

The influence of hydrography and
predation by herring (*Clupea harengus*)
and sprat (*Sprattus sprattus*) on
mesozooplankton long-term dynamics in
the Central Baltic Sea

Dissertation

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1. INTRODUCTION

In marine pelagic food webs zooplankton plays an important role in the energy transfer between primary producers and fish populations and is thus a key factor influencing fish production. Cushing's match-mismatch hypothesis points to the importance of the onset and the peak of the plankton production on growth and survival of larvae, and ultimately on the recruitment of fish stocks (Cushing, 1974). Specifically he related the magnitude of the abundance of the copepod *Calanus finmarchicus* to the recruitment success of herring (*Clupea harengus*) (Cushing, 1962, 1967), as well as the gadoids haddock (*Melanogrammus aeglefinus*) and cod (*Gadus morhua*) in the North Sea (Cushing, 1984). Similarly Rothschild (1998) demonstrated the cooccurrence of abundant cod and herring year-classes in the North Sea with either high abundances of *Calanus* or *Paracalanus/Pseudocalanus*. A further example for the dependence of fish stock recruitment on the food supply for fish larvae is Astthorsson et al.'s (1994) significant positive correlation between zooplankton biomass and abundance of 0-group cod in southwestern Icelandic waters. The general importance of *Calanus* populations for the recruitment of Atlantic cod stocks was discussed by Sundby (2000) in relation to temperature and advection.

Besides developmental success of early life-stages, fluctuations in the availability of zooplanktonic food may have an impact on certain population characteristics of planktivorous fish. For example, Verheye (2000) related increases in ovary mass and ovary-free condition of sardines (*Sardinops sagax*) to the long-term increase in abundance of cyclopoid copepods in the Southern Benguela System. A series of studies investigated the effect of the food supply on Cape anchovy (*Engraulis capensis*) in the southern Benguela current (e.g. Hutchings et al., 1998; Peterson et al., 1992; Painting et al., 1998; Plaganyi et al., 2000; Richardson et al., 1998). Variable feeding conditions mainly influenced egg production via ovarian atresia (Painting et al., 1998) as well as growth of juvenile fish (Plaganyi et al., 2000; Richardson et al., 1998).

Also for the major fish stocks in the Central Baltic Sea, zooplankton dynamics are of crucial importance. For example, recent individual-based modelling approaches

demonstrated the dependence of larval survival and consequently recruitment of cod on the dynamics of their main prey species (Hinrichsen et al., submitted). Similarly Köster et al. (in press) related copepod nauplii abundance to a measure of first-feeding cod larval survival. Reduced growth of herring in the Northern Baltic Sea was explained by declining abundances of larger calanoid copepods (Flinkman et al., 1998), and similarly changes in the species composition of the mesozooplankton community have been suggested to influence the growth herring in the Central Baltic basins (Cardinale and Arrhenius 2000; Horbowy, 1997). Also condition and growth of sprat (*Sprattus sprattus*) was found to be positively correlated to zooplankton abundance affecting further sprat egg production (Köster et al., in press). These examples demonstrate the necessity to explore temporal and spatial population dynamics of major zooplankton species, as well as factors governing the dynamics.

Long-term changes in zooplankton biomass were recorded in many areas of the world ocean and have been linked to climate variability (e.g. Aebischer et al., 1990; Roemmich and McGowan, 1995). In the North Atlantic e.g. 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. Karl et al., 1995; McGowan, 1985; Lavaniegos et al., 1998).

Also in the brackish Baltic Sea the hydrographic regime is ultimately controlled by meteorological factors (Dippner et al., 2000; Hänninen et al., 2000). In the central Baltic deep basins (Bornholm Basin, Gdansk Deep, Gotland Basin) (Figure 1.1) 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 on relatively rare occasions 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 runoff (Malmberg and

Svansson, 1982; Launiainen and Vihma, 1990) and air temperature respectively, triggered both also by meteorological conditions.

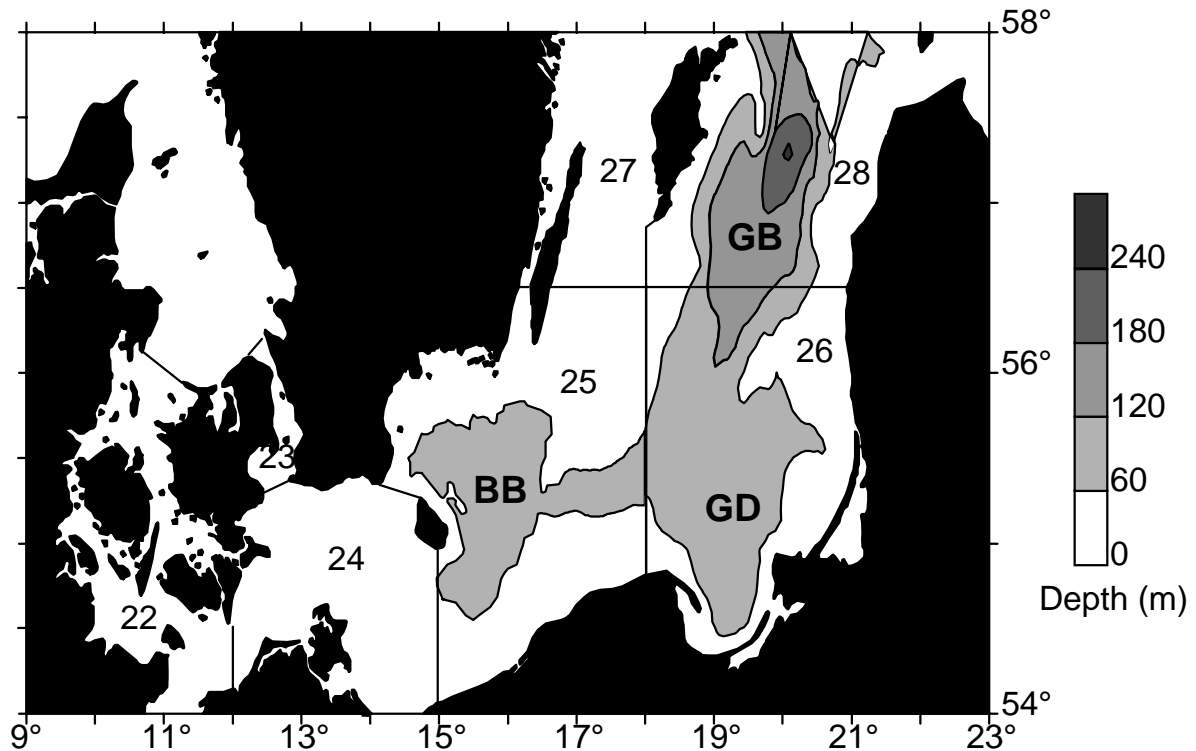


Figure 1.1. Map of the Baltic Sea with deep basins of the Central Baltic in greyscale (BB - Bornholm Basin; GD - Gdansk Deep; GB - Gotland Basin; numbers - ICES Subdivisions).

In the Central Baltic Sea the abiotic environment changed significantly during the last decades. The salinity level decreased due to lacking inflows of North Sea waters (Matthäus and Franck, 1992; Matthäus and Schinke, 1994; Matthäus and Lass, 1995) and increased runoff (Bergström and Carlsson, 1994). Population dynamics of various zooplankton species in the Northern Baltic Sea have been suggested to depend mainly on ambient salinity and temperature conditions (Viitasalo et al., 1995; Vuorinen et al., 1998; Ojaveer et al., 1998). For shallower areas of the Baltic Sea (Gulf of Finland and Gulf of Riga) Ojaveer et al. (1998) demonstrated the mesozooplankton species composition to be related to temperature and salinity. Especially the abundance of

Pseudocalanus elongatus was found to be significantly correlated to salinity. Also for shallow areas of the Northern Baltic, Vuorinen et al. (1998) demonstrated that a reduction of salinity caused by increased river runoff initiated the decline of large neritic copepods and the increase of species with freshwater origin, i.e. cladocerans. They discussed further the same mechanism to be responsible for changes in the mesozooplankton community of the open sea areas of the Central Baltic, investigated in the present study.

Beside hydrography, a trophodynamic control of zooplankton population dynamics through food limitations and/or predation by planktivorous fish may occur. Variability in the quantity and quality of food for mesozooplankton species affecting reproduction and growth (e.g. Berggreen et al., 1988; Lacoste et al., 2001; Campbell et al., 2001; Niehoff and Hirche, 2000; Hirche et al., 1997) is, however, difficult to assess for the Central Baltic Sea due to lacking data series. Nevertheless, the strong eutrophication of the area suggests that food limitations of mesozooplankton species are not very likely (e.g. Hansson and Rudstam, 1990).

Variability in standing stocks of plankton has for long been regarded as unrelated to fish and fisheries in the marine environment (Verheye, 2000), while the importance of those predator-prey interactions were an accepted concept in freshwater ecology (Kitchell and Carpenter, 1993). Recently marine studies increasingly focused on predation effects on zooplankton populations. In the Southern Benguela System decreasing stocks of small pelagic sardines (*Sardinops sagax*) coincided with a long-term increase of their preferential food, i.e. mainly cyclopoid copepods (Verheye and Richardson 1998; Verheye et al. 1998; Verheye 2000). Cury et al. (2000) reviewed indications for top-down control of zooplankton by small pelagics in upwelling areas and found evidence for the effect off South Africa, Ghana, Japan and the Black Sea. Also exploratory correlation analyses of long-term time-series from the North Sea indicated the existence of top-down controls (Reid et al. 2000). For the North Pacific Shiomoto et al. (1997) described inverse year-to-year patterns of pink salmon (*Oncorhynchus gorbuscha*) and macrozooplankton biomass.

Also for the Baltic Sea, planktivory is hypothesized to influence mesozooplankton dynamics, especially causing the late summer/early autumn decline in mesozooplankton biomass (Rudstam et al., 1994). For the Northern Baltic Sea, bioenergetic modelling of herring and sprat (*Sprattus sprattus*) resulted in consumption estimates which elucidated the potential of clupeids to control zooplankton populations, but beside a likely seasonal no interannual effect could be detected (Arrhenius and Hansson, 1993; Rudstam et al., 1994). Consumption estimates for the Central Baltic basins confirmed the lack of association to zooplankton abundance also for this area (Rudstam et al., 1994; Möllmann and Köster, 1999).

The upper trophic levels of the Central Baltic changed during the last 20 years from a cod- to a sprat-dominated system (Schnack, 1997; Köster et al., submitted). The decline of the cod stock due to recruitment failure and high fishing pressure released the sprat stock from predation pressure. The combination with high reproductive success, due to in general favourable temperature conditions enhancing egg and larval survival, resulted in exceptionally high sprat stock sizes in the 1990s (Köster et al., 2001a). This drastic increase in the stock of the planktivorous sprat suggests a strong predation pressure on their food and thus a possible control of the zooplankton dynamics.

In conclusion, mesozooplankton species in the Central Baltic deep basins faced during the last decades marked changes in their abiotic and biotic environment. The aim of this study is thus to investigate (i) the influence of hydrography and (ii) predation by planktivorous clupeid fish on mesozooplankton long-term dynamics.

Target species of the study were calanoid copepods and cladocerans, the dominant species in the open sea areas of the Central Baltic Sea and main food items of planktivorous fish (Möllmann and Köster, 1999). Calanoid copepods are the most important constituent of the plankton in every area of the world ocean, comprising at least 70% of the plankton fauna (Raymont, 1983). In the Central Baltic Sea, *Pseudocalanus elongatus*, *Temora longicornis* and different *Acartia* species are the dominant copepods (Sidrevics, 1979 and 1984). *P. elongatus* is an univoltine species with

peak reproduction in spring, i.e. May (Line, 1979 and 1984). During the summer and autumn mainly copepodites CIV and CV accumulate and form the overwintering stock. *T. longicornis* and *Acartia* spp. differ from *P. elongatus* in that they have multiple generations, in maximum 5 and 7 respectively (Line, 1984). Highest seasonal abundances occur in summer. The two copepods overwinter mainly in CIII-CIV, with the stock being generally low. *T. longicornis* and *Acartia* spp. are known to produce resting eggs. These dormant stages are produced to overcome low winter temperatures (Madhupratab et al., 1996) and are activated in spring due to the rise in temperature. Whereas resting eggs of *Acartia* spp. have been found in the Baltic (Katajisto et al., 1998; Madhupratab et al., 1996; Viitasalo and Katajisto, 1994), *T. longicornis* resting eggs are until now only observed in the North Sea (Lindley, 1986). However, it is very likely that they occur also in the Baltic (Madhupratab et al., 1996).

Cladocerans are usually an important group of crustaceans in fresh waters, while in marine zooplankton they are of comparatively little importance (Raymont, 1983). In the marine environment cladocerans are represented by only three genera, *Penilia*, *Podon* and *Evadne*. The latter two and additionally *Bosmina coregoni maritima* (cf. *B. longispina maritima*), characteristic for dilute estuarine waters, are found in the Baltic Sea (Ackefors, 1971). These crustaceans are extremely seasonal with high densities over short periods, usually in the warm period (Raymont, 1983). The mechanism for reaching extreme population sizes is a rapid parthenogenetic reproduction which is in case of the taxonomic family *Podonidae* (including *Podon* and *Evadne*) accelerated by pædogensis. At the end of the reproductive season cladocerans switch to a gamogenic reproductive mode and produce also diapausing embryos ("resting eggs") which in marine environments usually sink to the bottom. In spring these eggs normally hatch, depending mainly on temperature conditions. For a review see Egloff et al. (1997).

The influence of hydrography on mesozooplankton dynamics was in the present study investigated by relating standing stocks of copepod and cladoceran species to salinity and temperature in different deep basins of the Central Baltic Sea. For a further identification of population dynamics processes possibly influenced by a variable

physical environment, time-trends in stage-specific abundance of copepods were investigated concentrating on the best covered area, i.e. the Gotland Basin. To investigate the **influence of predation** the seasonal and interannual predation pressure by herring and sprat on copepod populations in the Gotland Basin was determined by comparing copepod production and fish consumption rates according to species/stages. Further, mortality rates were computed for copepod species/stages identified to suffer significantly from predation. As cladocerans are an important prey item only for sprat (Möllmann and Köster, 1999), the predatory influence on major cladoceran species was investigated for this fish species only. Sprat consumption rates were therefore related to cladoceran production rates. As a prerequisite for these investigations, reliable estimates of predator abundances in a given subarea of the Central Baltic Sea were needed. To derive this, Multispecies Virtual Population Analyses (MSVPA) have been performed based on an extensive recompilation of international catch-data (ICES, 1997a) and thoroughly validated by using independent information on stock developments. A further basis for the present study were long-term time-series on (i) abundance of Baltic mesozooplankton species, (ii) salinity and temperature and (iii) stomach contents of clupeid fish. These were compiled by the *Latvian Fisheries Research Institute* (LATFRI) in Riga within the frame of the EU-Project BASYS (www.io-warnemuende.de/Projects/Basys/en_home.htm).

2. MATERIAL AND METHODS

2.1. The influence of hydrography

The first part of the present study addresses the influence of hydrography on mesozooplankton long-term dynamics. First, an analysis of the spatio-temporal variability of the total biomass of the copepod species *P. elongatus*, *T. longicornis*, and *Acartia* spp. was performed. Following this, detailed stage-specific abundance data according to copepod species was used to study the temporal variability in stage-structure dynamics. For cladocerans, a detailed analysis of the spatio-temporal variability was conducted on the species level, i.e. *B. coregoni maritima*, *E. nordmanni* and *Podon* spp.

2.1.1. Salinity and temperature

Hydrographic information was available from LATFRI derived on various seasonal cruises in the period 1961 to 1997 and different stations in the Central Baltic (Table 2.1.1 and Figure 2.1.1). Salinity (psu) was measured either by the Knudsen Method (until 1992) or with an Inductivity Salinometer (since 1993). Temperature (°C) was recorded by using a water sampler (Nansen type; 1l capacity) and a Deep Sea Reversing Thermometer in 5 or 10m steps.

Table 2.1.1. Number of stations covered per season for hydrography and mesozooplankton in ICES Sub-divisions (SD) in the period 1959 to 1997.

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

Average values of hydrographic parameters were calculated for the depth range 0 – 50m, being the water layer mainly inhabited by *T. longicornis* and *Acartia* spp. as well as cladocerans (Sidrevics, 1979 and 1984). As *P. elongatus*, especially older stages show a

deeper distribution (Sidrevics, 1979 and 1984), for this species also the layer between 50 – 100m was considered.

2.1.2. Copepod and cladoceran standing stocks

Standing stocks of major mesozooplankton species in the central Baltic Sea were recorded by LATFRI during seasonal surveys, i.e. mainly in February, May, August and November (further on called winter, spring, summer and autumn respectively) conducted in 1959 to 1997. Sampling was performed mostly at daytime using a Jedy Net (UNESCO Press, 1968) operating vertically with a mesh size of 160 μ m and an opening diameter of 0.36m. The gear is considered to quantitatively catch all copepodite stages as well as adult copepods, whereas nauplii may be underestimated (Hernroth, 1979).

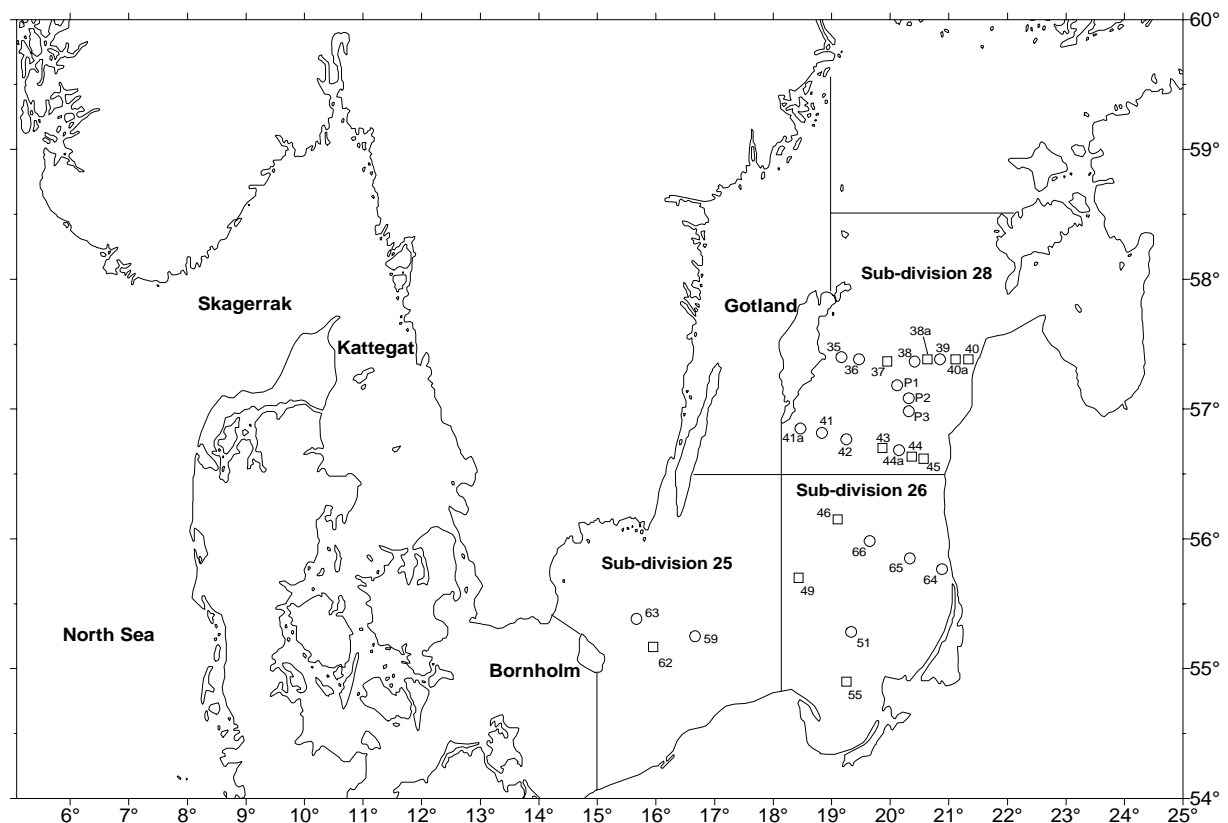


Figure 2.1.1. The Baltic Sea with ICES Sub-divisions 25, 26 and 28 as well as stations covered (○ - zooplankton sampling only; □ - zooplankton sampling and hydrographic measurements).

For sample analysis, a sample was divided in two subsamples and the number of a certain copepod species and stage was determined. A mean value was calculated from

both subsamples to derive the number per m³. To estimate the biomass of each species/stage per m³, standard weights were applied (Hernroth, 1985).

Data on major mesozooplankton species were considered in the present analysis, i.e. calanoid copepods *P. elongatus*, *T. longicornis* and *Acartia* spp. (including *A. bifilosa*, *A. longiremis* and *A. tonsa*) as well as cladocerans *B. coregoni maritima*, *E. nordmanni* and *Podon* spp. (including *P. polyphemoides*, *P. leuckarti* and *P. intermedius*). From copepods nauplii (N), copepodites I to V (CI-CV) as well as adult females (CVI-f) and males (CVI-m) were identified in the samples.

2.1.3. Numerical analyses

2.1.3.1. Spatio-temporal variability in biomass of copepod species

A first step in the analysis was the investigation of the spatio-temporal variability in the total biomass of copepod species. Therefore either hydrographic data and copepod biomasses 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 (Figure 2.1.1). For numbers of stations included in the analysis per area and season see Table 2.1.1.

Biological and physical data were normalized by transforming to natural logarithms. The seasonal cycle was removed by subtracting long-term quarterly means from annual quarterly means. Resulting non-seasonal anomalies were grouped to 5-year periods and subareas for performing a 2-way analysis of variance (ANOVA). For Post-hoc tests to distinguish differences between single means the Newman-Keuls-Test was used. For correlation analysis of non-seasonal anomalies among variables Pearson product-moment correlation analysis was utilized excluding dates with lacking data of one or the other variable.

To account for autocorrelation in the data we adjusted the degrees of freedom (d.f.) in the statistical tests using the equation by Chelton (1984), modified by Pyper and Peterman (1998):

$$\frac{1}{N^*} = \frac{1}{N} + \frac{2}{N} \sum_j r_{XX}(j)r_{YY}(j) \quad (1)$$

where N^* , is the “effective number of degrees of freedom” on the time-series X and Y , N is the sample size and $r_{XX}(j)$ as well as $r_{YY}(j)$ are the autocorrelation of X and Y at lag j . The latter were estimated using an estimator by Box and Jenkins (1976):

$$r_{XX}(j) = \frac{\sum_{t=1}^{N-j} (X_t - \bar{X})(X_{t+j} - \bar{X})}{\sum_{t=1}^N (X_t - \bar{X})^2} \quad (2)$$

where \bar{X} is the overall mean. Approximately $N/5$ lags were applied in Eq. (1) which ensures the robustness of the method (Pyper and Peterman, 1998).

2.1.3.2. Temporal variability in stage-specific abundance of calanoid copepods

For the investigation of temporal variability in population dynamics of calanoid copepods stage-specific abundance data were calculated for the combined area of ICES Subdivisions 26 and 28, i.e. the Gdansk Deep and Gotland Basin (Figure 2.1.1). Data were also log-transformed and missing values in the original time-series were interpolated using a linear trend regression (Statsoft, 1996). Principal component analyses (PCA) for classification (Le Fevre-Lehoerff et al., 1995) were conducted in order to investigate (i) differences in the time trends between the different copepod stages, and (ii) associations between specific stages and salinity and temperature. PCA summarizes in a few

dimensions (i.e. principal axes) most of the variability of a large number of descriptors (e.g. Fromentin et al., 1997; Legendre and Legendre, 1984). One PCA was performed for every season and species on the covariance matrices of the log-values with 8 biological descriptors (stages N, CI, CII, CIII, CIV, CV, CVI-f, CVI-m) as well as salinity and temperature as supplementary variables. Associations between the variables were displayed by correlations among the first two principal components.

Additionally, correlation analyses were performed as described above for the main reproduction periods, i.e. spring for *P. elongatus* as well as spring and summer for *T. longicornis* and *Acartia* spp.

2.1.3.3. Spatio-temporal variability in abundance of cladoceran species

The study of the spatio-temporal variability in abundance of cladoceran species was performed for ICES Sub-divisions 26 and 28 separately. It thus concentrated on the subareas with the best temporal and spatial data coverage (Table 2.1.1 and Figure 2.1.1.). Also for this analysis data were log-transformed and missing values were interpolated using a linear trend regression (Statsoft 1997). The different types of time-series were compared by linear regression analysis as described above.

2.2. The influence of clupeid predation

This section investigates the influence of clupeid predators herring and sprat on the population dynamics of mesozooplankton species in the Gotland Basin, the area for which the best data sets were available. The approach to study the seasonal and interannual predation pressure by the clupeid predator populations on copepod populations was to compare production and fish consumption rates according to species/stages. Further mortality rates were computed for copepod species/stages identified to suffer significantly from predation.

As cladocerans are an important prey item only for sprat (Möllmann and Köster, 1999), the predatory influence on major cladoceran species was investigated for this fish species only. Sprat consumption rates were therefore related to cladoceran production rates.

As a prerequisite for these investigations, reliable estimates of predator abundances in a given subarea of the Central Baltic Sea were needed. To derive this, Multispecies Virtual Population Analyses (MSVPA) have been performed and thoroughly validated by using independent information on stock developments.

2.2.1. Clupeid abundance

Multispecies Virtual Population Analysis (MSVPA) has been applied addressing the biological interactions between fish stocks in the North Sea (Pope, 1991; Stokes, 1992) and the Baltic (Sparholt, 1991 and 1994). Sparre (1991) and Magnusson (1995) present the theory and methods employed in the MSVPA as well as underlying assumptions. The model considers predation by specific piscivores on their major fish prey species as biological interactions affecting the population dynamics of the prey stocks. In the Central Baltic, cod, herring and sprat are the most important fish species and are presently the only species incorporated into the MSVPA (Sparholt, 1994). Cod is assumed to be the top predator in the system exhibiting cannibalistic behaviour, while herring and sprat are treated as prey species. These interactions are based on the analyses of over 62 thousand cod stomach contents, the majority of samples originating from ICES Sub-

divisions 25, 26 and 28 in the Central Baltic (Figure 2.1.1), collected during the period from 1977-1993 and compiled by ICES (1997a).

Within the Central Baltic, the abundance and biological characteristics of the three species are heterogeneous both spatially (between Sub-divisions) and temporally (inter- and intra-annually). For example, population sizes of Central Baltic cod, as resolved by international bottom trawl (Sparholt and Tomkiewicz, 2000) and ichthyoplankton surveys (Köster et al., 2001a), have revealed distinct distributional trends. Furthermore, for cod substantial differences in weight at age and maturity ogives have been reported for different Sub-divisions (ICES, 1997a; Tomkiewicz et al., 1997). The abundance and characteristics of herring and sprat have also been observed to vary spatially and temporally in the different Sub-divisions of the Central Baltic (e.g. Ojaveer, 1989). The herring stock in the Central Baltic is comprised of a number of different spawning components exhibiting variations in spawning period and growth rates as well as meristic, morphometric and otolith characteristics (e.g. Ojaveer, 1981; Parmanne et al., 1994). For sprat the existence of distinct populations is controversial as deviations in growth rates observed between sub-areas have been explained by immigration from the western Baltic and by migration between different basins (Parmanne et al., 1994). However, other authors state that sprat in the eastern Central Baltic form local populations (Ojaveer, 1989), which can be separated, primarily by otolith characteristics (Aps et al., 1981).

In this study, as a prerequisite to estimate the predation pressure of herring and sprat on mesozooplankton species, area dis-aggregated MSVPA runs were conducted to resolve the dynamics of cod, herring and sprat sub-populations in the different Sub-divisions (Figure 2.1.1) corresponding roughly to the Central Baltic basins (Ojaveer and Elken, 1995).

Resolution of a number of issues is necessary before determining the applicability of the area dis-aggregated MSVPA approach. First is the validation of the area dis-aggregated MSVPA results with respect to temporal trends in abundance and biomass of cod, herring and sprat. In order to address this issue, results from trawl and

hydroacoustic surveys are compared to the MSVPA output. Secondly, the impact of migration on population abundance may invalidate the approach. This issue is addressed by examining the relative horizontal distributions between Sub-divisions as determined by area dis-aggregated MSVPA and research surveys. Finally, in order to assess the estimates relative to existing information of stock fluctuations, population sizes derived by the MSVPA runs were integrated over Sub-divisions 25, 26 and 28 and compared to standard ICES stock assessments (ICES, 1998).

2.2.1.1. Area dis-aggregated MSVPA parameterisation

Cod, herring and sprat in Sub-divisions 25, 26 and 28 (Figure 2.1.1) were assumed to be unit stocks composed of the age-groups 0 to 9 for cod and herring and 0 to 7 for sprat with the oldest age-groups not handled as plus-groups. Quarterly catch at age in numbers and weight at age in the catch were utilised for the different Sub-divisions for years 1977-1992 as revised by ICES (1997a) with inputs for 1993-1996 based on national data reported to ICES (1997b).

Estimates of cod predation on herring and sprat as well as of cannibalism are based on quarterly cod stomach content data by Sub-division as revised in ICES (1997a). Average age-specific quarterly consumption rates were estimated by Sub-division as described in ICES (1999a). The residual natural mortality rate was assumed to be 0.2 per year, equally distributed over quarters, corresponding to standard MSVPA runs in the Baltic (Sparholt, 1991). Suitability coefficients of prey species age-groups as food of specific predator age-groups (Sparre, 1991) were estimated according to the standard suitability sub-model implemented in the Baltic MSVPA (ICES, 1997a). The tuning of the MSVPAs was performed by iteratively running Extended Survivor Analyses (Shepherd, 1999) and MSVPAs exchanging updated terminal F and predation mortalities until convergence was achieved (Vinther, 2001). Abundance indices utilized for tuning originated from the international bottom trawl survey directed to cod, performed annually in February/March (Sparholt and Tomkiewicz, 2000) and the international hydroacoustic

survey directed to herring and sprat, conducted annually in September/October (ICES, 1998).

2.2.1.2. Validation of area dis-aggregated MSVPA results

In order to assess the feasibility of employing the area dis-aggregated MSVPA for resolving temporal trends of stock abundance in the different basins, results from the model are compared to trawl and hydroacoustic surveys estimates. Data from these sources fall into two categories, those being data used to tune the area dis-aggregated MSVPA thus non-independent, and data not employed for tuning purposes. The international surveys utilised for tuning, although having an impact on the MSVPA results during the later part of the time series, have a reduced effect on the outputs back in time. This feature makes these data valid for a comparison of trends for a major part of the time series.

As a second mode of validation, independent population size indices are available from other research surveys, e.g. directed to spawning concentrations and young fish abundance. These indices although independent are typically not focused on monitoring population sizes and hence are of a lower quality than the non-independent data designed for this task. For the purposes of validation however these sources are applicable for examining trends in abundance.

The third method of validation involves the temporal coherence of population abundance and structure in the various basins. The comparison of relative horizontal distributions and corresponding age structures of the different sub-populations from area dis-aggregated MSVPA runs and corresponding research surveys will validate the suitability of the approach regarding age specific migration between Sub-divisions.

Finally, spawning stock sizes and recruitment derived by the area-disaggregated MSVPAs were summed over Sub-divisions 25, 26 and 28 and compared to corresponding estimates from the standard stock assessment for the Central Baltic. These are comparable as the standard assessment utilises predation mortalities from area aggregated MSVPAs as input. This exercise resolves whether the approach of running a

suite of independent MSVPAs generates robust results when compared to the best available information on stock development.

2.2.2. Clupeid fish consumption

Herring and sprat were sampled by pelagic trawling on research cruises by LATFRI. Sampling was performed during daytime only, which corresponds to the diurnal feeding time of clupeids in the area (Köster and Schnack, 1994). Stomach content data gathered in different months during the period 1977 to 1996 were aggregated to quarters. For every copepod species, groups of developmental stages (CII, CIII/IV, and CV/VI) were identified in the stomachs. A fixed number of stomachs was randomly taken from each sampled station, thus no weighting according to the length-frequency distribution of the clupeid stocks was necessary. The numbers of stomachs analysed per year and quarter are given in Table 2.2.1. Missing values in specific seasons of specific years were interpolated using a linear trend regression (Statsoft, 1996).

Based on these data obtained from LATFRI, individual daily rations (F_T) of herring and sprat within a season were calculated by using an exponential form of the general model of gastric evacuation (Tyler, 1970; Jones, 1974) which incorporates the actual ambient temperature as a variable (Temming, 1996):

$$F_T = R' \times S \times T \times e^{(A \times C)} + S_t - S_0 \quad (3)$$

where R' is a food type constant, S is stomach content, T is duration of the feeding period, A is a temperature coefficient, C is ambient temperature, and S_t the average stomach content at the end as well as S_0 the average stomach content at the beginning of the feeding period. A detailed description of the evacuation model and the parameter values and sources is given in Möllmann and Köster (1999).

Multiplying daily rations per fish with predator abundance from the MSVPA runs, finally resulted in seasonally time-series of daily consumption rates by both clupeid populations. For a comparison with production rates, these were scaled to values per m^2

($38.4 * 10^9 * m^{-2}$ for the central Gotland Basin; personal communication: Hans-Harald Hinrichsen, Institute of Marine Sciences, Kiel, Germany.)

Table 2.2.1. Number of copepod/cladoceran sampling stations (winter only used for copepods), as well as herring and sprat stomachs (only sprat used for cladocerans) included in the diet composition analysis for the investigation of a predatory effect in the Gotland Basin.

year	Copepods/Cladocerans				Herring				Sprat			
	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
1977	4	8	8	2	250	90	25	96	90	65	45	70
1978	3	4	3	6	75	166	200	-	60	148	273	-
1979	-	-	4	9	20	40	80	-	-	80	317	-
1980	5	4	8	2	150	235	39	80	80	155	60	-
1981	2	5	7	5	62	75	110	40	-	170	222	-
1982	4	8	7	6	55	103	73	-	10	125	383	-
1983	2	2	5	3	131	183	231	98	126	161	80	29
1984	3	4	6	3	-	-	-	-	78	208	190	-
1985	4	5	7	2	309	30	240	-	130	110	98	-
1986	3	5	10	1	128	448	309	492	29	395	192	-
1987	3	4	7	8	-	-	317	-	-	211	114	284
1988	3	9	10	2	386	79	191	199	511	178	47	89
1989	5	8	6	4	172	238	239	38	208	242	162	19
1990	2	9	7	5	118	230	129	47	236	261	272	-
1991	2	7	4	-	-	-	-	-	-	-	-	50
1992	2	-	-	-	32	-	-	-	57	97	78	180
1993	-	9	-	5	20	-	-	60	-	-	70	-
1994	4	7	3	4	100	77	63	103	118	104	205	122
1995	2	7	5	5	-	95	89	59	90	65	45	70
1996	4	8	13	6	44	-	150	136	60	148	273	-

(- no sampling)

2.2.3. Copepods

2.2.3.1. Abundance and vertical distribution

Data on copepod abundance were sampled as described in Chapter 2.1.2. The investigation of a predation effect by clupeids on copepod populations concentrated on the Gotland Basin, and LATFRI stations 35 to 46 and P1-3 were used in the analysis (Figure 2.1.1). Due to the availability of fish feeding data, the analysis was restricted to the period 1977 to 1996 (see Chapter 2.2.2). For numbers of stations included per year and season see Table 2.2.1. Missing values in specific seasons of specific years were interpolated using a linear trend regression (Statsoft, 1996). To match the stomach content analysis scheme (see Chapter 2.2.2), copepod life-stages were grouped to CII, CIII/IV and CV/VI.

The vertical distribution of the copepods was used to compute the weighted mean depths (WMD; e.g. Bollens and Frost, 1989) per season and year:

$$WMD = (\sum n_i d_i) / \sum n_i \quad (4)$$

where n_i is the abundance ($n \cdot m^{-3}$) in each stratum with the midpoint d_i . Average seasonal WMDs over the whole covered period were determined from years with a sufficient vertically resolving sampling, i.e. in 10m depth intervals. As the samples were taken mainly by daylight, an investigation of diurnal vertical migrations (DVM) of copepods (e.g. Bollens and Frost, 1989) could not be performed.

2.2.3.2. Development times and production

Assuming non-limiting food conditions, copepod production per developmental stage was calculated using quarterly abundances in Edmondson and Winberg's (1971) equation:

$$P_i = N_i \times \Delta w_i / D_i \quad (5)$$

where P_i is the daily potential production of stage i (wet weight), N is the abundance of stage i ($n \cdot m^{-2}$), Δw_i is the weight increase of stage i (wet weight), D_i is the development time of stage i (days^{-1}) and i the development stage. Season specific wet weights of the copepodite stages (CII to CV) and adults (CVI) were taken from Hernroth (1985).

D_i of developmental stages were computed using Belehrádek's temperature function (1957):

$$D_i = a(T - \alpha)^{-b} \quad (6)$$

where a for single copepodite stages is 3044, 1466 and 1288 and α is 13.9, 10.4 and 10.5 for *P. elongatus*, *T. longicornis* and *Acartia* spp. respectively and b is 2.05, all estimated by McLaren (1978 – for *T. longicornis* and *Acartia* spp.) and McLaren et al. (1989 – for *P. elongatus*), with T being the ambient temperature (°C). Seasonal data on average species/stage specific temperatures in WMDs (vertical distribution) were measured on LATFRI stations 37, 38a, 40, 40a, 43, 44, 45, 46 (Fig. 2.1.1). Production rates of adult females, i.e. egg production, were estimated by using the P/B ratio computed for CV, whereas consequently adult males were assumed to have 0 production (Hansson et al., 1990).

2.2.3.3. Copepod mortality

Seasonal data on copepod abundance allowed only a vertical life table approach to estimate daily mortality rates (Aksnes and Ohman, 1996). As only open localities were investigated, this approach has the advantage that estimates were not biased by advection or other sources of horizontal patchiness. The method assumes that the daily recruitment rate to a stage i is constant over a time corresponding to the duration of that specific stage (D_i), the duration of a stage is the same for all individuals, and that the mortality for the period D_i can be expressed by a single constant rate. Further it is assumed that stage abundances are sampled without bias through stage-specific efficiency of the gear and/or transport processes, and that the mortality rate is equal for a period corresponding to the duration of two consecutive stages ($D_i + D_{i+1}$). A mortality estimate is then derived for two consecutive stages:

$$\left[e^{(d_i D_i)} - 1 \right] / \left[1 - e^{(-d_i D_{i+1})} \right] = f_i \quad (\text{two juvenile stages}) \quad (7)$$

and

$$d_{q-1} = \ln(f_{q-1} + 1) / D_{q-1} \quad (\text{juvenile and adult stage}) \quad (8)$$

where $d_{i+1} = d_i$ (and $d_q = d_{q-1}$) is the common mortality rate for the two stages analysed, D_i is the development time of stage i , $f_i = n_i/n_{i+1}$ where n_i is the abundance of individuals in development stage i , and q denotes the final stage which individuals are leaving by dying only (Aksnes and Ohman, 1996; Aksnes et al., 1997).

2.2.4. Cladocerans

2.2.4.1. Cladoceran biomass

Data on copepod were sampled as described in Chapter 2.1.2. As biomass values were needed for the estimation of production rates (see Chapter 2.2.4.2), abundance data were converted to biomass using standard weights (Henroth, 1985). As for copepods, the investigation of a predation effect by clupeids on cladoceran populations concentrated on the Gotland Basin, and LATFRI stations 35 to 46 and P1-3 were used in the analysis. (Fig. 2.1.1). Due to the availability of fish feeding data, the analysis was restricted to the period 1977 to 1996 (see Chapter 2.2.2). For numbers of stations included per year and season see Table 2.2.1. As cladoceran are not present in the water column in winter, only data from the other seasons were used. Missing values in specific seasons of specific years were interpolated using a linear trend regression (Statsoft, 1996).

2.2.4.2. Cladoceran production

Rates of daily production by the different cladoceran species was estimated using an empirical relationship by Kankaala et al.(1984) derived for *B. coregoni maritima* in the Bothnian Bay (Northern Baltic):

$$P/B = 0.007 \times T - 0.012 \quad (9)$$

where P is the daily production (wet weight), B is the biomass (wet weight * m^{-2}) and T is temperature. As cladocerans concentrate in shallow water areas (Sidrevics, 1979 and 1984), the average temperature of the 0-25m depth layer was used for the calculation of production rates.

3. RESULTS

3.1. The influence of hydrography

3.1.1. Salinity and temperature

Mean salinities in the upper water layer (0-50m) showed almost no seasonal variation in all subareas with long-term quarterly means of 8.0, 7.6 and 7.5 psu for Sub-divisions 25, 26 and 28 respectively (Table 3.1.1.1). The same seasonal stability is visible for the deeper layers (50-100m), characterised by average salinities of 14.6, 9.7 and 9.1 psu (Table 3.1.1.1). A clear seasonality is obvious for the temperature in the upper depth range with maximum values regularly in summer (> 11 °C) and minimum values in winter (~ 2 °C). On the contrary, temperature in the deeper waters exhibited not such a pronounced seasonal development, but a clear difference between Sub-division 25 with on average 6.3 °C compared to 4.3 and 4.0 in Sub-divisions 26 and 28 respectively (Table 3.1.1.1).

Table 3.1.1.1. Long-term seasonal means (\pm standard deviation) for hydrographic variables (in °C) in ICES Sub-divisions (SD).

Variable	SD	Winter	Spring	Summer	Autumn
Salinity 0-50m	25	8.11 \pm 0.07	8.00 \pm 0.06	7.96 \pm 0.06	8.04 \pm 0.08
	26	7.73 \pm 0.12	7.65 \pm 0.01	7.61 \pm 0.01	7.58 \pm 0.01
	28	7.63 \pm 0.01	7.53 \pm 0.01	7.46 \pm 0.01	7.45 \pm 0.01
Salinity 50-100m	25	14.63 \pm 0.23	14.52 \pm 0.20	14.63 \pm 0.24	14.57 \pm 0.18
	26	9.88 \pm 0.06	9.64 \pm 0.06	9.51 \pm 0.06	9.71 \pm 0.06
	28	9.22 \pm 0.05	9.11 \pm 0.05	9.03 \pm 0.04	9.14 \pm 0.05
Temperature 0-50m	25	2.05 \pm 0.13	5.24 \pm 0.19	11.47 \pm 0.47	9.33 \pm 0.21
	26	2.21 \pm 0.05	4.84 \pm 0.09	11.07 \pm 0.25	9.18 \pm 0.13
	28	1.95 \pm 0.03	4.62 \pm 0.06	11.46 \pm 0.15	9.18 \pm 0.07
Temperature 50-100m	25	6.68 \pm 0.18	5.32 \pm 0.17	6.01 \pm 0.13	7.28 \pm 0.15
	26	4.44 \pm 0.05	4.05 \pm 0.05	3.95 \pm 0.05	4.59 \pm 0.07
	28	3.79 \pm 0.040	3.78 \pm 0.04	3.79 \pm 0.04	4.50 \pm 0.07

Non-seasonal anomalies of salinity (Figures 3.1.1.1 and 3.1.1.2) show in general the same interannual developments in all three considered Sub-divisions, but with a noticeable higher variability in the Bornholm area. In the upper water layers (0-50m)

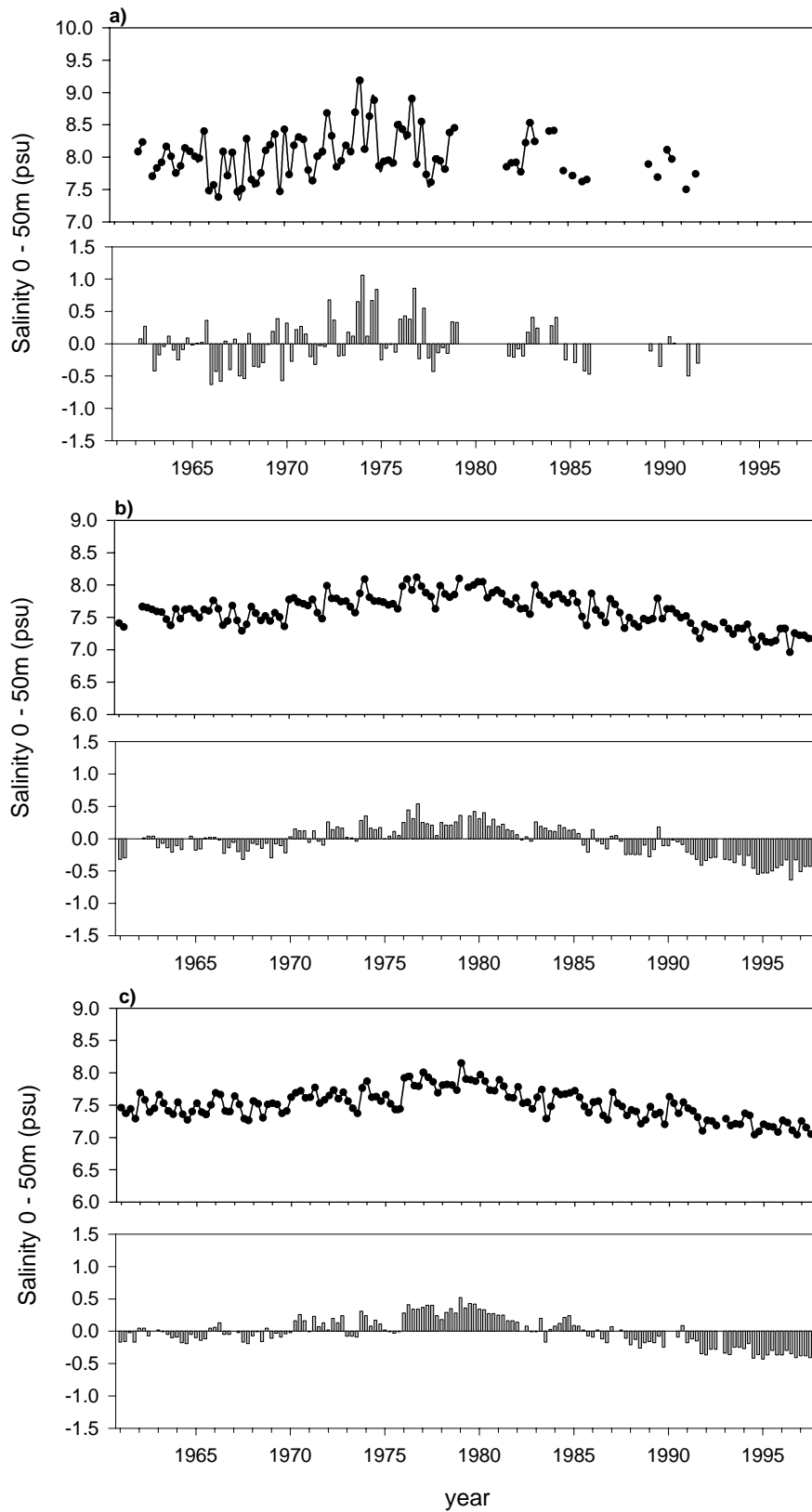


Figure 3.1.1.1. Time-series of quarterly means (above) and non-seasonal anomalies (below) of salinity in the layer of 0-50m in ICES Sub-divisions 25 (a), 26 (b) and 28 (c) in the period of 1961 to 1997.

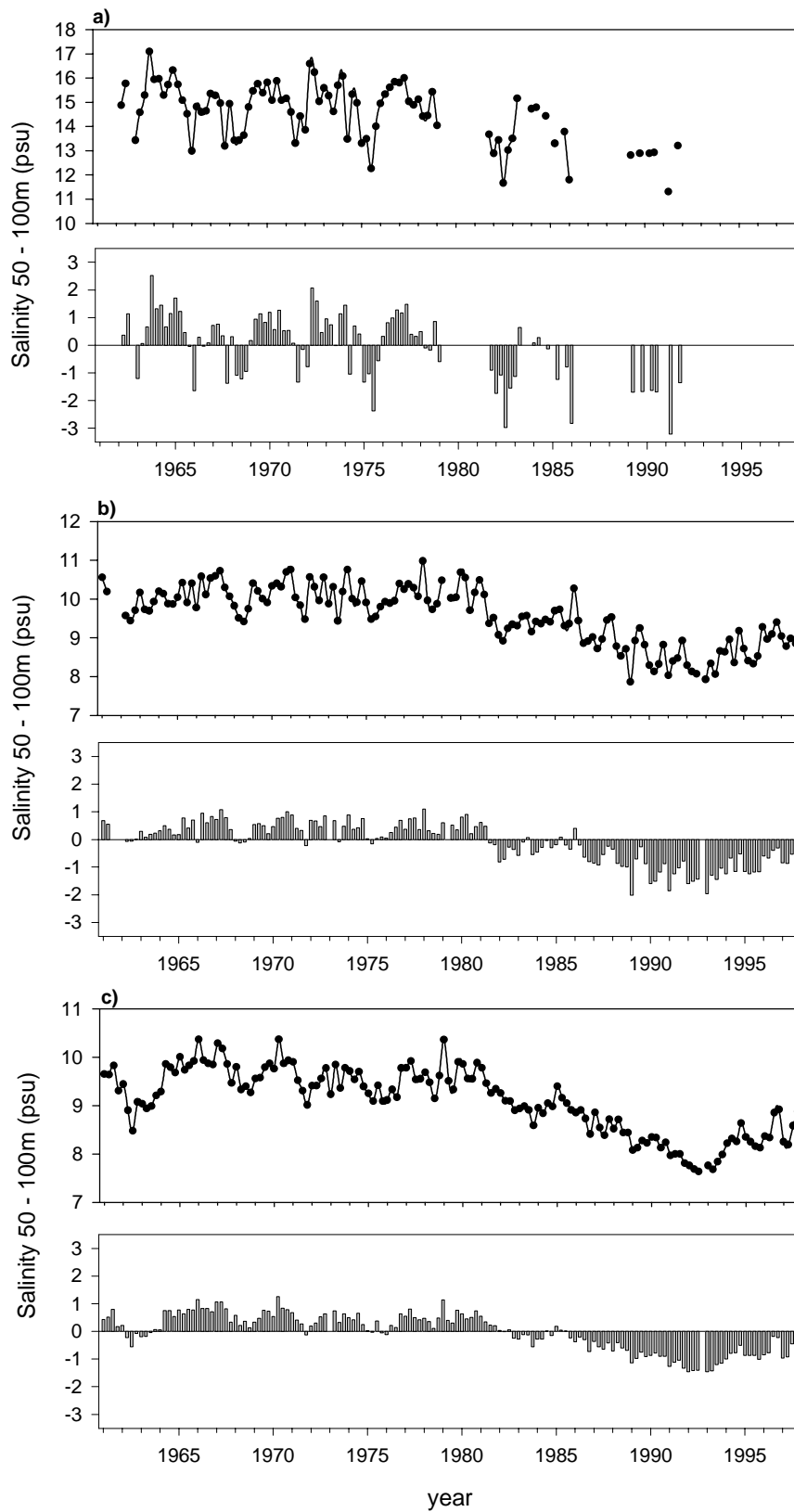


Figure 3.1.1.2. Time-series of quarterly means (above) and non-seasonal anomalies (below) of salinity in the layer of 50-100m in ICES Sub-divisions 25 (a), 26 (b) and 28 (c) in the period of 1961 to 1997.

negative anomalies of salinity were found in the 1960s. Increasing salinities were regularly recorded after the major Baltic inflows in 1969, 1971 and 1975/76 (Matthäus and Franck, 1992). During the 1980s a clear negative trend in all central Baltic areas is obvious, which lasts still in the 1990s. The deeper water layers (50-100m) exhibited similar interannual developments in salinity, but showing obviously a more pronounced response to inflow events. In contrast to the upper water layers, positive anomalies were found in the 1960s.

In all subareas negative anomalies of temperature were found in the layer of 0-50m until the mid 1960s (Figure 3.1.1.3). An in general positive trend is then visible until the middle of the 1970s. During the period between the end of the 1970s to the beginning of the 1990s, a wavelike development was recorded, ending up in highest positive anomalies in the early 1990s. In the 50-100m layer (Figure 3.1.1.4) all subareas showed increasing temperature anomalies until the early 1970s and afterwards negative ones until 1989. Positive anomalies turned then again negative after 1993.

Table 3.1.1.2. Means of non-seasonal anomalies for hydrographic variables (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.

<i>Variable</i>	1960- 64	1965- 69	1970- 74	1975- 79	1980- 84	1985- 89	1990- 94	1995- 97	F	P
Salinity 0-50m	-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
Salinity 50-100m	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
Temperature 0-50m	-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
Temperature 50-100m	-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

2-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 (0-50m: $F = 3.75$, $p = 0.03$; 50-100m: $F = 8.98$, $p < 0.001$). To match the statistical analysis of mesozooplankton (see Chapter 3.1.2.1.) also an additional 1-way ANOVA was calculated aggregating areas and including the 1990s (Table 3.1.1.2).

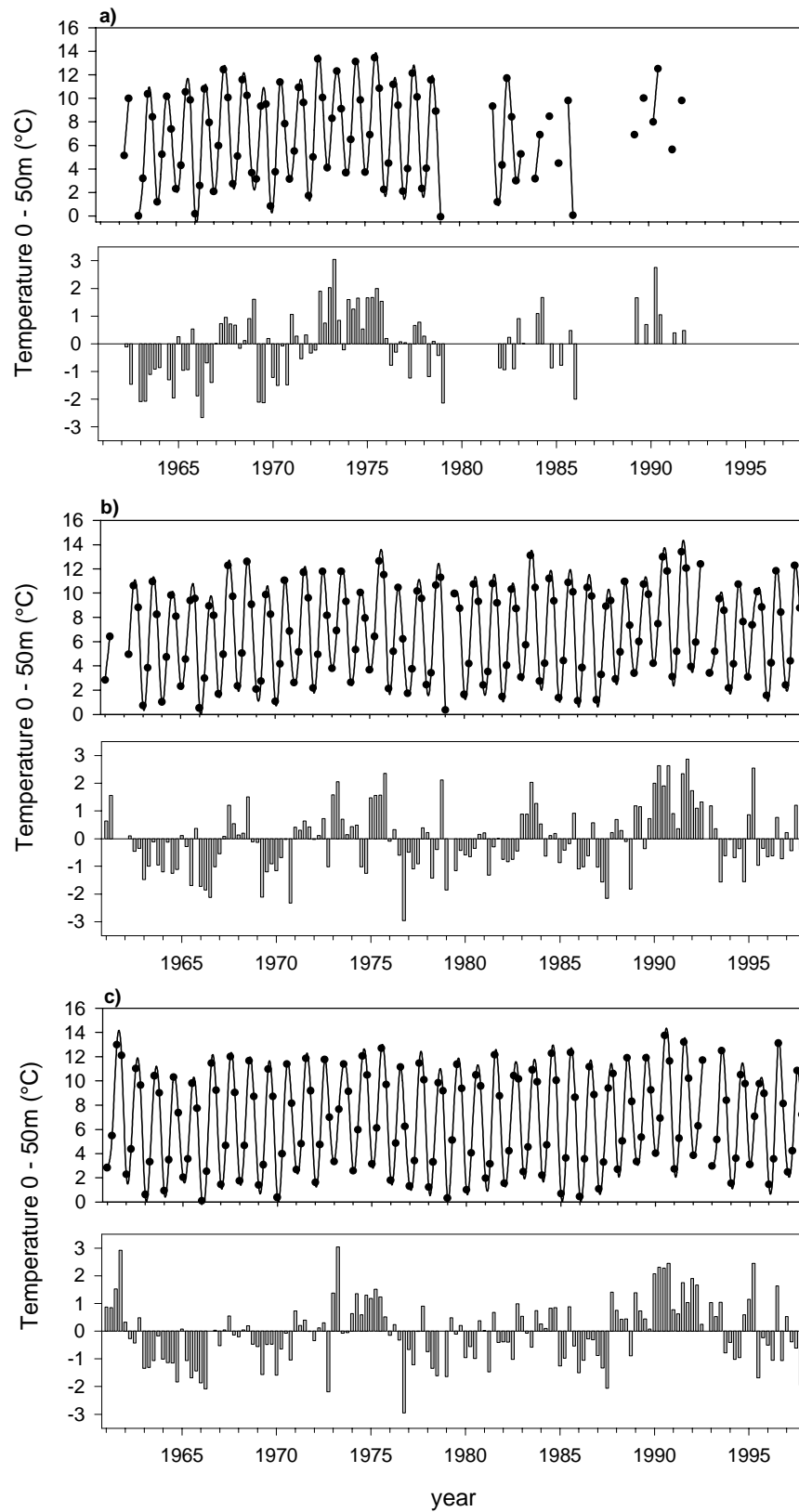


Figure 3.1.1.3. Time-series of quarterly means (above) and non-seasonal anomalies (below) of temperature in the layer of 0-50m in ICES Sub-divisions 25 (a), 26 (b) and 28 (c) in the period of 1961 to 1997.

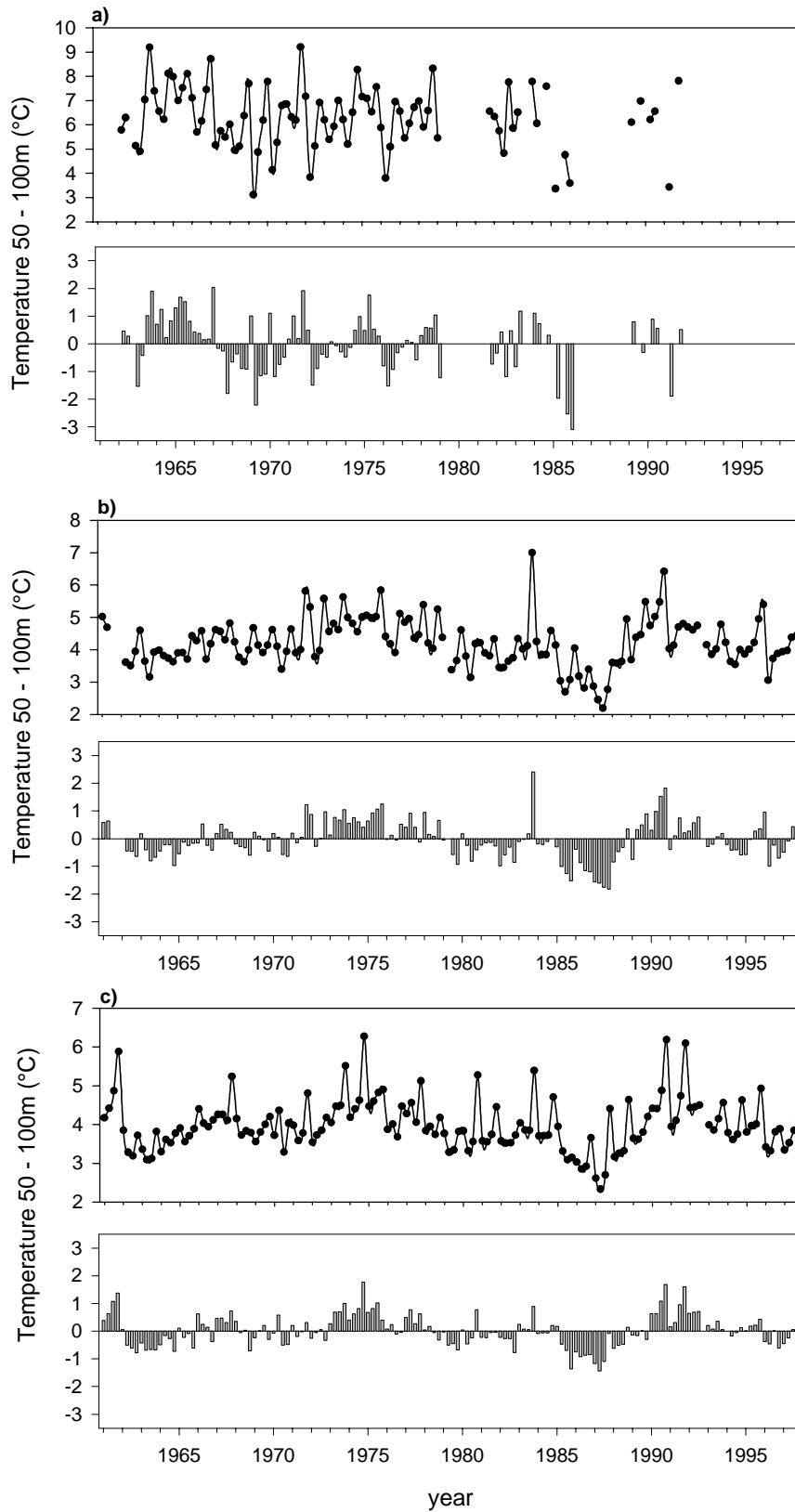


Figure 3.1.1.4. Time-series of quarterly means (above) and non-seasonal anomalies (below) of temperature in the layer of 50-100m in ICES Sub-divisions 25 (a), 26 (b) and 28 (c) in the period of 1961 to 1997.

Posthoc-tests indicate a negative trend in salinity in both layers with significantly lowest 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.

3.1.2. Spatio-temporal variability in biomass of copepod species

The biomass of all considered species is highly seasonal in all areas considered, showing also some geographic variability (Figure 3.1.2.1). After an increase from low values in the beginning of the year, peak biomass of all copepod species were found in the most western subarea (Sub-division 25) regularly in July. In contrast, in the more eastern regions (Sub-divisions 26 and 28) the highest values were observed later in August/September. Cladocerans appear in considerable amounts from spring onwards with a maximum in biomass in August, visible for all areas. Independent of the area, the most important copepod species in terms of biomass is *P. elongatus* followed by *T. longicornis* and *Acartia* spp. In general biomass did not differ between areas. Only for *P. elongatus* considerable deviations were encountered between the more southern Sub-divisions 25 and 26 compared to 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 3.1.2.1).

Table 3.1.2.1. Long-term seasonal means (\pm standard deviation) for biomass (In $\text{mg}\cdot\text{m}^{-3}$) of copepod species in ICES Sub-divisions (SD).

<i>Species</i>	SD	Winter	Spring	Summer	Autumn
<i>P. elongatus</i>	25	3.97 \pm 0.61	4.85 \pm 0.88	5.22 \pm 0.64	4.74 \pm 0.71
	26	4.35 \pm 0.96	4.56 \pm 1.20	5.01 \pm 1.26	3.86 \pm 1.84
	28	3.96 \pm 1.18	4.02 \pm 1.18	4.43 \pm 1.47	3.84 \pm 1.58
<i>T. longicornis</i>	25	3.30 \pm 0.54	2.71 \pm 1.08	4.55 \pm 1.10	3.89 \pm 0.88
	26	2.68 \pm 0.98	2.51 \pm 1.53	5.01 \pm 1.23	3.93 \pm 0.93
	28	2.47 \pm 0.90	2.08 \pm 1.23	4.92 \pm 1.04	3.79 \pm 0.83
<i>Acartia</i> spp.	25	1.98 \pm 0.70	2.93 \pm 1.09	3.67 \pm 1.18	3.33 \pm 1.10
	26	1.96 \pm 0.91	3.00 \pm 1.27	4.09 \pm 1.11	3.41 \pm 0.87
	28	1.78 \pm 1.08	2.77 \pm 1.14	4.24 \pm 1.04	3.31 \pm 0.97

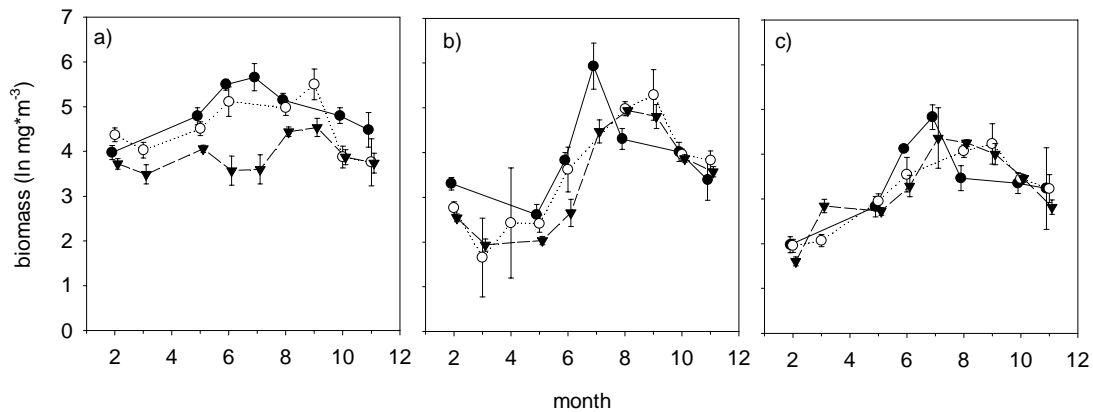


Figure 3.1.2.1. Long-term monthly means of *Pseudocalanus elongatus* (a), *Temora longicornis* (b) and *Acartia* spp. (c) in the Central Baltic (Sub-division 25 - black circles, solid line; Sub-division 26 - white circle, dotted line; Sub-division 28 - black triangle, dashed line) in the period of 1959 to 1997. Symbols and error bars represent means and standard deviations.

The biomass of *P. elongatus* (Figure 3.1.2.2) 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, turning also 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 3.1.2.3) exhibited a high variability without clear trends. Undulating developments were observed with a period of remarkably high anomalies in the end of the 1980s followed by sharply declining and mostly negative biomass anomalies in the 2nd half of the 1990s. Clear trends are obvious for the biomass of *Acartia* spp. (Figure 3.1.2.4) showing negative anomalies from the 1960s to the early 1970s.

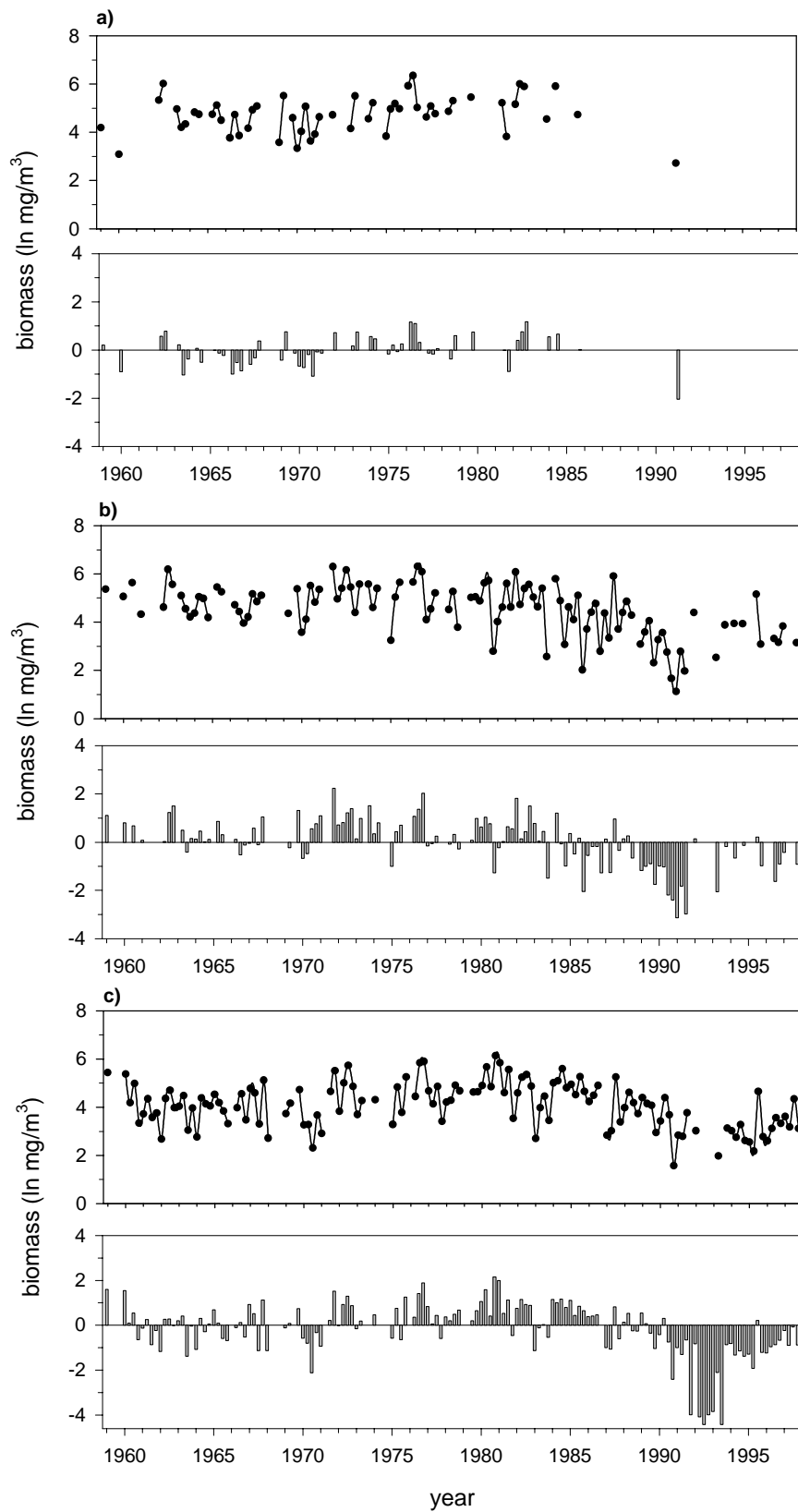


Figure 3.1.2.2. Time-series of quarterly means (above) and non-seasonal anomalies (below) of *Pseudocalanus elongatus* biomass in ICES Sub-divisions 25 (a), 26 (b) and 28 (c) in the period of 1959 to 1997.

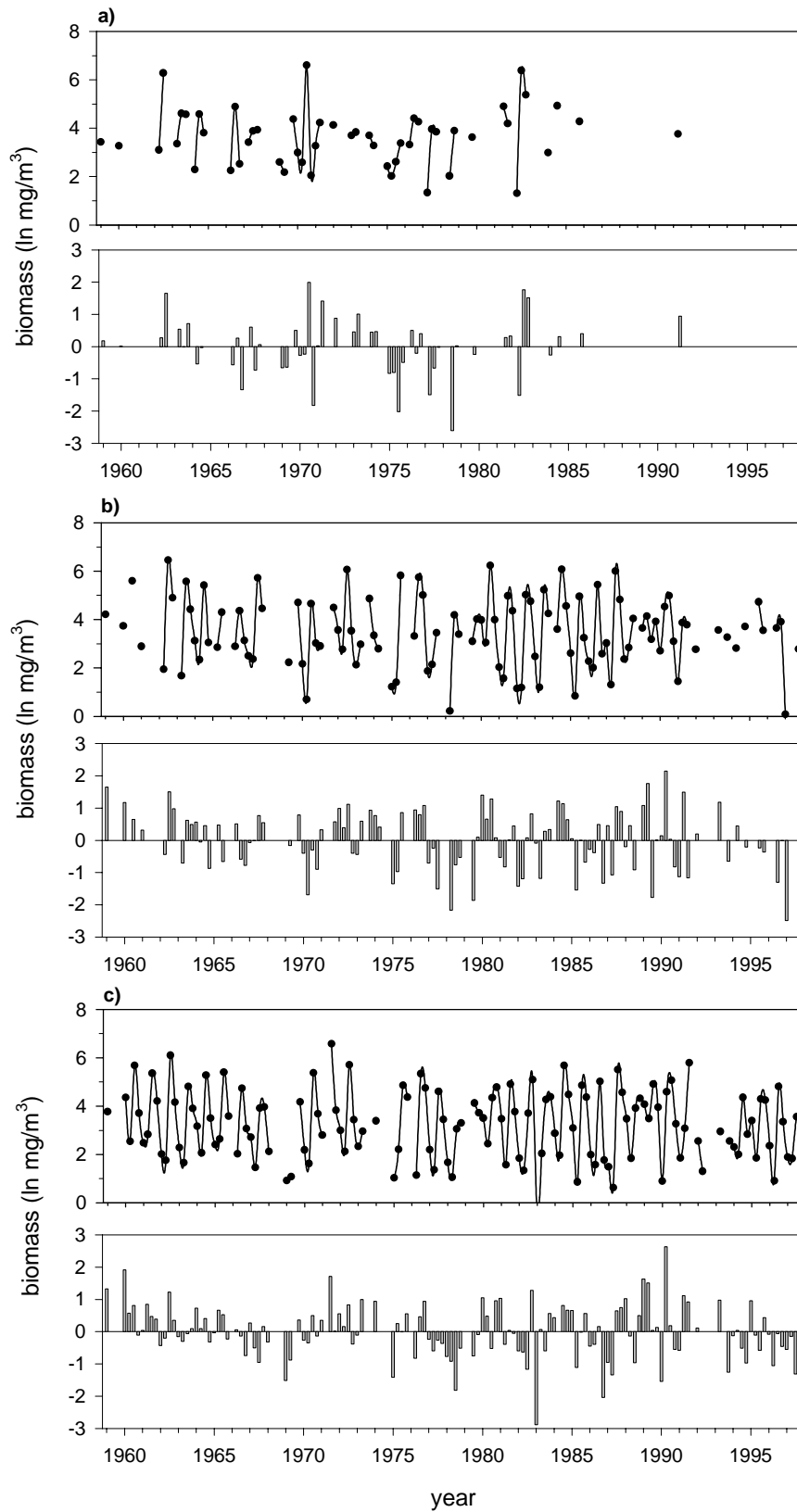


Figure 3.1.2.3. Time-series of quarterly means (above) and non-seasonal anomalies (below) of *Temora longicornis* biomass in ICES Sub-divisions 25 (a), 26 (b) and 28 (c) in the period of 1959 to 1997.

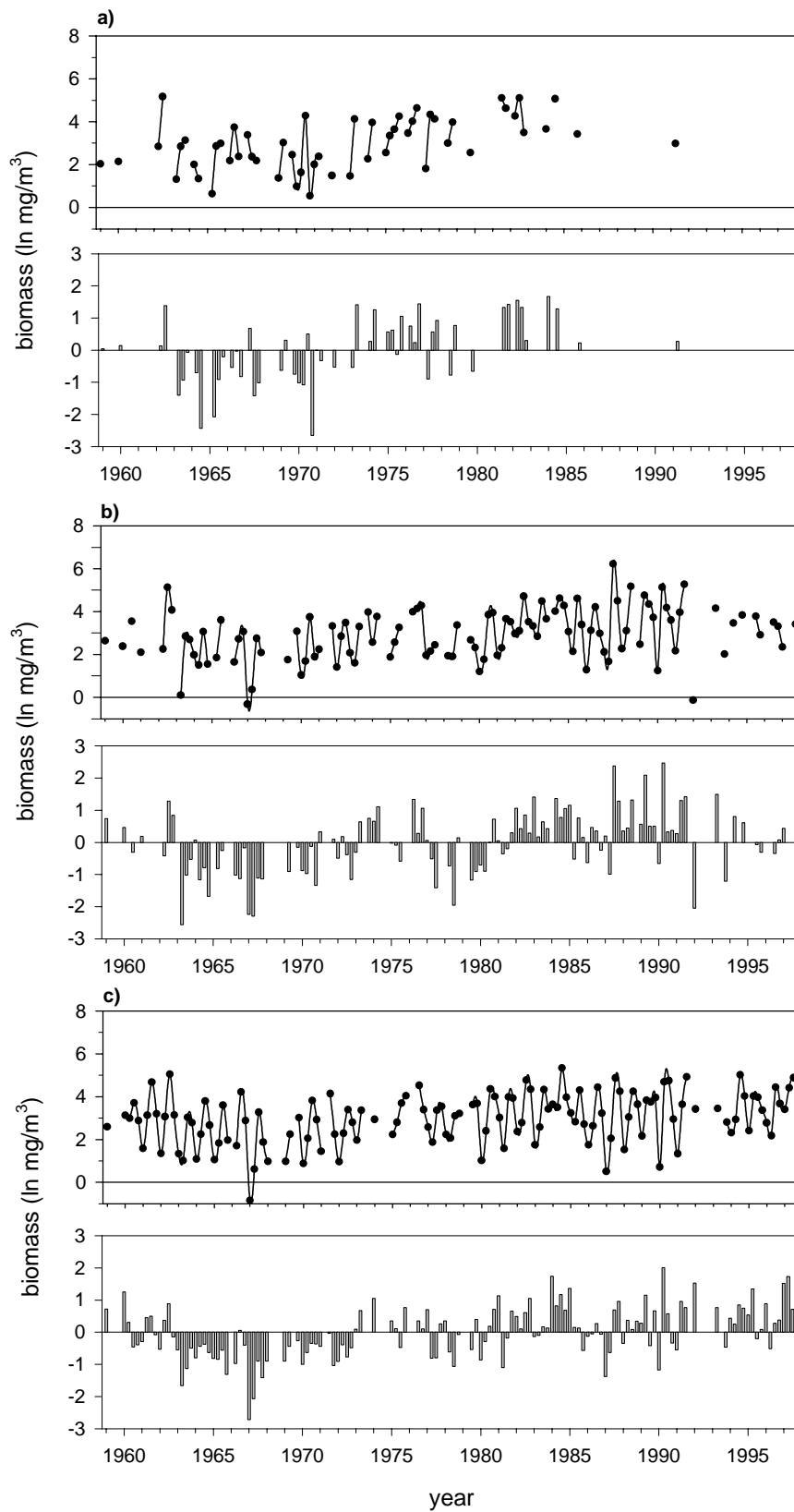


Figure 3.1.2.4. Time-series of quarterly means (above) and non-seasonal anomalies (below) of *Acartia* spp. biomass in ICES Sub-divisions 25 (a), 26 (b) and 28 (c) in the period of 1959 to 1997.

A short increase and again a subsequent drop in standing stocks characterized the development in the 1970s. The most obvious feature in the biomass development of *Acartia* spp. are the mostly positive anomalies during the 1980s, lasting in Sub-division 28 also in the 1990s.

No distinct differences between the biomass developments in the three subareas are apparent for all considered species. This is supported by the performed statistical analysis. Due to lack of data for the 1990s in Sub-division 25, the statistical comparison of non-seasonal anomalies of mesozooplankton 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 significant differences for the factor 5-year period, but not for the factor area. Thus an additional 1-way ANOVA was performed aggregating all subareas allowing to include also the data for the 1990s (Table 3.1.2.2). Posthoc-tests showed *P. elongatus* biomass anomalies since the later 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 later 1990s being significantly lower than in other time-intervals. *Acartia* spp. biomass anomalies were steadily increasing throughout the time-series with significant positive anomalies since the 1980s.

Table 3.1.2.2. Means of non-seasonal anomalies for biomass (ln mg*m⁻³) of copepod species and the taxonomic group of cladocerans 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.

Variable	1960-64	1965-69	1970-74	1975-79	1980-84	1985-89	1990-94	1995-97	F	P
<i>P. elongatus</i>	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
<i>T. longicornis</i>	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
<i>Acartia</i> 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

Table 3.1.2.3. Correlation tests between biomass of copepod species and the taxonomic group of cladocerans, and hydrographic variables in different seasons of the year; N = sample size, N* = "effective" number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α).

Variable	Season	N	Salinity 0-50m			Salinity 50-100m			Temperature 0-50m			Temperature 50-100m		
			N*	r	p	N*	r	p	N*	r	p	N*	r	p
<i>P. elongatus</i>	Winter	33	13	0.60	<0.001*	11	0.44	0.10	21	-0.18	0.322	18	0.16	0.386
<i>T. longicornis</i>			16	0.02	0.909	-	-	-	25	0.05	0.778	-	-	-
<i>Acartia spp.</i>			12	-0.02	0.933	-	-	-	20	0.17	0.343	-	-	-
<i>P. elongatus</i>	Spring	34	9	0.71	<0.001*	8	0.66	<0.001*	19	-0.04	0.819	16	0.22	0.216
<i>T. longicornis</i>			16	-0.08	0.657	-	-	-	24	0.59	<0.001**	-	-	-
<i>Acartia spp.</i>			13	-0.28	0.159	-	-	-	24	0.66	<0.001**	-	-	-
<i>P. elongatus</i>	Summer	31	12	0.55	0.001*	10	0.14	0.452	22	-0.39	0.030	18	-0.40	0.026
<i>T. longicornis</i>			14	0.16	0.378	-	-	-	23	0.12	0.536	-	-	-
<i>Acartia spp.</i>			11	-0.35	0.051	-	-	-	20	0.16	0.378	-	-	-
<i>P. elongatus</i>	Autumn	33	8	0.57	0.001	8	0.64	<0.001*	22	-0.27	0.134	16	0.13	0.475
<i>T. longicornis</i>			23	0.31	0.076	-	-	-	31	0.13	0.459	-	-	-
<i>Acartia spp.</i>			10	0.03	0.863	-	-	-	24	0.28	0.116	-	-	-

*significant at 0.05 and ** at 0.01 niveau

Correlation analysis were performed separately for seasons (Table 3.1.2.3). In all seasons, except autumn, the biomass of *P. elongatus* was significantly positively correlated to salinity in the upper layer. For the deeper water layer significant relationships were found in spring and autumn. Also a relatively strong, but insignificant inverse relation was observed for *P. elongatus* and temperature in summer. Highly significant positive correlations were also found for *T. longicornis* as well as *Acartia* spp. and temperature in spring.

3.1.3. Temporal variability in stage-specific abundance of calanoid copepods

3.1.3.1. *Pseudocalanus elongatus*

The overwintering stock of *P. elongatus* is dominated by CIV and CV copepodites and additionally lower proportions of CIII and CVI (Fig. 3.1.3.1). Peak reproduction takes place in spring, when mainly N and CI constituted the *P. elongatus* stock. In summer, these stages have further developed resulting in a dominance of CII, CIII and CIV. The overwintering stock builds up in autumn, comprising mainly CIII, CIV and CV.

The time-series display a period of a high overwintering stock in the late 1970s to the middle of the 1980s. Before and after this period abundance was low and decreased especially since the late 1980s. This development is also found in spring for CVI-f as well as for the dominating N and CI. The latter two stages, however, showed a period of high abundance also at the beginning of the time-series. All other copepodite stages experienced an undulating development during the observed period. In summer and autumn the dominating stages (CII-CV) again showed the peak abundance period in the 1970s and 1980s and the drastic decline especially during the 1990s.

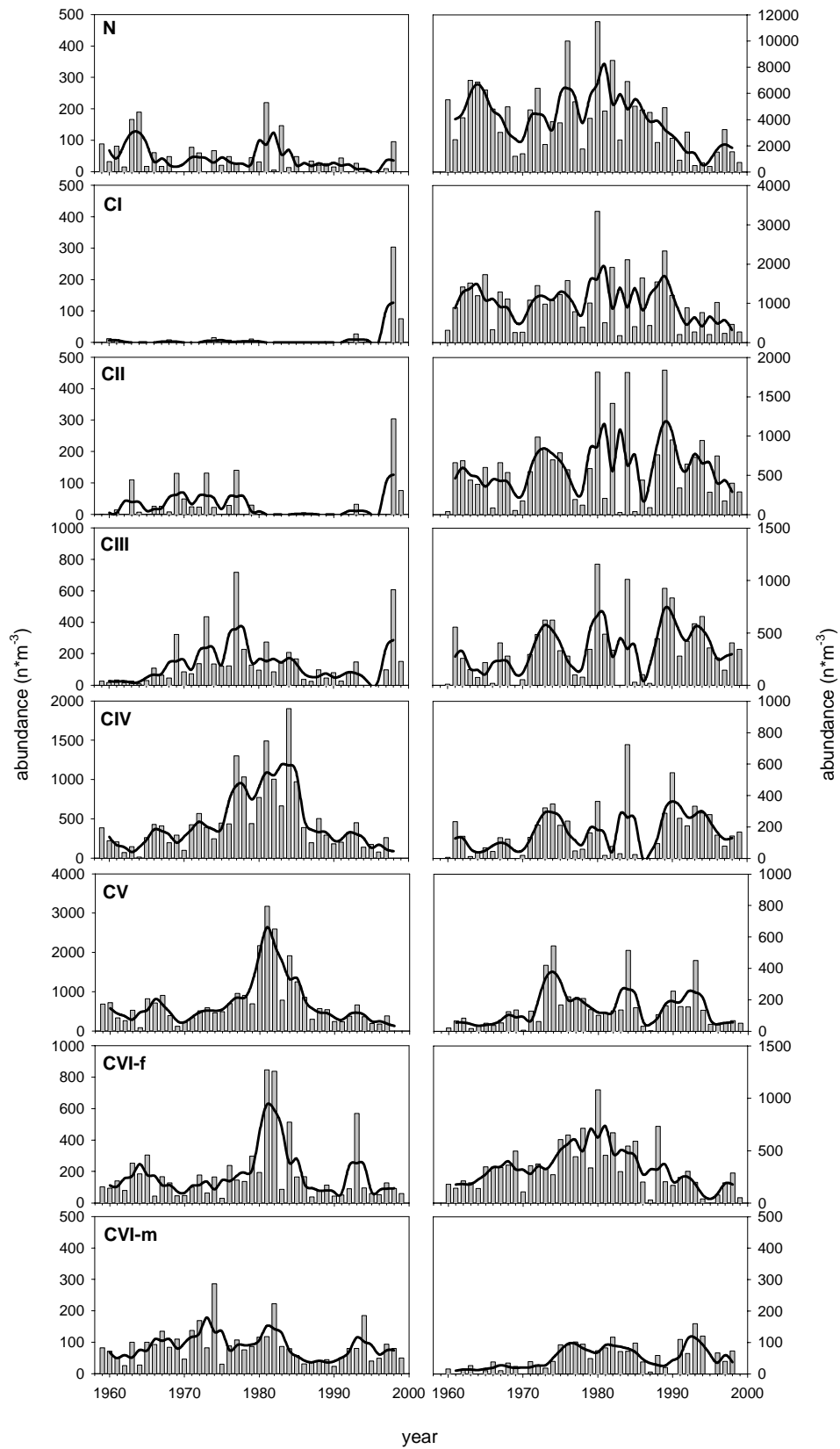


Figure 3.1.3.1a. Seasonal time-series on stage-specific abundance of *Pseudocalanus elongatus*.; 1st row – winter, 2nd row – spring. Superimposed solid lines represent a three-point running mean.

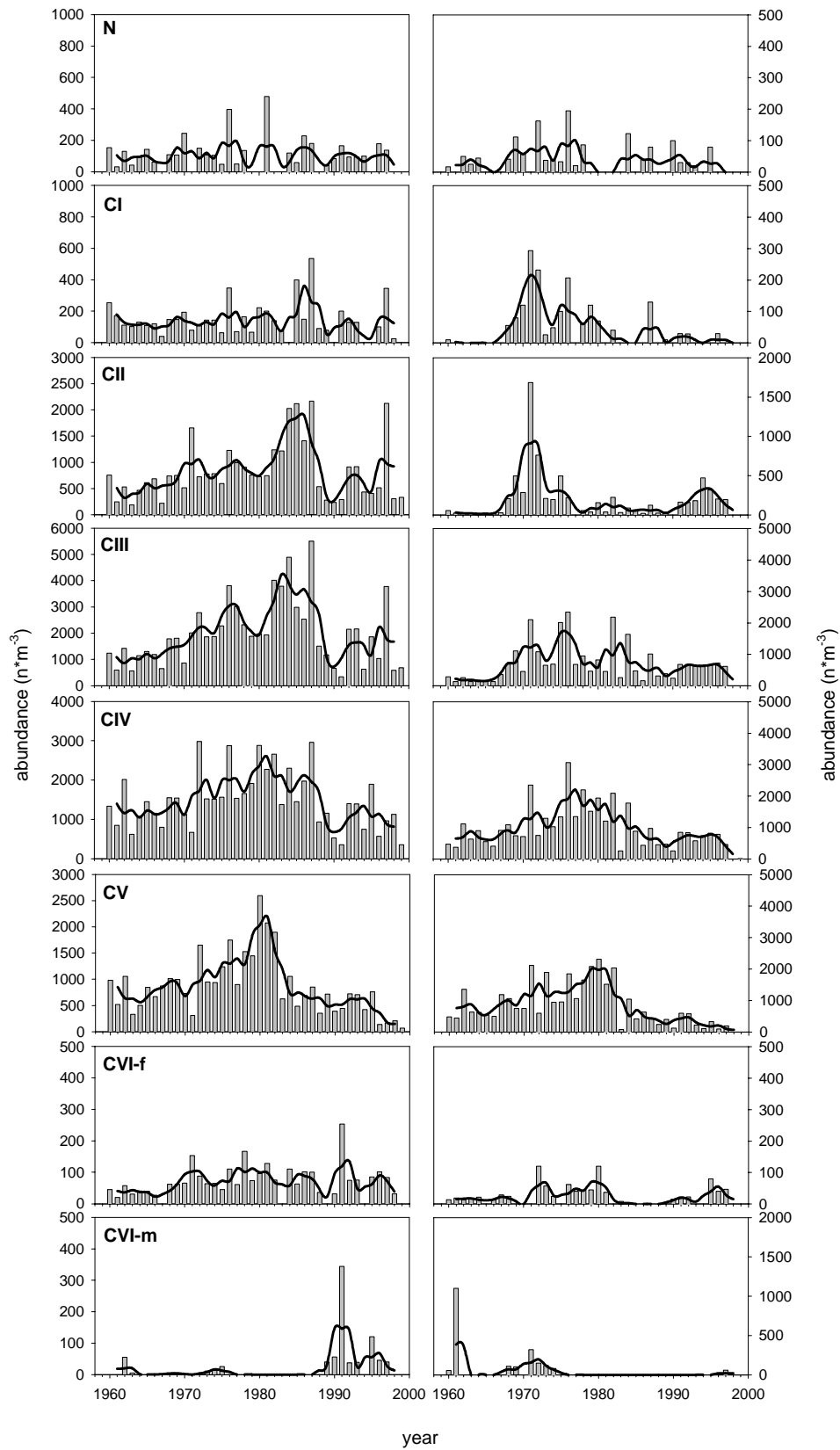


Figure 3.1.3.1b. Seasonal time-series on stage-specific abundance of *Pseudocalanus elongatus*; 1st row – summer, 2nd row – autumn. Superimposed solid lines represent a three-point running mean.

PCAs revealed pronounced differences in the behaviour of the seasonally dominating stages in spring (Fig. 3.1.3.2). A group comprising the adult (CVI) and the youngest stages (N, CI) is separated from the intermediate copepodites (CII-CV). Both groups showed also a different association to hydrography with the first group being associated to salinity in both depth horizons and the second group being connected to temperature. Correlation analyses confirmed the pattern with significant positive associations among N and salinity as well as an indication of a relationship of CVI-f and salinity (Table 3.1.3.1). Contrary intermediate copepodite stages were significantly related to temperatures. A relatively high negative correlation among N and temperature was as well detected, however being insignificant.

Table 3.1.3.1. Correlation tests between *Pseudocalanus elongatus* stage-specific abundance, and temperature and salinity time-series in spring. N* = "effective" number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α)

Stage	Salinity			Temperature		
	N*	r	p	N*	r	P
N	13	0.61	<0.001*	26	-0.25	0.119
CI	16	0.31	0.056	28	0.10	0.562
CII	16	-0.08	0.627	29	0.43	0.006*
CIII	27	-0.15	0.352	35	0.48	0.002**
CIV	19	-0.11	0.491	29	0.64	<0.001**
CV	19	-0.07	0.670	27	0.50	0.001**
CVI-f	15	0.41	0.009	23	0.05	0.748
CVI-m	21	-0.10	0.563	32	-0.14	0.399

*significant at 0.05 and ** at 0.01 niveau

3.1.3.2. *Temora longicornis*

T. longicornis hibernates mainly as CIV-CVI, although generally the overwintering stock is low compared to *P. elongatus* (Fig. 3.1.3.3). Reproduction starts in spring and lasts throughout the year as indicated by the continuous occurrence of N and the younger copepodite stages. Highest total abundance was found in summer, which coincides with the highest

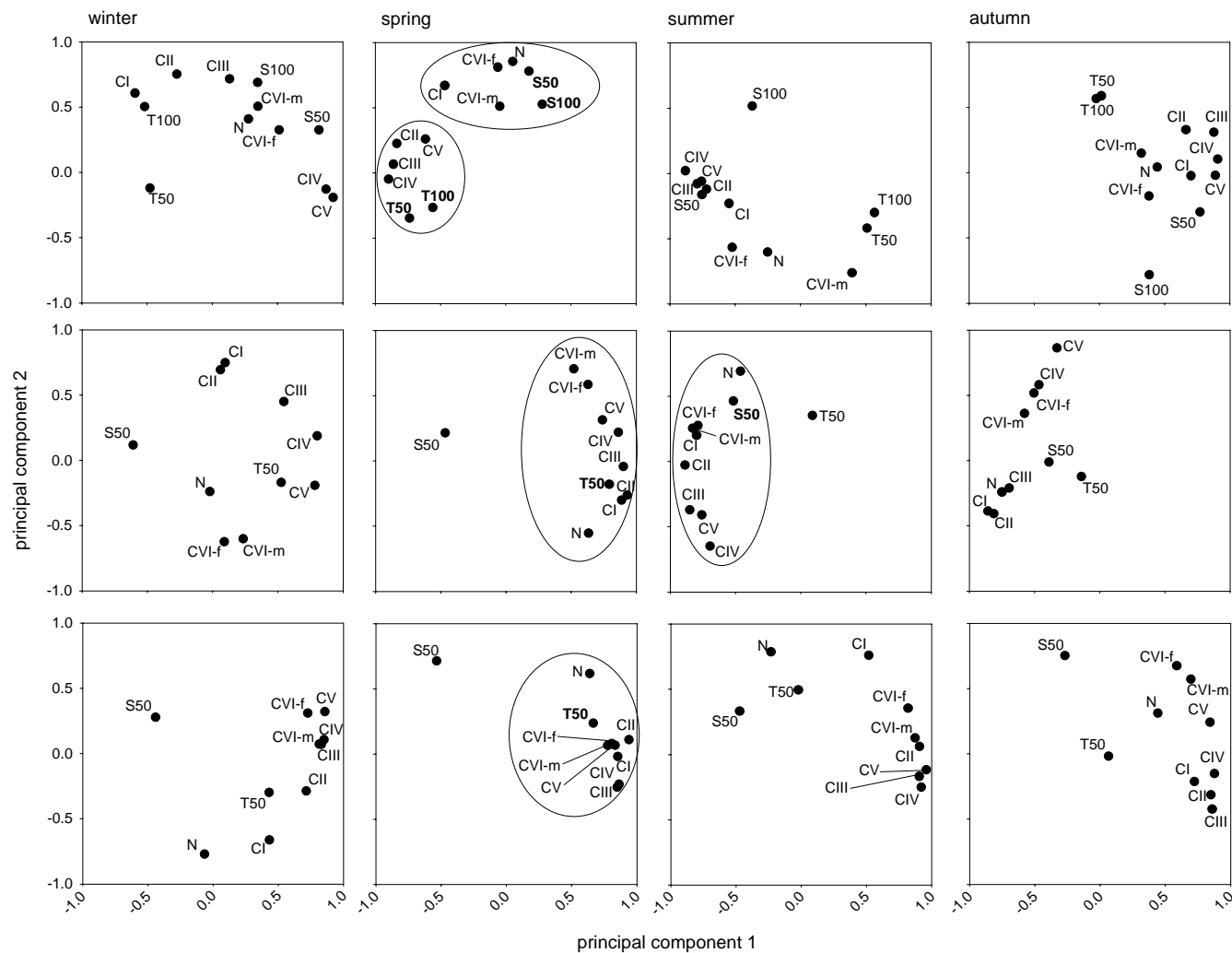


Figure 3.1.3.2. Results of Principal component analyses (PCA): Correlation between the first 2 principal components per season and copepod species: 1st row – *Pseudocalanus elongatus*, 2nd row – *Temora longicornis*, 3rd row – *Acartia* spp.; T50 and S50 – average temperature and salinity in 0-50m depth; T100 and S100 – average temperature and salinity in 50-100m depth.

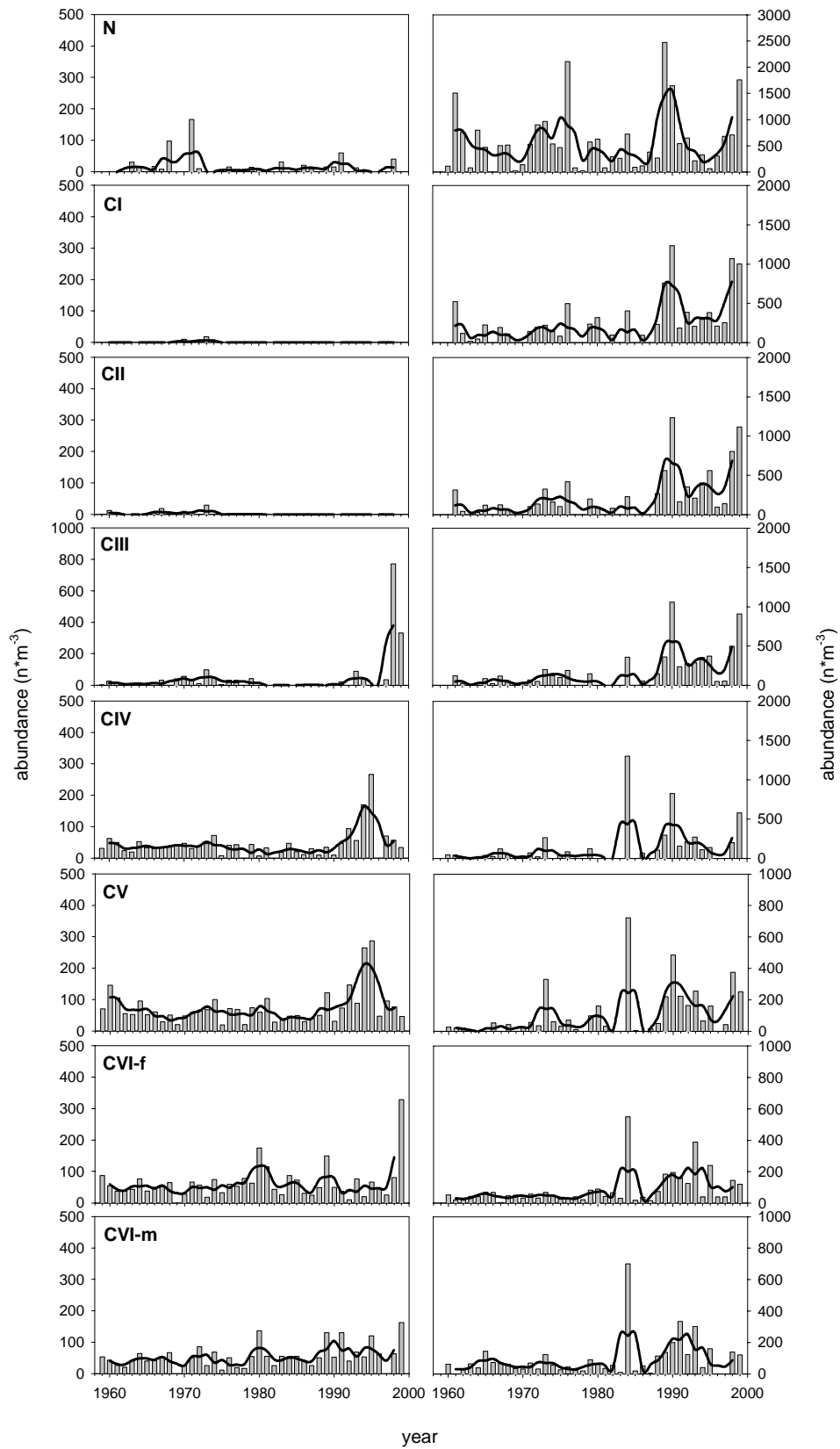


Figure 3.1.3.3a. Seasonal time-series on stage-specific abundance of *Temora longicornis*.; 1st row – winter, 2nd row – spring. Superimposed solid lines represent a three-point running mean.

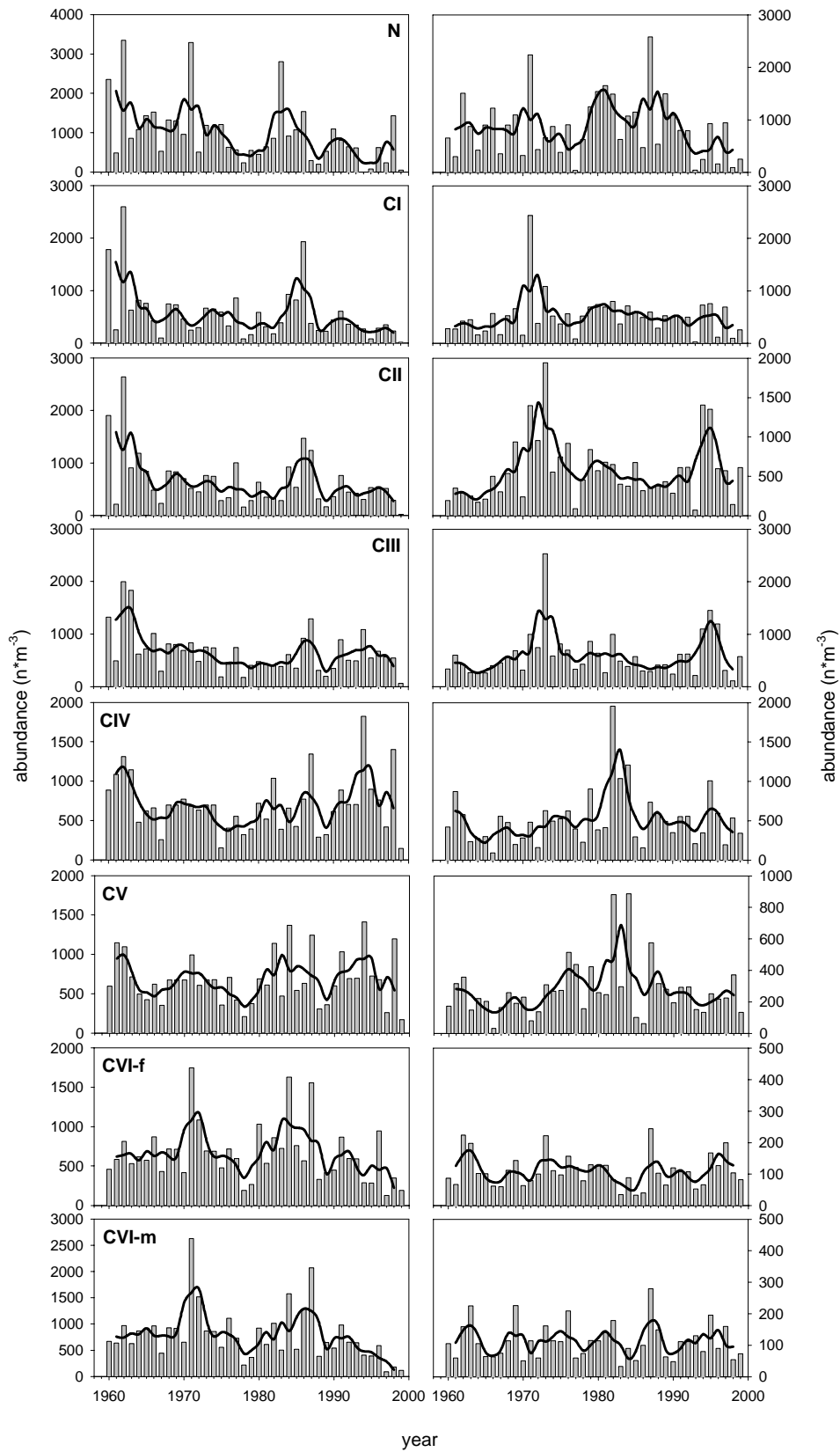


Figure 3.1.3.3b. Seasonal time-series on stage-specific abundance of *Temora longicornis*.; 1st row – summer, 2nd row – autumn. Superimposed solid lines represent a three-point running mean.

amount of CVI within the yearly cycle. In autumn N and copepodites CI to CIV dominate with similar abundances.

The winter time-series showed increasing abundances of CIII-CV and CVI-f in the 1990s. Similarly in spring exceptionally high standing stocks were observed since the late 1980s for all stages. Before the mid 1980s, spring abundances of all stages were low with an intermediate rise in the mid 1970s, however only pronounced in N. Contrary to spring, the summer time-series is characterized by mainly low and decreasing abundances in the 1990s with the exception of CIII-CV, which were relatively abundant. Generally a high variability is encountered in the summer time-series with high values at the beginning for N and copepodites, but lower ones for CVI. A similar high variability is found in autumn with peaks in the middle of the 1970s for N and CI-III and in the early 1980s for CIV-CV. In the 1990s the standing stock of N and CI was low and on average higher for CII-CIV.

PCAs revealed no clear associations between the stage-specific abundance of *T. longicornis* and the hydrographic variables in winter and autumn (Fig. 3.1.3.2). Contrary in spring, all stages had high positive correlations with the first principal axis as was observed for temperature. In summer no association to temperature was obvious, while all stages showed negative correlations to the second principal axis, as was found for salinity. Correlation analyses for the main reproductive periods confirmed a clear positive relation of all stages to temperature in spring (Table 3.1.3.2). The association to salinity is negative in spring, however significant only for CI and CII. In summer correlations with salinity were positive, however significant only for CI and CII as well as CVI.

3.1.3.3. *Acartia* spp.

The seasonal dynamics of *Acartia* spp. were similar to *T. longicornis* (Fig. 3.1.3.4). The overwintering stock is relatively small, reproduction starts in spring and last throughout the year. Peak abundance is found in summer.

Table 3.1.3.2. Correlation tests between *Temora longicornis* stage-specific abundance, and temperature and salinity time-series.

N* = "effective" number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α)

Stage	Spring						Summer					
	Salinity			Temperature			Salinity			Temperature		
	N*	r	p	N*	r	p	N*	r	P	N*	r	p
N	17	-0.17	0.302	31	0.63	<0.001**	22	0.38	0.018	34	0.16	0.317
CI	20	-0.44	0.005*	32	0.66	<0.001**	26	0.43	0.006*	34	0.03	0.835
CII	19	-0.46	0.003*	32	0.73	<0.001**	28	0.45	0.004*	36	-0.21	0.196
CIII	14	-0.47	0.003	28	0.66	<0.001**	26	0.25	0.129	35	-0.20	0.218
CIV	23	-0.34	0.033	34	0.60	<0.001**	29	0.07	0.680	37	-0.17	0.289
CV	19	-0.15	0.367	31	0.56	<0.001**	23	0.15	0.362	35	0.05	0.770
CVI-f	19	-0.31	0.055	32	0.35	0.028**	23	0.39	0.015*	34	0.10	0.548
CVI-m	21	-0.01	0.948	32	0.32	0.045**	18	0.54	<0.001*	31	-0.04	0.800

*significant at 0.05 and ** at 0.01 niveau

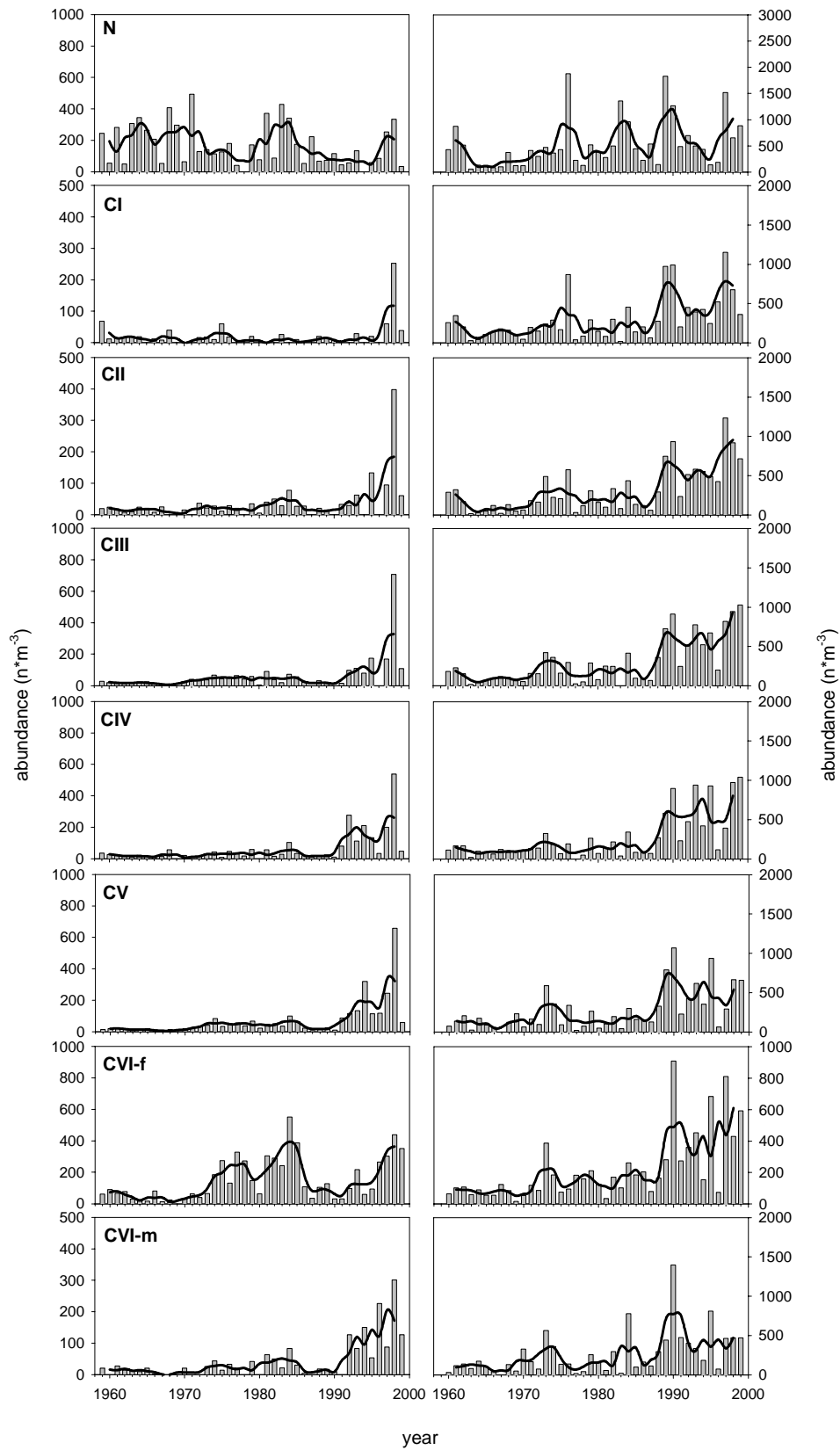


Figure 3.1.3.4a. Seasonal time-series on stage-specific abundance of *Acartia* spp.; 1st row – winter, 2nd row – summer. Superimposed solid lines represent a three-point running mean.

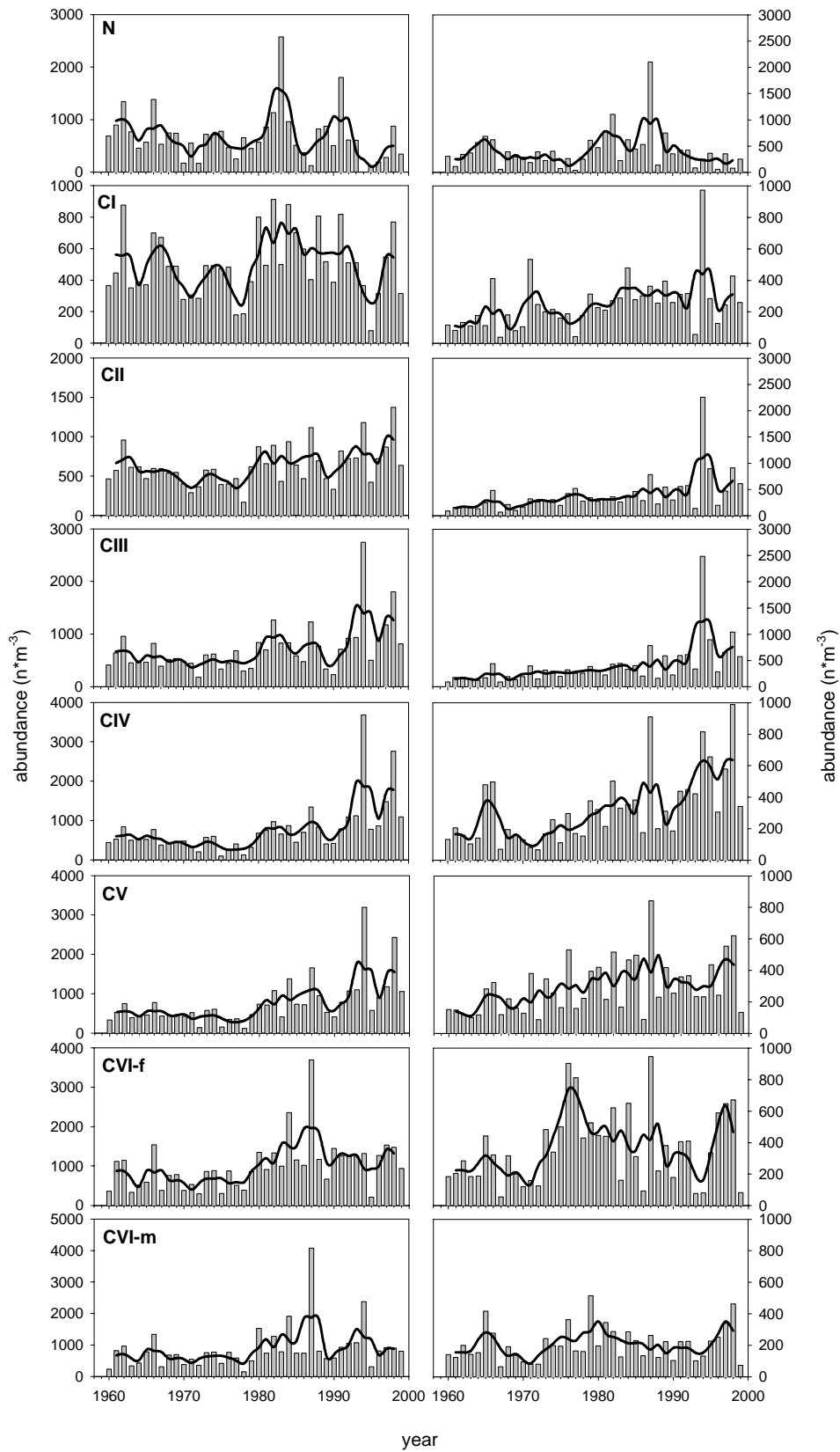


Figure 3.1.3.4b. Seasonal time-series on stage-specific abundance of *Acartia* spp.; 1st row – summer, 2nd row – autumn. Superimposed solid lines represent a three-point running mean.

Increasing winter abundances of all stages were observed in the 1990s. Compared to *T. longicornis* higher abundances of N and CVI-f of *Acartia* spp. were encountered showing an undulating development. Also in spring the time-trend was comparable with *T. longicornis*, i.e. with a marked increase in abundance since the late 1980s visible for all stages. Contrary to *T. longicornis* this stepwise increase in standing stock was as well encountered in summer and autumn, although mainly for CII and older stages.

Similar to *T. longicornis* PCAs for *Acartia* spp. showed only weak association of hydrographic variables to stage-specific abundance in winter and autumn, and additionally in summer (Fig. 3.1.3.2). In spring all stages were associated to temperature, whereas there is a clear opposition to salinity. Correlation analyses confirmed a clear positive and highly significant relationship of all stages to temperature in spring (Table 3.1.3.3). The association to salinity is negative in spring (significant only for CIII and CIV) and in summer (significant only for CIII-CV).

3.1.4. Spatio-temporal variability in abundance of cladoceran species

Clear abundance peaks were found for all three cladoceran species in summer (Fig. 3.1.4.1). *B. coregoni maritima*, not observed in spring, had the highest average abundance in summer, whereas *E. nordmanni* constituted most of the cladoceran abundance in spring and autumn. *Podon* spp. was in all seasons the least abundant species. A similar seasonality for all species was found in both investigated areas

A general rise in abundance of *B. coregoni maritima* is visible in the summer time-series until the late 1980s, with a decrease in most recent years especially in Sub-division 28 (Fig. 3.1.4.2). In contrast, autumn abundances exhibited a general downward trend with abundance values in Sub-division 26 being more stable than in Sub-division 28.

The abundance of *E. nordmanni* was more variable in spring and autumn compared to the season of peak abundance in summer (Fig. 3.1.4.3). Spring abundances were found to generally increase and the summer time-series to be relatively stationary with

Table 3.1.3.3. Correlation tests between *Acartia* spp. stage-specific abundance and temperature, and salinity time-series. N* = "effective" number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α)

Stage	Spring						Summer					
	Salinity			Temperature			Salinity			Temperature		
	N*	r	p	N*	r	p	N*	r	p	N*	r	p
N	18	-0.04	0.797	29	0.48	0.002**	22	0.19	0.240	32	0.19	0.244
CI	15	-0.39	0.013	29	0.44	0.005*	24	-0.01	0.990	32	0.27	0.097
CII	11	-0.41	0.009	26	0.55	<0.001**	22	-0.37	0.021	33	-0.03	0.860
CIII	15	-0.50	0.001*	29	0.44	0.005*	21	-0.43	0.007*	31	-0.14	0.399
CIV	14	-0.58	<0.001*	28	0.55	<0.001**	13	-0.58	<0.001*	26	-0.11	0.524
CV	16	-0.37	0.020	30	0.46	0.003**	14	-0.51	0.001*	27	-0.03	0.863
CVI-f	11	-0.43	0.006	26	0.63	<0.001**	19	-0.17	0.303	30	0.10	0.539
CVI-m	18	-0.33	0.042	32	0.50	0.001**	25	-0.17	0.301	34	-0.06	0.703

*significant at 0.05 and ** at 0.01 niveau

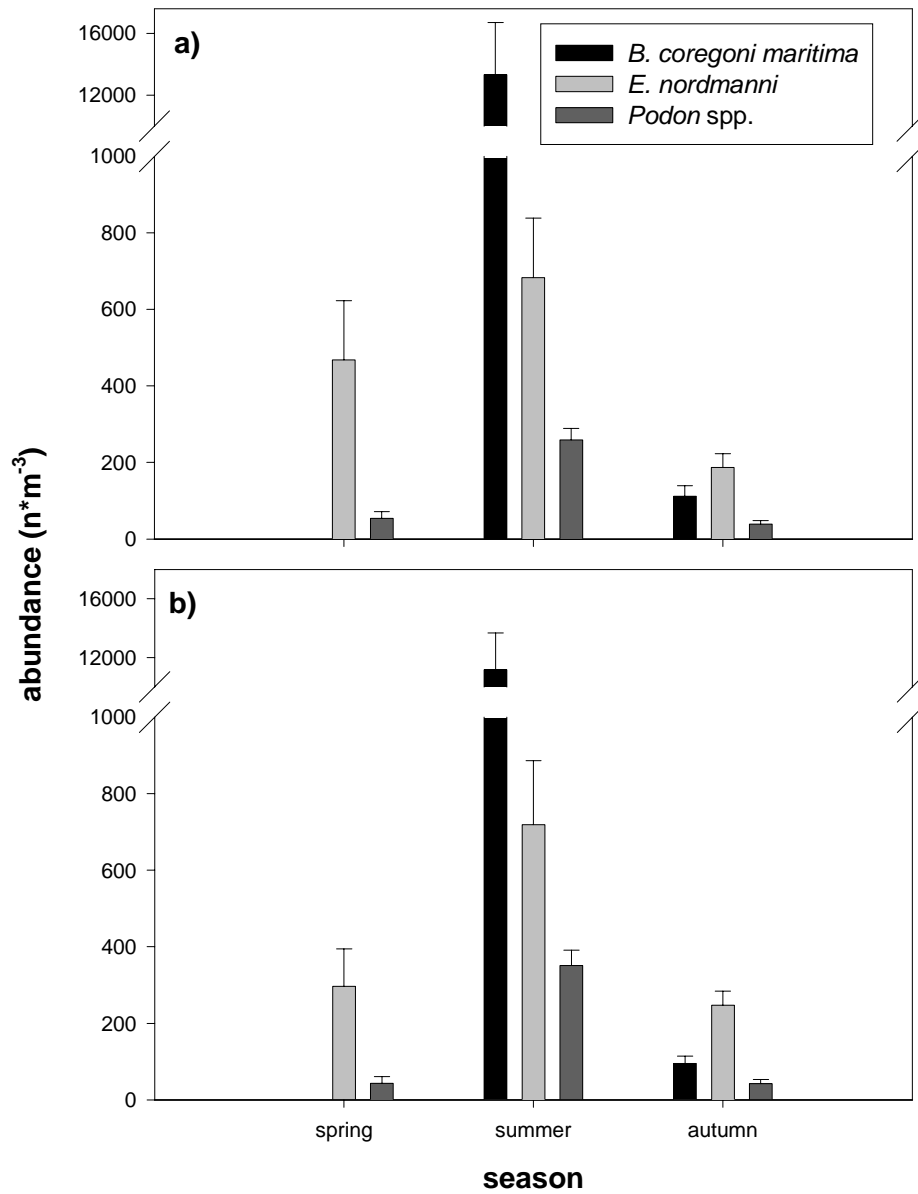


Figure 3.1.4.1. . Long-term seasonal means of abundance of cladoceran species in Sub-divisions 26 (a) and 28 (b). Error bars represent standard errors.

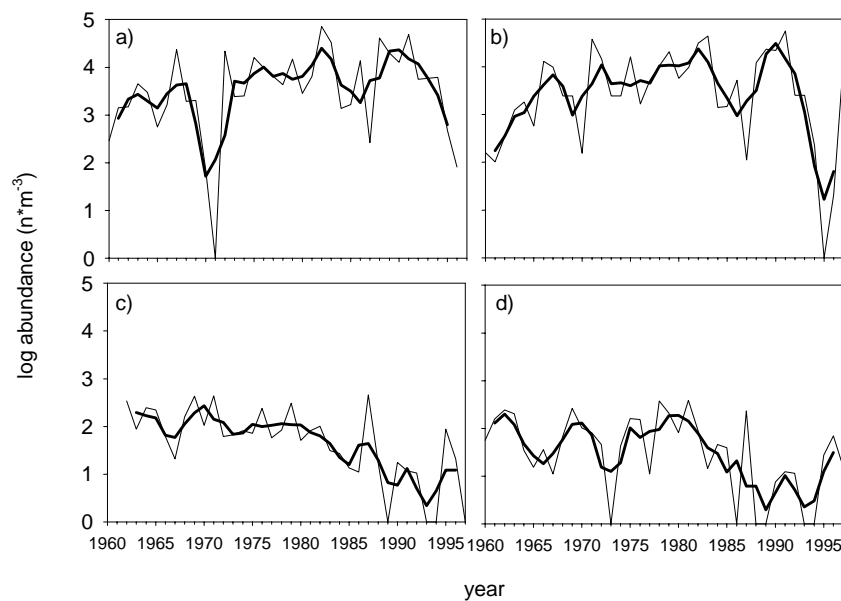


Figure 3.1.4.2. Log abundance time-series of *B. coregoni maritima*; a) summer, Sub-division 26; b) summer, Sub-division 28; c) autumn, Sub-division 26; d) autumn Sub-division 28. Superimposed solid lines represent a three-point running mean.

the exception of 0-values in the 1990s in Sub-division 26. Abundances in autumn were observed to generally decline, especially in the 1990s.

Table 3.1.4.1. Correlation tests between cladoceran abundance and temperature time-series in Sub-division 26 and 28. N = sample size, N* = "effective" number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α)

Species	Season	Sub-division 26				Sub-division 28			
		N	N*	r	p	N	N*	r	p
<i>Bosmina coregoni maritima</i>	Summer	35	32	0.39	0.022*	37	35	0.27	0.106
	Autumn	36	26	0.01	0.939	37	32	0.17	0.323
<i>Evadne nordmanni</i>	Spring	33	31	0.58	<0.001**	37	32	0.59	<0.001**
	Summer	35	31	-0.16	0.927	37	35	-0.13	0.438
	Autumn	36	29	-0.05	0.773	37	31	0.11	0.521
<i>Podon spp.</i>	Spring	33	29	0.50	0.003**	37	32	0.63	<0.001**
	Summer	35	34	-0.08	0.655	37	35	0.17	0.318
	Autumn	36	31	-0.01	0.949	37	33	0.20	0.240

*significant at 0.05 level; **significant at the 0.01 level

Similar time-trends as for *E. nordmanni* were found for *Podon* spp. in all three seasons (Fig. 3.1.4.4). Compared to the former species, the latter exhibited a more pronounced increase in standing stocks in the 1990s during spring.

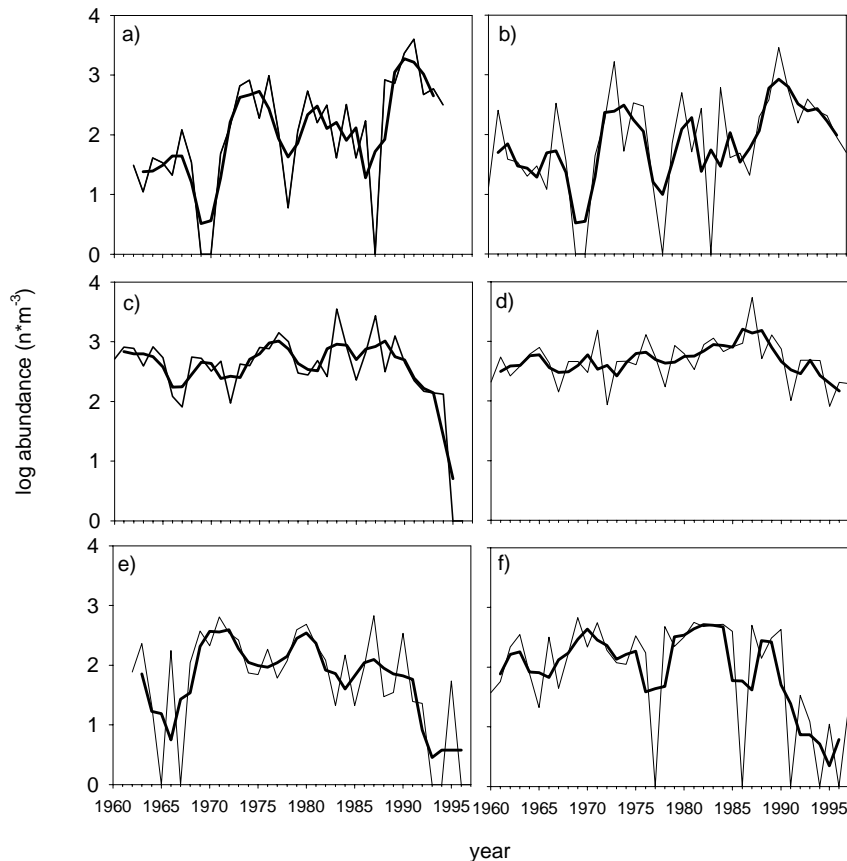


Figure 3.1.4.3. Log abundance time-series of *E. nordmanni*; a) spring, Sub-division 26; b) spring, Sub-division 28; c) summer, Sub-division 26; d) summer, Sub-division 28; e) autumn, Sub-division 26; f) autumn Sub-division 28. Superimposed solid lines represent a three-point running mean.

Test of association between *B. coregoni maritima* abundance and temperature in summer revealed a significant relationship ($p < 0.05$) in Sub-division 26, but not in Sub-division 28 (Table 3.1.4.1). Highly significant relationships ($p < 0.01$) were found between *E. nordmanni* and *Podon* spp. spring abundance and temperature in both subareas.

Tests of synchrony among standing stocks of *B. coregoni maritima* and salinity revealed no significant association (Table 3.1.4.2). However, all correlations with autumn time-series showed relatively strong positive relationships, being almost significant.

Table 3.1.4.2. Correlation tests between cladoceran abundance and salinity time-series in Sub-division 26 and 28. N = sample size, N* = "effective" number of degrees of freedom, r = Pearson correlation coefficient, p = associated probability (α)

Species	Season	Sub-division 26				Sub-division 28			
		N	N*	r	P	N	N*	r	P
<i>Bosmina coregoni maritima</i>	Summer	35	23	0.16	0.346	37	21	0.25	0.142
	Autumn	36	13	0.45	0.006	37	18	0.35	0.035
<i>Evadne nordmanni</i>	Spring	33	18	-0.05	0.793	37	23	-0.25	0.142
	Summer	35	17	0.73	<0.001**	37	24	0.17	0.321
	Autumn	36	17	0.51	0.002*	37	18	0.50	0.002*
<i>Podon</i> spp.	Spring	33	19	-0.08	0.668	37	20	-0.22	0.196
	Summer	35	27	0.60	<0.001**	37	24	0.18	0.299
	Autumn	36	19	0.48	0.003*	37	20	0.10	0.566

*p < 0.05 **p < 0.01

E. nordmanni and *Podon* spp. abundances in Sub-division 26 were significantly positive related to salinity in summer and autumn. In contrast to the more southerly situated subarea, we found rarely significant associations in Sub-division 28, only *E. nordmanni* abundance and salinity in autumn. A conspicuous result are negative correlation coefficients for *E. nordmanni* and *Podon* spp. in spring in Sub-division 28, however not significant, which are found also in Sub-division 26, but on a lower level.

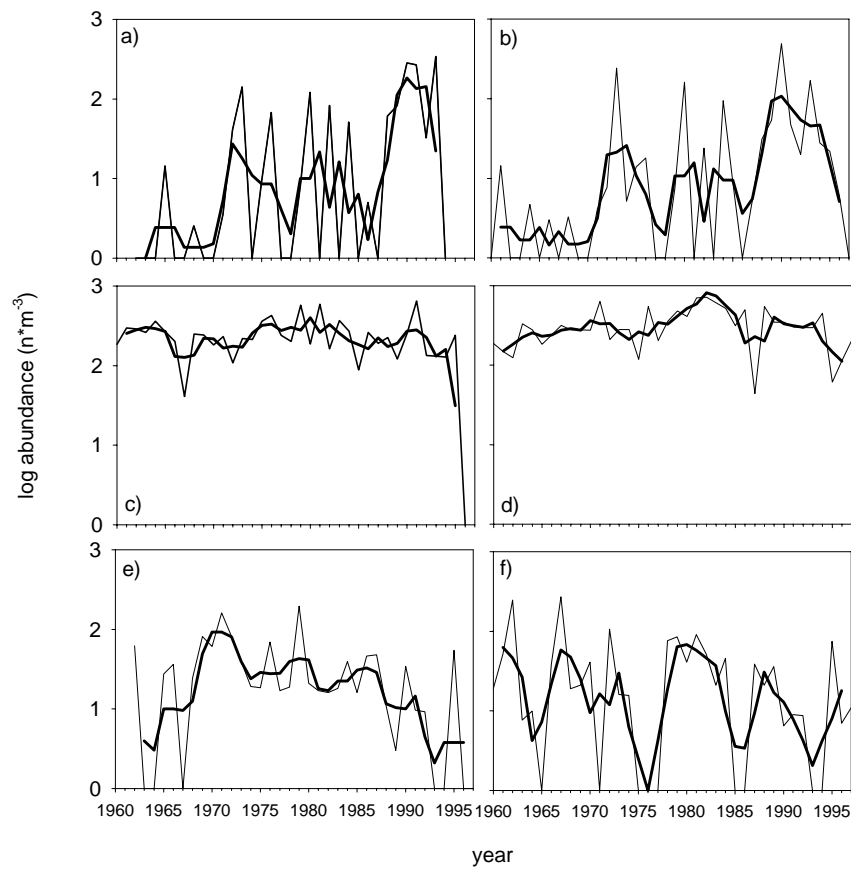


Figure 3.1.4.4. Log abundance time-series of *Podon* spp.; a) spring, Sub-division 26; b) spring, Sub-division 28; c) summer, Sub-division 26; d) summer, Sub-division 28; e) autumn, Sub-division 26; f) autumn Sub-division 28. Superimposed solid lines represent a three-point running mean.

3.2. The influence of predation

3.2.1. Clupeid abundance

3.2.1.1. Output from area dis-aggregated MSVPA runs

The development of the cod stock in all subareas is characterized by a peak in population size at the beginning of the 1980s and a subsequent drop to historical low stock levels in the early 1990s (Figure 3.2.1.1). Concurrently to the declining cod stock, the sprat stock exhibited a drastic increase to highest population size on record at the end of the period

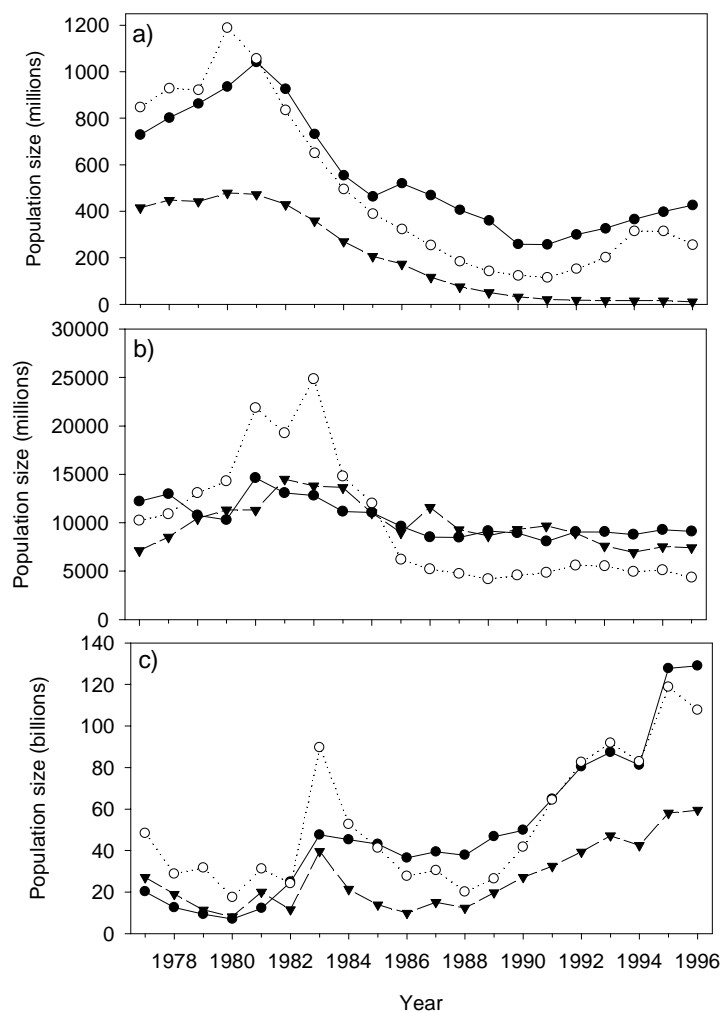


Figure 3.2.1.1. Total abundance (1st quarter) of cod (a), herring (b) and sprat (c) (all age 1+) from area-disaggregated MSVPA in different Sub-divisions (SD) of the Central Baltic (solid circles, SD 25; open circles, SD 26; triangles, SD 28).

covered. The herring stock in Sub-divisions 25 and 28 experienced a rather stable development. Contrarily, the population size in Sub-division 26 increased to a maximum in 1983, collapsing afterwards and remaining on a stable low level since 1986.

3.2.1.2. Validation of area dis-aggregated MSVPA results

Validation employing trawl and hydroacoustic surveys used for MSVPA tuning

For the cod population size (age-group 2+) significant linear relationships were obtained between area dis-aggregated MSVPA estimates (Appendix Table 1) and abundance indices based on bottom trawl surveys (Appendix Table 2) in all three sub-areas (Figure 3.2.1.5). The lowest r^2 -values were observed in Sub-division 25 ($r^2 = 0.64$), intermediate in Sub-division 26 ($r^2 = 0.69$) and highest in Sub-division 28 ($r^2 = 0.80$). Intercepts were significant for Sub-division 26 and 28 ($p = 0.039$ and 0.041), but not in Sub-division 25 ($p = 0.052$). Large inter-annual variability was observed in the international trawl survey in Sub-division 25 in 1980-1982 and 1985-1987 causing large deviations between observed and modelled population abundance. Similarly in Sub-division 26,

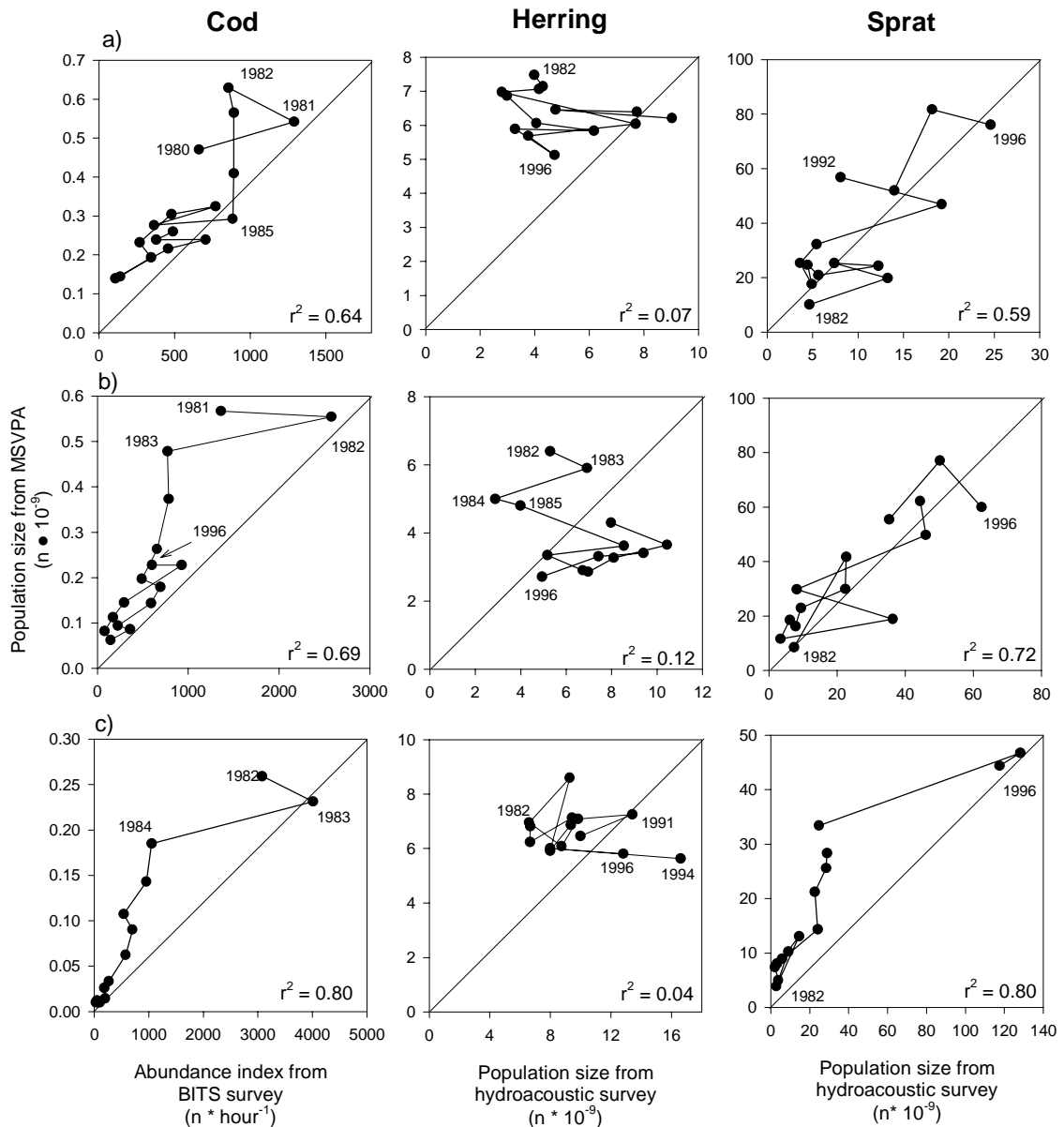


Figure 3.2.1.2. Population sizes of cod (age-group 2+), herring and sprat (age-group 1+) derived by area dis-aggregated MSVPA at time of survey vs. abundance indices from tuning fleets (a – Sub-division 25; b – Sub-division 26; c – Sub-division 28). Coefficient of determination (r^2) from a linear regression model, allowing for an intercept. BITS, Baltic International Trawl Survey.

considerable deviations occurred in the beginning of the time series with a high trawl survey abundance index in 1982 and a relatively low one in 1983. Interestingly, in Sub-division 28 the 1983 survey revealed highest abundance indices on record, potentially indicating a shift in distribution compared to 1982 and subsequent years. Apart from this observation, evidence of interannual shifts in distribution between different sub-areas

was not apparent. Correlating the age-specific abundance values obtained from the area dis-aggregated MSVPA runs against corresponding indices from the trawl survey revealed a dome-shaped pattern of r^2 -values with age, being lowest in oldest age-groups. This might indicate tuning problems encountered for these age-groups, while the decreasing fit in younger age-groups can be explained mainly by trawl selectivity. Cod recruitment at age 1 derived by area dis-aggregated MSVPA runs (Appendix Table 1) were nevertheless significantly correlated to abundance indices from the survey (Appendix Table 3), with highest variability in Sub-division 25 (Table 3.2.1.1). Here, especially a low abundance index of the year-class 1979 in the survey 1980 does not coincide with high recruitment estimated by the area dis-aggregated MSVPA. Excluding this year-class from the correlation improved the relationship between both recruitment estimates considerably ($r^2 = 0.60$).

Table 3.2.1.1. Linear regressions performed to validate cod and sprat recruitment (age-group 1) from area dis-aggregated MSVPA (dependent variable, unit: numbers) using results from the international bottom trawl survey for cod (unit: $n \cdot \text{hour}^{-1}$) and the international hydroacoustic survey for sprat (unit: numbers); parameter estimates, their significance level and r^2 -values.

Sub-division	year-classes	parameter	parameter estimates	p	r^2
Cod					
25	1979-95	slope	$6.2329 \cdot 10^6$	0.015	0.34
		intercept	$1.4396 \cdot 10^8$	<0.001	
26	1980-95	slope	$3.2003 \cdot 10^6$	<0.001	0.73
		intercept	$9.1831 \cdot 10^7$	<0.001	
28	1981-95	slope	$8.3191 \cdot 10^6$	<0.001	0.88
		intercept	98953	<0.001	
Sprat					
25	1981-95	slope	5.4102	<0.001	0.68
		intercept	$2.1162 \cdot 10^{10}$	<0.001	
26	1981-95	slope	1.3676	0.012	0.42
		intercept	$1.1497 \cdot 10^{10}$	0.146	
28	1981-95	slope	0.2798	0.002	0.35
		intercept	$9.8700 \cdot 10^{10}$	0.024	

In contrast to cod, correlation between abundance estimates of herring from area dis-aggregated MSVPA runs (Appendix Table 1) and hydroacoustic surveys (Appendix Table 2) revealed no significant relationships for any of the Sub-divisions (Figure 3.2.1.2).

For sprat, the comparison between international hydroacoustic survey results (Appendix Table 2) and area dis-aggregated MSVPA output (Appendix Table 1) revealed similar trends to those observed for cod (Figure 3.2.1.2), with lowest r^2 -values also in Sub-division 25 ($r^2 = 0.59$) and highest in 28 ($r^2 = 0.80$). The increase in population size in the 1990s observed in the MSVPA estimates for Sub-division 25 is less pronounced in the hydroacoustic surveys. In particular, the survey estimate obtained in 1992 appears to be rather low. Due to technical and area coverage problems, the hydroacoustic surveys in 1992 and 1993 (the latter omitted here) have been suggested to be the most unreliable in the present time series and are in fact excluded from regular assessment runs (ICES, 1997b). In Sub-division 28 contrary to Sub-division 25, the increase in population size in recent years is more pronounced in the hydroacoustic survey than in the area dis-aggregated MSVPA. A similar comparison for sprat recruitment at age 1 (Appendix Tables 1 and 3), revealed significant correlations for all sub-areas, with highest r^2 -values in Sub-division 25 and lowest in 28 (Table 3.2.1.1). In the latter area as well as in Sub-division 26, large deviations occurred for the year-class 1982, with the MSVPA estimates being significantly higher. Excluding this year from the correlation increased the r^2 -values considerably (Sub-division 26: 0.65 and 28: 0.79). Thus, recruitment of the 1982 year-class appears to be severely overestimated by the area dis-aggregated MSVPA, while in general hydroacoustic and MSVPA derived recruitment are in good agreement.

Validation employing independent research surveys

Validation of the area dis-aggregated MSVPA estimates for cod was performed against Latvian bottom trawl surveys conducted in Sub-division 26 and 28 in January and November/December 1976 to 1991 (Appendix Table 2). These estimates of age-group 3+ cod abundance were significantly correlated with the corresponding area dis-

aggregated MSVPA output (Figure 3.2.1.3), with r^2 values ranging from 0.52 to 0.90. Despite these significant relationships, a number of noteworthy deviations were evident. Outstandingly high abundances of 3+ cod in Sub-division 28 were encountered in the

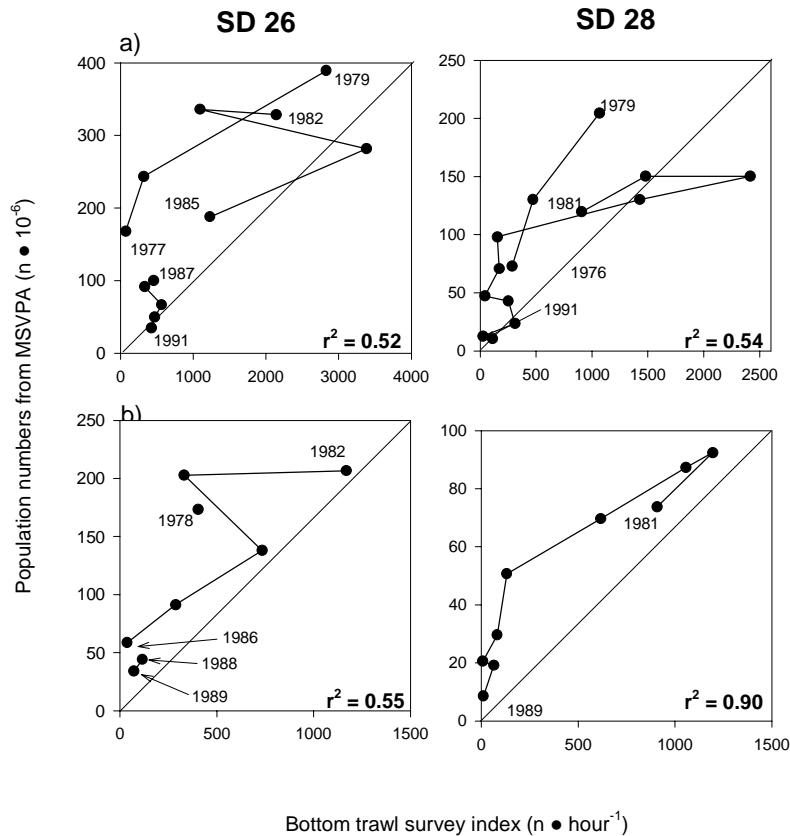


Figure 3.1.2.3. Population sizes of cod (age-group 3+) derived by area dis-aggregated MSVPA vs. abundance indices from the Latvian Bottom Trawl Survey in Sub-divisions (SD) 26 and 28 (a – January; b – November/December). Coefficient of determination (r^2) from a linear regression model, allowing for an intercept.

trawl surveys in January 1983, a result not reflected in the MSVPA estimates. In Sub-division 26, a reverse situation was encountered with comparatively low catch rates in January and November/October 1983 as compared to estimated high population abundance by the MSVPA. These results may indicate an anomalous distribution of the stock in 1983 as in the previous section identified by the international bottom trawl survey.

Further corroborative results come from Latvian demersal trawl surveys on cod spawning concentrations in the Gotland Basin (Uzars, et al. 1991). These show a decline in biomass indices of 84% in the period 1980 to 1989, a result corresponding to a similar

decline of the SSB derived by the area dis-aggregated MSVPA for the same period. Catch rates from pelagic trawl surveys covering the Bornholm Basin at different times of the spawning season revealed on average a 53% reduction in abundance of sexually mature cod from 1995 to 1996 (ICES, 1999b), a trend which is not obvious from the area dis-aggregated MSVPA. Comparing the daily egg production at peak spawning time as derived by ichthyoplankton surveys with corresponding potential annual egg production from 1986 to 1996 (Köster et al. 2001b), revealed maximum egg production by both methods in the Bornholm Basin in 1994 and 1995. In 1996 a large potential egg production (only 5% lower than the maximum in 1994) is contrasted by a 46% lower egg production as obtained from the ichthyoplankton survey. This indicates an overestimation of the most recent cod population size obtained by the area dis-aggregated MSVPA for Sub-division 25.

Unfortunately hydroacoustic surveys by the former GDR/USSR conducted in May/June 1979-1986 (Sjöstrand, 1989) are not representative for the abundance of herring. The majority of the spring spawning herring aggregate outside the survey area on their spawning grounds during this period (e.g. Aro, 1989; Parmanne et al., 1994) making these observations unreliable for estimating abundance and distribution. Other independent survey information, e.g. the Polish young fish survey, showed either high inter-annual variability (ICES, 1998) or did not cover comparable areas or sufficient time periods (Sjöstrand, 1989). Thus, the available independent data material on herring abundance appears to be insufficient for validation of the area dis-aggregated MSVPA results.

Validation of area dis-aggregated MSVPA derived biomass values of sprat were performed using above mentioned hydroacoustic surveys (Table 3.2.1.2) conducted in May/June 1979-1986 (data compiled by Sjöstrand, 1989) as well as Danish and Russian hydroacoustic surveys conducted in May/June 1995 (Tomkiewicz, Institute of Marine Sciences, Kiel, Germany, personal communication; Vasilieva, Atlantic Scientific Research Institute of Marine Fisheries and Oceanography, Kaliningrad, Russia, personal communication). The correlation between area dis-aggregated MSVPA output and

hydroacoustic survey results was high in all Sub-divisions (r^2 -values: 0.83 to 0.91), driven mainly by the increase in stock biomass from the mid 1980s to 1995.

Table 3.2.1.2 Comparison of sprat biomass estimates (age-group 1+; in 1000 tonnes) in different Sub-divisions (SD) as derived from hydroacoustic surveys in May/June and area dis-aggregated Multispecies Virtual Population Analyses (2nd quarter).

Year	SD 25		SD 26		SD 28	
	survey	MSVPA	survey	MSVPA	survey	MSVPA
1979	161	56	118	104	162	49
1981	68	73	76	101	41	51
1982	149	143	70	83	110	40
1984	159	341	120	319	147	92
1985	-	-	152	285	173	84
1986	153	295	128	215	165	63
1995	465	722	560	737	440	448

Note: A dash indicates that a reliable survey was not conducted that specific date

Population spatial dynamics

In order to validate the spatial distribution of adult cod in the Central Baltic, the area specific relative abundance of age-group 3+ from bottom trawl surveys in February/March (Sparholt and Tomkiewicz, 2000), is plotted against the relative population abundance from the area dis-aggregated MSVPAs (Figure 3.2.1.4). In Sub-division 26 the population remained stable throughout the time period, with the highest abundance observed in both the trawl survey and MSVPA estimates in 1996. In Sub-division 25, the proportions estimated by the MSVPA were in general higher than that observed in the trawl surveys, whereas in Sub-division 28 the MSVPA estimates were in general lower. Within the latter area a clear time trend of decreasing importance of the stock component is indicated by both data sources, with recent years being similarly low in the area dis-aggregated MSVPA and trawl survey results.

Cod recruits (age-group 1) showed a different distribution pattern than adult cod. Highest proportions were encountered by the trawl survey in Sub-division 26, while the MSVPA

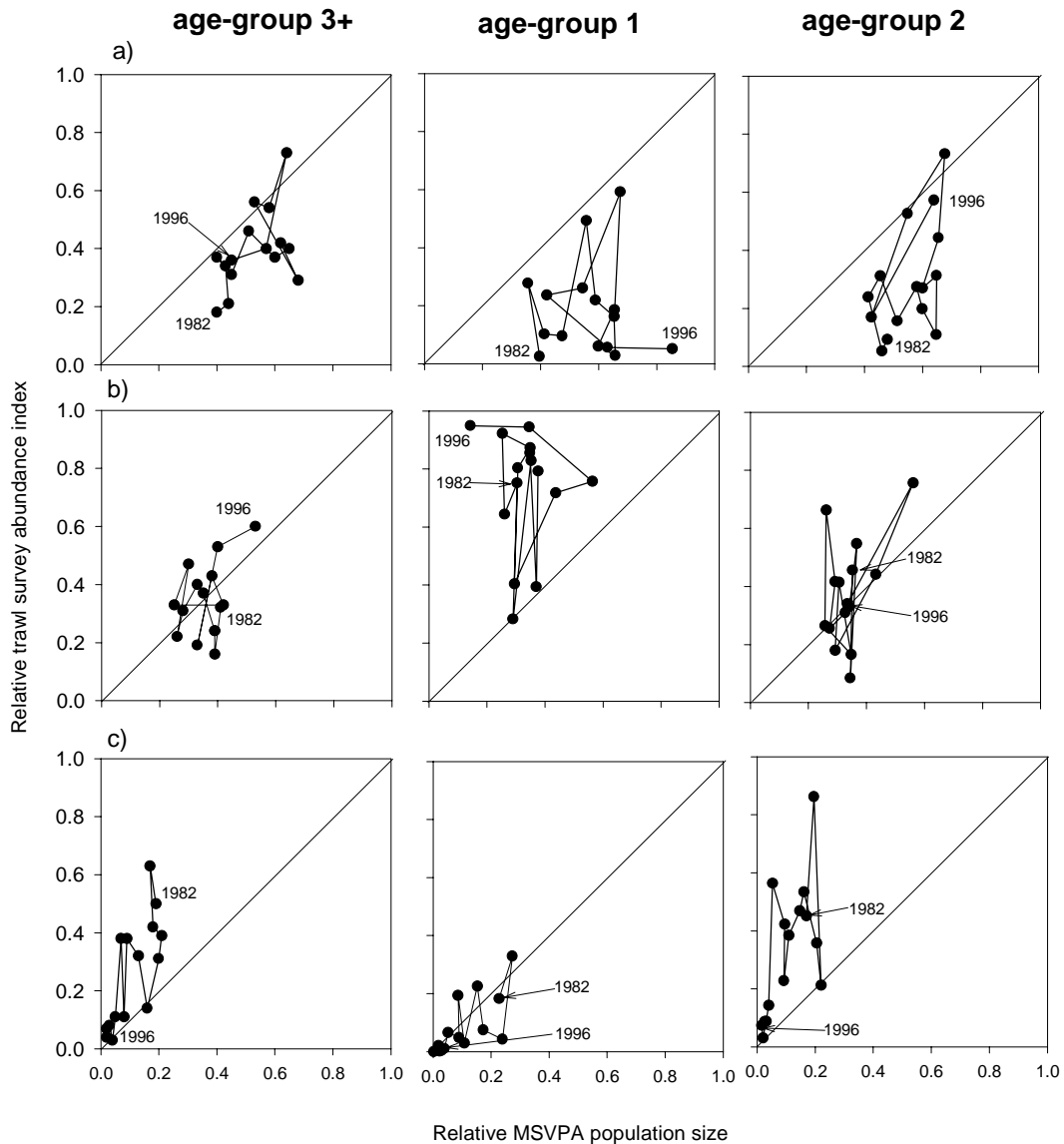


Figure 3.2.1.4. Relative horizontal distributions of total cod abundance indices (age-groups 3+, 1 and 2 and 3+) from the Baltic International Trawl Survey vs. corresponding relative distributions estimated by area dis-aggregated MSVPA (a – Sub-division 25; b – Sub-division 26; c – Sub-division 28).

estimated intermediate proportions (Figure 3.2.1.4). On the contrary, in Sub-division 25 the MSVPA derived recruitment is in general high and the corresponding fractions in the trawl surveys are comparatively low, with a time trend of increasing importance of the

area determined by the former but not by the latter. For Sub-division 28, independent of the method, rather similar low proportions were calculated, especially in recent years. The distribution pattern of age-group 2 by the area dis-aggregated MSVPA changed only slightly from that of the 1-group. However, in the trawl survey considerable changes with age were observed with increased proportions in Sub-division 25 and 28 and decreased in Sub-division 26.

The higher fraction of the cod stock derived by the trawl surveys in Sub-division 28 and a lower in Sub-division 25 may be interpreted as a spawning migration from the Gotland to the Bornholm Basin taking place after the bottom trawl survey is performed in the 1st quarter. These migrations have been previously described (Lablaika and Lishev, 1961).

The distribution pattern from the trawl survey changes with age, i.e. recruits of age-group 1 concentrate in Sub-division 26. A biological explanation for this dislocation relative to the area dis-aggregated MSVPA results, may be a drift of larvae and pelagic juveniles out of the Bornholm Basin into the neighbouring Sub-division, which has been identified through the application of hydrodynamic models (Voss et al., 1999; Hinrichsen et al., 2000). The change in relative distribution of age-group 2 indicates either a higher mortality of juveniles in Sub-division 26, not accounted for in the MSVPA, or a movement out of the area. In fact, an analysis of catch rates obtained from Latvian trawl surveys conducted at different times of the year in the Gotland Basin (see above) revealed indications of an expansion of juvenile cod into the Gotland Basin from southern areas.

The relative distribution of herring obtained by hydroacoustic surveys in September/October and the area dis-aggregated MSVPA match on average for Sub-division 28, whereas the fraction inhabiting Sub-division 25 estimated by the MSVPA was slightly higher (Figure 3.2.1.5). Pronounced long-term changes in the relative distribution of the herring populations were not obvious in any of the time series. Although not commonly agreed it has been argued (e.g. Ojaveer, 1989) that there exist three distinct herring groups in the Baltic, the open sea and the coastal spring spawning herring as well as the autumn spawning herring, represented by various independent stocks, showing

different migration patterns. Additionally the intensity of these migrations depend on

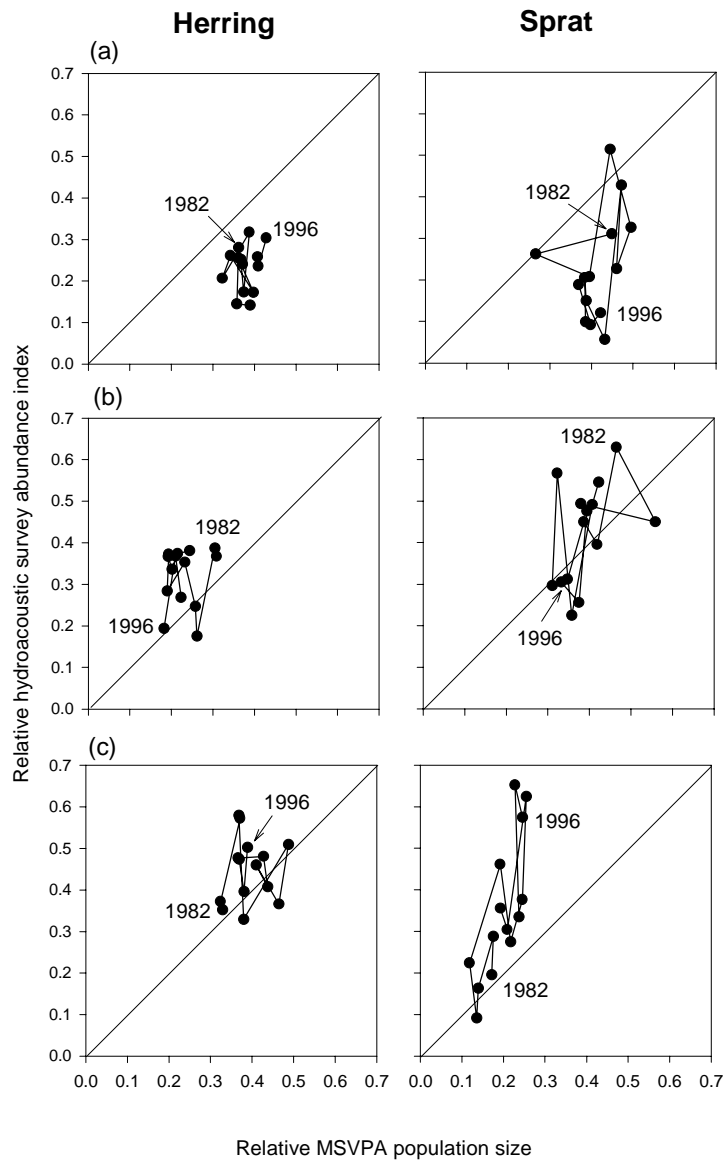


Figure 3.1.2.5. Relative horizontal distributions of total sprat and herring abundance (age-group 1+) from the International Hydroacoustic Survey vs. corresponding relative distributions derived by area dis-aggregated MSVPA (a – Sub-division 25; b – Sub-division 26; c – Sub-division 28).

environmental conditions and food supply (Parmanne et al., 1994). Hence, due to this complex stock structure and the migratory behaviour of herring within and between Sub-divisions (e.g. Aro, 1989; Ojaveer, 1989), an evaluation of the obtained relative distribution patterns from the area dis-aggregated MSVPA is extremely difficult.

When repeating the exercise for sprat using the international hydroacoustic survey from September/October, a similar picture to cod is obtained. Higher proportions are estimated for Sub-division 25 by the MSVPA, and lower abundance in Sub-division 28, with increasing deviations with time, and on average similar fractions in Sub-division 26 (Figure 3.2.1.5). A comparison of the average distribution patterns obtained from both data series with corresponding values derived by hydroacoustic surveys in May/June 1979-1986 (ICES, 1999a), shows that the similarity to the area dis-aggregated MSVPA output is considerably higher than to the hydroacoustic survey in autumn. The former allocated on average 37% of the stock to Sub-division 25 and 42% to 26. The survey in May/June revealed a corresponding fraction of the stock inhabiting Sub-division 25 and on average similar population levels in both eastern areas. In contrast the hydroacoustic survey in September/October identified the highest population sizes to be in Sub-division 26 (52%) and considerably lower fractions of the stock in Sub-division 25 (26%). This could be interpreted as spawning migrations from Sub-division 26 into the Bornholm and the central Gotland Basin. However, when interpreting the encountered deviations in relative distributions, an exchange between not covered Sub-divisions 27 and 29 and the study area must be considered. Additionally sprat from the western Baltic migrate to some extent to the Bornholm Basin for spawning (Aro, 1989; Parmanne et al., 1994).

Comparison of standard stock assessment and area dis-aggregated MSVPA results

For the Central Baltic cod stock (Sub-divisions 25-32), the Central Baltic herring stock (Sub-divisions 25-29 + 32, including Gulf of Riga) and the Baltic sprat stock (Sub-divisions 22-32) (ICES 1998), standard assessment results allow validation of the output of the area dis-aggregated MSVPA (summed over Sub-divisions 25, 26 and 28). The standard assessment utilises area aggregated MSVPA derived predation mortalities as input and is thus comparable to the integrated results obtained by the area dis-aggregated MSVPAs. However, stock units for all three species are not the same, as the regular assessment also includes at least Sub-divisions 27, 29 and 32. The major part of

the cod catch (90-98%) is nevertheless taken in the areas covered by the present study (Sparholt and Tomkiewicz, 2000).

Herring population estimates for Sub-divisions 25-28 can be obtained from standard assessment results (ICES, 1998) encompassing Sub-divisions 25-29 and 32, when subtracting stock estimates for Sub-division 29 and 32 determined by ICES (1998). However, Sub-division 27 is still included as an area which sustains a substantial herring fishery and for which the international hydroacoustic survey on average estimates 21% of the entire population in the Central Baltic.

The standard assessment of sprat treats the entire Baltic as one stock unit. To account for sprat in the western Baltic (Sub-divisions 22-24), population estimates derived by an earlier MSVPA (ICES, 1997a) were subtracted from the estimates for the entire Baltic. Sub-divisions 25, 26 and 28 covered in the present study sustain the major part of the sprat catch in the Baltic (79-83% in recent years). Nevertheless, the area dis-aggregated MSVPA population sizes should to a certain degree underestimate the Central Baltic sprat stock compared to the standard assessment (excluding Sub-divisions 22-24), as Sub-divisions 27, 29 and 32 are still not included.

Standard assessment and area dis-aggregated MSVPA derived estimates of cod SSB show a similar development from 1986 to 1995 (Figure 3.2.1.6). The standard assessment estimates are in general slightly higher, due to the incomplete area coverage by our dis-aggregated multispecies assessment. A relatively large discrepancy occurred in 1996 with the regular assessment estimate being substantially lower. This result confirms the overestimation by the area dis-aggregated MSVPA of the population size in Sub-division 25 in recent years (described above). In the first part of the time series, considerably higher SSB values were estimated by the standard assessment. This can not be explained by the lack of inclusion of Sub-divisions 27, 29 and 32 in the present area dis-aggregated MSVPA runs. Other factors, e.g. differences in the recompiled catch and especially weight at age data (see below) obviously contribute to this deviation.

For herring the trends in SSB estimates from standard assessment and area dis-aggregated MSVPA were rather similar, with a less rapid decline in the stock predicted by

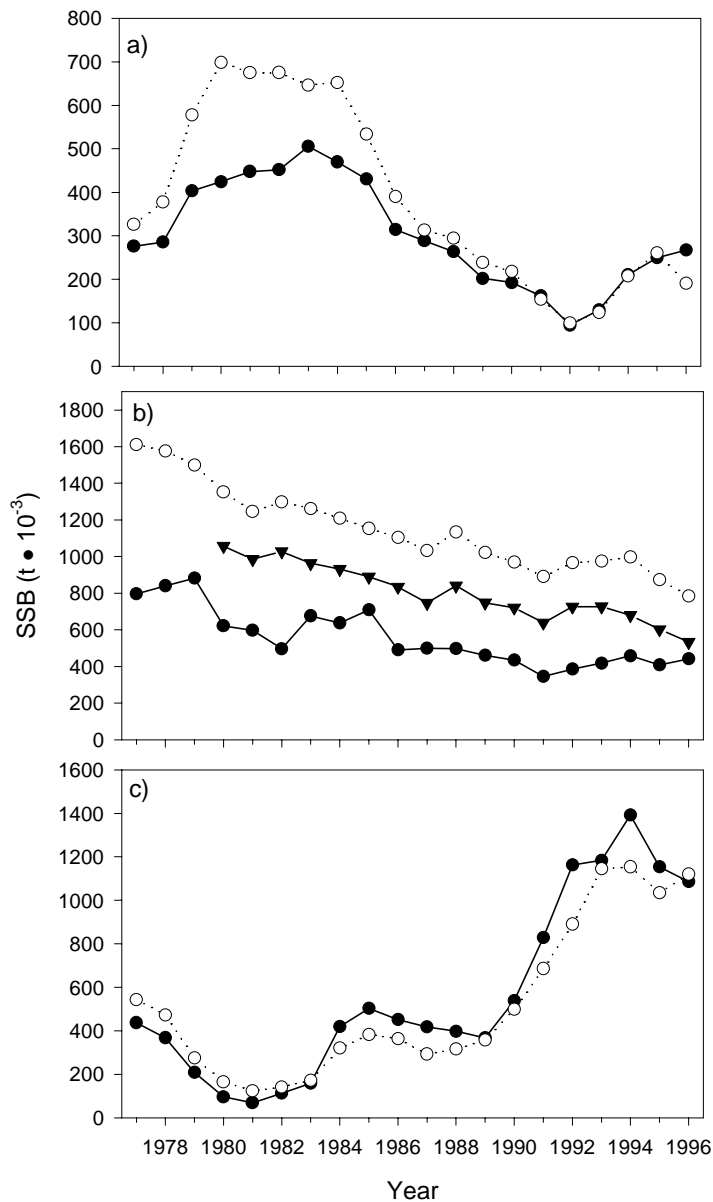


Figure. 3.2.1.6. SSB derived by area dis-aggregated MSVPA and standard stock assessments (XSA) (both beginning of the year) of cod (a), herring (b) and sprat (c) (solid circles, MSVPA; open circles, XSA for standard assessment areas; triangles (Fig. 3.2.1.9b), XSA Sub-divisions 25-28). See text for a detailed description of standard assessment areas.

the latter (Figure 3.2.1.6). The difference between the estimates from Sub-divisions 25-28 and the area dis-aggregated MSVPA output are higher than expected from the lack of

area coverage, which is caused by deviations in the revised and the standard assessment catch at age database (ICES 1999a).

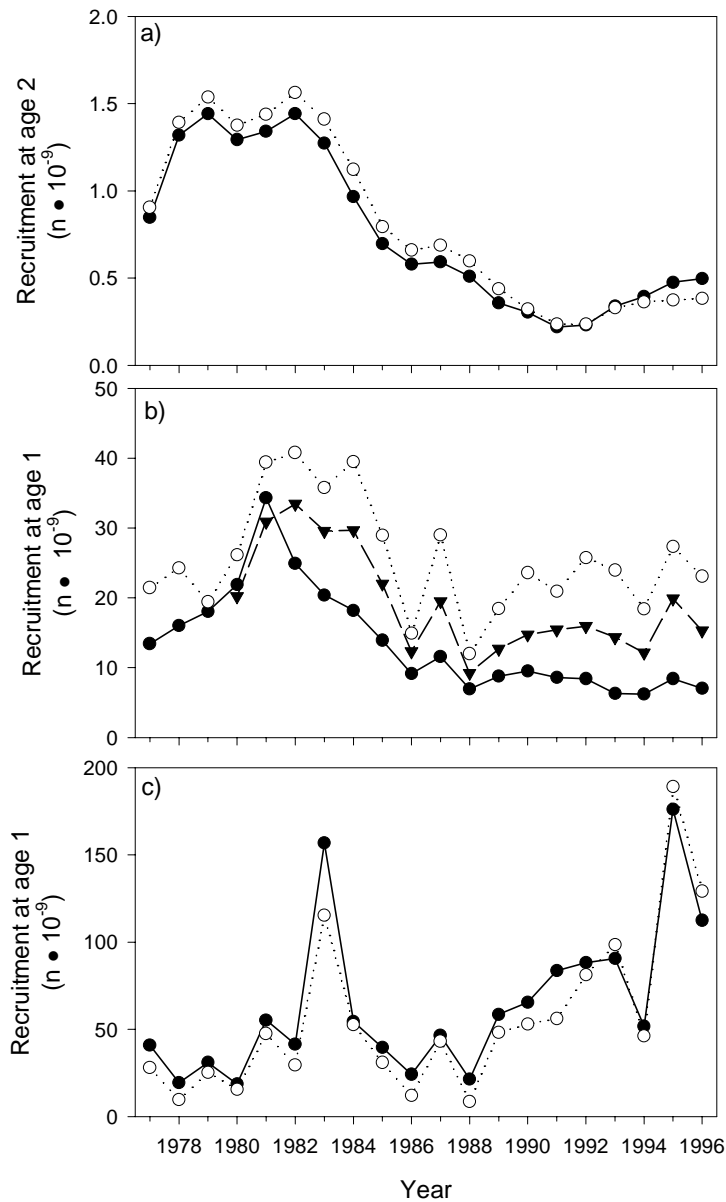


Figure 3.2.1.7. Recruitment derived by area dis-aggregated MSVPA and standard stock assessments (XSA) (beginning of the year) of cod (a), herring (b) and sprat (c) (solid circles, MSVPA; open circles, XSA for standard assessment areas; triangles (Fig. 3.2.1.10b), XSA Sub-divisions 25-28). See text for a detailed description of standard assessment areas.

Standard assessment and area dis-aggregated MSVPA estimates for sprat SSB are relatively similar throughout the entire time series (Figure 3.2.1.6). Until 1983, the standard assessment SSBs are higher than the corresponding multispecies estimates;

this could be expected due to the differences in area coverage. However, since 1984 the area dis-aggregated MSVPA derived spawning stocks were in general slightly higher.

Cod recruitment estimates derived by both assessments (age-group 2) were similar throughout the time series (Figure 3.2.1.7). This clearly demonstrates that the large deviations encountered in the SSB early in the time series are generated to a large extent by deviations in weight at age in the stock. These are set as constant in the regular assessment before 1983.

For herring standard assessments give a similar impression with respect to recruitment (age-group 1) development than our multispecies assessment until the mid 1980s, but show increasing differences afterwards (Figure 3.2.1.7). As expected recruitment values generated by the area dis-aggregated MSVPA runs were in general lower. However, especially in the beginning of the time series the deviation was less than expected. This indicates, that the major changes in SSB during this period were to a large extent due to deviations in weight at age.

Sprat recruitment (age-group 1) as determined by both methods were rather similar in all years considered. The area dis-aggregated MSVPA revealed in general slightly higher values, with the exception of recent years (Figure 3.2.1.7).

3.2.2. Clupeid fish consumption

3.2.2.1. Copepods

Highest individual daily rations by herring on *P. elongatus* were found in winter, spring and summer, whereas individual consumption was neglectable in autumn (Figure 3.2.2.1). In winter and spring mainly CII were consumed, whereas in summer preferred food items were CV/VI. Feeding rates on CIII/IV were generally relatively low. In all seasons individual daily ingestion rates declined drastically with time to almost 0-values in the mid 1990s.

Main feeding season by herring on *T. longicornis* was summer, however significant individual feeding rates were also calculated for the other seasons (Figure 3.2.2.1). The

stage-composition was similar to *P. elongatus* with mainly CII and CV/VI and lower

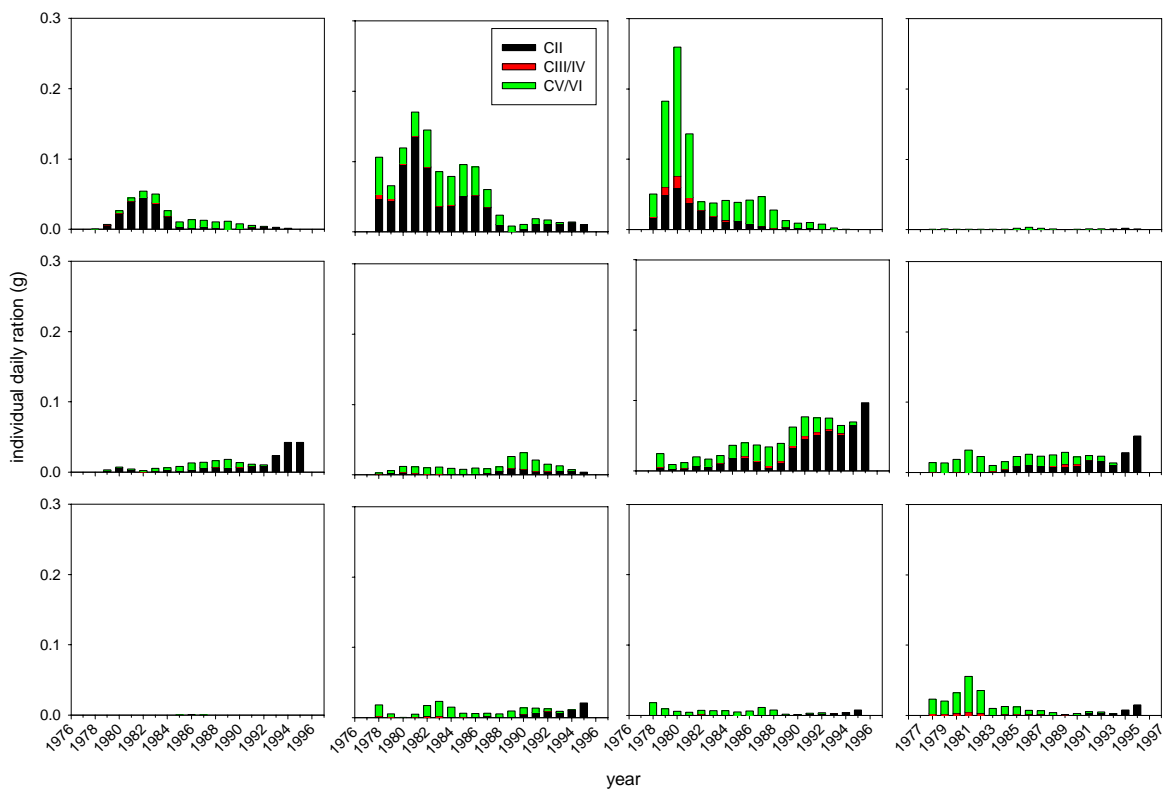


Figure 3.2.2.1. Average seasonal individual daily ration by herring on copepod life-stages (CII, CIII/IV, CV/VI) of *P. elongatus* [1st row], *T. longicornis* [2nd row] and *Acartia* spp. [3rd row]; data have been smoothed by a two-point running mean.

proportions of CIII/IV found in the diet. In all seasons, except spring, individual consumption rates increased in general with time, which went along with a switch from CV/VI to CII as main food item.

Individual herring predation on *Acartia* spp. was low compared to the other two copepod species, with predation taking place in spring, summer and especially autumn (Figure 3.2.2.1). Individual ingestion rates generally decreased with time. A marked change in stage-composition was observed, similar to *T. longicornis*, with herring preying upon CV/VI until the late 1980s, switching to CII during the 1990s.

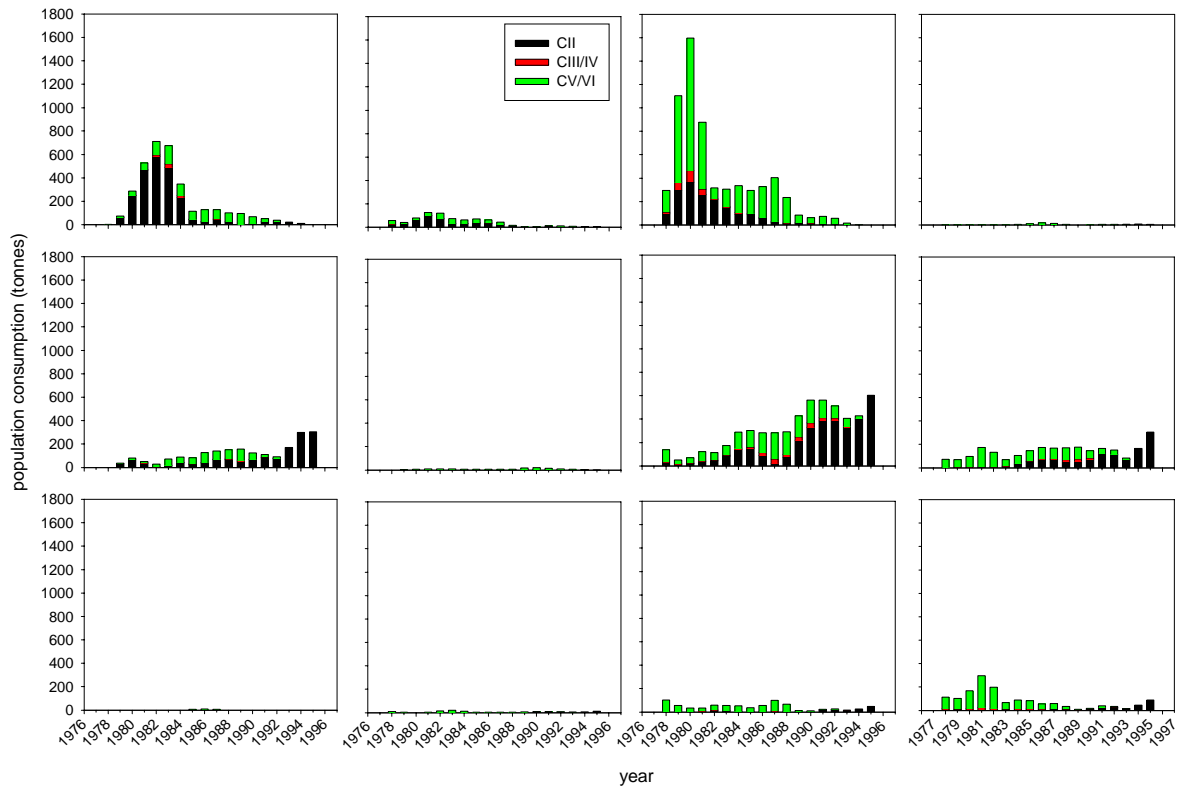


Figure 3.2.2.2. Average seasonal daily population consumption by herring on copepod life-stages (CII, CIII/IV, CV/VI) of *P. elongatus* [1st row], *T. longicornis* [2nd row] and *Acartia* spp. [3rd row]; data have been smoothed by a two-point running mean.

Population consumption rates by herring on displayed the same trend as found for individual daily rations (Figure 3.2.2.2). Only the absence of most of the herring population in spring due to spawning activity in coastal areas resulted in negligible population consumption.

Sprat fed exclusively on CV/CVI of all three copepod species (Fig. 3.2.2.3). *P. elongatus* was mainly preyed upon in winter, spring and summer. In all three seasons, a peak in individual daily rations was observed in the early 1980s decreasing afterwards. *T. longicornis* was consumed by individual sprat in all seasons with a clear and very pronounced decrease in feeding rates in autumn. *Acartia* spp. was a food item of sprat in all seasons except winter, showing a moderate increase in individual consumption during the 1980s, slightly decreasing during the 1990s.

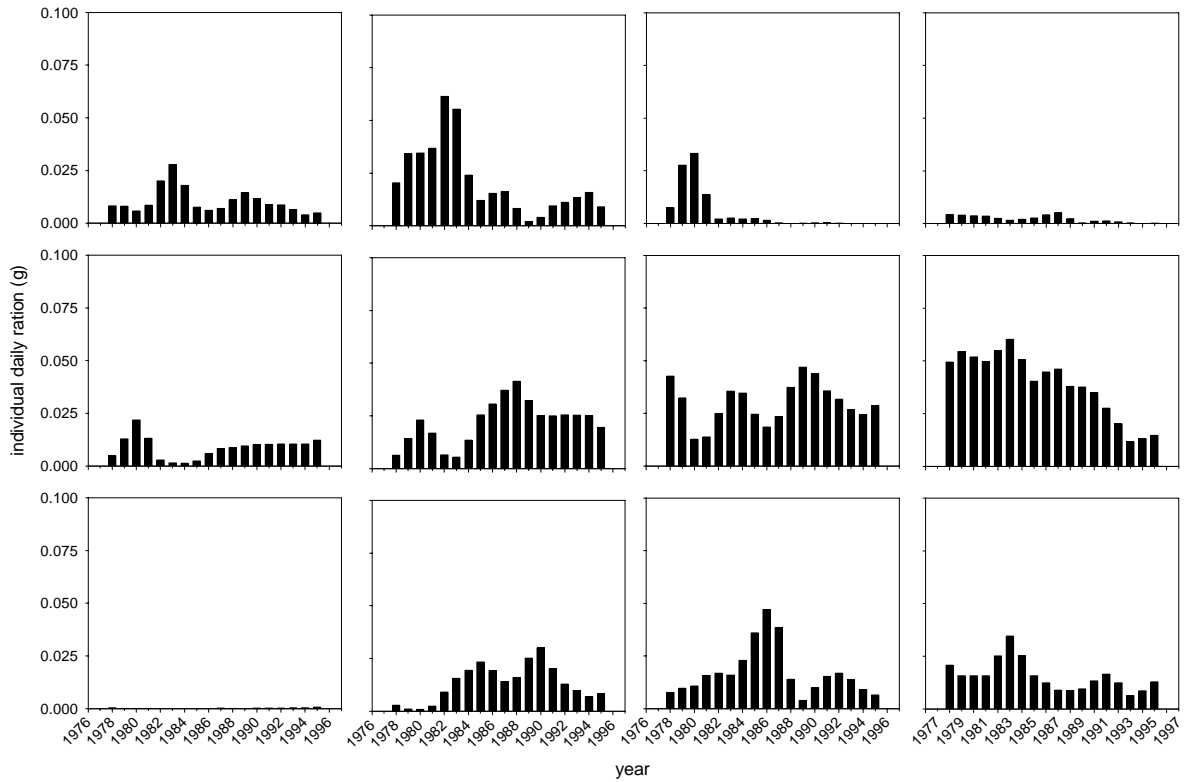


Figure 3.2.2.3. Average seasonal individual daily ration by sprat on CV/VI of *P. elongatus* [1st row], *T. longicornis* [2nd row] and *Acartia* spp. [3rd row]; data have been smoothed by a two-point running mean.

The drastic increase in sprat stock size during the 1990s, resulted in a general rise in daily population consumption rates (Figure 3.2.2.4). This stock enlargement resulted in generally high population consumption on all copepods, however most pronounced in *T. longicornis*.

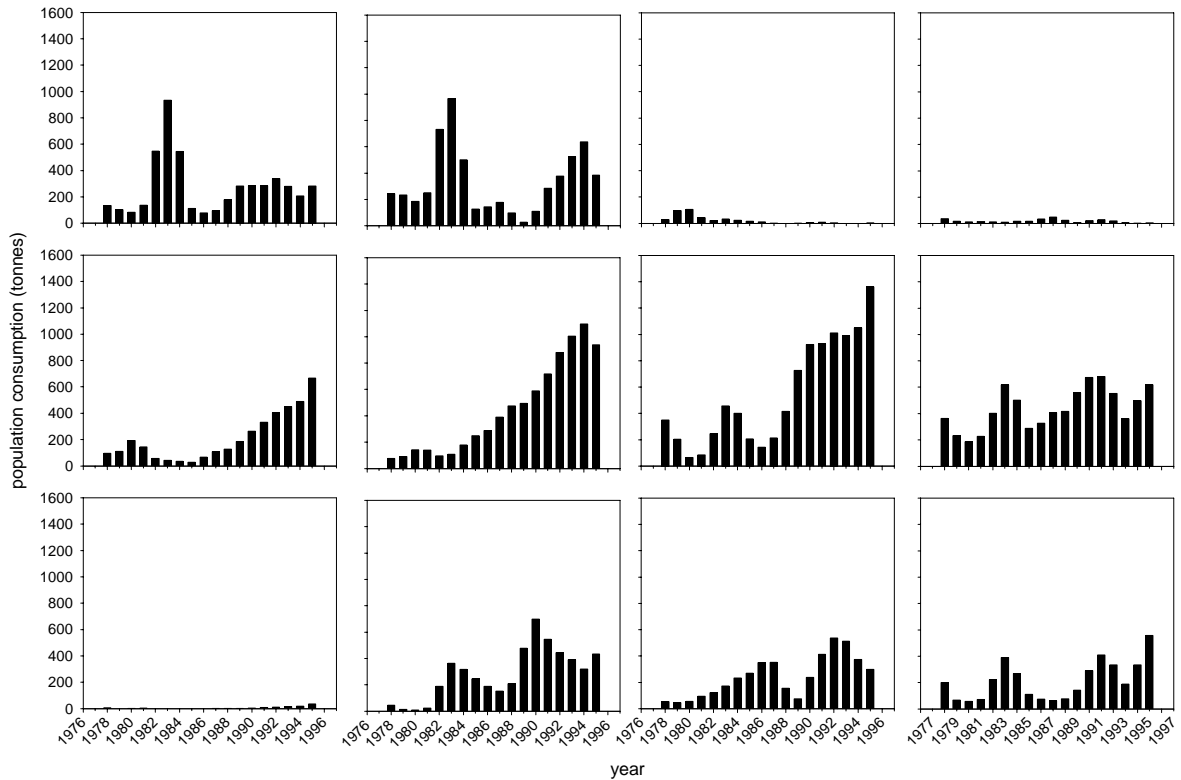


Figure 3.2.2.4. Average seasonal daily population consumption by sprat on CV/VI of *P. elongatus* [1st row], *T. longicornis* [2nd row] and *Acartia* spp. [3rd row]; data have been smoothed by a two-point running mean.

3.2.2.2. Cladocerans

Sprat was found to consume *B. coregoni maritima* in the Gotland Basin in summer and autumn (Figure 3.2.2.5). In general there was a tendency to decreasing individual daily rations with time, especially in the 1990s. In contrast, sprat preyed upon *Podon* spp. and *E. nordmanni* in spring and summer. Whereas individual ingestion by sprat on *Podon* spp. decreased continuously since the beginning of the 1980s, a highly variable predation pressure was estimated for *E. nordmanni* with two maxima in spring (early 1980s and 1990s). A three-modal distribution appeared in the summer time-series. A concentration of 0-values was found in the latest years of the time-series which is to a higher degree true for *Podon* spp.

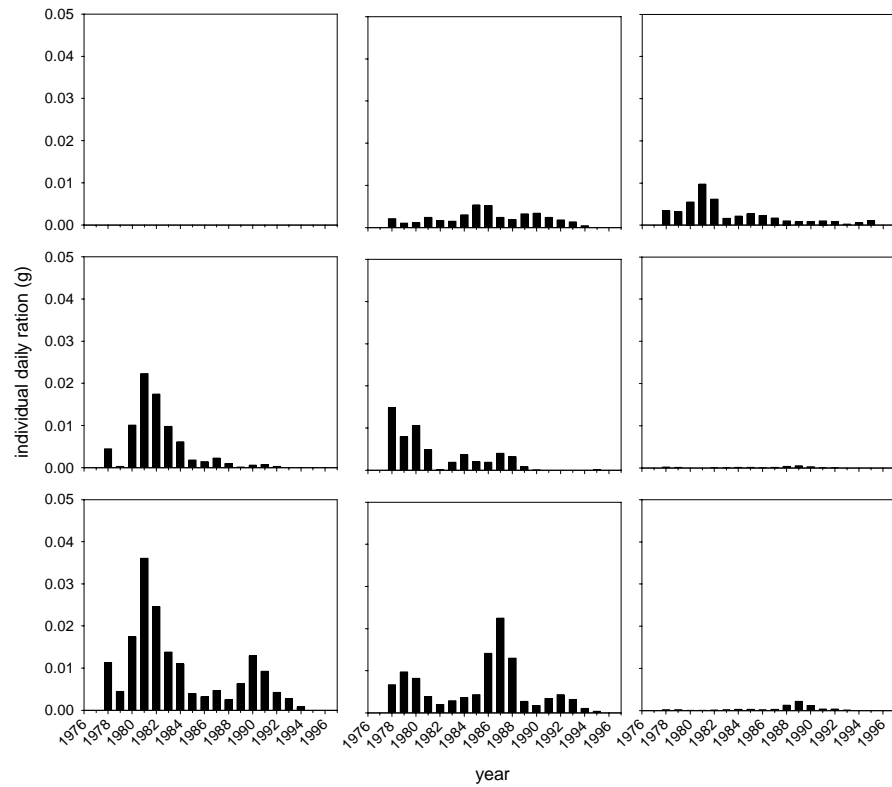


Figure 3.2.2.5. Average seasonal individual daily ration by sprat on *B. coregoni maritima* [1st row], *Podon* spp. [2nd row] and *E. nordmanni* [3rd row] in spring [1st column], summer [2nd column] and autumn [3rd column];; data have been smoothed by a two-point running mean.

Combing individual daily rations with sprat stock size (Figure 3.2.2.6) resulted in estimates of the population consumption. Similar time-trends as for individual daily

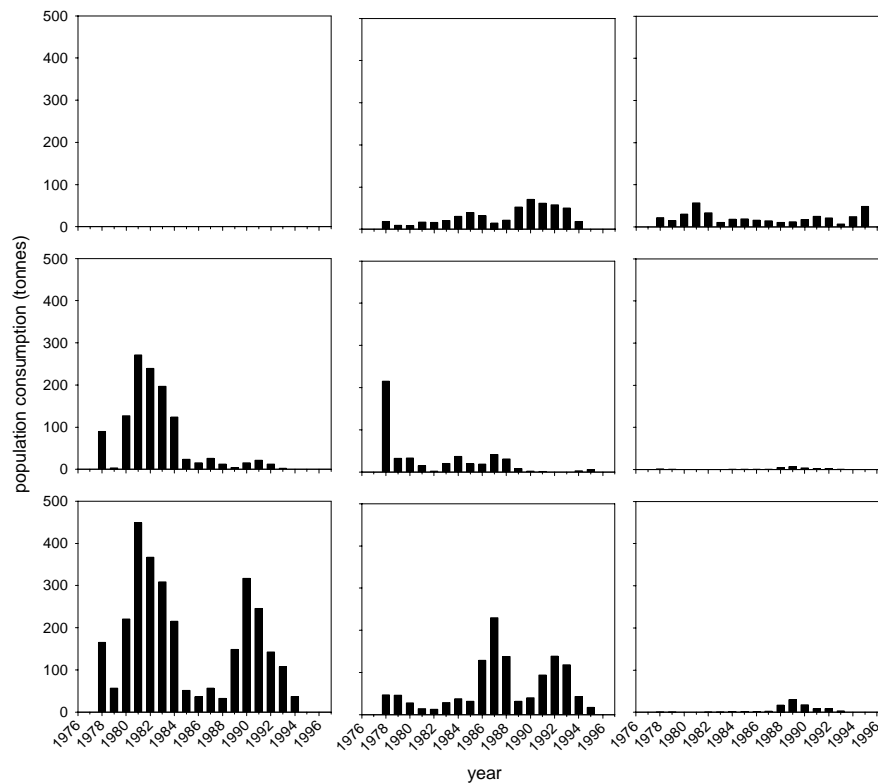


Figure 3.2.2.6. Average seasonal population consumption by sprat on *B. coregoni maritima* [1st row], *Podon* spp. [2nd row] and *E. nordmanni* [3rd row] in spring [1st column], summer [2nd column] and autumn [3rd column]; data have been smoothed by a two-point running mean.

ingestion rates were encountered in the time-series (Figure 3.2.2.5). Only during the 1990s, the drastically enlarged sprat stock counteracted decreasing individual daily rations.

3.2.3. Copepods

3.2.3.1. Copepod abundance and vertical distribution

The standing stock of *P. elongatus* in winter was mainly composed of CIII/IV and CV/CVI with lower values of both stage-groups since the mid 1980s. (Figure 3.2.3.1). Due to reproduction in spring CII appeared in larger numbers being relatively stable over time, but having a minimum in the mid 1980s. *P. elongatus* CIII/IV abundance was higher in

the 1990s compared to the preceding decade, whereas CV/CVI showed the opposite development. In summer the stock constituted mainly of CIII/CIV and total abundance declined over time. This decline was obvious for all stages, but especially in pronounced CII and CV/CVI. The development of the autumn stock of *P. elongatus* showed the same time-trend as in winter with the proportion of CIII/IV being higher.

The *T. longicornis* winter stock was composed of CV/VI on a stable low level (Figure 3.2.3.1). The same situation was encountered in spring until the end of the 1980s, whereas afterwards a stepwise increase in all stage-groups was observed. Also the summer stock was composed of all stage-groups with CV/CVI dominating, and the total abundance generally increasing. The autumn stock of *T. longicornis* was relatively stable in time being mainly composed of CIII/IV.

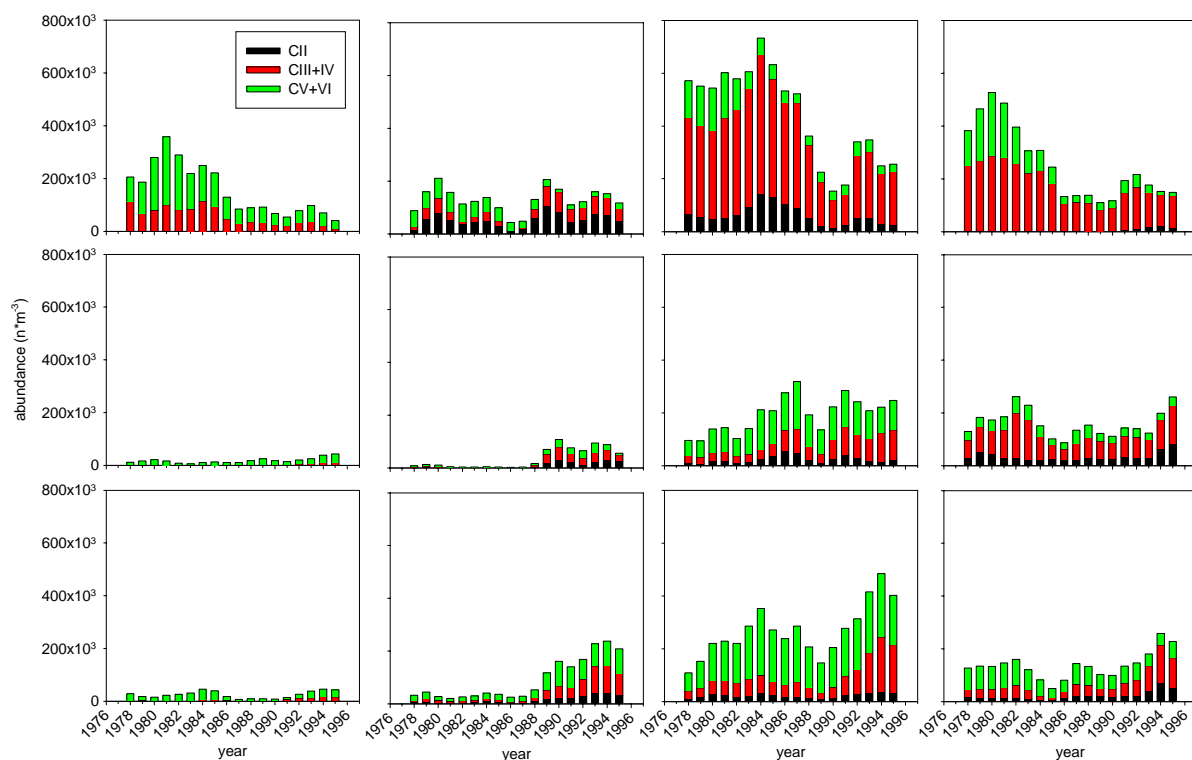


Figure 3.2.3.1. Seasonal abundance of copepod life-stages (CII, CIII/IV, CV/VI) of *P. elongatus* [1st row], *T. longicornis* [2nd row] and *Acartia* spp. [3rd row]; data have been smoothed by a two-point running mean.

The population development of *Acartia* spp. was similar to *T. longicornis* (Figure 3.2.3.1). However, the stepwise increase in abundance in spring was even more pronounced in *Acartia* spp., and the total summer standing stock was rising in the 1990s due to increased CIII/IV abundance.

The vertical preference of *P. elongatus* (Figure 3.2.3.2) showed a clear ontogenetic trend with CII dwelling shallowest in the water column (average annual WMD = 34m) and the oldest stages CV, CVI-f and especially CVI-m having the deepest distribution (average annual WMDs = 56m, 53m and 66m respectively). Clear seasonal differences were obvious for CIII and older stages having a shallower distribution in winter compared to the other seasons.

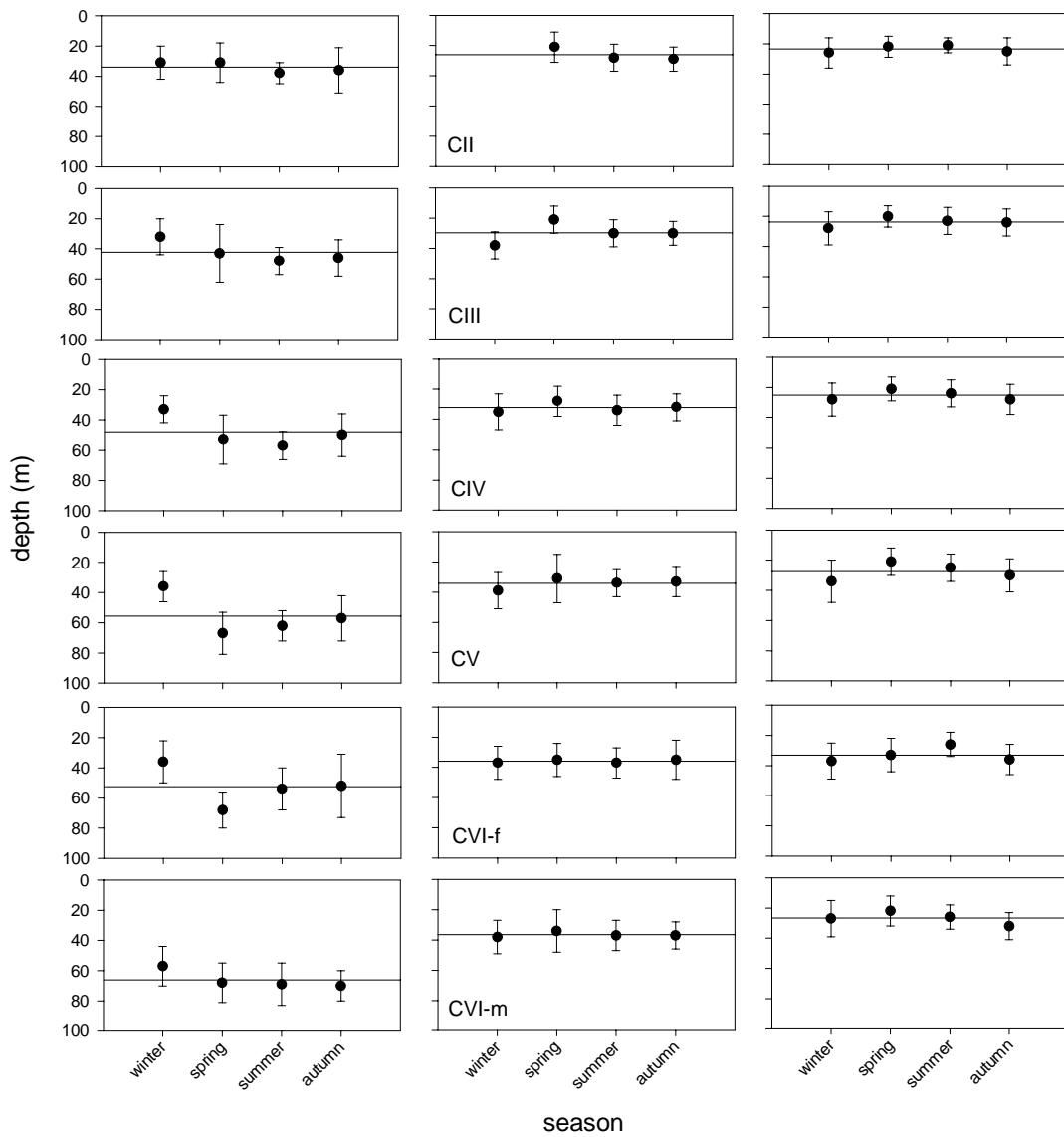


Figure 3.2.3.2. Seasonal weighted mean depth (WMD) copepod life-stages (CII-V, CVI-f and CVI-m) of *P. elongatus* [1st column], *T. longicornis* [2nd column] and *Acartia* spp. [3rd column].

T. longicornis and *Acartia* spp. showed a less pronounced ontogenetic increase in depth from CII (annual average WMD = 26 and 24m respectively) to CVI (annual average WMD

= 36 and 33m respectively). Generally weak seasonal variation was found with a slightly deeper distribution of all stages in winter.

3.2.3.2. Copepod development times and production

Temperature-dependent development times (Appendix Table 4) resulted in average daily production rates having a higher variability than observed copepod abundance (Appendix-Table 5). However, the main trends were still visible, showing a general decline of all *P. elongatus* stages in all seasons. In contrast, production rates of *T. longicornis* and *Acartia* spp. life-stages, although highly variable, increased, especially in the 1990s.

3.2.3.3. Clupeid fish consumption versus copepod production

Average ratios of consumption to production (C/P-ratios) for the herring population were generally low, with values mainly far below 0.10 (Table 3.2.3.1; Appendix-Table 6). Relatively high C/P-ratios were found for *P. elongatus* CII in spring, with four outstanding high values during the 1970s and 1980s. During the 1990s C/P-ratios for CII of *P. elongatus* were as well low. C/P-ratios of *T. longicornis* CII in summer were in general high, especially during the last decade.

Significant proportions of the production of *P. elongatus* and *T. longicornis* CV/VI were consumed by sprat in spring (Table 3.2.2.1; Appendix-Table 7). Again high ratios were mainly found in the 1990s, but for *T. longicornis* also in the second half of the 1980s

Table 3.2.3.1. Consumption/production-ratios of copepod species/stages in seasons with a strong predation pressure by herring and sprat (see text for details).

Year	Herring		Sprat	
	Spring	Summer	Spring	
	<i>P. elongatus</i>	<i>T. longicornis</i>	<i>P. elongatus</i>	<i>T. longicornis</i>
	CII	CII	CV/VI	CV/VI
1977	0.54	0	0.04	0.07
1978	0.05	0.76	0.02	0.21
1979	0.04	<0.01	0.09	0.04
1980	0.02	0	0.02	0.10
1981	>1	0.10	<0.01	0.24
1982	0.06	0	0.08	0.02
1983	0.20	0.44	0.22	0.32
1984	0.02	0.12	0.04	0.16
1985	>1	0.27	0.01	>1
1986	0.11	0.04	0.04	0.37
1987	0.54	<0.01	>1	>1
1988	<0.01	0	<0.01	0.76
1989	0	>1	0.02	0.10
1990	0	0.43	0.02	0.05
1991	0.02	0.15	0.36	0.17
1992	<0.01	0.68	0.08	0.23
1993	<0.01	0.45	0.33	0.07
1994	<0.01	0.40	>1	0.91
1995	<0.01	>1	>1	0.62
1996	<0.01	0.39	0.02	0.06
Mean	0.23	0.39	0.39	0.57

3.2.3.4. Copepod mortality

CII of *P. elongatus* in spring and CII of *T. longicornis* in summer were identified by C/P-ratios to suffer from predation pressure by herring. Additionally CV/VI of *P. elongatus* and *T. longicornis* in spring were significantly preyed upon by sprat. To validate the predation effect, mortality rates for these stages were computed. Mortality rates were not calculated for CII of *P. elongatus* in spring, because of the low frequency of high C/P-ratios, suggesting that a significant predation pressure by herring on this stage is unlikely or happens sporadically only.

As a vertical life table approach was used, where daily mortality rates can only be computed for consecutive stages, mortality rates for CI/II and CII/III of *T. longicornis* in

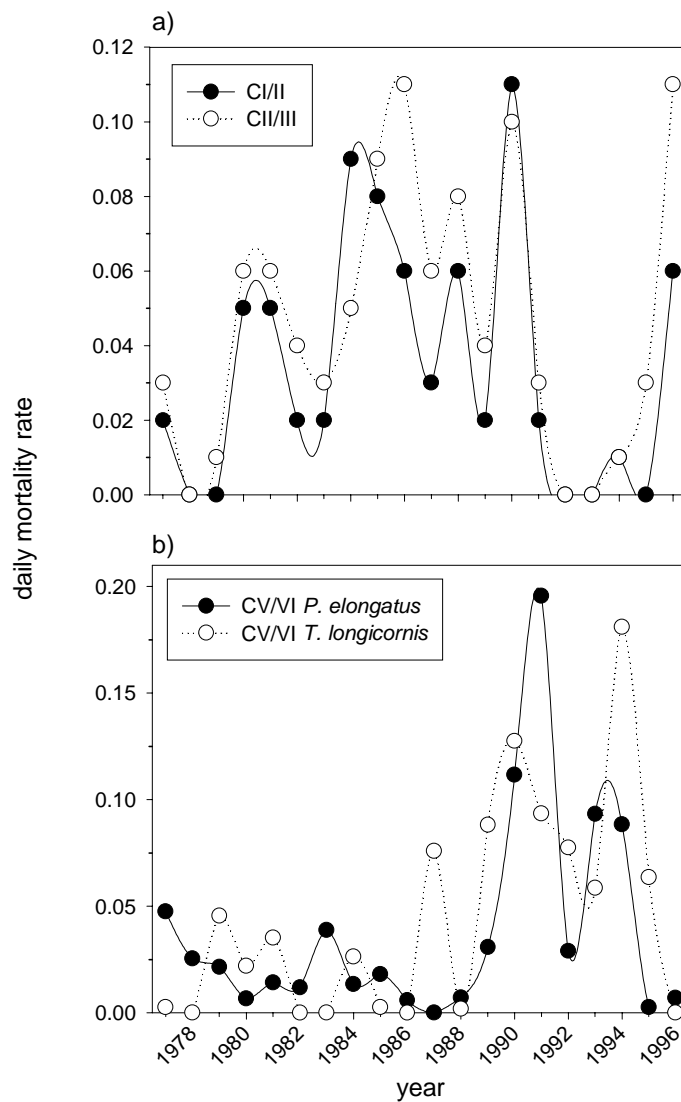


Figure 3.2.3.3. Daily mortality rates of CI/II and CII/III of *T. longicornis* in summer (a), as well as CV/VI of *P. elongatus* and *T. longicornis* in spring (b).

summer were calculated to check the influence of herring predation (Fig. 3.2.2.8a). The time-series of mortality rates of both stage-groups showed generally a parallel development with increasing values until the early 1980s to in maximum 0.11. High rates during the 1980s were followed by low mortality (0-values) in the beginning of the 1990s, increasing afterwards

Mortality rates of CV/VI of *P. elongatus* in spring were on average 0.02 until 1989, whereas afterwards they increased to 0.08 (Fig. 3.2.2.8b). Two distinct periods within

the considered time-series were also found for *T. longicornis* in spring with low rates until 1986 (on average 0.01) afterwards mortality rates were higher (on average 0.08).

3.2.4. Cladocerans

3.2.4.1. Cladoceran biomass

Considerable biomasses of *B. coregoni maritima* were only encountered in summer (Figure 3.2.4.1). Within the considered time-series two peaks, in 1982 and 1991, were

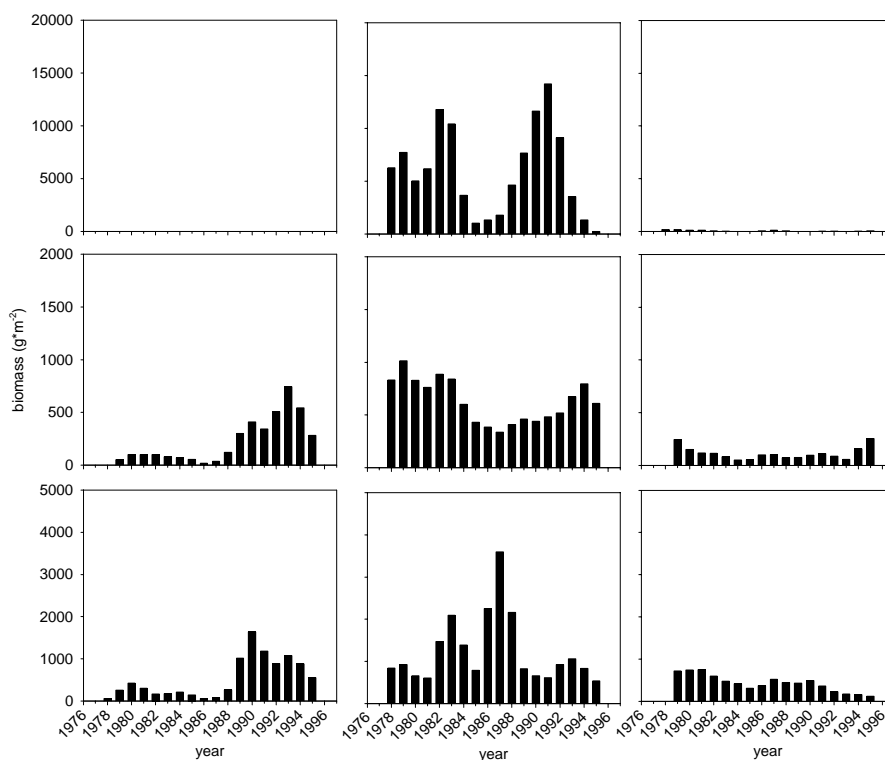


Figure 3.2.4.1. Biomass of *B. coregoni maritima* [1st row], *Podon* spp. [2nd row] and *E. nordmanni* [3rd row] in spring [1st column], summer [2nd column] and autumn [3rd column]; data have been smoothed by a two-point running mean.

observed. A stepwise increase in *Podon* spp. and *E. nordmanni* biomass was observed in spring. Summer biomass of *Podon* spp. decreased until the mid 1980s and increased afterwards, whereas *E. nordmanni* exhibited an opposite development. In autumn biomass of cladocerans was generally low, with *Podon* spp. showing no stable time-trend, whereas *E. nordmanni* biomass declined continuously.

3.2.4.2. Cladoceran production

Temperature-dependent average seasonal daily production rates of the different cladoceran species showed to a large extent the same time pattern as observed for biomass (Appendix-Table 8). Highest production regularly appeared in summer and the most productive species is *B. coregoni maritima*.

3.2.4.3. Sprat consumption versus cladoceran production

Significant C/P-ratios were found for *B. coregoni maritima* regularly in autumn with in maximum 0.80 (Table 3.2.4.1). High C/P-ratios were seldom found for *Podon* spp. with the exception of three values larger than 0.30 in spring and summer. Regularly in spring *E. nordmanni* was heavily predated by the sprat stock, consuming in maximum the full production of this cladoceran species. However, these high C/P-ratios were exclusively computed for earlier years, i.e. 1977-1987.

Table 3.2.4.1. Average seasonal sprat consumption/production-ratios of cladocerans.

Year	<i>B. coregoni maritima</i>		<i>Podon</i> spp.			<i>E. nordmanni</i>		
	Summer	Autumn	Spring	Summer	Autumn	Spring	Summer	Autumn
1977	0	0.24	-	0.36	-	>1	0	-
1978	0	0.05	-	0.02	0	>1	0.03	0
1979	0	0.03	0	0	0	0	0.01	0
1980	0	0	0	0.03	0	0	0.02	0
1981	0	0.24	-	0	0	>1	0	0
1982	0	0.12	0.36	0	0	0.15	0	0
1983	0	0.02	-	0	0	>1	0	0
1984	0.01	0.45	0.7	0.03	0.01	0.4	0.02	0
1985	0.02	0.59	0	0	-	0.31	0	0
1986	0	0.34	-	0	0	0.13	0.02	0
1987	0	0.04	>1	0.15	0	>1	0.02	0
1988	0	-	0	0.01	0.02	0	0.03	0
1989	0	-	0	0	0.07	0.03	0.01	0.06
1990	0	0.21	0.01	0	0	0.11	0	0
1991	0	0.32	0.12	0	0.01	0.20	0.08	0.02
1992	0	0.36	0.02	0	0.01	0.13	0.03	0.02
1993	0	-	0	0	-	0.09	0.04	0
1994	0	0	0	0	0	0	0	0
1995	0	0.80	0	0.01	0	0	0	0
1996	0.01	0.01	0	0	0	0	0.03	-

- 0 production resulted in unrealistic C/P-ratios.

4. DISCUSSION

4.1. The influence of hydrography

4.1.1. Copepods

Estimates of zooplankton abundance are always sensitive to the sampling efficiency of the gear in use which may not be constant for all stages (Båmstedt, 2000). The gear used for this study is however considered to quantitatively sample all copepodite stages (Hernroth, 1979), thus measurements may only be biased for the nauplii stages. Furthermore copepod abundance estimates may be uncertain due to a low number of stations sampled in specific seasons/years, and may be furthermore affected by advective transport which appears to be difficult to separate from biological events (Aksnes and Blindheim, 1996). However, the analysis of long-term biomass dynamics of these copepod species revealed the same time trends in standing stocks in all Central Baltic deep basins (Chapter 3.1.2) and similar time-trends were found independently in more coastal areas of the Baltic Sea (Ojaveer et al., 1998; Vuorinen et al., 1998). Consequently the observed abundance values are considered as reliable.

The results of the present study revealed earlier peak biomasses of the considered copepod species within a season in the Bornholm Basin (Sub-division 25) compared to the more eastern areas, i.e. the Gdansk Deep (Sub-division 26) and the Gotland Basin (Sub-division 28). This is explainable 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, using 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 subareas for all species/taxonomic groups. However, it has to be pointed out that Sub-division 25 is covered by a very limited number of stations only. Average hydrographic variables were also rather similar in all subareas considered, except of salinity and temperature in the 50 to 100m layer, being significantly higher in Sub-division 25 than in the other areas. The reason for this is the greater depth in Sub-divisions 26 and 28, allowing highly saline water from the North

Sea to flow deeper than 100m. Thus, these water masses do not influence the layer between 50 and 100m 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 detected time-trends can partly be explained by the hydrographic situation encountered during different periods of the time-series.

4.1.1.1. *Pseudocalanus elongatus*

Correlation analyses with the combined biomass of all life-stages showed *P. elongatus* to be positively dependent on salinity in all seasons. This dependence on salinity is reflected in the positive development of *P. elongatus* in the 1970s and early 1980s as a result of increased salinities due to the 1971 and 1975/76 major inflows of saline water from the North Sea. Since the early 1980s salinity decreased as a result of lacking inflow events (Matthäus and Schinke, 1994) in combination with high precipitation and river runoff (Bergström and Carlsson, 1994). Consequently biomass of *P. elongatus* decreased in parallel, a development weakened by the 1993 major inflow.

The affinity of *P. elongatus* to higher salinity characterises this species as a typical marine copepod (Raymont, 1983). The positive correlations with biomass indicate the need of a relatively high salinity level for processes such as maturation, reproduction and growth. Investigating the dynamics of single copepod life-stages revealed indeed a clear stage-specific response of *P. elongatus* to the prevailing hydrographic conditions during the season of peak reproduction in spring. At this time of the year most of the CV mature, which is obviously dependent on the salinity level, as indicated by the significant positive correlation to salinity. If salinity is low, fewer CV mature and consequently offspring production and thus N abundance is also low. Contrary, the development of the intermediate stages CII-CV in spring and thus, the fast production and growth of older stages, is highly dependent on temperatures.

However, as *P. elongatus* is an univoltine species in the Central Baltic (Line, 1979 and 1984) the long-term dynamics of this species was triggered by the magnitude of the

CVI-f stock formed in spring, which depends mainly on the salinity level. The peak recruitment period from the middle of the 1970s to the early 1980s is obviously caused by high CVI-f standing stocks during a period of high salinity. This peak in reproduction is carried through the rest of the year and determines the overwintering stock. With decreasing salinities in the last two decades the abundance of CVI-f decreased and so did N. Contradicting to this, a period of high N abundance in parallel to relatively low CVI-f numbers is encountered during the 1960s. A possible explanation may be low temperatures in this period favouring reproduction. This is indicated by the negative correlation of N and temperature in spring, although not being significant. Similarly a strong, but insignificant negative correlation of total *P. elongatus* biomass in summer and temperature was found. This indicates that the optimal thermal conditions for production and development of the copepodite stages is on the lower limit of temperatures encountered in summer.

4.1.1.2. *Temora longicornis*

Results of the correlation analysis showed the total biomass of *T. longicornis* to be positively related to temperature in the upper 50m of the water column in spring. This is apparent especially in the period between 1976 and 1993, when the biomass development followed to a large extent the development of the temperature. This result confirms the description of the species in the literature as thermophil (Chojnacki et al., 1984; Corkett and McLaren, 1978). Although *T. longicornis* has in the Baltic a long reproduction period (March – October) and up to five generations per year (Line, 1979 and 1984), the peak reproduction period is placed in spring (Line, 1984). Higher temperatures at this time of the year shorten the development time and are thus of advantage to build up the populations. This is supported by the investigation of the stage-specific dynamics. All life-stages of *T. longicornis* showed a uniform association to higher temperatures in spring. The building up of the population in spring is obviously strongly dependent on the warming of upper water layers. Thus, the drastic increase in spring standing stocks during the 1990s appears to be coupled to the high water

temperatures. The increase in standing stocks in winter of the 1990s may be related to an earlier onset of the warming period.

A further mechanism may be the activation of resting eggs due to the spring rise in temperature. *T. longicornis* is known to produce these dormant stage to overcome low winter temperatures (Madhupratap et al., 1996). Although the eggs are until now only found in the North Sea (Lindley, 1986), it is very likely that they occur also in the Baltic (Madhupratap et al., 1996).

No significant relationships could be established between salinity and the total biomass of *T. longicornis*. This is not surprising since this species is described to be in the Central Baltic to prefer salinities up to 16 psu (Chojnacki et al., 1984; Raymont, 1983), a situation rarely encountered in the upper water layers of the area. However, association tests among the abundance of single life-stages in spring revealed strong negative correlations of all stages with salinity. This result can be considered as a consequence of the opposite development of temperature and salinity, because as stated above, *T. longicornis* is a species of marine origin not favouring explicitly low saline conditions (Raymont, 1983). Statistically, the d.f. adjustment showed that the high correlations were mostly due to their contradicting trends, as only the correlations among salinity and CI and CII remained significant.

In summer generally the association of the different life-stages to salinity was positive. Interestingly, significant correlations could be found only for CVI and the early stages CI and CII (with N being almost significant). This may indicate that maturation and consequently reproductive success of *T. longicornis* in summer, when temperature is generally sufficiently high, depends on the salinity level. The observed general decrease in summer abundance may thus be caused by the decreasing salinity.

4.1.1.3. *Acartia* spp.

Results of the correlation analysis with the total biomass of *Acartia* spp. were similar to *T. longicornis* with significant positive relationships to temperature in spring. Even more pronounced than in *T. longicornis*, the biomass development of *Acartia* spp. followed to a

large extent the development of the temperature in the period between 1976 and 1993. This result confirms *Acartia* spp. to be thermophil (Chojnacki et al., 1984; Corkett and McLaren, 1978), having also a similar life-cycle as *T. longicornis* with up to seven generations per year (Line, 1979 and 1984). PCAs as well as correlation analyses with the abundance of single copepod life-stages revealed also a significant association of all stages to temperature in spring. Apparently, also for *Acartia* spp. the beginning of the population development is strongly dependent on spring warming, which explains the drastic increase in abundance during the warm 1990s. Especially for this copepod, the activation of resting eggs may be of importance as their occurrence is well known for the Baltic (Katajisto et al., 1998; Madhupratap et al., 1996; Viitasalo and Katajisto, 1994).

Again negative correlations with salinity were found in spring and, in contrast to *T. longicornis*, also in summer. The significant negative correlations may point to the favouring of low saline conditions, which cannot be ruled out, as the group of *Acartia* spp. comprise species with slightly different preferences (Raymont, 1983). It may, however, also be a spurious correlation due to the mainly opposite trend in temperature and salinity as discussed before. The difference in summer response to salinity between *Acartia* spp. and *T. longicornis* is clearly visible in the time-series. A generally high abundance was found for *Acartia* spp. during the 1990s, whereas the standing stock of *T. longicornis* decreased.

4.1.2. Cladocerans

The average seasonal abundance of *B. coregoni maritima* found within this study was well in agreement with abundances reported for the Finnish Archipelago Sea (Vuorinen and Ranta, 1987; Viitasalo et al., 1995), while they were significantly higher than those reported for the north-east coast of Sweden (Kankaala, 1982). Abundances of *E. nordmanni* and *Podon* spp. were low compared to values found in the Northern Baltic (Vuorinen and Ranta, 1987; Viitasalo et al. 1995) as well as in Kiel Fjord (Poggensee and Lenz, 1981). A reason may be a better food supply in these coastal areas compared to the open-sea areas investigated in the present study.

The observed average seasonal pattern of abundance showed a clear peak for all investigated cladoceran species in summer, which confirms results derived in the Northern Baltic (Kankaala, 1982; Vuorinen and Ranta, 1987; Viitasalo et al., 1995). This finding demonstrates the clear association of these crustaceans to high temperatures having positive effects on their population dynamics (Allan, 1976). The dominant species in summer was *B. coregoni maritima*, whereas in spring and autumn *E. nordmanni* was most abundant. This is explainable by the characteristic preferences of the different species. *B. coregoni maritima* is one of the few endemic forms in the Baltic Sea originating from fresh water (Kankaala, 1982). The species may thus be best adapted to the prevailing low salinity conditions. On contrary *E. nordmanni* and *Podon* spp. are considered to be "marine cladocerans" and are thus more confined to higher salinities (Egloff et al., 1997). *E. nordmanni* is known as especially eurythermic and euryhaline (Bryan and Grant, 1979), which explains the relative constant occurrence throughout the year. The different *Podon* species prefer higher salinities (Bryan and Grant, 1979), which may explain the low abundances relative to *B. coregoni maritima* and *E. nordmanni*.

The results of the association tests among cladoceran abundance and temperature with significant positive correlations for *E. nordmanni* and *Podon* spp. in spring and *B. coregoni maritima* in summer, confirm results of earlier studies in the Baltic (Poggensee and Lenz, 1981; Kankaala, 1982; Vuorinen and Ranta, 1987; Viitasalo et al., 1995). *E. nordmanni* and *Podon* spp. appeared in the plankton already in spring and higher temperatures initiate hatching of neonates from resting eggs (Iwasaki et al., 1977) and support population growth (Allan, 1976). The same is true for *B. coregoni maritima*, but later in summer, which indicates a general higher temperature to be necessary for the population development of this species compared to the two podonid species. This is confirmed by different optimum temperature ranges of 14-18°C for *B. coregoni maritima* found in the Baltic (Ciszewski, 1984) and 11-15°C for *E. nordmanni* as well as >8°C for *Podon* spp. derived in Chesapeake Bay (Bryan and Grant, 1979).

In contrast to temperature, the results of correlation analyses with salinity were less consistent. A tendency to a positive association of *B. coregoni maritima* to salinity in

autumn was found, however statistically insignificant. Significant positive relationships were derived for *E. nordmanni* and *Podon* spp. in summer and autumn in Sub-division 26, whereas in Sub-division 28 only the former species showed a positive association in autumn. No significant correlation between the podonid cladocerans and salinity in spring was detected. Interestingly the correlation coefficients are negative, with higher values in Sub-division 28. In summary, the results of the correlation analyses with salinity were threefold: (i) a difference between on the one hand *B. coregoni maritima* and on the other hand *E. nordmanni* and *Podon* spp., and for the podonid species a difference between (ii) subareas and (iii) seasons.

The relative weak association of *B. coregoni maritima* to salinity indicates that the salinity range encountered by this species in the investigated areas is not critical. According to Ackefors (1969, 1971) the optimal range for *B. coregoni maritima* is 2-8 psu, the encountered conditions were thus in the upper part of this range, but never above. Contrary the optimal salinity range found for *E. nordmanni* in Chesapeake Bay is considerably higher (>20psu) and even higher for *Podon* spp. (>25 psu) (Bryan and Grant, 1979). Assuming these ranges to be valid also for the Central Baltic where salinities are well below, increasing salinities will be favourable for the development of these cladoceran species. This is reflected in significant positive relationships among abundances of *E. nordmanni* and *Podon* spp. and salinity especially in summer ($p < 0.01$), and also in autumn ($p < 0.05$). Additionally the negative correlation coefficients in spring, although weak, indicate an opposite association as found for later in the year. This seasonal difference may point to different conditions conducive for the hatching of resting eggs in spring than for the population growth later in the year. Correlation analyses among cladoceran abundance and salinity in the Northern Baltic, however not resolved to seasons, revealed significant negative relationships with salinity for *B. coregoni maritima* and *Podon polyphemoides* biomass (Viitasalo et al., 1995), contradicting findings of the present study. However, their study did not comprise the period of the pronounced decrease in salinity in the Baltic since the late 1980s and a prolongation of the time-series did not confirm the significant negative correlations among *Podon* spp. and salinity

(Vuorinen et al., 1998). Nevertheless also Vuorinen et al. (1998) found a significant negative relation of *B. coregoni maritima* to salinity, although weaker than found by Viitasalo et al. (1995). Explaining the encountered regional and temporal differences on the basis of the time-series investigated has to remain rather speculative. A potential candidate is a different adaptation of the species to the regional physical environment indicating different populations.

4.2. The influence of predation

4.2.1. Clupeid abundance

The results of the area dis-aggregated MSVPA runs performed here revealed distinct trends in population abundance, spawning biomass, recruitment and predation mortalities of cod and sprat in different areas of the Central Baltic. These results were in general similar to time trends in population sizes of cod and sprat as estimated by standard assessments, research surveys utilised for tuning of the MSVPA runs as well as independent estimates of stock abundance. The application of the area dis-aggregated MSVPA was inconclusive for Baltic herring stocks due to timing and area coverage of surveys, complexity of stock structure and migratory behaviour. Hence, due to the limited amount of other suitable data series on herring abundance, a conclusive validation on distribution of the stock appears at present to be impossible. The area dis-aggregated MSVPA does however capture the temporal dynamics of the Baltic herring population as estimated by the standard assessment.

A number of data related and methodological problems impact upon the utility of the present approach for cod and sprat. For example, the newly compiled catch at age data for cod and sprat (ICES, 1997a) showed considerable fluctuations in some age-groups, quarters and years. High variability in the catch in numbers of the last age-group of cod caused problems in tuning the terminal-F values. For sprat, tuning of the last year in the time series was problematic in Sub-divisions 25 and 26 due to trends in F at age as well as changes in the exploitation pattern (ICES, 1998) caused by the commencement of a large-scale reduction fishery.

The VPA-technique assumes that catch at age are exact input data, which due to several reasons is seldom the case. The present analysis covers a time period with well established reporting systems in the Baltic introduced in the mid 1970s. The data compilation procedure utilizing information submitted by the responsible national laboratories is described in detail in ICES (1997a and 1999a). However, discarding and mis-reporting takes place in Baltic cod and is not accounted for in the present catch at age data. The estimated discards of age-group 1-2 in 1998 and 1999 amounted to 17

and 4%, 9 and 2% as well as 3 and 2% of the total catch in numbers in Sub-divisions 25, 26 and 28 respectively (ICES, 2000). These preliminary data indicate considerable inter-annual variability in discards and a potential bias of recruitment estimates in years of intensive discarding. Mis-reporting in the cod fishery has been identified by ICES (1997b) especially for the period 1992-1994 with restrictive fisheries management measures enforced. Mis-reporting is partly accounted for by national catch estimates treated in the assessment as unallocated catches according to Sub-division. However, for the above period, nevertheless a considerable underestimation of the catch may have occurred, affecting the spawning stock size estimation in 1991-1994 and recruitment of the year-classes 1990-1992. Another source of bias is errors in age reading of Baltic cod otoliths (Bagge et al., 1994), with deviations in estimated age of 1-2 years between different countries commonly occurring (ICES, 2000). This affects especially the estimation of year-class strength and its inter-annual variability.

Migration between different areas of the Central Baltic is expected to have an impact on the area dis-aggregated MSVPA results for all stocks. As stated by ICES (1999a) explicit inclusion of the migration process into the MSVPA-context is difficult and at present no adequate methodology is available. Reliable migration rates are missing for all stocks under consideration and databases required for the implementation of statistically based spatial multi-species models, e.g. BORMICON (Stefánsson and Pálsson, 1998) are not readily available. Even with these databases at hand, however, conflicting output trends depending on considered data sources might as well be encountered, as recently demonstrated for the BORMICON application in the Icelandic system (Stefánsson, 1998). At present the only feasible way of resolving spatial distribution in the Baltic is to run a suite of independent MSVPAs for the different sub-areas, as performed in this study. Following this approach, migration is accounted for by fluctuations in the catch at age data only.

4.2.2. Clupeid fish consumption

Results of stomach content analyses, which formed the basis for the consumption estimation, were in detail described by earlier studies (Möllmann, 1996; Möllmann and Köster, 1999). As shown by other authors, copepod species, *P. elongatus* in late winter/spring, *Acartia* spp. and especially *T. longicornis* in summer and autumn as well as to a lesser extend cladocerans in late summer/early autumn, formed the major parts of the diet (e.g. Hinrichs, 1985; Patokina, 1996; Starodub and Kondratjeva, 1988; Szyplula, 1985). Interannual variations in the diet composition with a decreasing importance of *P. elongatus* and an increasing importance of *T. longicornis* in late 1980s and early 1990s have also been described by several authors before (Starodub et al., 1992; Davidyuka, 1996; Davidyuk et al., 1992; Fetter and Davidyuk, 1993).

However, this is the first study resolving stomach content data on groups of copepod developmental stages and single cladoceran species. The study revealed that herring in the Gotland Basin was preying upon all groups of copepod life-stages. This is contradictory to findings in the northern Baltic (Flinkman et al., 1992) and off western Norway (Dalpadado et al., 2000) where herring prey selectively on larger copepodite stages and especially reproducing females. This difference may indicate that herring of the Central Baltic are not able to fulfill food requirements by feeding on older stages alone. As in other areas, the older copepod stages CV/VI were intensively consumed, but a surprisingly high consumption on CII was observed, whereas CIII/IV were encountered more seldom in the diet. This selection pattern by herring which is observed for all three copepod species is hardly explainable. Neither vertical distribution nor seasonal occurrence give hints on the reasons for herring to select CII and not CIII/IV. Contrary to herring, sprat almost exclusively selected CV/VI which characterizes the species as visual selective predator.

Möllmann (1996) and Möllmann and Köster (1999) have shown, that individual daily rations determined with the model used here, were generally lower than former estimates by applying a simple linear evacuation model coupled to a Bajkov (1935) approach (Zalachowski et al., 1976; Szyplula, 1985). The latter studies derived

consumption values of 2.5 - 4.2% and 1.1 - 1.7% body weight d^{-1} for sprat and herring, respectively in summer, compared to estimates by Möllmann and Köster (1999) of 0.5 - 1.6% and 0.1 - 1.5%. Rather similar daily rations were found in winter/spring with 0.1 - 0.8% body weight d^{-1} for sprat and 0.1 - 1.7% for herring, compared to estimates derived by the evacuation model used in the present study of 0.2 - 0.8% for sprat and 0.1 - 0.5% for herring. For herring, average daily rations of 1.1% body weight d^{-1} were estimated by Fetter and Davidyuka (1996) on basis of a series of 24-hour fisheries conducted in Sub-division 26 and 28 in summer 1978 - 87, thus confirming the low summer feeding rates of herring determined by Möllmann and Köster (1999). Patokina (1996), however, estimated higher daily rations ingested by both sprat and herring of 1.5 - 2.9% and 1.3 - 5.4% body weight d^{-1} , respectively, using a similar approach as Fetter and Davidyuka (1996). Application of bioenergetics models revealed in general also considerably higher daily rations (yearly averages) of 3.4 - 3.5% for sprat (Lankov, 1988; northern Baltic) and 1.2 - 1.9% (Aneer, 1980; swedish coastal waters), 3.3 - 4.7% (Rudstam, 1988; swedish coastal waters) and 2.6 - 2.8% of body weight d^{-1} (Chekunova, 1979; Eastern Baltic) for herring. This was confirmed for cod in the North Sea (Hansson et al., 1996) and in the Baltic (ICES, 1999a). Thus, the consumption estimates derived within the present study were obviously conservative compared to former estimates, however, the utilized evacuation model is thought to be a considerable improvement compared to earlier approaches. For an extended discussion on the suitability and shortcomings of the applied model of gastric evacuation also in comparison to bioenergetics modelling, the underlying assumptions and the performed evacuation experiments see Temming (1996).

Population consumption rates by herring on copepods were highest in winter and summer on *P. elongatus* and *T. longicornis*. The latter copepod was additionally preyed upon intensively in autumn. Spring feeding rates were generally low due to low predator abundance, as spring spawning herring concentrate in their coastal spawning areas outside the basins (Aro, 1989). Within the time-series two main trends were detectable: (i) population consumption on *P. elongatus* decreased, and (ii) predation on *T. longicornis*

increased but mainly on CII. The first trend may be explained by the drastic decline in abundance of *P. elongatus*. The second trend indicates that herring suffered from increased competition with the enlarged sprat stock. For all copepod species consumption rates by sprat on CV/VI increased drastically, whereas the amount of these older stages declined in herring consumption. This suggests that herring was during the 1990s forced to switch to younger stages by the increased sprat stock.

Estimates of consumption on cladocerans revealed sprat to prey intensively upon *Podon* spp. and *E. nordmanni* in spring during the early 1980s. Afterwards consumption rates decreased, although the biomass of both cladoceran species increased drastically. This may be due to the drastically enlarged sprat stock size, reducing the number of food items per individual sprat. Another explanation may be the increased abundance of the copepods *T. longicornis* and *Acartia* spp. in the 1990s (Chapter 3.1.2, 3.1.3 and 3.2.2.1), being the main food items of sprat (Möllmann and Köster, 1999; Chapter 3.2.2.3). This increased copepod prey abundance may have had the result that cladocerans were less selected by sprat, and may also explain the general low individual consumption on all cladoceran species in summer and autumn during the 1990s.

4.2.3. Copepods

4.2.3.1. Copepod abundance and vertical distribution

Possible biases in the estimation of copepod abundance are discussed in Chapter 4.1.1. The population dynamics of *P. elongatus* showed a steady decrease in the overwintering stock and especially in CV/VI. This decrease in abundance of older stages, related to declining salinities, resulted in the decline of the total *P. elongatus* stock (Chapter 3.1.3). The population developments of *T. longicornis* and *Acartia* spp. followed largely the same trends with a marked increase during the 1990s, most pronounced in *Acartia* spp. This stepwise rise in abundance is mainly explainable by the warmer thermal conditions due to less severe winters in the Central Baltic Sea (Dippner et al., 2000; and Chapter 3.1.2) probably favouring activation of resting eggs, reproduction, growth and survival (Chapter 3.1.3).

As no regularly vertically resolving sampling was performed, only data from a subset of sampling dates could be used for the investigation of the vertical distribution. Thus integration over the whole covered period had to be performed, not considering interannual changes in the vertical distribution as have been demonstrated by Kornilovs et al. (2001) for *T. longicornis* and *Acartia* spp. in the area. Additionally the sampling was performed only at daylight, allowing not to investigate potentially predator-induced diurnal vertical migration (e.g. Bollens and Frost, 1989).

The results clearly indicate an ontogenetic distribution of increasing depth with age for *P. elongatus*, and further that especially older stages perform a seasonal descent in spring. This is explainable by the preference of this copepod for high salinities and low temperatures for reproduction, encountered in the study region only in the permanent halocline of the deep Baltic basins (Chapter 3.1.2 and 3.1.3). The shallower distribution in winter may be interpreted as a predator avoidance, as planktivorous fish, especially herring, feed on the overwintering stock of older stages (see below) in the region of the permanent halocline in about 60m (Köster and Schnack, 1994). Hence a shallower distribution at this time of the year may be of advantage for the survival of the copepod. In contrast, *T. longicornis* and *Acartia* spp. showed a more shallower and uniform distribution, which is explainable by their preference for higher temperature (Dippner et al., 2000; Chapter 3.1.2 and 3.1.3).

4.2.3.2. Copepod development times and production

Production estimates of copepods in the present study could only be based on a temperature dependent function, which does not take into account variations due to quantity and quality of food shown to affect production (e.g. Berggreen et al., 1988). Furthermore, parameters for the estimation of temperature-dependent stage development times were derived from the literature, potentially not reflecting the special environmental conditions in the Baltic, e.g. the low salinity. Finally available data did not allow an incorporation of diurnal vertical migrations of copepods (e.g. Bollens and Frost, 1989) in the calculations of average ambient temperatures. For an assessment of the

production estimates direct estimates via the egg production method (Runge and Roff, 2000) are needed, but are not yet available for the area. Nevertheless, the estimated daily production rates in summer were very similar to those calculated for *T. longicornis* and *Acartia* spp. in the Northern Baltic (Hansson et al., 1990). However, values computed for the 1990s, when the stocks drastically increased, were higher than in Hansson et al. (1990). Although the estimates rely on a number of assumptions and parameters from the literature, the results are considered to reflect realistically seasonal daily production rates of the copepod species.

4.2.3.3. Clupeid fish consumption versus copepod production

The present study revealed that clupeid fish in the central Gotland Basin consumed at times large proportions and in maximum the full potential production of a certain group of copepod life-stages. This has been shown in earlier studies for northern Baltic areas (Arrhenius and Hansson, 1993; Hansson et al. 1990) and for the Central Baltic (Möllmann et al., 1999; Rudstam et al., 1994). However, this is the first study calculating C/P-ratios for single or groups of copepodite stages of single species in different seasons and for a period of twenty years. Using this large data set, herring was found at times to exert a high predation pressure in spring on CII of *P. elongatus*. However, this was observed only in four of twenty years, and especially not in the 1990s. Thus, this predation pressure on CII had not the potential to contribute to the decline of the *P. elongatus* stock. Contrary, high C/P-ratios were computed regularly and especially during the 1990s for CII of *T. longicornis* in summer. As during the 1990s also the observed abundance of this copepodite stage declined, it is very likely that herring controlled to some extent these younger stages during the 1990s. This might have prevented an even more pronounced increase in standing stock of *T. longicornis* as has been shown for *Acartia* spp. not heavily preyed upon by clupeid fish.

The highest predation pressure by the sprat population, with frequently high C/P-ratios of *P. elongatus* and *T. longicornis* CV/VI, was found in spring. In case of the first copepod this might have contributed or amplified the decline of the whole stock since the

late 1980s, whereas for the latter species this may have prevented an even more pronounced temperature-driven increase in abundance.

The finding of a major predation pressure by sprat in spring is contradicting to results derived for the Northern Baltic (Adrian et al., 1999; Arrhenius and Hansson, 1993; Hansson et al., 1990; Rudstam et al., 1994) and in freshwater ecology (Kitchell and Carpenter, 1993), where the decline of the zooplankton populations in late summer and autumn is attributed to a strong planktivory. At this time of the year neglectable C/P-ratios were observed, clearly indicating a limited influence of sprat predation.

4.2.3.4. Copepod mortality

Copepod mortality rates were calculated to evaluate the effect of clupeid consumption on copepod populations. A vertical life-table approach was used to estimate mortality rates, which has the advantage that estimates are not biased by advection or other sources of horizontal patchiness. The method requires a constant sampling efficiency of the different stages (Aksnes and Ohman, 1996), which is the case with the sampling gear used (Hernroth, 1979). Negative mortality rates are likely to occur with the method, when mortality is low and the stage composition is variable from one sample to another (Aksnes and Ohman, 1996). This was avoided for CI/II and CII/III of *T. longicornis* by setting individual negative point estimates equal to 0 as proposed by Aksnes and Ohman (1996), being aware that the final value will be overestimated.

As for production rates, computation of mortality rates depends on independent estimates of stage durations. Parameters for the temperature-dependent stage development times were derived from the literature and may not fully reflect the special environmental conditions in the Baltic Sea (see above). On the other hand Aksnes and Ohman (1996) stated that moderate variability in stage durations is not critical for mortality estimation by the vertical method. By simulation modeling the authors found the main drawback of the vertical approach to be the sensitivity to trends in recruitment (Aksnes and Ohman, 1996), which is not encountered in the present study. Additionally, the authors found that ten replicates assure precision of estimates, which however were

mostly not available for this study. Nevertheless, the estimated daily mortality rates calculated in this study are well in agreement with earlier studies using vertical as well as horizontal life-table approaches (e.g. Aksnes and Ohman, 1996; Ohman, 1986; Ohman and Wood, 1996) and are thus considered to be reliable.

By calculating C/P ratios, the strongest predation pressure by herring on CII of *T. longicornis* was found in summer, especially during the 1990s. Mortality rates, however, were in parallel mainly very low not confirming a significant influence of herring predation on *T. longicornis* dynamics.

Strongest predation pressure by sprat was found in spring during the late 1980s/early 1990s, which was due to the drastically increased stock size. In parallel peak daily mortality rates for both CV/VI of *P. elongatus* (Mann-Whitney U-test, $p < 0.05$; 1977-89/1990-96) and *T. longicornis* (Mann-Whitney U-test, $p < 0.05$; 1977-86/1987-96) were apparent, indicating an impact of sprat predation on population dynamics of both copepod species in spring.

4.2.4. Cladocerans

4.2.4.1. Cladoceran biomass

Abundance and biomass estimates may be uncertain, as discussed for copepods (Chapter 4.1.1), due to a low number of stations sampled in specific seasons/years, as well as due to advective transport. In addition some bias may have been introduced by the seasonal sampling strategy. As cladocerans are extremely seasonal with high densities over short periods (Raymont 1983), due to rapid parthenogenetic and/or pædogenic reproduction, the occurrence of peak biomasses may have been at times missed by the sampling. In consequence, the observed standing stocks may sometimes be underestimates. However, long-term abundance dynamics of the considered cladoceran species revealed the same time trends in two Central Baltic deep basins, i.e. Gdansk Deep and Gotland Basin (Chapter 3.1.4). Distinct time-trends were encountered with increasing biomass of *Podon* spp. and *E. nordmanni* in spring during the 1990s, explainable by increased temperatures (Chapter 4.1.2). Biomass trends in the

remaining seasons were mainly due to species-specific adaptations to the prevailing temperature and salinity conditions (Chapter 4.1.2).

4.2.4.2. Cladoceran production

Production estimates of cladocerans in the present study could only be based on a temperature dependent empirical function for *B. coregoni maritima* (Kankaala et al., 1984). The production rates thus represent only a very rough estimates, which does not take into account species-specific differences. As *B. coregoni maritima* may be the cladoceran best adapted to the brackish conditions in the Baltic, displayed by there dominating abundance (Chapter 4.1.2), production estimates for *Podon* spp. and *E. nordmanni* may be overestimated. Further the empirical relationship by Kankaala et al. (1984) was derived in the Bothnian Sea, an area farther north from the Gotland Basin with different hydrographic conditions. Hence, the relationship may not fully reflect the situation in the Gotland Basin, especially the higher salinity.

4.2.4.3. Sprat consumption versus cladoceran production

The present study showed sprat in the central Gotland Basin to consume frequently large proportions and in maximum the full potential production of a certain cladoceran species. *B. coregoni maritima* is heavily preyed upon in autumn, when abundance is generally low. Thus sprat predation may contribute to the seasonally decline of this cladoceran species. High C/P-ratios were also found for *E. nordmanni* in spring, being however low during the 1990s. This temporal development may lead to the conclusion that sprat predation controlled *E. nordmanni* biomass during the 1980s, whereas high biomass in the 1990s were a result of a release in predation pressure. This is however unlikely, as also *Podon* spp. biomass drastically increased during the 1990s, but is obviously not affected by sprat predation. Thus the warmer thermal conditions are very likely the reason for this increase in cladoceran biomass.

Generally the results suggest that sprat predation has a restricted influence on cladoceran population dynamics, which may be due to the rapid turnover rates of these

plankton species, assuring high standing stocks even in presence of strong predation pressure. This rapid development is mainly steered by the hydrographic conditions, being thus to a large degree responsible for the population development (**Chapter 4.1.2**). Nevertheless, other factors as food availability as well as invertebrate (e.g. medusae) and larval fish (e.g. cod and sprat) predation may have contributed to the observed biomass trends of cladocerans.

5. CONCLUSIONS

This study investigated the influence of hydrography and predation by clupeid fish on mesozooplankton long-term dynamics in the deep basins of the Central Baltic Sea. The analyses of the association between standing stocks of mesozooplankton species and hydrography indicated clear salinity and temperature preferences of the different copepod and cladoceran species:

- *P. elongatus* was related to high salinities and low temperatures, probably influencing maturation and reproduction in spring, whereas higher temperatures favoured intermediate life-stage development.
- *T. longicornis* development was positively associated with higher temperatures in spring, whereas higher salinity may favour maturation and reproduction in summer.
- *Acartia* spp. showed a uniform positive relationship for all developmental stages to temperature in spring.
- *B. coregoni maritima* dynamics were mainly influenced by high temperatures in spring.
- *E. nordmanni* and *Podon* spp. showed clear positive associations to temperature in spring and salinity in summer.

It could be shown that the distinct trends in hydrography encountered by the mesozooplankton species have resulted in different abundance trends. The most pronounced pattern is the change in species dominance within the copepod community. The formerly dominating stock of *P. elongatus* declined due to the decreasing salinity and increasing temperatures, especially since the late 1980s. Contrary, *T. longicornis* and *Acartia* spp. increased in abundance, mainly due to the warmer thermal regime. The increase of *T. longicornis* was less pronounced, potentially due to the effect of salinity on reproduction. All investigated cladoceran species took advantage of increasing temperatures at the beginning of their seasonal population development, whereas

indications exist that lower salinities negatively affected the population development of *E. nordmanni* and *Podon* spp.

As demonstrated by the MSVPAs, the fish stock development in the Central Baltic is characterized by a drastic decrease of the top-predator cod. The released predation pressure has resulted in a drastic increase of the sprat stock, especially during the 1990s, which suggested a growing influence of planktivory by clupeid fish on mesozooplankton species. The present analysis identified significant predation pressures by sprat on CV/VI of *P. elongatus* and *T. longicornis* in spring since the late 1980s, paralleled by high mortalities of these copepods. This indicates that sprat predation contributed to the decline of *P. elongatus* and hindered a more pronounced temperature-driven increase of the *T. longicornis* population.

For cladocerans, the results indicate an influence of sprat predation of *B. coregoni maritima* and *E. nordmanni* standing stocks. However, it was found that predation by the sprat population has a restricted influence on cladoceran population dynamics.

Although the present work revealed clear indications of the role of hydrography on mesozooplankton dynamics, the processes behind the found relationships remain speculative. Future research should thus encompass experimental investigations on the effect of salinity and temperature on processes such as maturation, egg production and growth. In a further conclusive evaluation of the population dynamics of copepods and cladocerans in the Central Baltic, beside hydrography and clupeid predation other abiotic and biotic variables have to be taken into account. For example, physical processes as advection and diffusion (e.g. Davis, 1984; Pedersen et al., 2001) as well as turbulence (e.g. Incze et al., 2001) may be of importance for demography and spatial distribution of zooplankton species. Turbulence may further enhance encounter and thus grazing rates of plankton species affecting reproduction and growth (e.g. Alcaraz, 1997; Kiørboe et al., 1996; Saiz and Kiørboe, 1995) as do quantity and quality of food (e.g. Lacoste et al., 2001; Campbell et al., 2001; Niehoff and Hirche, 2000; Hirche et al., 1997). Also predation by other vertebrate and invertebrate predators, i.e. medusae (e.g. Behrends and Schneider, 1995; Suchman and Sullivan, 2000), larval and 0-group fish (Arrhenius

and Hansson, 1999), mysids (Mohammadian et al., 1997), copepod egg cannibalism (Kang and Poulet, 2001; Ohman and Hirche, 2001) or predation among copepod species (Sell et al., 2001; Titelman, 2001) have to be investigated.

After identifying the most important processes for the population dynamics of mesozooplankton species, these should be incorporated in population models which are able to forecast, based on available biotic and abiotic variables, the future development. These could then be useful indicators for prognosis of growth and developmental success of commercially important fish species.

A possible and promising approach, which is also able to resolve the relative effects of different physical and biological variables and their spatial heterogeneity, may be the coupling of individual-based population models (de Angelis and Gross, 1992) to physical hydrodynamic circulation models forced by realistic atmospheric conditions. This has been successfully performed in other areas of the world ocean simulating the dynamics of copepod populations (e.g. Davies, 1984; Gupta et al. 1994; Miller et al, 1998; Lynch et al, 1998; Pedersen et al., 2001) and represents a useful approach also for the Baltic Sea.

6. SUMMARY

The present study investigated the influence of hydrography, as well as predation by clupeid fish on mesozooplankton long-term dynamics in the deep basins of the Central Baltic Sea. The dominating copepod species *Pseudocalanus elongatus*, *Temora longicornis* and *Acartia* spp. as well as the cladocerans *Bosmina coregoni maritima*, *Evadne nordmanni* and *Podon* spp. were considered in the analyses.

The analysis of long-term temperature and salinity data revealed clear changes in the physical environment of the mesozooplankton species, especially in the last two decades. The dominating pattern was a decreasing salinity since the beginning of the 1980s, due to lacking inflows of highly saline water from the North Sea as well as increased river runoff. Additionally a general increase of water temperature was observed in the 1990s due to mainly warm winters.

Correlation analyses revealed a clear association between the biomass of *P. elongatus* and higher salinities, as well as lower temperatures in spring. Principal component analyses (PCAs) identified the dependence of the abundance of Nauplii and adult *P. elongatus* on higher salinities, indicating an influence on maturation and reproduction. Contrary, PCAs displayed the affinity of all intermediate copepodite stages to higher temperatures.

Based on the results of the correlation analyses, the general increase in the biomass of *T. longicornis* and *Acartia* spp., especially during the 1990s, can be attributed to the increase in water temperature. PCAs confirmed the affinity of all developmental stages of these two copepod stages to temperature in spring. The temperature-driven increase in the standing stock of *T. longicornis* was not as pronounced as for *Acartia* spp., which based on the results of the PCAs can be interpreted, similarly to *P. elongatus*, as a result of the negative effect of salinity on maturation and reproduction in summer.

Correlation analyses with the abundance of the cladoceran species also indicated that these mesozooplankton species took advantage of the increase in water temperatures during the beginning of their population development in spring. The

decreasing salinity, however, hindered obviously a more pronounced increase in abundance of *E. nordmanni* and *Podon* spp.

Multispecies Virtual Population Analyses (MSVPAs) displayed the stock development of the commercially most important fish species in the Central Baltic Sea. Whereas the abundance of the top-predator cod (*Gadus morhua*) drastically decreased, the release in predation pressure resulted in a substantial increase in the major forage fish sprat (*Sprattus sprattus*), especially during the 1990s. In contrast, the population of the second important clupeid fish herring (*Clupea harengus*) slightly decreased.

The drastic increase in the total clupeid abundance suggested a potential top-down control of the major food items of planktivorous fish, i.e. mesozooplankton species. Within this study, predation rates of the clupeid fish populations were computed by a combination of a model of gastric evacuation, which estimates individual daily rations based on stomach content data, and stock sizes derived by MSVPAs. Resulting population consumption rates were compared to production rates of mesozooplankton species. The analyses revealed no substantial impact of herring predation on the mesozooplankton dynamics, whereas a significant predation pressure of sprat in spring on copepodite stages CV/VI of *P. elongatus* and *T. longicornis* was identified since the end of the 1980s. In parallel mortality rates of these copepods increased, which indicates a contribution of the sprat population to the decline of the *P. elongatus* population and further hindered a more pronounced temperature-driven increase of the *T. longicornis* abundance.

Contrary to copepods, this study revealed a general limited influence of sprat predation on the dynamics of cladocerans which is discussed to be a result of short generation times and high turnover rates due to parthenogenetic and pædogenic reproduction. Only a small influence of sprat predation on the seasonal decline of *B. coregoni maritima* and *E. nordmanni* in autumn could be identified.

7. ZUSAMMENFASSUNG

Die vorliegende Studie untersuchte den Einfluss von Hydrographie, sowie von Prädation durch clupeide Fische auf die Langzeitdynamik von Mesozooplanktonarten in den tiefen Becken der Zentralen Ostsee. In der Analyse wurden die in Abundanz und Biomasse dominierenden Copepodenarten *Pseudocalanus elongatus*, *Temora longicornis* und *Acartia* spp., sowie die Cladoceren *Bosmina coregoni maritima*, *Evadne nordmanni* und *Podon* spp. untersucht.

Die Analyse von Langzeitdatenserien von Temperatur und Salzgehalt zeigte deutliche Veränderungen in der physikalischen Umgebung der untersuchten Mesozooplanktonarten, insbesondere in den letzten zwei Jahrzehnten. Die dominierenden Muster waren dabei abnehmende Salzgehalte seit Mitte der 1980er Jahre, verursacht durch das Ausbleiben von Einstromsituation aus der Nordsee und einem Anstieg im Süßwassereintrag, sowie der Anstieg der Wassertemperaturen in den 1990er Jahren, ausgelöst durch eine Vielzahl von milden Wintern.

Korrelationsanalysen zeigten einen deutlichen Zusammenhang zwischen der Biomasse von *P. elongatus* und hohen Salzgehalten, sowie niedrigen Temperaturen im Frühling. Hauptkomponentenanalysen (PCAs) identifizierten eine Abhängigkeit der Grösse des Bestandes an adulten Individuen und Nauplien von *P. elongatus* von hohen Salzgehalten, was auf einen Einfluss auf Reife- und Reproduktionsprozesse schliessen lässt. Im Gegensatz dazu, zeigten die PCAs einen positiven Einfluss von hohen Temperaturen auf die Entwicklung der intermediären Copepoditstadien.

Der generelle Anstieg der Biomasse von *T. longicornis* und *Acartia* spp., insbesondere in den 1990er Jahren, wurde dagegen auf Basis der Korrelationsanalysen, auf den generellen Anstieg der Wassertemperatur zurückgeführt. PCAs bestätigten dabei den Zusammenhang zwischen der Abundanz aller Lebensstadien der beiden Copepodenarten und höheren Temperaturen im Frühling. Die Zunahme der Bestandsgrösse von *T. longicornis* war dabei vergleichsweise geringer, was auf Basis der PCA-Ergebnisse, in ähnlicher Weise als für *P. elongatus*, mit dem negativen Einfluss des

abnehmenden Salzgehaltes auf die Reifung und Reproduktion dieser Copepodenart im Sommer begründet wurde.

Korrelationsanalysen mit der Abundanz der untersuchten Cladocerenarten liessen den Schluss zu, dass diese Mesozooplankter offensichtlich ebenfalls vom Anstieg der Umgebungstemperaturen zu Beginn ihrer saisonalen Populationsentwicklung profitierten. Der abnehmende Salzgehalt verhinderte dagegen offensichtlich eine starke Zunahme der Bestände von *E. nordmanni* und *Podon* spp.

Mittels eines Mehrarten-Populationsmodelles (Multispecies Virtual Population Analysis; MSVPAs) wurde die Bestandsentwicklung der kommerziell wichtigsten Fischarten der Zentralen Ostsee dokumentiert. Während der Bestand des Top-Prädatoren Dorsch (*Gadus morhua*) drastisch abnahm, führte die resultierende Abnahme im Fraßdruck zu einer substantiellen Zunahme der Population der Sprotte (*Sprattus sprattus*), insbesondere in den 1990er Jahren. Im Gegensatz zur Sprotte, zeigte der Bestand der anderen Clupeidenart im System, des Hering (*Clupea harengus*), eine leicht negative Bestandsentwicklung.

Die drastische Zunahme in der gesamten Abundanz planktivorer Fische liess auf eine potentielle Top-down Kontrolle der Hauptnahrungsorganismen planktivorer Fische, d.h. von Mesozooplanktonarten, schliessen. Im Rahmen der vorliegenden Arbeit wurde mittels der Kombination eines Magenentleerungsmodelles, zur Bestimmung individueller Tagesrationen auf Basis von Mageninhaltsdaten, mit den Ergebnissen der MSVPAs, Wegfrassraten der clupeiden Fischpopulationen bestimmt und mit Produktionsraten der Mesozooplanktonarten verglichen. Während kein substantieller Wegfrass durch die Heringspopulation ermittelt werden konnte, wurde ein signifikanter Frassdruck im Frühling durch Sprotten auf die Copepoditstadien CV/VI von *P. elongatus* und *T. longicornis* seit dem Ende der 1980er Jahre identifiziert. Parallel wurde ein Anstieg in den Mortalitätsraten dieser Copepodenarten ermittelt, was auf einen Beitrag der verstärkten Konsumtion durch die Sprottenpopulation auf den Niedergang des Bestandes an *P. elongatus* schliessen lässt. Zusätzlich hat der verstärkte Frassdruck durch Sprotten

offensichtlich einen stärkeren temperaturbedingten Anstieg der Population von *T. longicornis* verhindert.

Im Gegensatz zu Copepoden wurde generell ein geringer Einfluss des Wegfrasses der Sprotten auf die Dynamik von Cladoceren ermittelt, was auf die kurzen Generationsfolgen und hohe Umsatzraten durch parthenogenetische und pädogenetische Reproduktion zurückgeführt wurde. Nur für *B. coregoni maritima* und *E. nordmanni* wurde ein geringer Einfluss der Prädation durch Sprotten auf den Niedergang der Cladocerenbiomasse im Herbst festgestellt.

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9. APPENDIX

Appendix-Table 1. Spawning stock biomass (2nd quarter), recruitment (age-group 1, 1st quarter) and stock size (cod: age-group 2+, 1st quarter; herring and sprat: age-group 1+, 4th quarter) in different Sub-divisions (SD) of the Central Baltic determined from area dis-aggregated Multispecies Virtual Population Analyses.

Year	Cod			Herring			Sprat		
	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28
Spawning stock biomass (in 1000 tonnes)									
1977	92	96	39	387	290	120	93	196	148
1978	96	110	63	384	325	131	82	169	116
1979	105	141	86	376	333	173	55	91	63
1980	110	181	72	343	199	81	26	45	26
1981	144	158	56	293	200	104	19	30	19
1982	135	148	65	261	207	63	29	50	34
1983	163	156	67	339	230	71	69	61	29
1984	118	131	62	312	183	52	161	195	64
1985	116	115	54	277	160	83	218	219	66
1986	87	70	39	273	137	81	223	181	48
1987	87	73	30	227	141	131	210	164	45
1988	88	67	21	225	113	159	199	136	63
1989	76	47	13	206	119	136	164	129	75
1990	79	47	8	195	100	139	239	178	121
1991	54	32	7	159	84	102	330	289	210
1992	41	37	3	170	113	103	469	471	223
1993	88	53	5	164	117	138	585	363	236
1994	116	61	5	198	111	149	569	512	310
1995	110	75	6	187	91	131	421	451	282
1996	113	118	4	179	75	189	417	413	256
Recruitment (in millions)									
1977	418	486	242	5532	5416	2934	10661	20896	9387
1978	327	375	159	6332	4801	4162	4910	8674	5963
1979	321	316	147	3874	6860	5955	4686	21695	4561
1980	465	611	235	4930	6980	6991	3915	9565	5249
1981	500	491	240	9756	12341	6485	10137	27512	17721
1982	296	281	170	6774	8166	9928	20950	14309	6191
1983	167	173	128	6558	5730	8156	38500	82162	36231
1984	146	123	85	5010	4385	8797	27486	16801	10174
1985	172	128	63	4814	4086	4953	19531	14208	5930
1986	243	127	67	3594	2502	3036	14144	6939	3124
1987	145	75	26	3318	2015	6245	20239	15555	10562
1988	101	40	13	3562	1757	1616	15402	3225	2924
1989	129	50	18	4645	1687	2436	30460	15867	12326
1990	65	38	6	3756	2023	3734	26584	25094	13783
1991	114	53	7	3237	1921	3458	34828	36335	12566
1992	160	70	7	3647	2259	2479	36522	36327	15408
1993	112	89	4	2846	1631	1812	34879	34823	20968
1994	127	170	4	2879	1567	1776	25023	20299	6382
1995	160	87	6	3788	2171	2442	80169	68414	27541
1996	168	28	1	3498	1532	2004	54916	38687	18811
Stock size (in millions)									
1977	311	363	174	7698	6227	4959	8563	22937	14762
1978	475	555	289	8049	5889	5120	5219	11290	7533
1979	541	606	295	6214	5466	5050	3498	9434	3434
1980	470	579	244	5556	4625	5554	2255	4182	2669
1981	542	567	232	7415	7591	5328	4393	11982	6153
1982	629	554	259	7483	8563	6807	10059	8490	3846
1983	565	478	231	7145	11147	6238	19794	41654	13065
1984	409	373	185	7064	9365	7133	25338	29829	8948
1985	292	262	143	6979	4359	6864	24358	22926	7415
1986	276	197	107	6044	3620	5920	20885	16295	4977
1987	324	179	90	5685	3347	8595	24599	18540	10261
1988	304	144	62	5122	2894	6948	17559	11545	8073
1989	232	94	33	5895	2850	6080	25254	18855	14349
1990	193	86	26	5840	3266	7087	32237	29792	21231
1991	143	63	15	6062	3643	7251	46885	49694	25551
1992	140	82	10	6871	4300	6458	56793	62174	28336
1993	215	113	12	6617	3872	5843	61041	67892	39274
1994	239	145	11	6210	3405	5628	52004	55477	33411
1995	239	228	10	6454	3314	6004	81700	77071	46772
1996	259	228	10	6391	2718	5805	76122	59937	44349

Appendix-Table 2. Indices of stock sizes for different Sub-divisions (SD): cod age-group 2+ from Baltic international trawl survey in February/March and age-group 3+ from Latvian bottom trawl survey in January (left column) and November/December (right column) (units: $n \cdot \text{hour}^{-1}$), herring and sprat age-group 1+ from international hydroacoustic surveys in September/October (in millions).

Note: A dash indicates that a reliable survey was not conducted that specific date.

Year	Cod age-group 2+			Cod age-group 3+				Herring			Sprat		
	SD 25	SD 26	SD 28	SD 26	SD 26	SD 28	SD 28	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28
1977	-	-	-	71	-	285	-	-	-	-	-	-	-
1978	-	-	-	320	405	473	-	-	-	-	-	-	-
1979	-	-	-	2830	-	1068	-	-	-	-	-	-	-
1980	663	-	-	-	-	-	-	-	-	-	-	-	-
1981	1290	1361	-	-	-	908	908	-	-	-	-	-	-
1982	855	2575	3080	2142	1169	1479	1195	3980	5290	6679	4651	7383	2925
1983	891	772	4011	1091	332	2415	1056	4303	6923	6652	13261	22696	14536
1984	891	786	1053	3383	734	1428	617	4156	2881	9429	7395	22405	5800
1985	884	658	957	1232	288	154	132	2798	3988	9350	12227	9394	2178
1986	365	491	539	-	38	170	83	7696	8547	7977	5647	7792	3878
1987	771	694	703	454	-	42	8	3761	5172	9283	4455	6120	9048
1988	479	590	574	332	117	253	65	4725	6738	6609	4917	3408	3155
1989	269	226	269	567	72	311	11	3279	6977	8745	3637	36389	24143
1990	344	358	182	469	-	25	-	6168	8096	9823	5447	8150	22656
1991	140	147	201	426	-	110	-	4058	10451	13408	19223	46071	28498
1992	109	79	27	-	-	-	-	2977	7978	9983	8084	44395	28923
1993	458	172	49	-	-	-	-	-	-	-	-	-	-
1994	706	293	68	-	-	-	-	9037	9399	16597	13983	35297	24849
1995	379	928	99	-	-	-	-	4759	7421	7985	18155	50214	128170
1996	489	603	66	-	-	-	-	7750	4937	12821	24594	62374	117462

Appendix-Table 3. Recruitment of cod, herring and sprat (age-group 1) derived from the Baltic international bottom trawl surveys (units: $n \cdot \text{hour}^{-1}$) and the international hydroacoustic survey (in millions).

Year	Cod			Herring			Sprat		
	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28	SD 25	SD 26	SD 28
1980	10.3	-	-	-	-	-	-	-	-
1981	309.7	3294.6	-	-	-	-	-	-	-
1982	26.5	816.2	187.5	768	1146	991	361	2832	1037
1983	36.8	52.2	43.8	966	1142	510	7166	15569	8610
1984	36.8	309.1	15.4	654	466	3315	581	10979	1140
1985	15.0	129.5	11.6	886	713	743	2036	1415	458
1986	11.9	6.8	5.5	2224	874	261	58	1127	59
1987	47.7	163.8	6.5	723	1023	1983	306	4002	5925
1988	7.7	30.6	9.2	552	510	171	92	44	22
1989	6.4	202.6	10.6	992	745	1230	1010	23345	7842
1990	7.9	113.9	8.7	940	1422	1926	339	3194	4576
1991	6.0	26.1	0.3	918	1762	1018	2665	26985	9254
1992	15.7	10.7	0.1	633	1998	456	636	16031	12222
1993	28.7	78.8	2.3	-	-	-	-	-	-
1994	71.1	227.1	1.7	536	827	277	245	8955	473
1995	18.4	310.2	0.1	781	952	459	8276	31382	75143
1996	2.3	41.7	0.0	373	506	330	3674	24698	29674

Note: A dash indicates that a reliable survey was not conducted that year.

Appendix-Table 4. Average seasonal (1977-1996) species and stage-specific (copepodite stages CII-CV) ambient temperature (T) and development times (D_i) \pm standard deviations.

Stage	Winter		Spring		Summer		Autumn	
	T (°C)	D_i (d)	T (°C)	D_i (d)	T (°C)	D_i (d)	T (°C)	D_i (d)
	<i>P. elongatus</i>							
CII	1.98 \pm 1.14	10.5 \pm 1.5	3.74 \pm 0.98	8.5 \pm 0.8	5.00 \pm 1.34	7.5 \pm 1.0	8.83 \pm 1.73	5.6 \pm 2.1
CIII	1.98 \pm 1.14	10.7 \pm 1.5	3.30 \pm 0.94	9.0 \pm 0.9	4.00 \pm 1.05	8.3 \pm 0.9	6.72 \pm 1.97	6.7 \pm 2.1
CIV	1.98 \pm 1.14	10.7 \pm 1.5	2.93 \pm 0.94	9.4 \pm 1.0	3.43 \pm 0.90	8.9 \pm 0.9	6.72 \pm 1.97	6.7 \pm 2.1
CV	2.13 \pm 1.08	10.4 \pm 1.4	3.24 \pm 0.84	9.1 \pm 0.9	3.43 \pm 0.90	8.9 \pm 0.9	5.32 \pm 1.72	7.6 \pm 1.9
	<i>T. longicornis</i>							
CII	2.17 \pm 10.6	8.4 \pm 1.4	4.52 \pm 1.13	5.8 \pm 0.8	7.42 \pm 1.52	4.1 \pm 0.7	10.17 \pm 0.88	3.0 \pm 0.3
CIII	2.17 \pm 10.6	8.4 \pm 1.4	4.52 \pm 1.13	5.8 \pm 0.8	7.42 \pm 1.52	4.1 \pm 0.7	10.17 \pm 0.88	3.0 \pm 0.3
CIV	2.17 \pm 10.6	8.4 \pm 1.4	3.77 \pm 0.88	6.5 \pm 0.8	7.42 \pm 1.52	4.1 \pm 0.7	10.17 \pm 0.88	3.0 \pm 0.3
CV	2.17 \pm 10.6	8.4 \pm 1.4	3.77 \pm 0.88	6.5 \pm 0.8	7.42 \pm 1.52	4.1 \pm 0.7	10.17 \pm 0.88	3.0 \pm 0.3
	<i>Acartia</i> spp.							
CII	2.02 \pm 1.11	7.4 \pm 1.3	4.52 \pm 1.13	5.1 \pm 0.7	13.76 \pm 1.96	1.9 \pm 0.4	10.17 \pm 0.88	2.6 \pm 0.2
CIII	2.02 \pm 1.11	7.4 \pm 1.3	4.52 \pm 1.13	5.1 \pm 0.7	13.76 \pm 1.96	1.9 \pm 0.4	10.21 \pm 0.87	2.6 \pm 0.2
CIV	2.02 \pm 1.11	7.4 \pm 1.3	4.52 \pm 1.13	5.1 \pm 0.7	13.76 \pm 1.96	1.9 \pm 0.4	10.17 \pm 0.88	2.6 \pm 0.2
CV	2.02 \pm 1.11	7.4 \pm 1.3	4.52 \pm 1.13	5.1 \pm 0.7	7.42 \pm 1.52	3.6 \pm 0.6	10.17 \pm 0.88	2.6 \pm 0.2

Appendix-Table 5a. Daily production rates (mg/C * m⁻²) of *Pseudocalanus elongatus* life-stages CII, CIII/IV and CV/VI.

Carbon in zooplankton 5% of wet weight (Mullin, 1969).

Year	Winter			Spring			Summer			Autumn		
	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI
1977	0.2	8.65	10.4	0.15	0.2	10.45	5.85	29.55	12.55	0	19.6	19.6
1978	0	4.7	10.2	0.1	0.25	12.95	4.3	31.3	31	0.2	31.5	31.7
1979	<0.1	1.85	7.05	0.9	1.15	3.9	5.5	29.25	23.8	<0.1	14.1	28.65
1980	0	3.05	24.05	2.85	3.2	17.95	2.7	23.45	23.6	1.05	48.85	101.35
1981	0	6.3	35.6	0.15	<0.1	8.2	5.25	34	40.9	<0.1	13.15	32.9
1982	0	3.35	26.95	1.75	0.5	12.55	4.7	36	18.9	0.6	35.65	39.15
1983	0	2.85	7.4	<0.1	0.1	8.35	4.6	26.3	4.1	<0.1	7.95	3
1984	0	7.75	23.05	2.45	2.65	8.25	16.65	64.35	17.65	0.4	39.55	31.55
1985	0	3.75	11.95	<0.1	<0.1	10.25	12.35	28.75	6.25	0.55	11.6	9.95
1986	<0.1	1.4	8.9	0.5	<0.1	3.85	5.65	22.6	6.8	0	5.1	2.85
1987	0	0.9	3.6	0.05	<0.1	0.15	10.45	42.3	6.15	0.5	20.05	8.7
1988	0	2.4	7.3	1	0.6	11.7	2.6	15.45	3.8	0.1	10.75	7.65
1989	0	1.85	9.9	3.9	3.85	1.4	1.85	15.85	9.95	0	10.1	7.6
1990	0	1.6	5.55	2.25	4.05	1.8	1.25	11.2	4.7	0	5.1	2.4
1991	0	0.7	3.5	0.65	1.5	1.35	1.3	2.55	6.25	1.3	20.9	17.85
1992	0	2.05	5.6	1.5	2.1	6.05	5.7	29.65	11.75	0.4	8.3	7.3
1993	<0.1	2.85	10.6	1.9	3.15	1.6	7	29.3	11.15	1.45	10.9	4.55
1994	0	0.45	3.9	1.95	3.2	1.2	1.05	5.55	1.6	4.1	15.9	2.15
1995	0	0.6	3.2	0.6	1.75	5	2.05	27.95	7.7	0.35	9.4	4.35
1996	0	0.35	2.9	1.5	1.1	0.95	2.75	9.95	2.6	0.95	14.55	1.6
Mean	0.01	2.87	11.08	1.34	1.83	6.40	5.18	25.77	12.56	0.70	17.65	18.24

Carbon in zooplankton 5% of wet weight (Mullin, 1969).

Appendix-Table 5b. Daily production rates (mg/C * m⁻²) of *Temora longicornis* life-stages CII, CIII/IV and CV/VI.

Carbon in zooplankton 5% of wet weight (Mullin, 1969).

Year	Winter			Spring			Summer			Autumn		
	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI
1977	0	0.5	2.75	0	0	1.15	1.35	4.95	21.3	0.3	8.15	27
1978	0	0	1.8	0	0	0.6	0.1	1.7	7.1	1.15	6.65	12.4
1979	<0.01	0.35	2	0.2	0.45	1.8	0.3	2.1	14.45	2.85	16.15	15.75
1980	0	0	4.25	<0.01	0	2.15	0.6	2.1	16.15	2.05	14.45	24.75
1981	0	0.1	4.4	0	0	1	1.05	5.8	35.45	0.7	3.05	8.05
1982	0	0	0.95	<0.01	0	1.25	0.2	1.95	9.9	2.3	46.4	56.2
1983	0	0.05	0.9	0	0	0.65	0.3	1.75	9.8	0.8	20.5	17.3
1984	0	0.15	2.75	<0.01	<0.01	0.8	1.55	4.45	61.8	0.5	15.65	34.25
1985	0	0.05	2.5	0	0	0.3	0.9	3.35	20.05	1.9	6.55	5.1
1986	0	0.1	1.1	0	0	0.65	3.05	6.7	20.15	0.5	1.95	1.25
1987	0	0.15	1.65	0	0	0.1	2.1	12.05	56.75	1.15	12.55	37.45
1988	0	<0.01	3.15	<0.01	0.05	0.9	0.55	2.75	11	1	9.75	15.05
1989	0	0.5	7.85	0.65	1.75	5.65	0.2	2.8	23	1.15	11.55	17.7
1990	0	0.1	3.05	2.2	6.5	16.65	0.9	7.1	31.95	0.95	6.95	8.65
1991	0	0.4	1.8	0.35	1.55	5.55	3.55	21.6	55.5	1.8	13.55	18.05
1992	0	1.6	7.25	0.45	1.25	4.65	0.75	5.4	22.3	0.45	3.2	4.2
1993	0	0.75	4.25	0.6	2.95	20.5	1	7.45	30.8	0.15	3.95	7.85
1994	0	1.8	5.75	1	2.25	1.3	0.65	16.25	35.3	2.9	14.2	6.55
1995	0	3.5	11.25	1.1	1.45	2.95	0.75	11.45	30.35	4.25	20.35	15.55
1996	0	0	2.05	0.15	0.15	0.2	1.65	10.7	46.1	1.35	16.2	15.55
Mean	<0.01	0.53	3.57	0.42	0.97	3.44	1.08	6.62	27.96	1.41	12.59	17.43

Appendix-Table 5c. Daily production rates (mg/C * m⁻²) of *Acartia* spp. life-stages CII, CIII/IV and CV/VI.

Year	Winter			Spring			Summer			Autumn		
	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI
1977	0	3.2	0.1	<0.01	<0.01	2.6	2.15	7.75	14.6	1.8	2.55	24.35
1978	0	2.5	0.05	0.1	0.05	2.6	0.25	1.65	5.7	0.75	1.85	19
1979	<0.01	0.9	0.1	0.45	1.15	4.7	1.15	3	16.35	1.15	3.35	17.7
1980	0	0.45	<0.01	0.05	0.1	1.6	3.3	8	16.1	0.75	3.1	21.4
1981	<0.01	2.55	0.15	0.05	0.25	0.7	2.25	8.6	25.6	0.7	2.05	15.1
1982	<0.01	2.3	0.05	0.3	0.45	3.15	1.2	9.25	25.2	1.35	6.85	39.9
1983	<0.01	2.35	<0.01	0.05	<0.01	1.5	1.85	7.8	15.9	0.35	2.2	8.55
1984	<0.01	5.15	0.2	0.6	0.85	3.9	2.9	9.1	62.15	0.6	1.35	23.55
1985	<0.01	3.05	0.2	0.1	0.1	3	2	5.5	22.35	0.2	0.3	3.5
1986	<0.01	0.7	<0.01	0.1	0.25	2.55	1.1	4.25	18.4	0.75	0.85	2.2
1987	0	0.35	<0.01	0.1	0.25	1.7	2.3	9.95	38.35	1.95	6.25	37.25
1988	<0.01	1.05	<0.01	0.3	0.5	3.3	1.4	5.1	16.6	0.8	1.65	8.65
1989	<0.01	1.35	<0.01	0.75	1.95	8.75	0.6	2.8	15.45	1.8	3.45	16.8
1990	0	0.5	<0.01	1.5	4.15	23.65	1.3	6.35	33.05	0.55	1.15	9.4
1991	0	0.1	0.2	0.65	1.45	7.3	3.05	12.75	41.45	1.75	5.35	19.05
1992	<0.01	0.6	0.7	1.05	2.85	10.05	1.4	7.95	24.6	0.45	1.3	4.55
1993	<0.01	2.05	0.35	1.55	8.45	16.95	2.6	15.05	34.65	0.45	4.15	6.6
1994	0	0.5	0.6	1.5	3.95	7.05	4.9	45.8	58.75	6.95	16.3	7.85
1995	0.1	0.55	0.7	0.95	7.75	24.15	1.35	16.65	17.4	2.05	7.95	15.1
1996	0	1.95	<0.01	0.95	0.95	1.4	4.25	23	33.95	0.75	3.9	16.65
Mean	<0.01	1.61	0.28	0.58	1.97	6.53	2.07	10.52	26.83	1.30	3.80	15.86

Carbon in zooplankton 5% of wet weight (Mullin, 1969).

Appendix-Table 6a. Seasonal consumption/production-ratios of herring preying upon groups of *P. elongatus* life-stages.

year	winter			spring			summer			Autumn		
	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI
1977	0	0	< 0.01	0.54	0.04	< 0.01	0	0	< 0.01	0	0	0
1978	0	0	0	0.05	0.03	< 0.01	0.02	< 0.01	< 0.01	0	0	< 0.01
1979	0	0	0	0.04	0	0	0.06	< 0.01	0.02	0	0	< 0.01
1980	0	< 0.01	< 0.01	0.02	< 0.01	< 0.01	0.29	< 0.01	0.11	0	0	< 0.01
1981	0	0	< 0.01	> 1	0.23	< 0.01	0	< 0.01	< 0.01	0	0	0
1982	0	0	< 0.01	0.06	< 0.01	< 0.01	0.12	< 0.01	0.01	0	0	< 0.01
1983	0	< 0.01	0.04	0.20	< 0.01	< 0.01	0	0	< 0.01	0	0	0
1984	0	< 0.01	< 0.01	0.02	< 0.01	< 0.01	0.01	< 0.01	0.03	<	0	< 0.01
1985	0	< 0.01	< 0.01	> 1	0	< 0.01	< 0.01	0	0.03	<	0	< 0.01
1986	0	0	0.02	0.11	0.03	< 0.01	0.02	< 0.01	0.03	0	0	0.01
1987	0	< 0.01	0.02	0.54	0.11	0.15	0	< 0.01	0.13	<	0	< 0.01
1988	0	0	< 0.01	< 0.01	0	< 0.01	0	< 0.01	0.03	0	0	< 0.01
1989	0	0	0.02	0	0	< 0.01	0.02	< 0.01	0.01	0	0	0
1990	0	0	0	0	0	< 0.01	0	0	< 0.01	0	0	0
1991	0	< 0.01	0.02	0.02	0	< 0.01	0.02	< 0.01	0.02	<	0	< 0.01
1992	0	0	0	< 0.01	0	< 0.01	< 0.01	0	< 0.01	0.01	0	< 0.01
1993	0	0	0	< 0.01	0	< 0.01	0	0	< 0.01	<	0	0
1994	0	0	0	< 0.01	0	0	0	0	0	<	0	0
1995	0	0	0	< 0.01	0	0	< 0.01	0	0	0	0	0
1996	0	0	0	< 0.01	0	0	0	0	0	0	0	0

Appendix-Table 6b. Seasonal consumption/production-ratios of herring preying upon groups of *T. longicornis* stages.

year	winter			spring			summer			Autumn		
	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI
1977	0	< 0.01	< 0.01	0	0	< 0.01	0	< 0.01	0.02	< 0.01	0	< 0.01
1978	0	0	0	0	0	< 0.01	0.76	< 0.01	0.01	0	< 0.01	< 0.01
1979	0	0	0	< 0.01	0	0	< 0.01	< 0.01	< 0.01	0	< 0.01	< 0.01
1980	0	0.15	< 0.01	0.36	0	< 0.01	0	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
1981	0	0	< 0.01	0	0	< 0.01	0.10	< 0.01	< 0.01	0	0	0.05
1982	0	0	< 0.01	0	0	< 0.01	0	0	< 0.01	< 0.01	< 0.01	< 0.01
1983	0	0.06	0.11	0	0	0.02	0.44	< 0.01	0.01	< 0.01	< 0.01	< 0.01
1984	0	0.02	0.02	0.07	0.01	0.01	0.12	< 0.01	< 0.01	0.10	< 0.01	< 0.01
1985	0	0	< 0.01	0	0	0.01	0.27	< 0.01	0.01	0.03	< 0.01	0.02
1986	0	0	0.17	0	0	0.01	0.04	< 0.01	< 0.01	0.17	< 0.01	0.11
1987	0	0.02	0.03	0	0	0.08	< 0.01	< 0.01	< 0.01	0.10	< 0.01	< 0.01
1988	0	0	0.02	0	0	< 0.01	0	< 0.01	0.01	0.02	< 0.01	< 0.01
1989	0	0.04	0.03	0.02	0	< 0.01	> 1	0.01	0.01	0.10	< 0.01	0.01
1990	0	0	0	< 0.01	< 0.01	< 0.01	0.43	< 0.01	< 0.01	0.04	0	< 0.01
1991	0	< 0.01	0.03	0.01	< 0.01	< 0.01	0.15	< 0.01	< 0.01	0.11	< 0.01	< 0.01
1992	0	0	0	< 0.01	< 0.01	< 0.01	0.68	< 0.01	< 0.01	0.42	< 0.01	0.01
1993	0	0	0	< 0.01	< 0.01	< 0.01	0.45	< 0.01	< 0.01	0.15	0	0
1994	0	0	0	< 0.01	0	0	0.40	0	0	0.05	0	0
1995	0	0	0	< 0.01	0	0	> 1	0	0	0.13	0	0
1996	0	0	0	0.02	0	0	0.39	0	0	0.23	0	0

Appendix-Table 6c. Seasonal consumption/production-ratios of herring preying upon groups of *Acartia* spp. stages.

year	Winter			spring			summer			autumn		
	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI	CII	CIII/IV	CV/VI
1977	0	0	< 0.01	0	0	< 0.01	< 0.01	< 0.01	0.02	< 0.01	< 0.01	< 0.01
1978	0	0	0	0	0	< 0.01	< 0.01	< 0.01	< 0.01	0	0.01	< 0.01
1979	0	0	0	0	< 0.01	0	< 0.01	< 0.01	< 0.01	0	< 0.01	< 0.01
1980	0	0	0	0	0	< 0.01	0	< 0.01	< 0.01	0	< 0.01	< 0.01
1981	0	0	0	0	0	< 0.01	0	0	< 0.01	0	0.03	0.04
1982	0	0	0	0	0	< 0.01	0.03	< 0.01	< 0.01	0	< 0.01	< 0.01
1983	0	0	0	0	0	0.02	0	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
1984	0	0	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	0.01	0.01	< 0.01
1985	0	0	< 0.01	0	0	< 0.01	0	< 0.01	< 0.01	0.05	0.04	0.03
1986	0	0	0.03	0	0	< 0.01	0	< 0.01	< 0.01	0	< 0.01	< 0.01
1987	0	0	< 0.01	0	0	< 0.01	< 0.01	< 0.01	< 0.01	0.01	< 0.01	< 0.01
1988	0	0	0	0	0	0	0	< 0.01	< 0.01	0	< 0.01	< 0.01
1989	0	0	0	< 0.01	0	< 0.01	0	0	0	0	< 0.01	< 0.01
1990	0	0	0	< 0.01	< 0.01	< 0.01	0	0	< 0.01	0	0	< 0.01
1991	0	0	< 0.01	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	0.02	< 0.01	< 0.01
1992	0	0	0	< 0.01	< 0.01	< 0.01	0.02	< 0.01	0	0.10	< 0.01	< 0.01
1993	0	0	0	< 0.01	0	< 0.01	< 0.01	< 0.01	0	0	0	0
1994	0	0	0	0	0	0	< 0.01	0	0	< 0.01	0	0
1995	0	0	0	0.03	0	0	0.07	0	0	0.08	0	0
1996	0	0	0	0.01	0	0	0.01	0	0	0.12	0	0

Appendix-Table 7. Seasonal consumption/production-ratios of sprat preying upon CV/VI of the copepod species.

Year	<i>P. elongatus</i>				<i>T. longicornis</i>				<i>Acartia</i> spp.			
	W	Sp	Su	A	W	Sp	Su	A	W	Sp	Su	A
1977	0.01	0.04	0	< 0.01	0.13	0.07	< 0.01	0.02	< 0.01	0.04	< 0.01	0.03
1978	0.02	0.02	0	< 0.01	< 0.01	0.21	0.10	0.04	< 0.01	0.02	0.02	< 0.01
1979	0.02	0.09	< 0.01	< 0.01	0.05	0.04	0.01	0.02	< 0.01	< 0.01	< 0.01	< 0.01
1980	< 0.01	0.02	< 0.01	< 0.01	0.08	0.10	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
1981	< 0.01	< 0.01	< 0.01	< 0.01	0.04	0.24	< 0.01	0.05	< 0.01	0.05	< 0.01	< 0.01
1982	< 0.01	0.08	< 0.01	< 0.01	0.01	0.02	0.01	< 0.01	0	0.01	< 0.01	< 0.01
1983	0.30	0.22	0.02	0	0.08	0.32	0.10	0.07	0	0.57	0.02	0.10
1984	< 0.01	0.04	< 0.01	< 0.01	0.02	0.16	< 0.01	0.01	0	0.04	< 0.01	< 0.01
1985	0.01	0.01	< 0.01	< 0.01	< 0.01	> 1	0.01	0.07	0	0.17	0.02	0.04
1986	< 0.01	0.04	< 0.01	< 0.01	0.08	0.37	< 0.01	0.19	0	0.04	0.02	0.04
1987	0.05	> 1	< 0.01	0.01	0.10	> 1	< 0.01	0.02	0.01	0.16	0.02	< 0.01
1988	0.01	< 0.01	0	0	0.04	0.76	0.04	0.01	< 0.01	0.05	< 0.01	0.02
1989	0.05	0.02	< 0.01	0	0.03	0.10	0.04	0.05	< 0.01	0.06	< 0.01	< 0.01
1990	0.05	0.02	< 0.01	0.02	0.11	0.05	0.04	0.10	0.01	0.06	< 0.01	0.05
1991	0.11	0.36	< 0.01	< 0.01	0.24	0.17	0.02	0.05	0.01	0.07	0.01	0.03
1992	0.08	0.08	0	< 0.01	0.07	0.23	0.06	0.21	0.01	0.05	0.03	0.13
1993	0.05	0.33	0	0	0.15	0.07	0.05	0.02	< 0.01	0.04	0.03	< 0.01
1994	0	> 1	0	< 0.01	0.10	0.91	0.02	0.10	0.01	< 0.01	< 0.01	0.05
1995	0.18	> 1	0	< 0.01	0.07	0.62	0.09	0.07	0.01	0.04	0.03	0.07
1996	0.11	0.02	< 0.01	0	0.64	0.06	0.03	0.02	0.04	0.37	< 0.01	0.03

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