Long-term dynamics of main mesozooplankton species in the central Baltic Sea

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Abstract. Long-term dynamics (1959–1997) of the copepod species *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia* spp. and *Centropages hamatus*, as well as the taxonomic group of cladocerans, are described for the open sea areas of the central Baltic Sea. Differences between areas, i.e. Bornholm Basin, Gdansk Deep and Gotland Basin, as well as between 5 year periods, were investigated by means of Analysis of Variance (ANOVA). No significant differences in mesozooplankton biomass between areas were found. On the other hand, clear time-trends could be demonstrated and related to salinity and temperature, with *P.elongatus* biomass mainly dependent on salinity and *T.longicornis*, *Acartia* spp. and cladocerans biomasses dependent, to a large extent, on thermal conditions. Decreasing salinities since the early 1980s due to a lack of major inflows of highly saline water from the North Sea and increased river run-off, both triggered by meteorological conditions, obviously caused a decrease in biomass of *P.elongatus*. Contrarily, the standing stocks of the other abundant copepod species and cladocerans followed, to a large degree, the temperature development and showed, in general, an increase. The shift in species composition during this period is considered to be a reason for decreasing growth rates of Baltic herring (*Clupea harengus*) since the early 1980s, and for sprat (*Sprattus sprattus*) since the early 1990s. Generally, it is suggested that low mesozooplankton biomasses in the 1990s were caused, at least partially, by amplified predation by clupeid fish stocks.

Introduction

In marine pelagic food webs, zooplankton plays an important role in the energy transfer between primary producers and pelagic fish populations, and is thus a key factor influencing fish production. Long-term changes in zooplankton biomass have been recorded in many areas of the world's oceans and have been linked to climate variability [e.g. (Aebischer *et al.*, 1990; Roemmich and McGowan, 1995)]. For example, in the North Atlantic, variability in zooplankton abundance, especially of *Calanus finmarchicus*, was related to the North Atlantic Oscillation (NAO) [e.g. (Fromentin and Planque, 1996; Planque and Taylor, 1998)]. Similarly, in the Pacific, the El Niño Southern Oscillation (ENSO) affects the pelagic ecosystem [e.g. (McGowan 1985; Karl *et al.*, 1995; Lavaniegos *et al.*, 1998)].

Also in the Baltic Sea, the hydrographic regime is ultimately controlled by meteorological factors. In the central Baltic deep basins (Bornholm Basin, Gdansk Deep and Gotland Basin), the hydrographic conditions are strongly dependent on the renewal of the bottom water through inflowing, highly saline and oxygenated water masses from the North Sea and the Skagerrak/Kattegat. This phenomenon occurs relatively rarely and is connected to the mean atmospheric circulation pattern (Matthäus and Franck, 1992; Matthäus and Schinke,

1994). Vertically, a permanent halocline restricts the water exchange between the bottom water and the surface layer. Salinity and temperature in upper water layers are thus more influenced by freshwater run-off (Malmberg and Svansson, 1982; Launiainen and Vihma, 1990) and air temperature, respectively, both triggered also by meteorological conditions.

For shallower areas of the Baltic Sea (Gulf of Finland and Gulf of Riga), Ojaveer *et al.* (Ojaveer *et al.*, 1998) demonstrated the mesozooplankton species composition to be related to temperature and salinity. The abundance of *P.elongatus* in particular was found to be significantly correlated to salinity. Also, for shallow areas of the Northern Baltic, Vuorinen *et al.* (Vuorinen *et al.*, 1998) demonstrated that a reduction of salinity caused by increased river run-off initiated the decline of large neritic copepods and the increase of species with freshwater origin, i.e. cladocerans. They further considered the same mechanism to be responsible for changes in the mesozooplankton community of the open sea areas of the Central Baltic.

The aim of our present work is (i) to demonstrate the long-term trends in biomass of major mesozooplankton species/taxonomic groups for the deep basins of the central Baltic Sea and (ii) to test the hypothesis that salinity and temperature are the major factors influencing their biomass.

Method

Data on biomass of major mesozooplankton species in the central Baltic Sea were derived from a database of the Latvian Fisheries Research Institute (LATFRI). Sampling was performed using a Jeddy Net (UNESCO, 1968), a zooplankton net operating vertically with a mesh size of 160 μm and an opening diameter of 0.36 m. Individual hauls were carried out to a maximum depth of 100 m. The data were derived from several surveys during the period of 1959 to 1997 (Figure 1).

The off-shore area of the central Baltic Sea has a topographic structure with three deep basins separated by shallow sills hindering the water exchange with the North Sea. As these areas also differ in their water balance, differing hydrographic conditions are encountered in these subsystems (MacKenzie *et al.*, 2000). Thus, for the present analysis, available data were aggregated to three areas: (i) ICES Sub-division 25 (LATFRI stations 59, 62 and 63), representing the Bornholm Basin; (ii) ICES Sub-division 26 (LATFRI stations 46, 49, 51, 55, 64, 65 and 66), representing the southern part of the Gotland Basin and the Gdansk Deep; and (iii) ICES Sub-division 28 (LATFRI stations 35 to 45 and P1–3), representing the central Gotland Basin. For numbers of stations included in the analysis per area and season, see Table I.

For analysis, two subsamples were taken from the whole sample from which the number of a certain mesozooplankton species was determined. The size of the subsamples was chosen depending on the abundances found in the sample. A mean value was calculated from both subsamples to derive the number per m³. Finally, standard weights (Henroth, 1985) were used to estimate the biomass of each species per m³.

Data on major mesozooplankton species were considered in the present
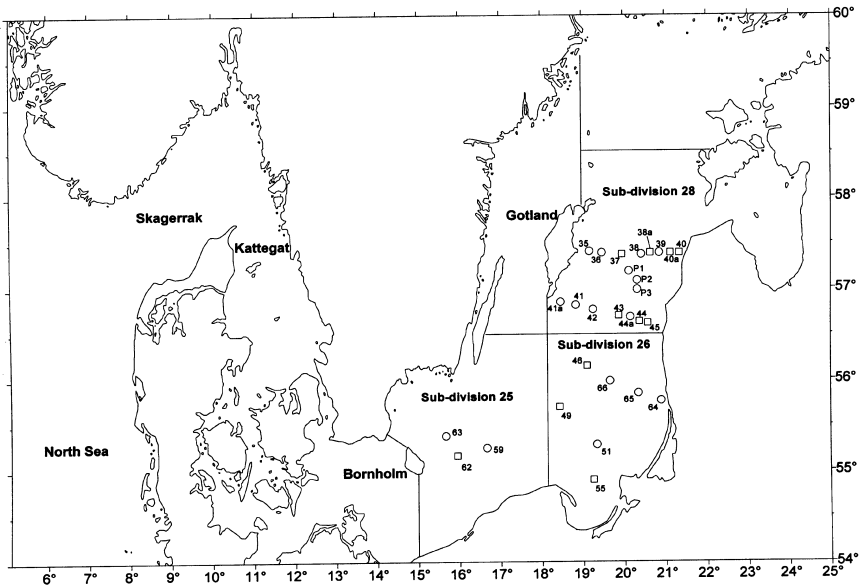
Fig. 1. The Baltic Sea with ICES Sub-divisions 25, 26 and 28 as well as stations covered within this study (○, zooplankton sampling only; □, zooplankton sampling and hydrographic measurements).

Table I. Number of stations covered per season for mesozooplankton and hydrography in ICES Sub-divisions (SD) in the period 1959–1997

Variable	SD	Winter	Spring	Summer	Autumn
Mesozooplankton	**25**	15	24	20	20
	26	45	71	66	73
	28	129	203	204	133
Hydrography	**25**	21	24	19	22
	26	80	82	77	75
	28	210	196	208	186

analysis, i.e. *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia* spp. (including *A.bifilosa*, *A.longiremis* and *A.tonsa*), *Centropages hamatus* and the taxonomic group of *Cladocera* (including *Bosmina coregoni maritima*, *Evadne nordmanni*, *Podon polyphemoides*, *Podon leuckarti* and *Podon intermedius*).

Time-series on salinity (psu) and temperature (°C) were compiled from a LATFRI database. Sampling was performed using a water sampler (Nansen type, 1 l capacity) and a Deep Sea Reversing Thermometer in 5 or 10 m steps. Salinity was measured either by the Knudsen Method or with an Inductivity Salinometer. Hydrographic information is available from various seasonal cruises during the period 1961 to 1997 and different stations in the Central Baltic (Table I). For the present study, station-specific information was used (Figure 1) according to the sub-areas described above for mesozooplankton (ICES Sub-division 25— LATFRI station 62; ICES Sub-division 26—LATFRI stations 46, 49, 55; ICES

Sub-division 28—LATFRI stations 37, 38a, 40, 40a, 43, 44, 45). Average values of hydrographic parameters were calculated for the depth range 0–50 m, being the water layer mainly inhabited by *T.longicornis*, *Acartia* spp., *C.hamatus* and clado-cerans (Sidrevics, 1979, 1984). As *P.elongatus*, especially older stages, show a deeper distribution (Sidrevics, 1979, 1984), the layer between 50 and 100 m was also considered for this species.

Biological data were normalized by transforming to natural logarithms. Hydrographic data and zooplankton biomasses were averaged over stations and aggregated to quarters. The seasonal cycle was removed by subtracting long-term quarterly means from annual quarterly means. For statistical analysis, resulting non-seasonal anomalies were aggregated to 5 year periods and sub-areas for performing a 2-way analysis of variance (ANOVA). For *post hoc* tests to distin-guish differences between single means, the Newman–Keuls test was used. For correlation of non-seasonal anomalies among variables, Pearson product–moment correlation analysis was used, excluding dates lacking data of one or the other variable.

Results

Mesozooplankton

The biomass of all considered species or taxonomic groups was highly seasonal in all areas considered, and also showed some geographic variability (Figure 2). After an increase from low values at the beginning of the year, peak biomasses of all copepod species were regularly found in the most western sub-area (Sub-division 25) in July. In contrast, in the more eastern regions (Sub-divisions 26 and 28), the highest values were observed later, in August/September. Cladocerans appeared in considerable numbers from spring onwards, with a maximum in biomass in August observed in all areas. Independent of the area, the most important copepod species in terms of biomass was *P.elongatus* followed by *T.longicornis*, *Acartia* spp. and *C.hamatus*. In summer, cladocerans showed biomass values of the same order as *P.elongatus* or even higher. In general, biomass did not differ between areas. Only for *P.elongatus* were considerable deviations encountered between the more southern Sub-divisions 25 and 26 compared with the northern Gotland Basin area (Sub-division 28). The seasonal development, with maximum biomass in summer, is confirmed by the quarterly long-term means for all species (Table II a).

The biomass of *P.elongatus* (Figure 3) showed positive non-seasonal anomalies in Sub-division 26 until the early 1980s. In Sub-divisions 25 and 28, more variable values were observed at the beginning of the time-series, also turning to positive anomalies in the early 1970s. Since the middle of the 1970s, high positive biomass anomalies were observed for *P.elongatus*, followed by a drastic decline in the following period until 1993. At the end of the time-series, still negative but slightly increased anomalies were recorded. The standing stock of *T.longicornis* (Figure 4) exhibited a high variability without clear trends. Undulating developments were observed, with a period of remarkably high anomalies at the end of the
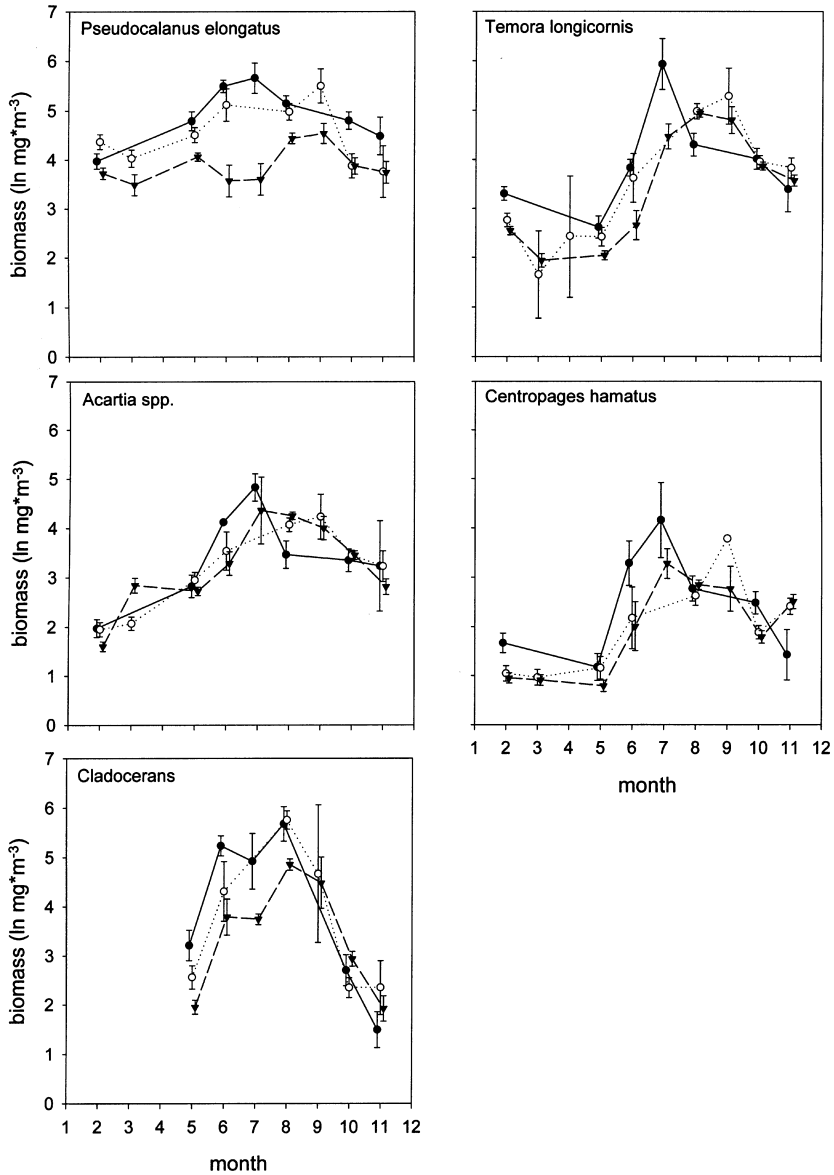
Fig. 2. Long-term monthly means of main mesozooplankton species/taxonomic groups in the central Baltic (Sub-division 25 – black circles, solid line; Sub-division 26 – white circle, dotted line; Sub-division 28 – black triangle, dashed line) in the period of 1959 to 1997. Symbols and error bars represent means and standard deviations.

1980s followed by sharply declining and mostly negative biomass anomalies in the 1990s. Clear trends were obvious for the biomass of *Acartia* spp. (Figure 5), showing negative anomalies from the 1960s to the early 1970s. A short increase and again, a subsequent drop in standings stocks, characterized the development
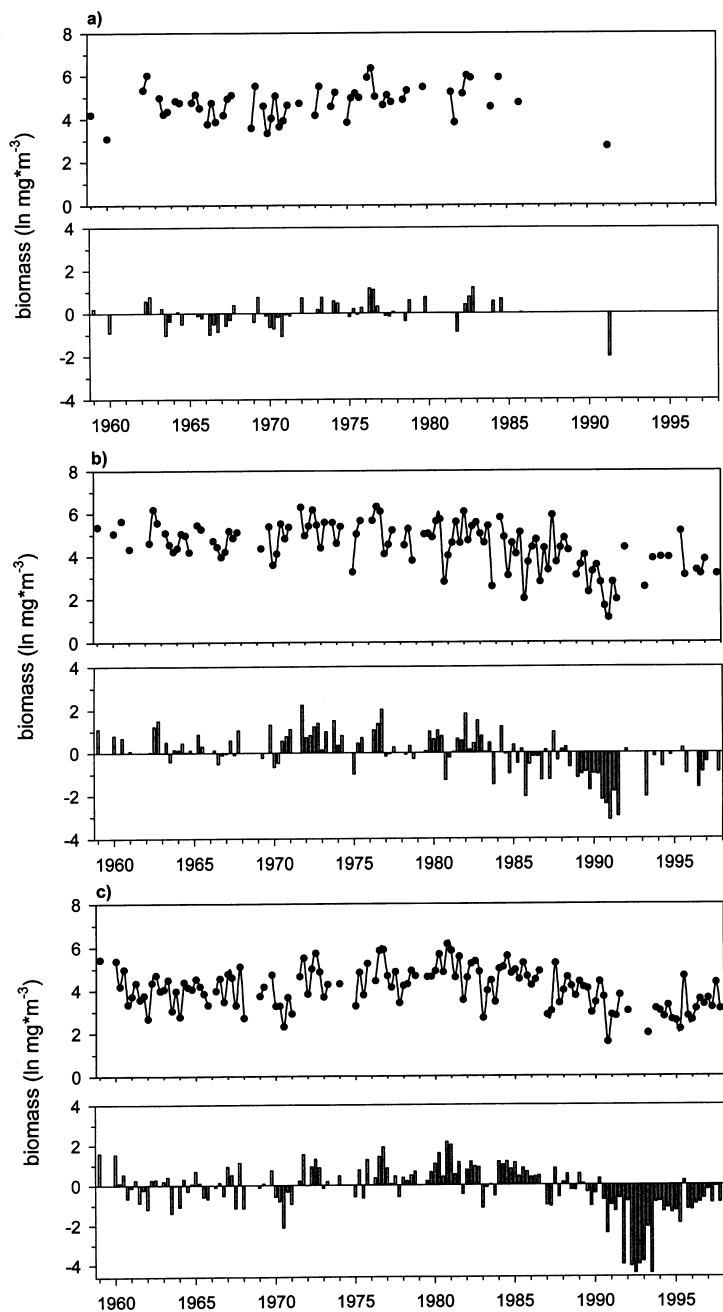
Fig. 3. Time-series of quarterly means (above) and non-seasonal anomalies (below) of *Pseudocalanus elongatus* biomass in ICES Sub-divisions 25 (**a**), 26 (**b**) and 28 (**c**) in the period of 1959 to 1997.
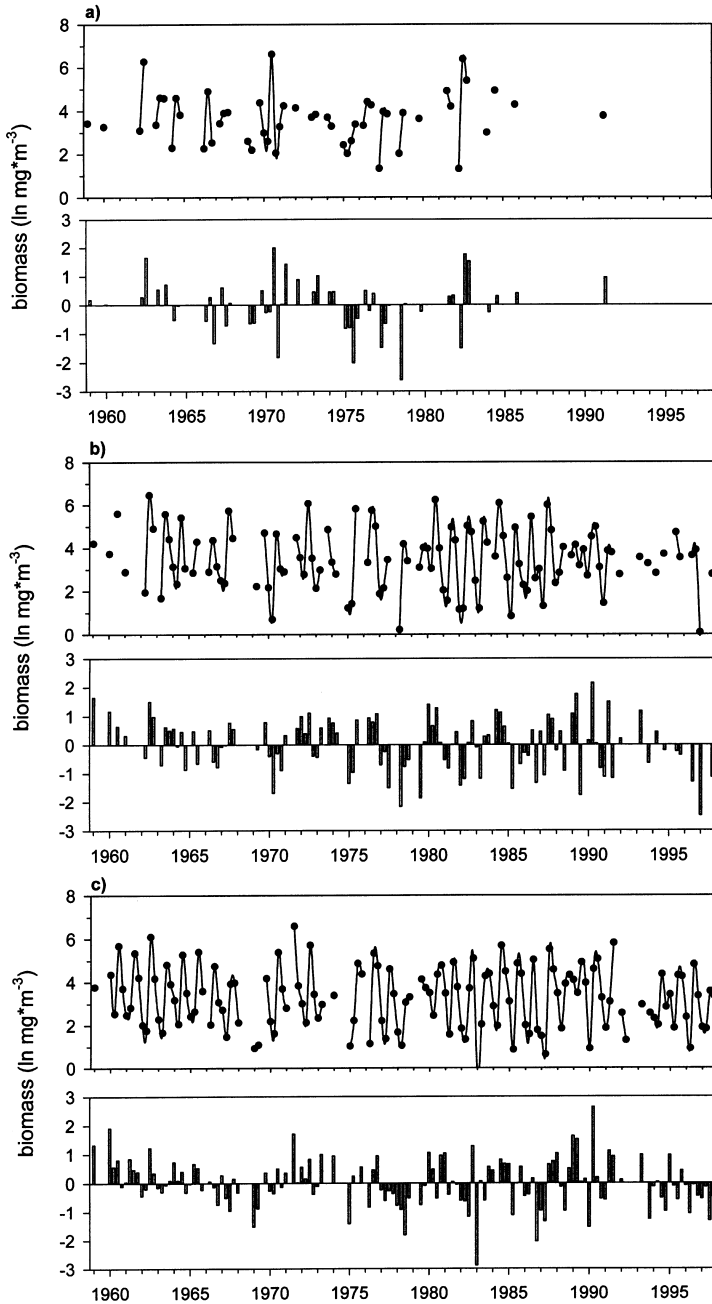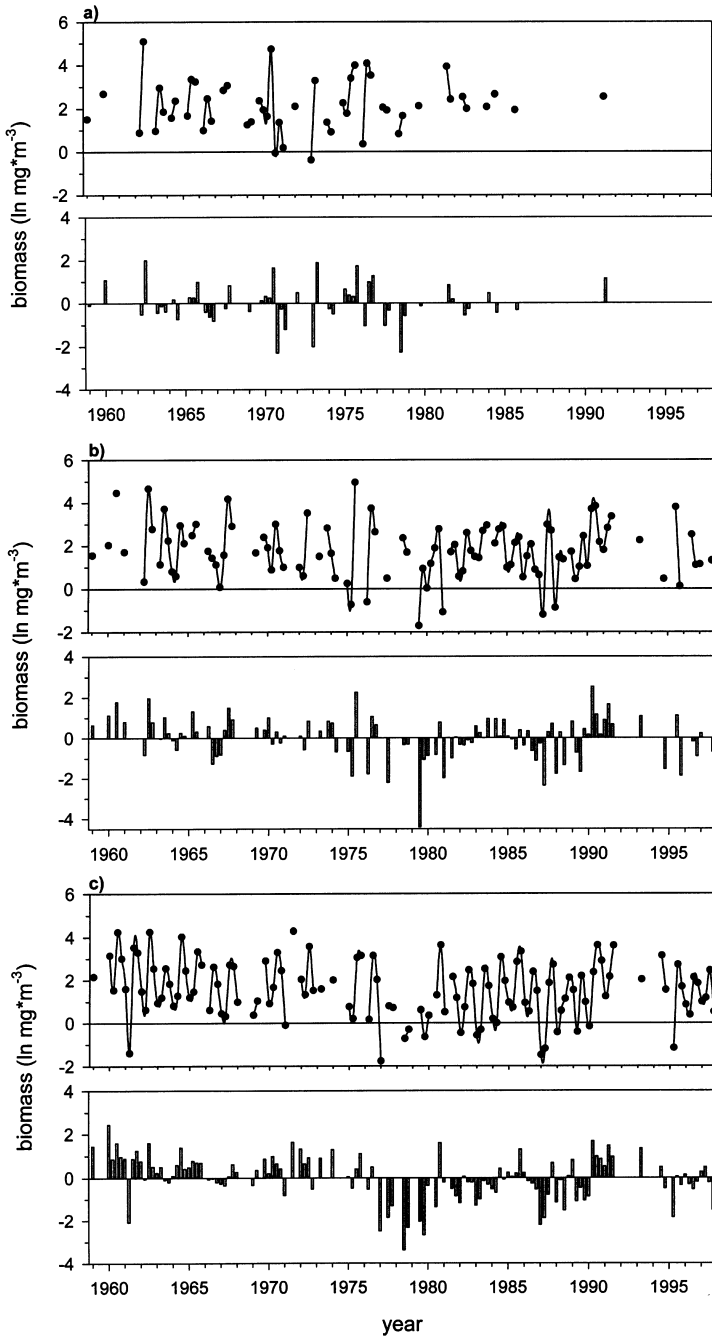
Fig. 4. Time-series of quarterly means (above) and non-seasonal anomalies (below) of *Temora longi-cornis* biomass in ICES Sub-divisions 25 (**a**), 26 (**b**) and 28 (**c**) in the period of 1959 to 1997.
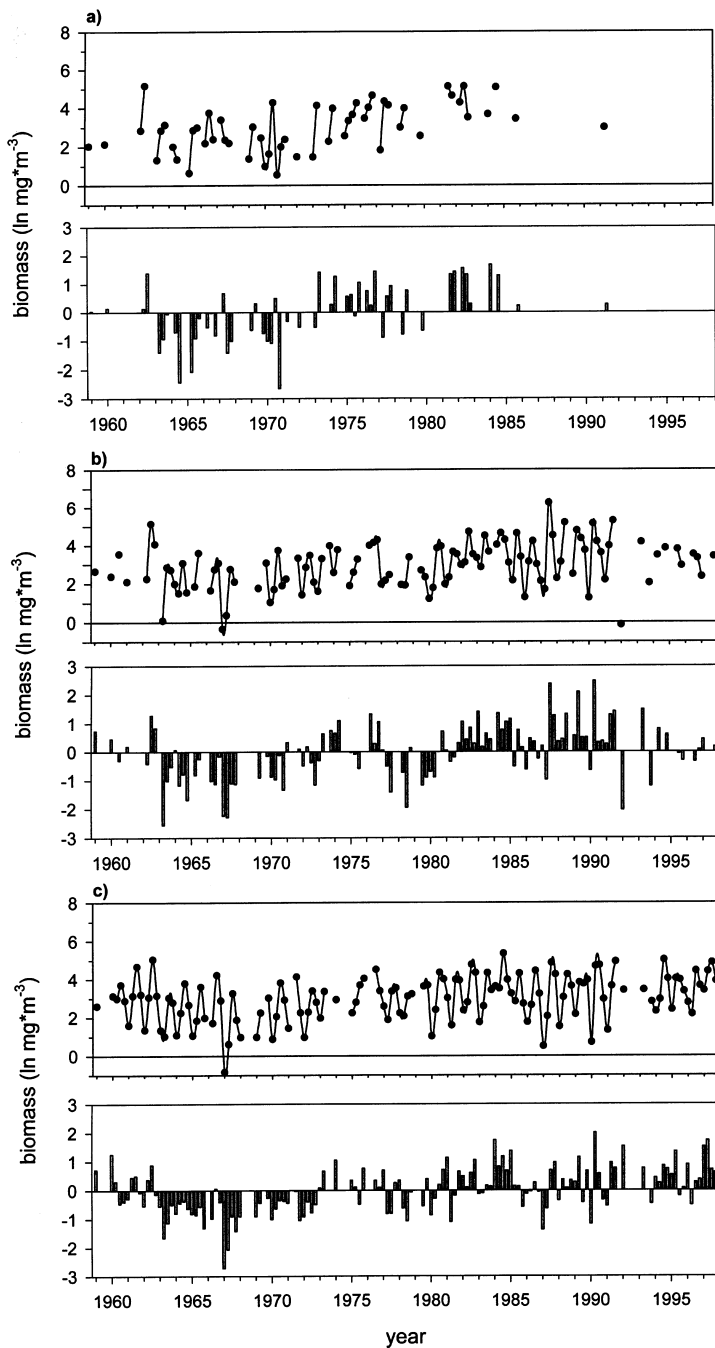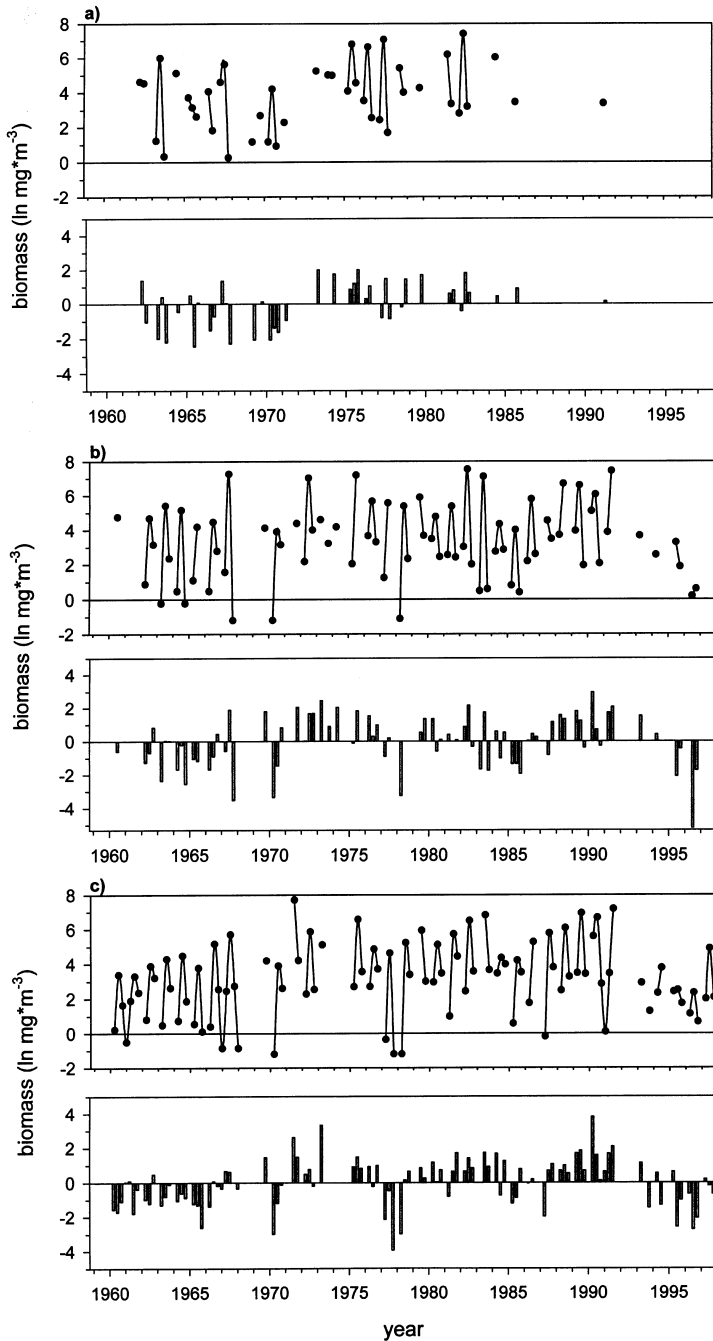
Fig. 5. Time-series of quarterly means (above) and non-seasonal anomalies (below) of *Acartia* spp. biomass in ICES Sub-divisions 25 (**a**), 26 (**b**) and 28 (**c**) in the period of 1959 to 1997.

Fig. 6. Time-series of quarterly means (above) and non-seasonal anomalies (below) of *Centropages hamatus* biomass in ICES Sub-divisions 25 (**a**), 26 (**b**) and 28 (**c**) in the period of 1959 to 1997.

Fig. 7. Time-series of quarterly means (above) and non-seasonal anomalies (below) of *Cladocera* biomass in ICES Sub-divisions 25 (**a**), 26 (**b**) and 28 (**c**) in the period of 1959 to 1997.

Table II. Long-term seasonal means (± standard deviation) for (**a**) biomass (in mg m^{-3}) of mesozooplankton species/taxonomic groups and (**b**) hydrographic variables (S-Salinity in psu; T-Temperature in °C) in ICES Sub-divisions (SD)

(**a**)

Species	SD	Winter	Spring	Summer	Autumn
P.elongatus	25	3.97 ± 0.61	4.85 ± 0.88	5.22 ± 0.64	4.74 ± 0.71
	26	4.35 ± 0.96	4.56 ± 1.20	5.01 ± 1.26	3.86 ± 1.84
	28	3.96 ± 1.18	4.02 ± 1.18	4.43 ± 1.47	3.84 ± 1.58
T.longicornis	25	3.30 ± 0.54	2.71 ± 1.18	4.55 ± 1.10	3.89 ± 0.88
	26	2.68 ± 0.98	2.51 ± 1.53	5.01 ± 1.23	3.93 ± 0.93
	28	2.47 ± 0.90	2.08 ± 1.23	4.92 ± 1.04	3.79 ± 0.83
Acartia spp.	25	1.98 ± 0.70	2.93 ± 1.09	3.67 ± 1.18	3.33 ± 1.10
	26	1.96 ± 0.91	3.00 ± 1.27	4.09 ± 1.11	3.41 ± 0.87
	28	1.78 ± 1.08	2.77 ± 1.14	4.24 ± 1.04	3.31 ± 0.97
C.hamatus	25	1.67 ± 0.78	1.41 ± 1.25	2.98 ± 1.17	2.27 ± 1.01
	26	1.04 ± 0.94	1.25 ± 1.56	2.69 ± 1.53	1.97 ± 1.02
	28	0.94 ± 0.99	0.85 ± 1.33	2.85 ± 1.29	1.96 ± 1.21
Cladocerans	25	0	3.42 ± 1.39	5.57 ± 1.38	2.46 ± 1.27
	26	0	2.70 ± 1.84	5.71 ± 1.50	2.35 ± 1.48
	28	−0.54 ± 0.45	2.13 ± 1.72	4.82 ± 1.60	2.73 ± 1.44

(**b**)

Variable	SD	Winter	Spring	Summer	Autumn
S 0–50 m	25	8.11 ± 0.07	8.00 ± 0.06	7.96 ± 0.06	8.04 ± 0.08
	26	7.73 ± 0.12	7.65 ± 0.01	7.61 ± 0.01	7.58 ± 0.01
	28	7.63 ± 0.01	7.53 ± 0.01	7.46 ± 0.01	7.45 ± 0.01
S 50–100 m	25	14.63 ± 0.23	14.52 ± 0.20	14.63 ± 0.24	14.57 ± 0.18
	26	9.88 ± 0.06	9.64 ± 0.06	9.51 ± 0.06	9.71 ± 0.06
	28	9.22 ± 0.05	9.11 ± 0.05	9.03 ± 0.04	9.14 ± 0.05
T 0–50 m	25	2.05 ± 0.13	5.24 ± 0.19	11.47 ± 0.47	9.33 ± 0.21
	26	2.21 ± 0.05	4.84 ± 0.09	11.07 ± 0.25	9.18 ± 0.13
	28	1.95 ± 0.03	4.62 ± 0.06	11.46 ± 0.15	9.18 ± 0.07
T 50–100 m	25	6.68 ± 0.18	5.32 ± 0.17	6.01 ± 0.13	7.28 ± 0.15
	26	4.44 ± 0.05	4.05 ± 0.05	3.95 ± 0.05	4.59 ± 0.07
	28	3.79 ± 0.04	3.78 ± 0.04	3.79 ± 0.04	4.50 ± 0.07

in the 1970s. The most obvious feature in the biomass development of *Acartia* spp. was the mostly positive anomalies during the 1980s, lasting in Sub-division 28 into the 1990s. A contradictory development was observed for *C.hamatus* (Figure 6), starting with generally positive values until the middle of the 1970s. The 1980s were characterized by negative anomalies, with the exception of a short period in the middle of the decade. The 1990s started with positive anomalies for *C.hamatus* which dropped in more recent years. Cladoceran standing stocks (Figure 7) were low at the beginning of the period covered, increasing up to the early 1970s. In the mid 1970s, a sharp drop in biomass occurred. During the 1980s,

anomalies were generally positive, but after 1993, standing stocks sharply decreased.

No distinct differences between the biomass developments in the three sub-areas were apparent for all considered species/taxonomic groups. This was supported by the statistical analysis. Due to lack of data for the 1990s in Sub-division 25, the statistical comparison of non-seasonal anomalies of mesozoo-plankton biomass data, using a 2-way ANOVA with factors area and 5 year periods, was performed as a first step only until the end of the 1980s. The analysis revealed, for all considered species/taxonomic groups, significant differences for the factor 5 year period, but not for the factor area. Thus, an additional 1-way ANOVA was performed aggregating all sub-areas, allowing the inclusion of the data for the 1990s (Table III a). *Post hoc* tests showed *P.elongatus* biomass anomalies since the late 1980s to be lower than for the other periods. Negative anomalies were found for *T.longicornis* in the second half of the 1980s and during the late 1990s, and were significantly lower than in other time-intervals. *Acartia* spp. biomass anomalies steadily increased throughout the time-series, with significant positive anomalies since the 1980s, whereas for *C.hamatus*, a decreasing trend was encountered with an intermediate high value in the early 1990s. An increasing trend until the early 1990s was identified for cladocerans. For the late 1990s, a *post hoc* test showed significantly lower biomass anomalies for this taxonomic group.

Hydrography

Mean salinities in the upper water layer (0–50 m) showed almost no seasonal variation in all sub-areas, with long-term quarterly means averaging 8.0, 7.6 and 7.5 psu for Sub-divisions 25, 26 and 28, respectively (Table II b). The same seasonal stability was visible for the deeper layers (50–100 m), characterized by average salinities of 14.6, 9.7 and 9.1 psu (Table II b). A clear seasonality was observed for the temperature in the upper depth range, with maximum values occurring regularly in summer (>11°C) and minimum values occurring in winter (~2°C). On the contrary, temperature in the deeper waters exhibited a less pronounced seasonal development but a clear difference between Sub-division 25, with on average 6.3°C, compared with 4.3 and 4.0 in Sub-divisions 26 and 28, respectively (Table II b).

Non-seasonal anomalies of salinity (Figures 8 and 9) generally showed the same inter-annual developments in all three Sub-divisions considered, but with a noticeably higher variability in the Bornholm area. In the upper water layers (0–50 m), negative anomalies of salinity were found in the 1960s. Increasing salinities were regularly recorded after the inflows in 1969, 1971 and 1975/76 (Matthäus and Franck, 1992). During the 1980s, a clear negative trend in all central Baltic areas was obvious and still exists in the 1990s. The deeper water layers (50–100 m) exhibited similar inter-annual developments in salinity, but showed an obviously more pronounced response to inflow events. In contrast to the upper water layers, positive anomalies were found in the 1960s.

In all sub-areas, negative anomalies of temperature were found in the 0–50 m

Table III. Means of non-seasonal anomalies for (**a**) biomass (in mg m^{-3}) of mesozooplankton species/ taxonomic groups and (**b**) hydrographic variables (S-Salinity in psu; T-Temperature in °C) for the combined area of investigation; results of 1-way ANOVA with factor 5 year period (F) and the significance (P); number of data points in parentheses

(a)

Variable	1960–64	1965–69	1970–74	1975–79	1980–84	1985–89	1990–94	1995–97	F	P
Pelongatus	0.55 (41)	0.01 (38)	0.30 (40)	0.39 (44)	0.50 (46)	-0.20 (39)	-1.78 (26)	-0.81 (18)	27.55	<0.001
T.longicornis	0.33 (41)	-0.14 (35)	0.28 (40)	-0.48 (44)	0.13 (46)	-0.03 (40)	0.08 (26)	-0.49 (18)	4.88	<0.001
Acartia spp.	-0.34 (41)	-0.87 (38)	-0.23 (40)	-0.02 (43)	0.51 (46)	0.33 (40)	0.44 (26)	0.41 (18)	13.31	<0.001
C.hamatus	0.49 (41)	0.18 (37)	0.23 (35)	-0.64 (37)	-0.19 (42)	-0.39 (40)	0.72 (19)	-0.38 (17)	7.55	<0.001
Cladocerans	-0.79 (32)	-0.52 (31)	0.35 (25)	0.21 (38)	0.50 (35)	0.28 (28)	1.05 (17)	-1.43 (13)	7.56	<0.001

(b)

Variable	1960–64	1965–69	1970–74	1975–79	1980–84	1985–89	1990–94	1995–97	F	P
S 0–50 m	-0.08 (39)	-0.12 (60)	0.15 (60)	0.21 (56)	0.14 (50)	-0.11 (45)	-0.25 (38)	-0.42 (24)	49.84	<0.001
S 50–100 m	0.37 (39)	0.41 (60)	0.51 (60)	0.29 (56)	-0.16 (50)	-0.66 (45)	-1.18 (38)	-0.75 (24)	51.20	<0.001
T 0–50 m	-0.52 (39)	-0.46 (60)	0.24 (60)	-0.05 (56)	-0.03 (50)	-0.22 (45)	0.89 (38)	-0.01 (24)	7.03	<0.001
T 50–100 m	-0.04 (39)	-0.01 (60)	0.20 (60)	0.18 (56)	-0.05 (50)	-0.74 (45)	0.39 (38)	-0.12 (24)	11.01	<0.001
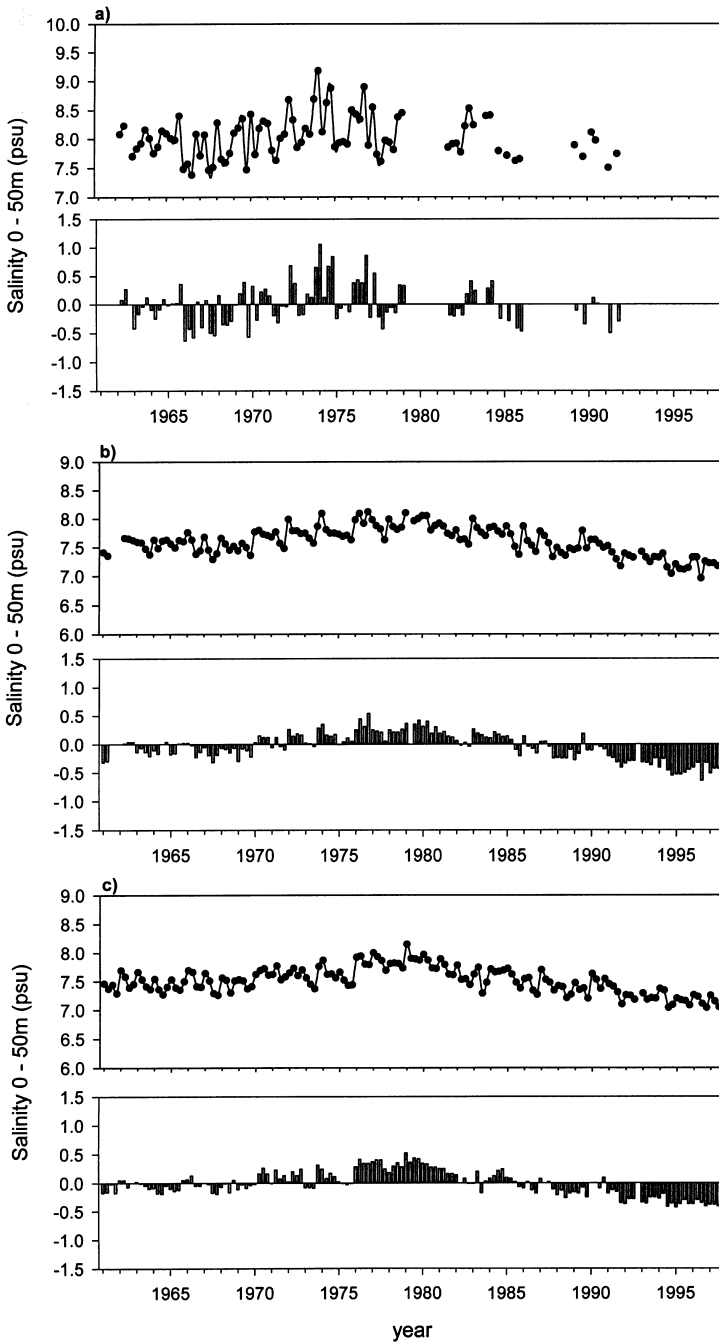
Fig. 8. Time-series of quarterly means (above) and non-seasonal anomalies (below) of salinity in the layer of 0–50 m in ICES Sub-divisions 25 (**a**), 26 (**b**) and 28 (**c**) in the period of 1961 to 1997.
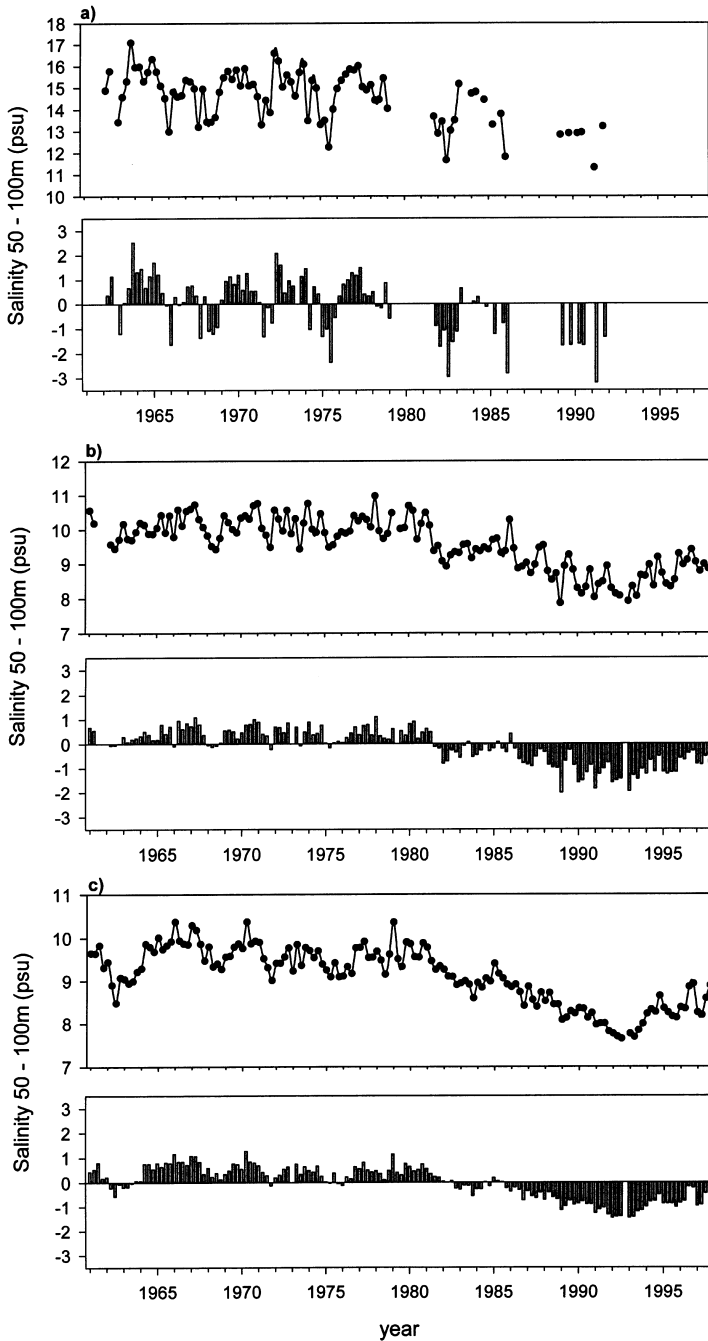
Fig. 9. Time-series of quarterly means (above) and non-seasonal anomalies (below) of salinity in the layer of 50–100 m in ICES Sub-divisions 25 (**a**), 26 (**b**) and 28 (**c**) in the period of 1961 to 1997.

layer until the mid 1960s (Figure 10). A generally positive trend was then visible until the middle of the 1970s. During the period between the end of the 1970s and the beginning of the 1990s, a wave-like development was recorded, ending in highest positive anomalies in the early 1990s. In the 50–100 m layer (Figure 11), all sub-areas showed increasing temperature anomalies until the early 1970s and afterwards, negative anomalies until 1989. Positive anomalies again turned negative after 1993.

Two-way ANOVAs with factors area and 5 year periods (excluding the 1990s) showed significant differences between periods for all variables, but for the factor area, only for salinity (0–50 m: $F = 3.75$, $P = 0.03$; 50–100 m: $F = 8.98$, $P < 0.001$). To match the statistical analysis of mesozooplankton, an additional 1-way ANOVA was calculated, aggregating areas and including the 1990s (Table III b). *Post hoc* tests indicated a negative trend in salinity in both layers, with significantly lower values since the second part of the 1980s. Highest and significantly different values for temperature in both depth ranges were observed in the early 1990s.

Correlation between mesozooplankton biomass and hydrography

Correlation analyses were performed separately for seasons (Table IV). In all seasons, the biomass of *P.elongatus* was significantly positively correlated to salinity in both layers, with the exception of the deeper water layer in summer. Also, a significant but inverse relationship was observed between *P.elongatus* and temperature in summer. Strong positive correlations were also found for *T.longicornis* and *Acartia* spp., and temperature, in spring, whereas cladocerans were significantly positively related to temperature in spring and to salinity in autumn. No significant correlations were found between *C.hamatus* and one of the hydrographic variables.

To test whether autocorrelations in the time-series possibly reduced the validity of the correlations, the Durbin–Watson test was used. With the exception of the correlations for *P.elongatus* and temperature (0.96 for the upper layer; 1.21 for the lower layer), all Durbin–Watson coefficients were in the range 1.5–2.5, indicating no autocorrelation of the residuals.

Discussion

The results of the present study revealed earlier peak biomasses of the copepod species within a season in the Bornholm Basin (Sub-division 25) than in the more eastern areas, i.e. the Gdansk Deep (Sub-division 26) and the Gotland Basin (Sub-division 28). This can be explained by the earlier onset of the phytoplankton bloom and thus, a better food supply in the more western Bornholm Basin (Wasmund *et al.*, 1996). However, the use of time-series of non-seasonal anomalies of mesozooplankton biomass to perform a 2-way ANOVA with the factors area and 5 year periods revealed insignificant differences between the investigated sub-areas for all species/taxonomic groups. Average hydrographic variables were also rather similar in all sub-areas, with the exception of salinity and
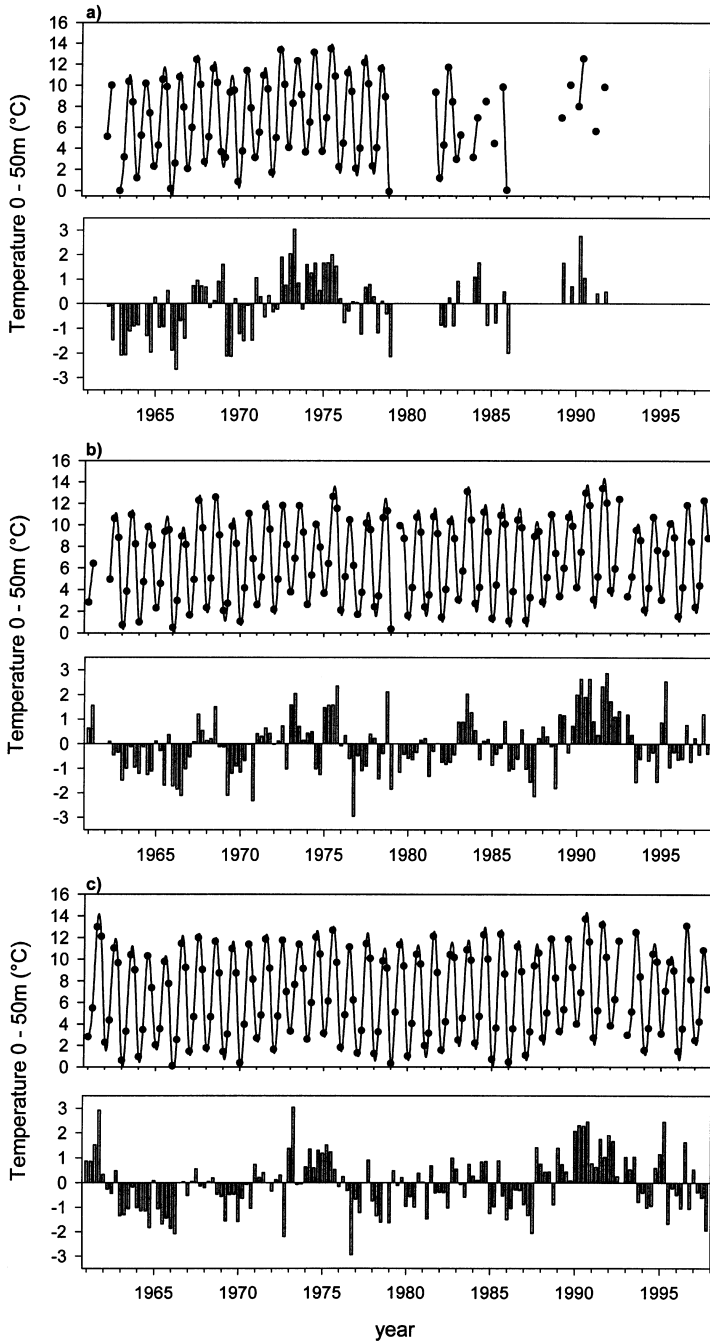
Fig. 10. Time-series of quarterly means (above) and non-seasonal anomalies (below) of temperature in the layer of 0–50 m in ICES Sub-divisions 25 (**a**), 26 (**b**) and 28 (**c**) in the period of 1961 to 1997.
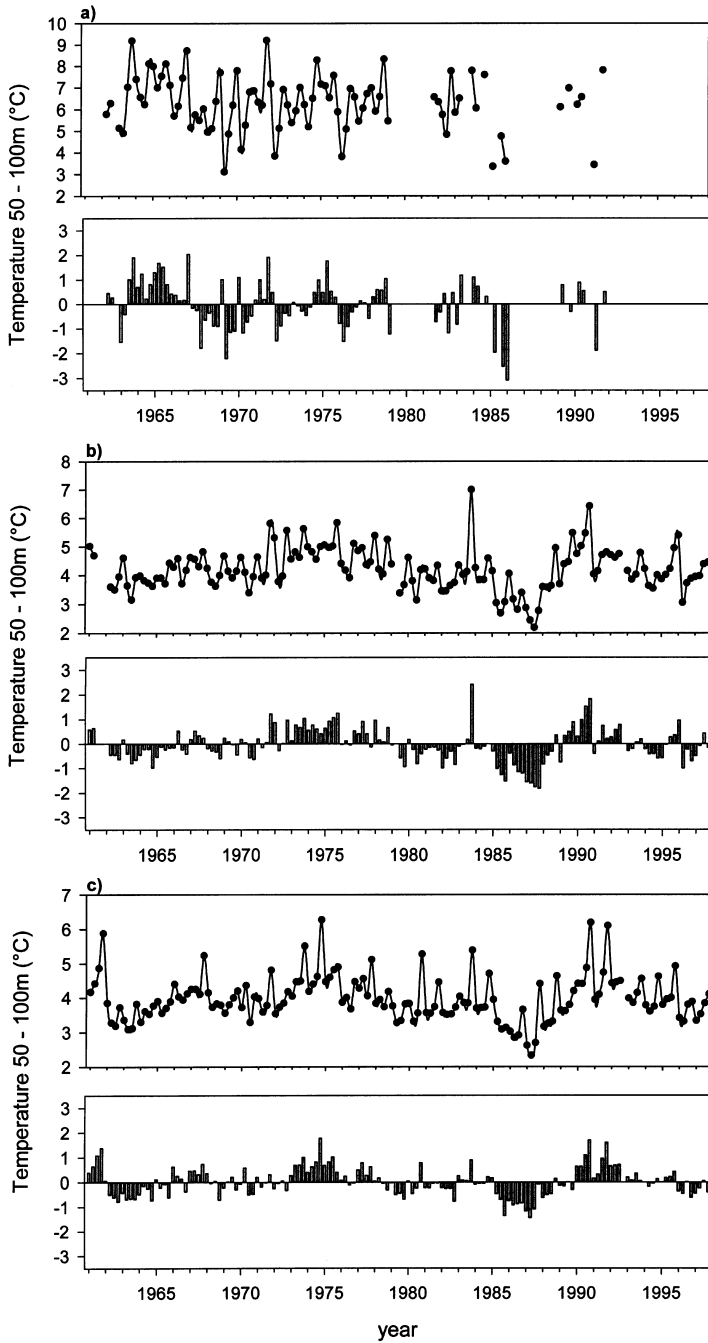
Fig. 11. Time-series of quarterly means (above) and non-seasonal anomalies (below) of temperature in the layer of 50–100 m in ICES Sub-divisions 25 (**a**), 26 (**b**) and 28 (**c**) in the period of 1961 to 1997.

Table IV. Correlation coefficients (*r*) among biomass of mesozooplankton species/taxonomic groups and hydrographic variables (S-Salinity; T-Temperature) in different seasons of the year using non-seasonal anomalies (*significant correlation at 0.05 level); number of data points in parentheses

Variable	Season	S 0–50 m	S 50–100 m	T 0–50 m	T50–100 m
P.elongatus		0.60* (33)	0.44* (33)	–0.18 (33)	0.16 (33)
T.longicornis		0.02 (33)	–	0.05 (33)	–
Acartia spp.	Winter	–0.02 (33)	–	0.17 (33)	–
C.hamatus		–0.09 (33)	–	0.04 (33)	–
Cladocerans		–	–	–	–
P.elongatus		0.71* (34)	0.66* (34)	–0.04 (34)	0.22 (34)
T.longicornis		–0.08 (34)	–	0.59* (34)	–
Acartia spp.	Spring	–0.28 (34)	–	0.66* (34)	–
C.hamatus		–0.04 (34)	–	0.11 (34)	–
Cladocerans		–0.12 (34)	–	0.74* (34)	–
P.elongatus		0.55* (31)	0.14 (31)	–0.39* (31)	–0.40* (31)
T.longicornis		0.16 (31)	–	0.12 (31)	–
Acartia spp.	Summer	–0.35 (31)	–	0.16 (31)	–
C.hamatus		–0.22 (31)	–	0.24 (31)	–
Cladocerans		0.28 (31)	–	0.25 (31)	–
P.elongatus		0.57* (33)	0.64* (33)	–0.27 (33)	0.13 (33)
T.longicornis		0.31 (33)	–	0.13 (33)	–
Acartia spp.	Autumn	0.03 (33)	–	0.28 (33)	–
C.hamatus		0.16 (33)	–	0.27 (33)	–
Cladocerans		0.46* (33)	–	0.10 (33)	–

temperature in the 50 to 100 m layer which were significantly higher in Subdivision 25 than in the other areas. The reason for this is the greater depth in Subdivisions 26 and especially 28, which allowed highly saline water from the North Sea to flow deeper than 100 m. Thus, these water masses do not influence the layer between 50 and 100 m in the more eastern areas as they do in the Bornholm Basin.

Results of the 1-way ANOVA with factor 5 year periods revealed significant differences for mesozooplankton biomasses between the time intervals. The time-trends detected can be explained partly by the hydrographic situation encountered during different periods of the time-series. Correlation analyses showed the biomass of *P.elongatus* to be positively dependent on salinity in all seasons. The dependence on salinity is reflected in the positive development of *P.elongatus* in the 1970s and early 1980s as a result of increased salinities caused by the 1971 and 1975/76 major inflows of saline water from the North Sea. Since the early 1980s, salinity decreased as a result of a lack of inflow events (Matthäus and Schinke, 1994) combined with high precipitation and river run-off (Bergström and Carlsson, 1994). Consequently, biomass of *P.elongatus* decreased in parallel, a development obviously weakened by the 1993 major inflow. The affinity of *P.elongatus* to higher salinity characterizes this species as a typical marine copepod. The positive correlations with biomass indicate the need for a relatively high salinity level for the maturing process at the beginning of the year, as well as for the main reproduction period from March to May (Line, 1979,

1984), and the successful development to the resting copepodite stage 5 at the end of the season. As indicated by the significant negative correlation coefficient, additionally in summer, low temperatures obviously favour the production and development of the younger copepodite stages in the upper water layers, where they concentrate at this time of the year (Sidrevics, 1979, 1984). When considering biomass values of *P.elongatus*, it must be noted that results from new vertically-resolving sampling in the Gdansk Deep and the Gotland Basin revealed that in times of a sufficient oxygen supply (>2 ml l^{-1}) in the Baltic deep basins, a part of the *P.elongatus* population, especially older stages, is distributed deeper than 100 m (CORE, 1998). They are thus not included in the sampling which covered the water column only down to 100 m. The biomass values presented may in these cases be underestimated.

Results of the correlation analysis showed the biomass of *T.longicornis* and *Acartia* spp. to be positively related to temperature in the upper 50 m of the water column in spring. This was apparent especially in the period between 1976 and 1993, when the biomass development, particularly of *Acartia* spp., largely followed the development of the temperature. This confirms the description of the two species in the literature as thermophilic (Corkett and McLaren, 1978; Chojnacki *et al.*, 1984). Although both copepod species have, in the Baltic, long reproduction periods (*T.longicornis*: March–October; *Acartia* spp.: March–December) and up to five (*T.longicornis*) and seven (*Acartia* spp.) generations per year (Line, 1979, 1984), the peak reproduction period is in spring (Line, 1984). Higher temperatures at this time of the year shorten the development time and are thus of advantage for building up the populations. Nevertheless, for the other seasons of the year as well, positive correlations were found, however insignificant, and confirm a positive influence of temperature on the biomass development. No significant relationships could be established between salinity and the biomass of *T.longicornis* and *Acartia* spp. This was not surprising as these species are described as being able to cope with salinities of up to 16 psu (Raymont, 1983; Chojnacki *et al.*, 1984), a situation rarely encountered in the upper water layers of the central Baltic.

No significant correlations between stock biomass and hydrographic variables were found for *C.hamatus*. Nevertheless, in the literature, this copepod is described as thermophilic, similarly to *T.longicornis* and *Acartia* spp. (Ackefors and Hernroth, 1970; Sidrevics, 1984). This is confirmed by the fact that the biomass development of *C.hamatus* was following, to a considerable extent, the temperature time-series, resulting in relatively high correlation coefficients, although not significant, in summer and autumn.

Cladocerans show a clear preference for higher temperatures in the upper layers with a highly significant relationship in spring. Although this taxonomic group constitutes in the present analysis of quite different species with varying preferences, the results nevertheless demonstrate the general affinity for higher temperatures as described in the literature (Chojnacki *et al.*, 1984; Vuorinen *et al.*, 1998). The significant correlation in spring refers to the period when overwintering eggs of cladoceran species start to develop (Sidrevics, 1980, 1984) and hence, warm ambient conditions obviously favour this development. Additionally, a significant

positive correlation was detected for cladocerans and salinity in autumn. This is surprising as most of the cladoceran species are freshwater species. The only species in the Baltic Sea which is described as being able to cope with higher salinities is *E.nordmannii* (Chojnacki *et al.*, 1984). It is nevertheless unlikely that higher salinities favour the development of this species in autumn when cladocerans are in general at the end of their reproduction cycle (Chojnacki *et al.*, 1984).

The present study showed the biomass development of major mesozooplankton species from 1959 to 1997 to be at least partially dependent on hydrographic variables. Whereas *P.elongatus* showed an affinity to higher salinity and lower temperatures, the other copepod species and cladocerans seemed to have a preference for higher temperatures. These different affinities with hydrographic variables obviously caused the change in mesozooplankton species composition during the stagnation period between 1976 and 1993, characterized by a lack of major inflow events. Decreased salinities resulted in drastically declining standing stocks of *P.elongatus*. All other species/taxonomic groups experienced undulating developments due to temperature fluctuations, finally resulting in comparatively high standing stocks in the early 1990s. This change in species composition was also described for other areas of the Baltic. Vuorinen *et al.* found a negative influence of reduced salinities for all neritic copepods in the Northern Baltic, i.e. for *T.longicornis*, *Acartia* spp. and *C.hamatus* (Vuorinen *et al.*, 1998). On the contrary, in the open sea areas of the central Baltic considered here, only *P.elongatus* seemed to be affected by low salinities. The reason for this difference might be generally lower salinities in the Northern Baltic also affecting more tolerant neritic copepods. Ojaveer *et al.* found a similarly high correlation between salinity and *P.elongatus* abundance/biomass in Estonian waters compared with the present work (Ojaveer *et al.*, 1998).

Salinity in the Baltic deeper layers is strongly dependent on the frequency and magnitude of pulses of inflowing water from the North Sea which are linked to the atmospheric circulation patterns (Matthäus and Schinke, 1994). The lack of major inflow events from the late 1970s until 1993 is controversial. Nevertheless, increased zonal atmospheric circulation obviously resulted in increased precipitation and river run-off (Bergström and Carlsson, 1994). By causing abnormal sea levels in the Baltic, the amplified river run-off decreased the frequency and intensity of major inflows in this period (Schinke and Matthäus, 1998). In the upper water layers, the increase of the freshwater component certainly decreased the salinity level. Thus, the decreased standing stock of *P.elongatus* from the middle of the 1980s appeared to be most likely a result of wetter climatic conditions in the area. The development of the other mesozooplankton species/taxonomic groups is also largely driven by the meteorological conditions determining the temperature regime in the Baltic. For example, lowest temperature anomalies since the beginning of the 1980s were associated with the ice winters in 1985 and 1986 (Omstedt and Nyberg, 1996) and contrarily, the period of extremely positive temperature anomalies in the early 1990s coincided with the warmest summers of this century in 1992 and 1994 (Tiesel, 1996). Additionally, when comparing the time-series of non-seasonal temperature anomalies in the upper

50 m with the sums of heat (sum of positive differences between daily average temperatures in summer and twice the yearly average temperature) as presented by Tiesel (Tiesel, 1996), an almost parallel development was apparent. Thus, clearly the meteorological forcing influences the development of the considered species/taxonomic groups by determining the water temperature.

The results of the present study support the hypothesis that the decrease in growth of Baltic herring (*Clupea harengus*) since the early 1980s (Sparholt, 1994) is caused by a changed food environment (Flinkman *et al.*, 1998; Vuorinen *et al.*, 1998). The hydrography-mediated decreased share of *P.elongatus* in the plankton, the main food item of herring (Möllmann and Köster, 1999), has probably contributed to this phenomenon. Since the early 1990s, a decreasing growth of sprat (*Sprattus sprattus*) in the central Baltic (ICES, 1999) has also been observed, which, on the basis of the results of this study, could be explained by the generally low standing stocks of mesozooplankton species during this decade, especially *T.longicornis* which is the main food item of sprat (Möllmann and Köster, 1999). The generally low standing stock of mesozooplankton might be attributed to the still low salinity level for *P.elongatus* and the average low temperatures for the other species/taxonomic groups. However, it may also be a direct result of intensified predation pressure by the drastically increased clupeid stocks, i.e. herring and especially sprat (CORE, 1998). Such a 'top-down control' of planktivorous fish on their prey species has already been postulated for the Baltic (Hansson *et al.*, 1990; Rudstam *et al.*, 1994) and demonstrated for other areas of the world ocean (Shiomoto *et al.*, 1997; Verheye *et al.*, 1998; Verheye and Richardson, 1998). Although the connection between mesozooplankton biomass and clupeid fish needs more thorough investigation, this study demonstrates the close connection between climate, mesozooplankton and clupeid fish in the central Baltic Sea.

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