Pseudocalanus* sp., *Temora longicornis*, *Acartia* spp., and mysids.
- Fig. 5b. Time-series on anomalies of the seasonal mean sprat stomach content (g wet weight) on *Pseudocalanus* sp., *Temora longicornis*, *Acartia* spp., and cladocerans.
- Fig. 6. Time-series on anomalies of the seasonal condition (g at the grand mean length) of herring and sprat. Solid lines represent a fitted cubic polynomial.
- Fig. 7. Time-series on anomalies of herring (black dots) and sprat (white dots) stock size (numbers).
- Fig. 8. Schematic description of relationships among climate, copepods and pelagic fish growth: Left part – relationships among variables; right part – resulting idealized time-trends; grey lines and arrows represent temperature-driven processes, black lines and arrows represent salinity-driven processes.

Fig. 1

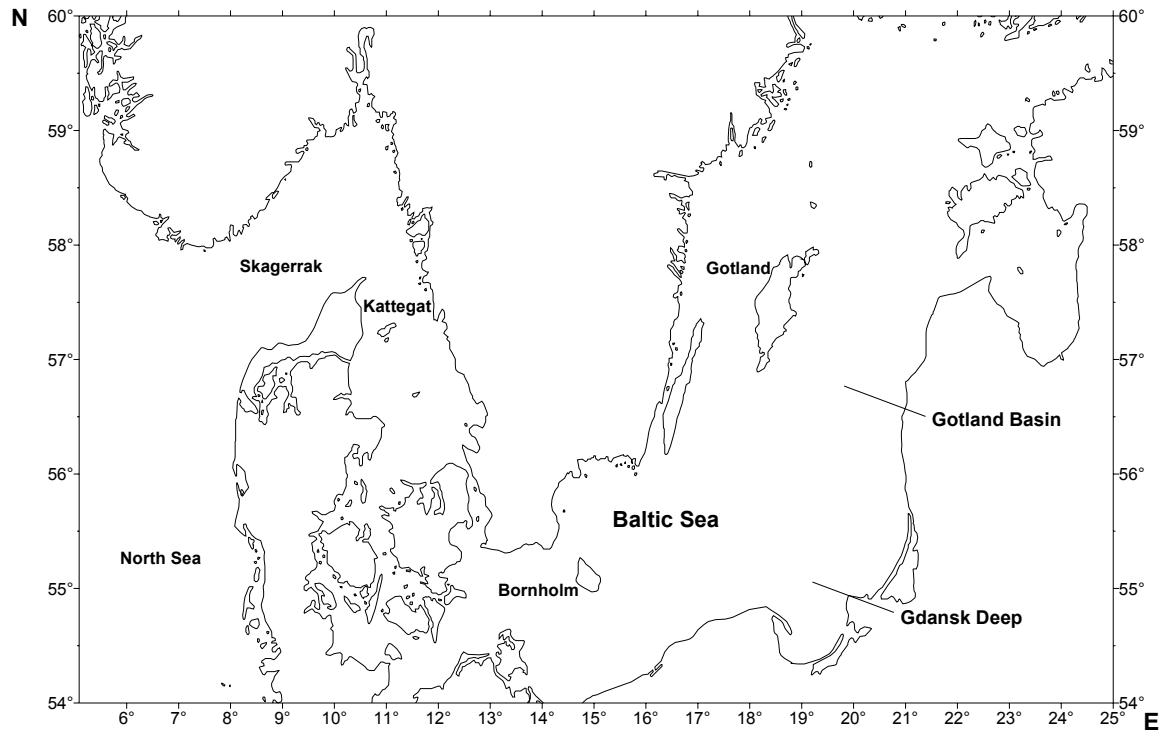


Fig. 2

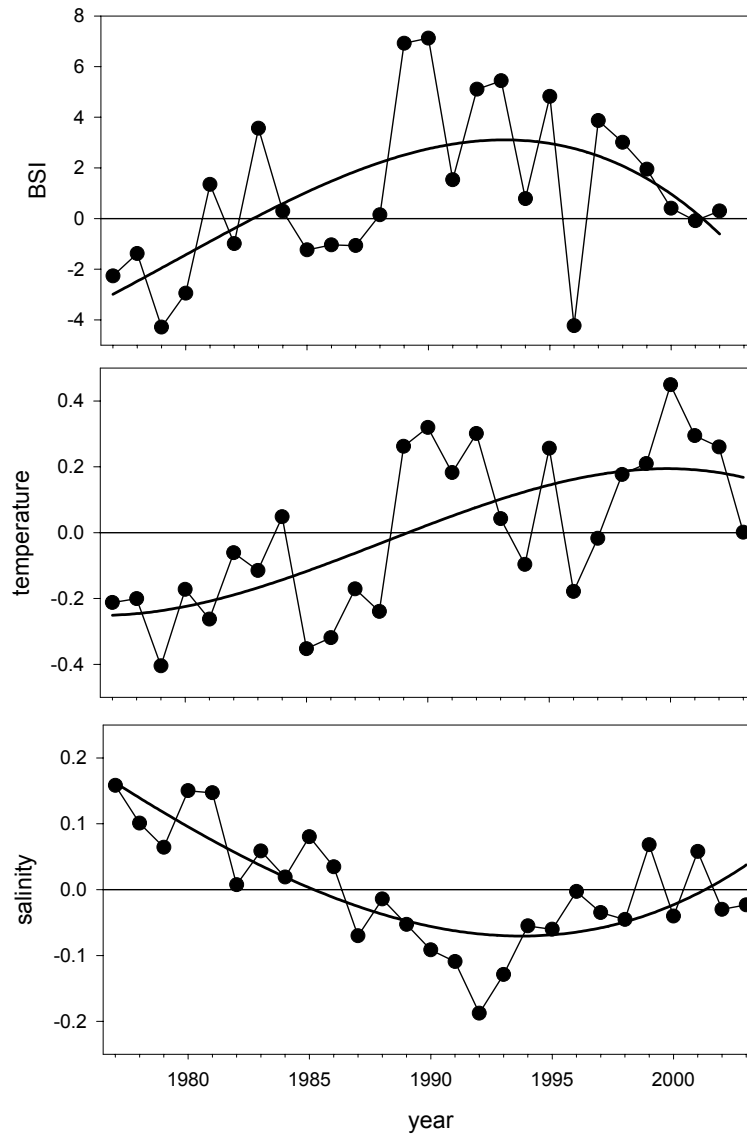


Fig. 3

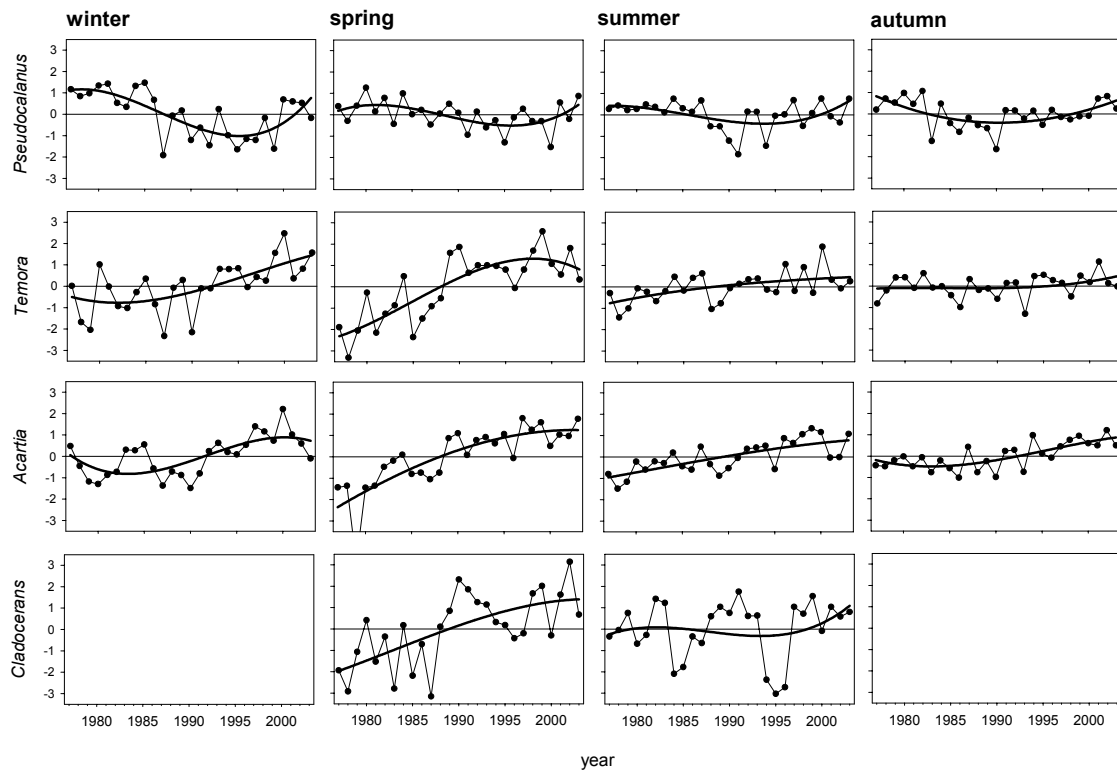


Fig. 4

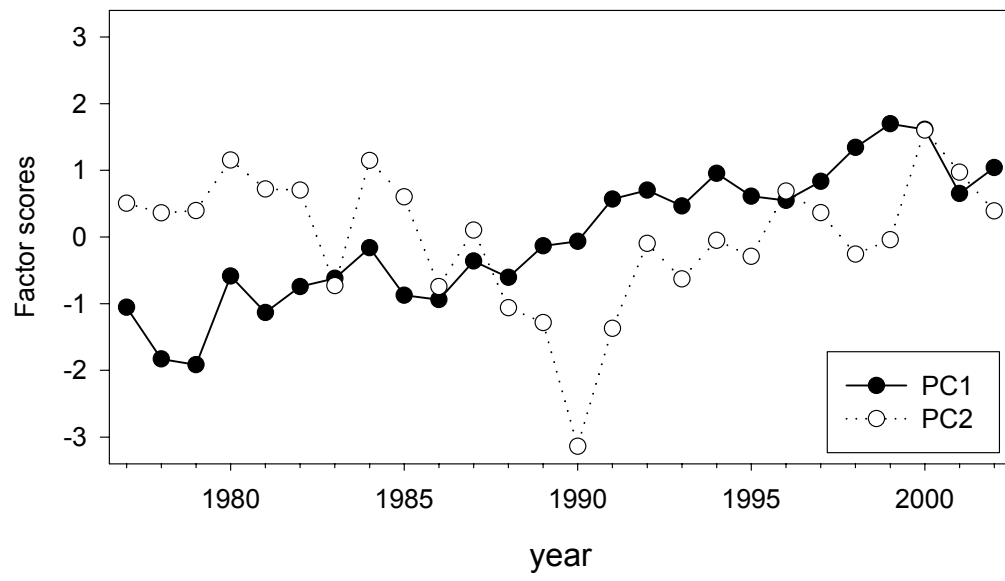


Fig. 5a

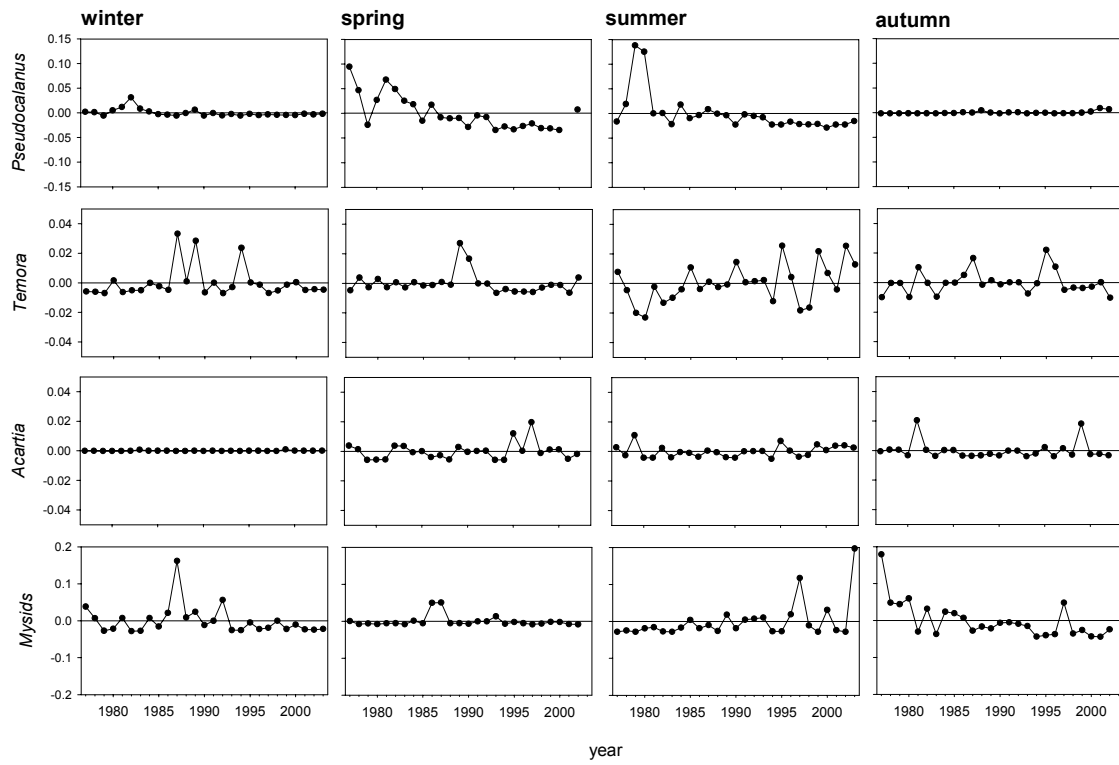


Fig. 5b

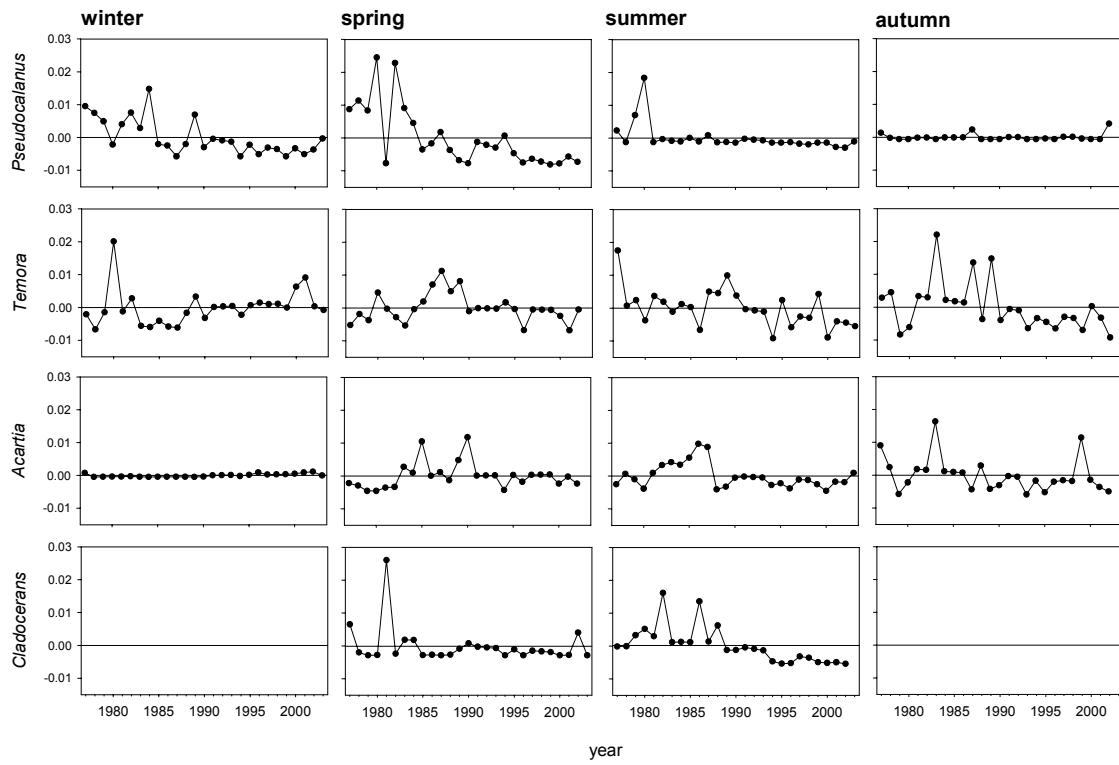


Fig. 6

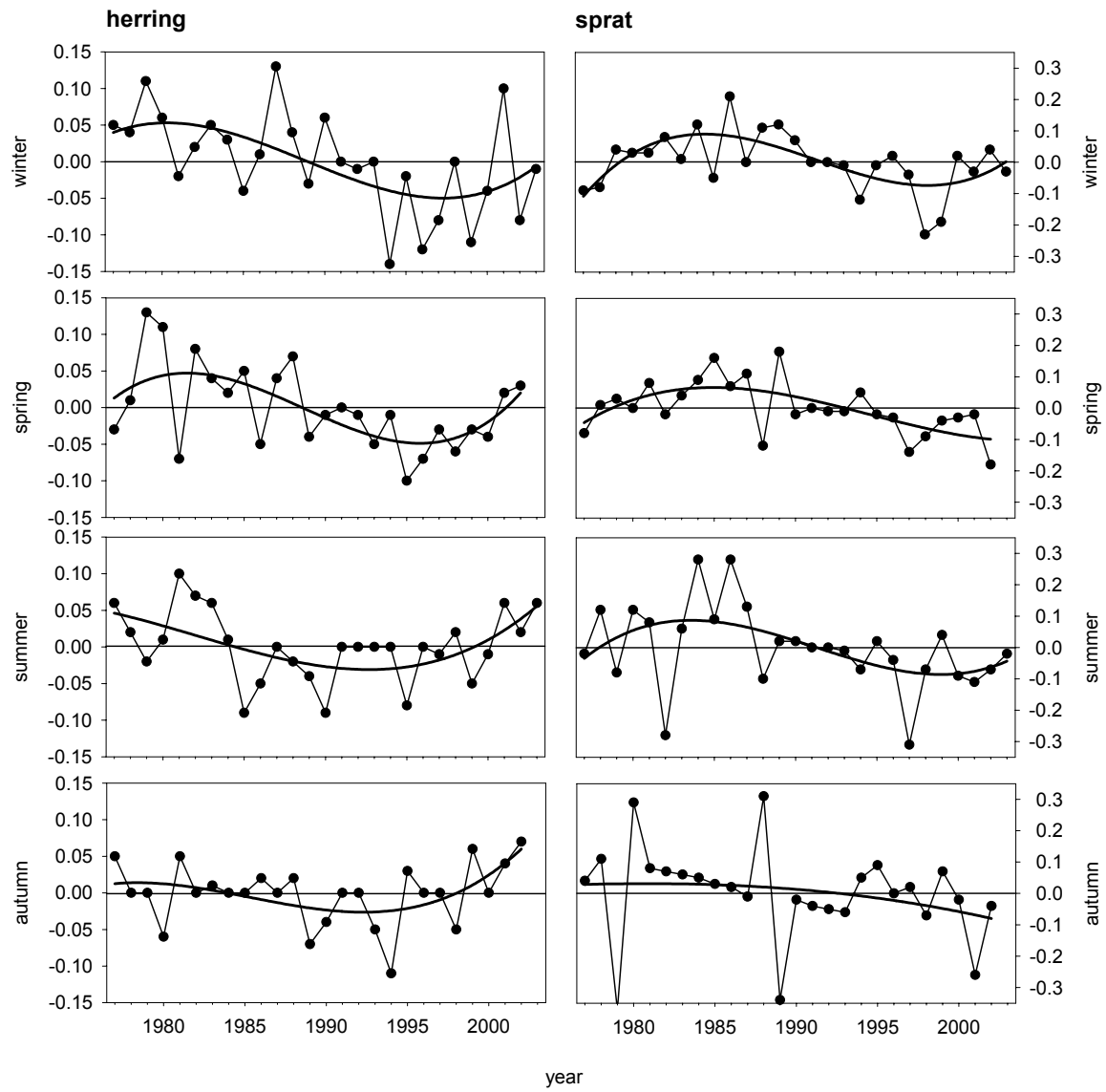


Fig. 7

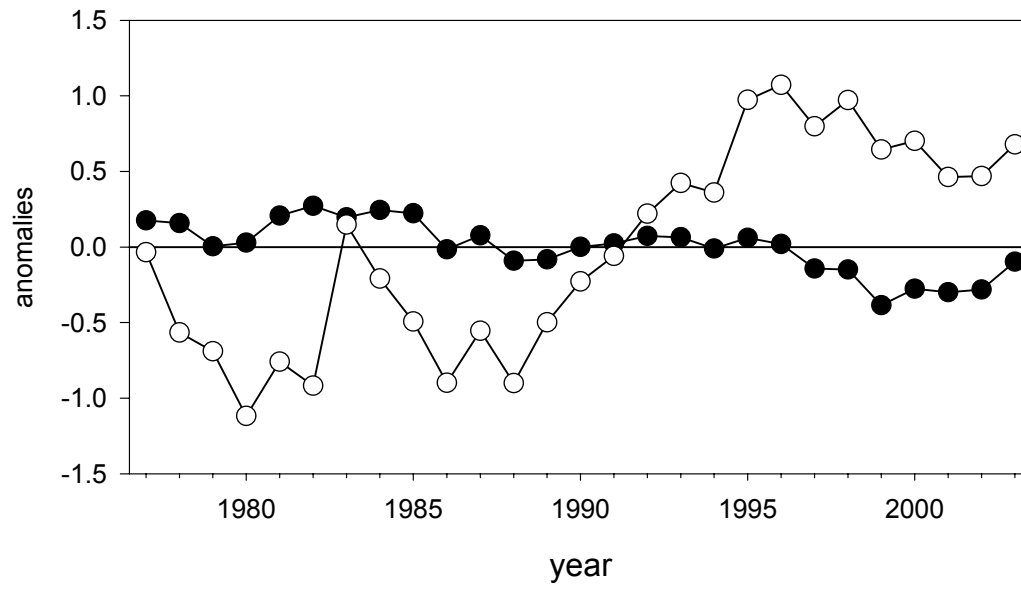


Fig. 8

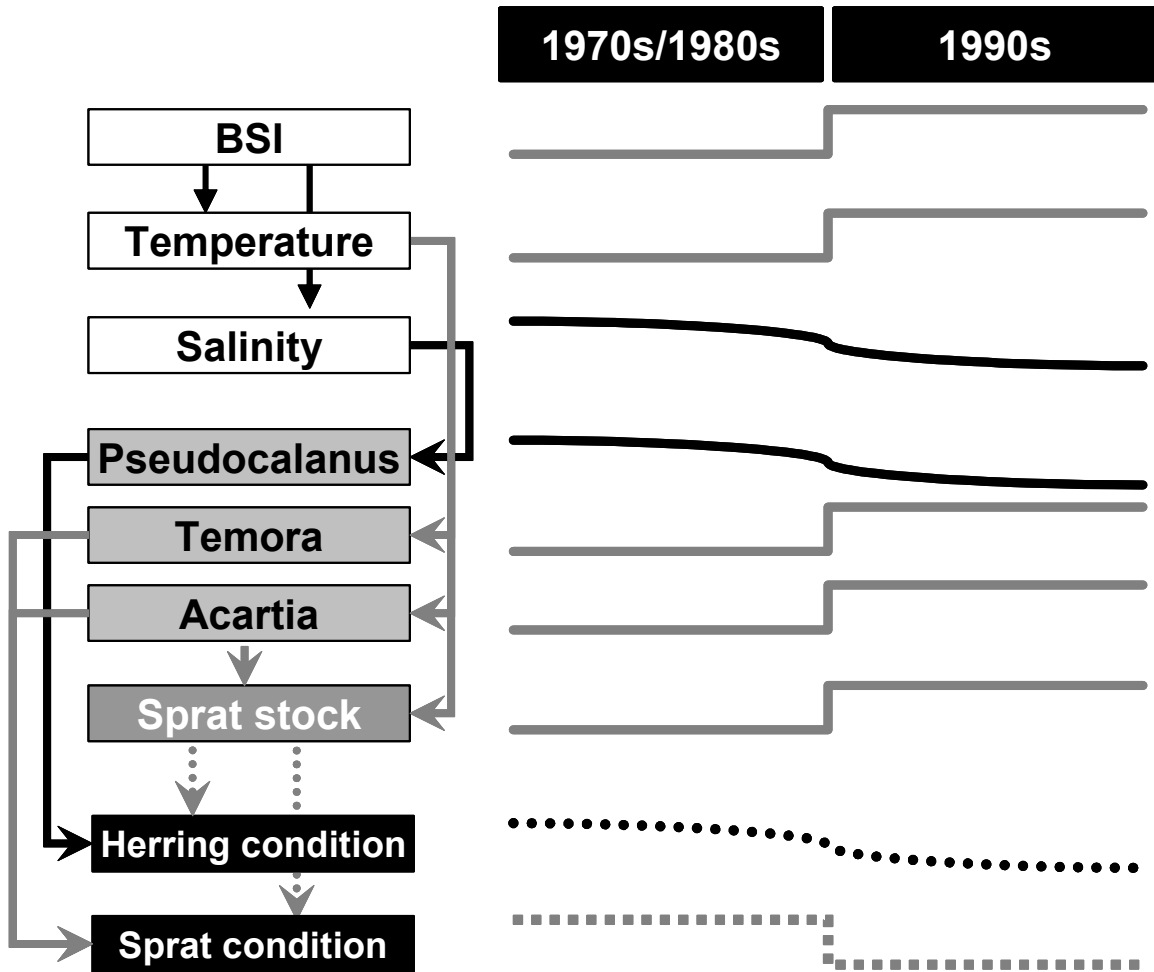


Table 1. Factor loadings of mesozooplankton seasonal abundance and principal components 1 and 2 (PC1 and PC2)

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

Table 2. Correlation tests between the BSI as well as temperature and salinity, and principal components 1 and 2 (PC1 and PC2) of the mesozooplankton abundance time-series. N^{eff} = “effective” number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α)

Variable	PC1			PC2		
	r	p	N^{eff}	r	P	N^{eff}
Temperature	0.76	<0.001	9**	-0.19	0.357	13
Salinity	-0.55	0.004	12*	0.47	0.016	17*

*significant at 0.05 and ** at 0.01 level

Table 3. Correlation tests between the seasonal and annual condition of herring and sprat, and principal components 1 and 2 (PC1 and PC2) of the mesozooplankton abundance time-series. N^{eff} = “effective” number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α)

Condition	PC1			PC2		
	r	p	N^{eff}	r	P	N^{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

Table 4. Correlation tests between the seasonal and annual condition of herring and sprat, and sprat stock size. N^{eff} = “effective” number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α)

Condition	Sprat stock size		
	r	p	N^{eff}
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