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Variability in population biology of calanoid copepods in the Central Baltic Sea

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Abstract

Interannual variability (1959-1999) in population biology of calanoid copepods *Pseudocalanus elongatus*, *Temora longicornis* and *Acartia* spp. in the Central Baltic Sea were described for different life-stages. By means of Principal component (PCA) and correlation analyses the association of the stage-specific abundance to salinity and temperature was investigated. *P. elongatus* dynamics were related to high salinities in spring favouring maturation and reproduction. Additionally low temperatures appear to be favourable for reproduction, whereas intermediate copepodite stages were positively correlated to temperature. *T. longicornis* and *Acartia* spp. life-stages were consistently associated to higher temperatures in spring. Furthermore indications exist that *T. longicornis* maturation and reproductive success in summer is affected by salinity levels similarly to *P. elongatus*.

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Introduction

Mesozooplankton species, especially calanoid copepods, play an important role in the Baltic Sea ecosystem. Changes in the species composition have been shown to influence the growth of their major predators, the clupeid fish herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (e.g. Flinkman et al., 1998; Möllmann and Köster, 2001). Recent individual-based modelling approaches additionally demonstrated the dependence of larval survival and consequently recruitment of cod (*Gadus morhua*) on the dynamics of their main prey species (Hinrichsen et al., 2001).

Long-term dynamics of copepod species have been investigated in different parts of the Baltic Sea and their abundance and biomass was shown to depend to a large extent on hydrographic conditions (Ojaveer et al., 1998; Viitasalo, 1992; Viitasalo et al., 1995; Vuorinen and Ranta, 1987; Vuorinen et al., 1998; Möllmann et al., 2000) controlled by climatic factors (Dippner et al., 2000 and 2001; Hänninen et al., 2000). In the Central Baltic basins especially decreasing salinities since the late 1970s, caused by increased river-runoff (Bergström and Carlsson, 1994) and lower frequency of pulses of saline water intrusions from the North Sea and Skagerrak (Matthäus and Franck, 1992; Matthäus and Schinke, 1994) caused obviously a declining biomass of *Pseudocalanus elongatus*, the dominant copepod in the area (Dippner et al., 2000; Möllmann et al., 2000). Two other important species, *Temora longicornis* and *Acartia* spp., were found to depend mainly on the prevailing temperature conditions in spring; especially *Acartia* spp. showed a general increase in biomass in the 1990s concurrently to prevailing relatively high temperature (Möllmann et al., 2000).

Former studies from the Central Baltic investigated trends in total standing stocks of copepod species, while no stage-specific dynamics were considered. The latter may result in the identification of a critical life-stage or population dynamic processes driving the dynamics. Here we explored the stage-specific long-term dynamics of *P. elongatus*, *T. longicornis* and *Acartia* spp. in the combined area of the Gdansk Deep and the central Gotland Basin (Fig. 1) and their association to temperature and salinity by means of Principal component (PCA) and correlation analyses.

Material and methods

Temperature and salinity

Temperature and salinity were measured by the Latvian Fisheries Research Institute (LATFRI) in Riga on 8 stations covering the Gdansk Deep and the central Gotland Basin. Measurements were performed during several cruises in 1961 to 1999 using a water sampler (Nansen type; 1l capacity) in 5 or 10m steps. A Deep Sea Reversing Thermometer was used for temperature measurements, whereas salinity was measured either by the Knudsen Method (until 1992) or with an Inductivity Salinometer (since 1993).

Average values of temperature and salinity per season were calculated for the depth range 0 – 50m, being the water layer mainly inhabited by *T. longicornis* and *Acartia* spp. (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.

Copepod stage-specific abundance

Copepod abundance data were sampled during seasonal surveys of LATFRI, i.e. mainly in February, May, August and November (further on called winter, spring, summer and autumn respectively) conducted in 1959 to

1999. Sampling was performed mostly at daytime using a Jeddy 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 (Anonymous, 1979).

Individual hauls were carried out in vertical steps, resulting in a full coverage of the water column to a depth of 100m on every station. For the present analysis data from LATFRI stations in the Gdansk Deep and the central Gotland Basin were used. 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. Nauplii (N), copepodites I to V (CI-CV) as well as adult females (CVI-f) and males (CVI-m) of the species *P. elongatus*, *T. longicornis* and *Acartia* spp. (including *A. bifilosa*, *A. longiremis* and *A. tonsa*) were identified in the samples.

Numerical analyses

Data were log-transformed to stabilize the variance. Missing values in the original time-series were interpolated using a linear trend regression (Statsoft, 1996).

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. One PCA was performed for every season and species 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, simple correlation analyses were performed for the main reproduction periods, i.e. spring for *P. elongatus* as well as spring and summer for *T. longicornis* and *Acartia* spp. To account for autocorrelation in the data the degrees of freedom (d.f.) in the statistical tests were adjusted 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. We applied approximately N/5 lags in Eg. (1) which ensures the robustness of the method (Pyper and Peterman, 1998).

Results

Temperature and salinity

Temperature in the upper 50m showed a rather high interannual variability (Fig. 2). Three marked peaks are visible in the winter and spring time-series: in the middle of the 1970s as well as the early 1980s and 1990s. Fluctuations were less pronounced in the deeper water layer (50-100m), but exhibited in general the same time-trend. Compared to the earlier decades the 1990s appeared to be the warmest period.

The time-series on salinity are characterized by a rather stable situation in the 1960s and 1970s. From the 1980s onwards salinity declined continuously in both depth layers. Whereas in the lower depth layer salinity increased again from the middle of the 1990s onwards, salinity declined further in the upper layer.

Pseudocalanus elongatus

The overwintering stock of *P. elongatus* is dominated by CIV and CV copepodites and additionally lower proportions of CIII and CVI (Fig. 3a). 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.

PCAs revealed pronounced differences in the behaviour of the seasonally dominating stages in spring (Fig. 4). 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 1a). 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.

Temora longicornis

T. longicornis hibernates mainly as CIV-CVI, although generally the overwintering stock is low compared to *P. elongatus* (Fig. 3b). 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 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. 4). 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 1b). 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.

Acartia spp.

The seasonal dynamics of *Acartia* spp. were similar to *T. longicornis* (Fig. 3c). The overwintering stock is relatively small, reproduction starts in spring and last throughout the year. Peak abundance is found in summer. 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, but also in summer (Fig. 4). 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 1c). The association to salinity is negative in spring (significant only for CIII and CIV) and in summer (significant only for CIII-CV).

Discussion

Pseudocalanus elongatus

A clear stage-specific response of *P. elongatus* to the prevailing hydrographic conditions during the season of peak reproduction in spring is indicated. At this time of the year most of the CVI-f mature, and their number is depending on the size of the overwintering stock, which is obviously dependent on the salinity level. If salinity is low, fewer individuals reach the CV-stage in winter and are available for maturation in spring. Consequently egg production and recruitment of N is low. Contrary, the development of the intermediate stages CII-CV in spring and thus, the fast production 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 were 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 (Möllmann et al., 2000). This is indicated by the negative correlation of N and temperature in spring, although not being significant.

Temora longicornis

Contrary to *P. elongatus*, all life-stages of *T. longicornis* showed a uniform association to higher temperatures in spring. For this copepod species, which has up to five generations per year (Line, 1979 and 1984), 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 (Madhupratab 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 (Madhupratab et al., 1996).

The negative correlation of all stages with salinity in spring can be considered as a result of the opposite development of temperature and salinity, because *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 the association 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). Obviously maturation and consequently reproductive success of *T. longicornis* in summer, when temperature is generally sufficiently high, depends on the salinity level. The general decrease in summer abundance may thus be caused by the decreasing salinity.

Acartia spp.

The group of *Acartia* species has a similar life-cycle as *T. longicornis* with up to seven generations per year (Line, 1979 and 1984) and PCAs as well as correlation analyses revealed also for *Acartia* spp. the significant association of all stages to temperature in spring. Obviously 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; Madhupratab et al., 1996; Viitasalo and Katajisto, 1994).

Again negative correlations with salinity were found in spring and, in contrast to *T. longicornis*, in summer. This indicates that reproduction of *Acartia* spp. in neither season is favoured by higher salinities. 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. 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.

Conclusions

Investigating the long-term stage-specific dynamics of major Central Baltic copepod species gave some new insights in the effect of hydrography. The study confirmed the impact of salinity during maturation and reproduction in spring on the stock development of *P. elongatus* (Möllmann et al., 2000), but additionally a stage-specific response to temperature was detected. While for reproduction lower temperatures are favourable, the development of intermediate copepodite stages is accelerated by warmer conditions. The dynamics of *T. longicornis* and *Acartia* spp. are mainly related to temperature in spring as demonstrated before (Dippner et al., 2000; Möllmann et al., 2000). Additionally, we could show that in summer, when temperature is not critical, higher salinities favour the maturation and subsequent reproduction of *T. longicornis*, similar to *P. elongatus*. Beside hydrography predation by planktivores (e.g. Rudstam et al., 1994) and/or food availability (e.g. Berggreen et al., 1988) may contribute to copepod dynamics. Especially the drastically enlarged sprat stock (Köster et al., 2001) may have the potential to control the stock of *P. elongatus* and *T. longicornis* (Möllmann and Köster, 1999 and 2001). Nevertheless, the main time-trends of the considered copepod species are explainable mainly by temperature and salinity changes.

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References

- Anonymous, 1979. Recommendations on methods for marine biological studies in the Baltic Sea. In: Hernroth, L. (Ed.), Baltic Marine Biologists, 15pp.
- Berggreen, U., Hansen, B., and Kiørboe, T. (1988). Food size spectra ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. *Marine Biology*, 99: 341-352.
- Bergström, S., and Carlsson, B. 1994. River runoff to the Baltic Sea 1950 - 1990. *Ambio* 23: 4-5.
- Box, G.E.P., and Jenkins, G.W. 1976. Time series Analysis: Forecasting and control. Holden-Day, San Francisco, CA xxi + 575pp.
- Chelton, D.B. 1984. Commentary: short-term climate variability in the Northeast Pacific Ocean: In the influence of ocean conditions on the production of salmonids in the North Pacific. Edited by W. Pearcy. Oregon State University Press, Corvallis, Oreg., USA: 87-99.
- Dippner, J.W., Kornilovs, G., and Sidrevics, L. 2000. Long-term variability of mesozooplankton in the Central Baltic Sea. *Journal of Marine Systems*, 25: 23-32.

- Dippner, J.W., Hänninen, J., Kuosa, H., and Vuorinen, I. 2001. The influence of climate variability on zooplankton abundance in the northern Baltic Archipelago Sea (SW Finland). *ICES Journal of Marine Science*, 58: 569-578.
- Flinkman, J., Aro, E., Vuorinen, I., and Viitasalo, M. 1998. Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s. top-down and bottom-up processes at work. *Marine Ecology Progress Series*, 165: 127-136.
- Hänninen, J., Vuorinen, I., and Hjelt, P. 2000. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnology and Oceanography*, 45(3): 703-710.
- Hinrichsen, H.-H., Möllmann, C., Voss, R., Köster, F.W., and Kornilovs, G. 2001. Bio-physical modelling of larval Baltic cod (*Gadus morhua*) growth and survival. Submitted to *Canadian Journal of Fisheries and Aquatic Sciences*.
- Katajisto, T., Viitasalo, M., and Koski, M. (1998). Seasonal occurrence and hatching of calanoid eggs in sediments of the northern Baltic Sea. *Marine Ecology Progress Series*, 163: 133-143.
- Köster, F.W., Möllmann, C., Neuenfeldt, S., St. John, M.A., Plikshs, M., and Voss, R. (2001). Developing Baltic cod recruitment models I: Resolving spatial and temporal dynamics of spawning stock and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 1516-1533.
- Le Fevre-Lehoerff, G., Ibanez, F., Poniz, P., and Fromentin, J.M. 1995. Hydroclimatic relationships with planktonic time series from 1975 to 1992 in the North Sea off Gravelines, France. *Marine Ecology Progress Series*, 129: 269-281.
- Lindley, J.A. 1986. Dormant eggs of calanoid copepods in sea-bed sediments of the English Channel and southern North Sea. *Journal of Plankton Research*, 8: 399-400.
- Line, R.J. 1979. Some observations on fecundity and development cycles of the main zooplankton species in the Baltic sea and the Gulf of Riga. In: *Fisheries investigations in the basin of the Baltic Sea*. Riga, Zvaigzne, 14: 3-10 (in russian).
- Line, R.J. 1984. On reproduction and mortality of zooplankton (Copepoda) in the South-eastern, Eastern and North-eastern Baltic. In: *Articles on biological productivity of the Baltic sea*. Moscow, 2: 265-274 (in russian).
- Madhupratap, M., Nehring, S., and Lenz, J. 1996. Resting eggs of zooplankton (Copepoda and Cladocera) from the Kiel Bay and adjacent waters (southwestern Baltic). *Marine Biology*, 125: 77-87.
- Matthäus, W., and Franck, H. 1992. Characteristics of major Baltic inflows - a statistical analysis. *Continental Shelf Research*, 12: 1375-1400.
- Matthäus, W., and Schinke, H. 1994. Mean atmospheric circulation patterns associated with major Baltic inflows. *Deutsche Hydrographische Zeitschrift*, 46: 321-339.
- Möllmann, C., and Köster, F.W. 1999. Food consumption by clupeids in the Central Baltic: evidence for top-down control? *ICES Journal of Marine Science*, 56 (suppl.): 100-113.
- Möllmann, C., Kornilovs, G., and Sidrevics, L. 2000. Long-term dynamics of main mesozooplankton species in the Central Baltic Sea. *Journal of Plankton Research*, 22(11): 2015-2038.
- Möllmann, C., and Köster, F.W. 2001. Interactions between clupeid fish and calanoid copepods in a Central Baltic Sea Basin. Submitted to *Sarsia*.
- Ojaveer, E., Lumberg, A., and Ojaveer, H. 1998. Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). *ICES Journal of Marine Science*, 55: 748-755.

- Pyper, B.J., and Peterman, R.M. 1998. Comparison of methods to account for autocorrelation in correlation analyses of fish data. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 2127-2210.
- Raymont, J.E.G. 1983. *Plankton and Productivity in the Oceans*, 2nd Edition, Volume 2: Zooplankton. Pergamon Press, 824 pp.
- Rudstam, L.G., Aneer, G., and Hildén, M. (1994). Top-down control in the pelagic Baltic ecosystem. *Dana*, 10:105-129.
- Sidrevics, L.L. 1979. Some peculiarities of vertical distribution of zooplankton in the Central Baltic. In: *Fisheries investigations in the basin of the Baltic sea*. Riga, Zvaigzne, 14: 11-19 (in russian).
- Sidrevics, L.L. 1984. The main peculiarities of zooplankton distribution in the South-eastern, Eastern and North-eastern Baltic. In: *Articles on biological productivity of the Baltic sea*. Moscow, 2: 172-187 (in russian).
- Statsoft. 1996. *STATISTICA for Windows*. StatSoft Inc., Tulsa, USA
- UNESCO Press. 1968. *Zooplankton sampling*. Monographs on oceanographic methodology, 2: 174pp.
- Viitasalo, M. 1992. Mesozooplankton in the Gulf of Finland and Northern Baltic proper – a review of monitoring data. *Ophelia*, 35: 147-168.
- Viitasalo, M., and Katajisto, T. 1994. Mesozooplankton resting eggs in the Baltic Sea: identification and vertical distribution in laminated and mixed sediments. *Marine Biology*, 120: 455-465.
- Viitasalo, M., Vuorinen, I., and Saesmaa, S. 1995. Mesozooplankton dynamics in the northern Baltic Sea: implications of variations in hydrography and climate. *Journal of Plankton Research*, 17(10): 1857-1878.
- Vuorinen, I., and Ranta, E. 1987. Dynamics of marine meso-zooplankton at Seili, Northern Baltic Sea, in 1967-1975. *Ophelia*, 21: 31-48.
- Vuorinen, I., Hänninen, J., Viitasalo, M., Helminen, U., and Kuosa, H. 1998. Proportion of copepod biomass declines together with decreasing salinities in the Baltic Sea. *ICES Journal of Marine Science*, 55: 767-774.

Figure captions

Fig. 1. Map of the Baltic Sea with the area of investigation, i.e. the Gdansk Deep and Gotland Basin (numbers-ICES Sub-divisions) shaded.

Fig. 2. Seasonal time-series on temperature (left panels) and salinity (right panels); 1st row – winter, 2nd row – spring, 3rd row – summer, 4th row – autumn; solid line 0-50m, dotted line 50-100m.

Fig. 3a. Seasonal time-series on stage-specific abundance of *Pseudocalanus elongatus*. Superimposed solid lines represent a three-point running mean.

Fig. 3b. Seasonal time-series on stage-specific abundance of *Temora longicornis*. Superimposed solid lines represent a three-point running mean.

Fig. 3c. Seasonal time-series on stage-specific abundance of *Acartia* spp. Superimposed solid lines represent a three-point running mean.

Fig. 4. 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.

Table 1a. Correlation tests between *Pseudocalanus elongatus* 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	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

Table 1b. 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

Table 1c. 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 1

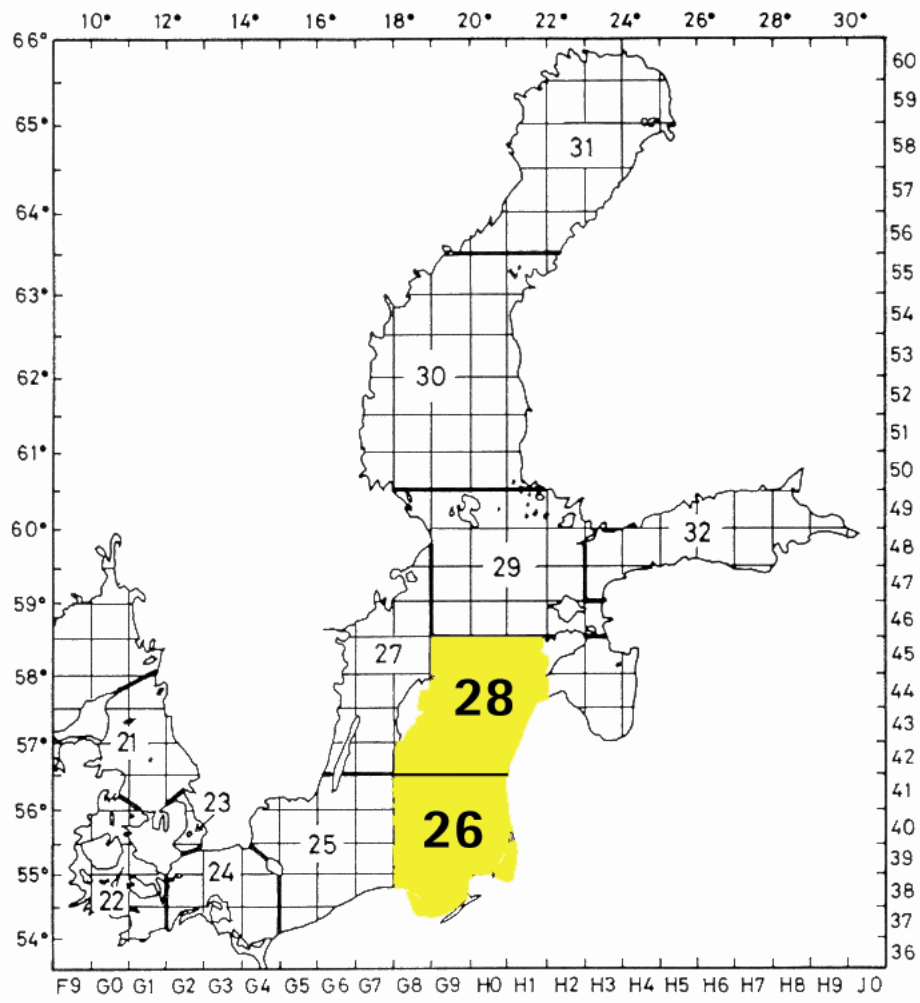


Figure 2

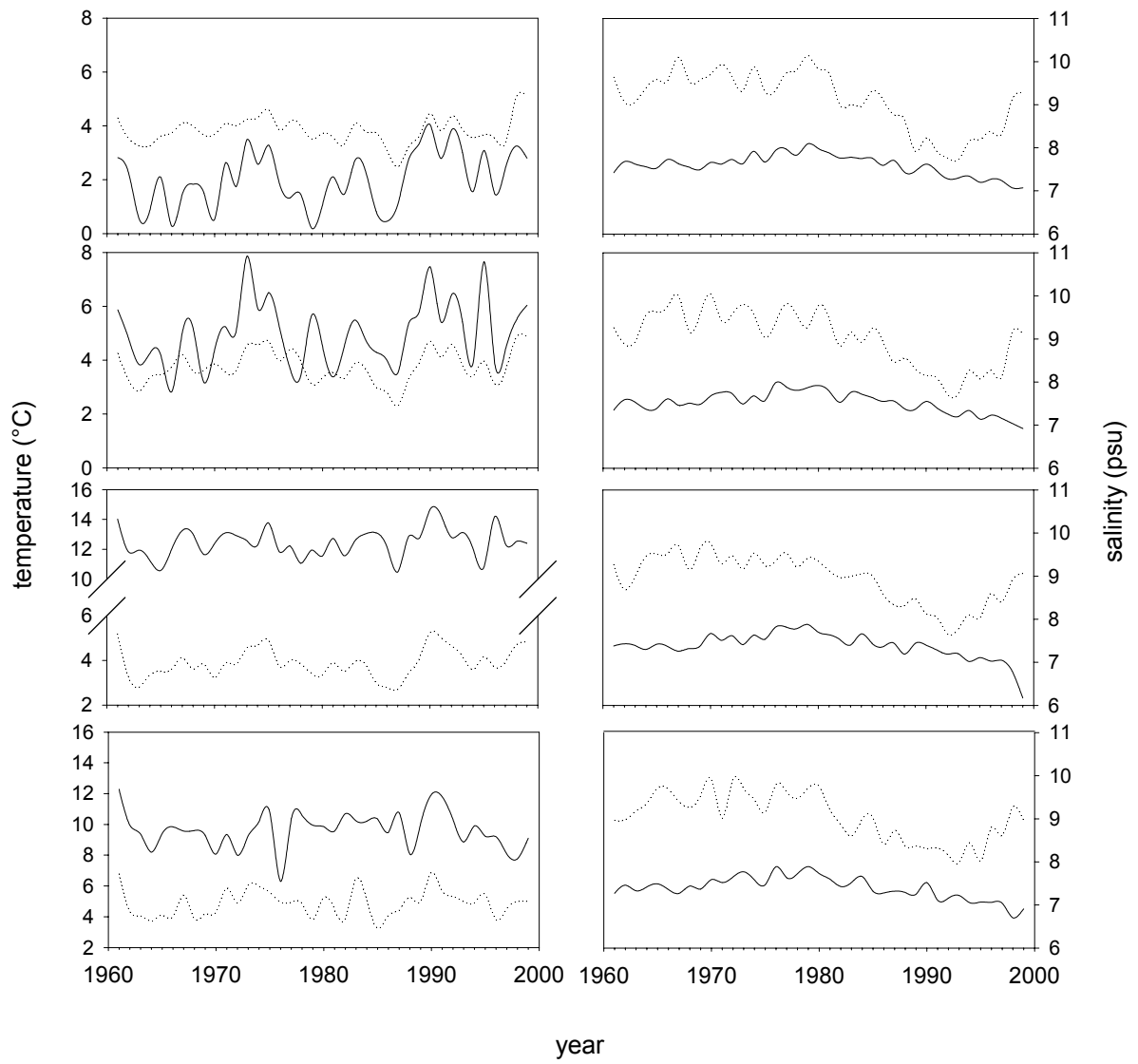


Figure 3a

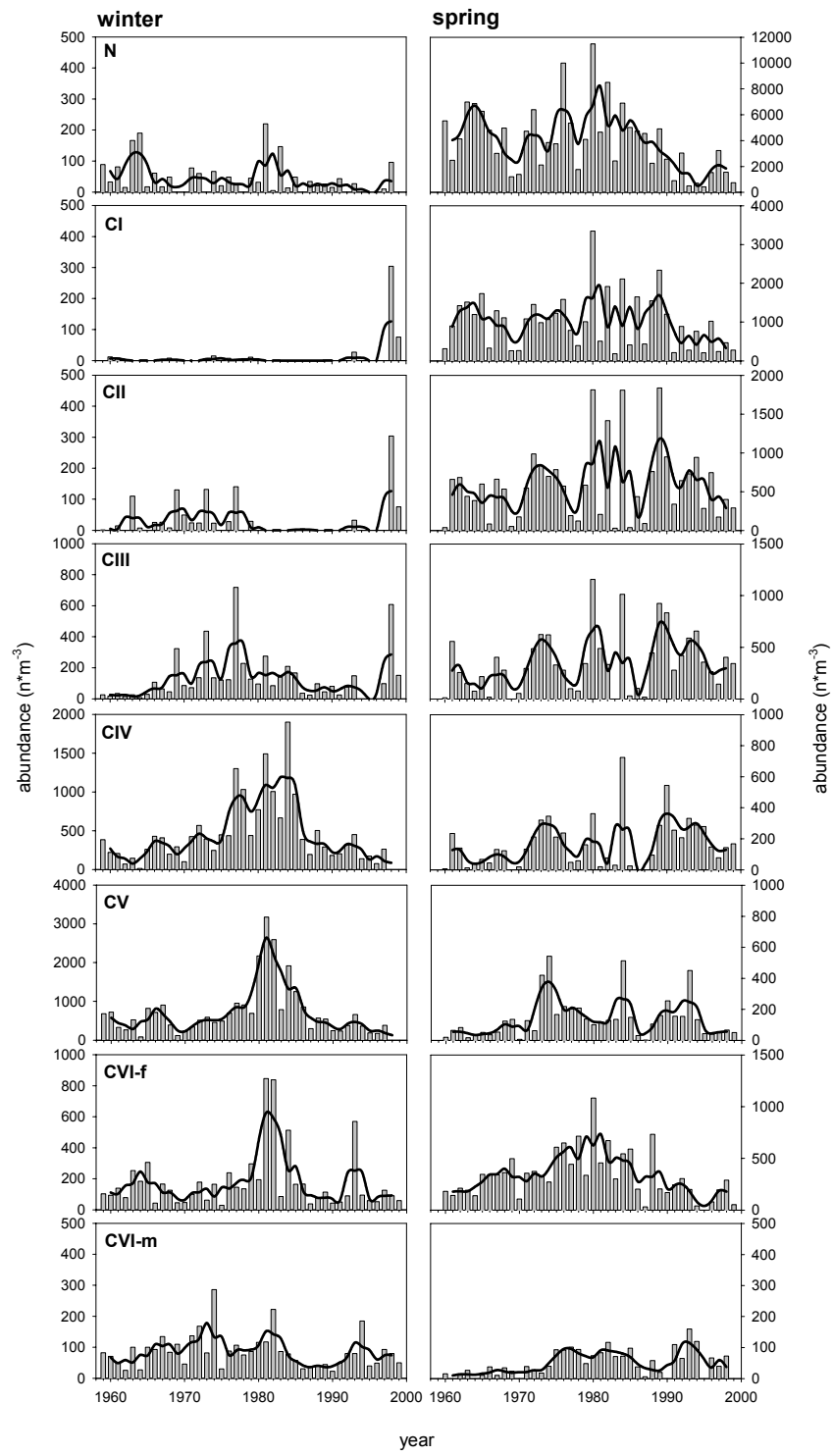


Figure 3a cont.

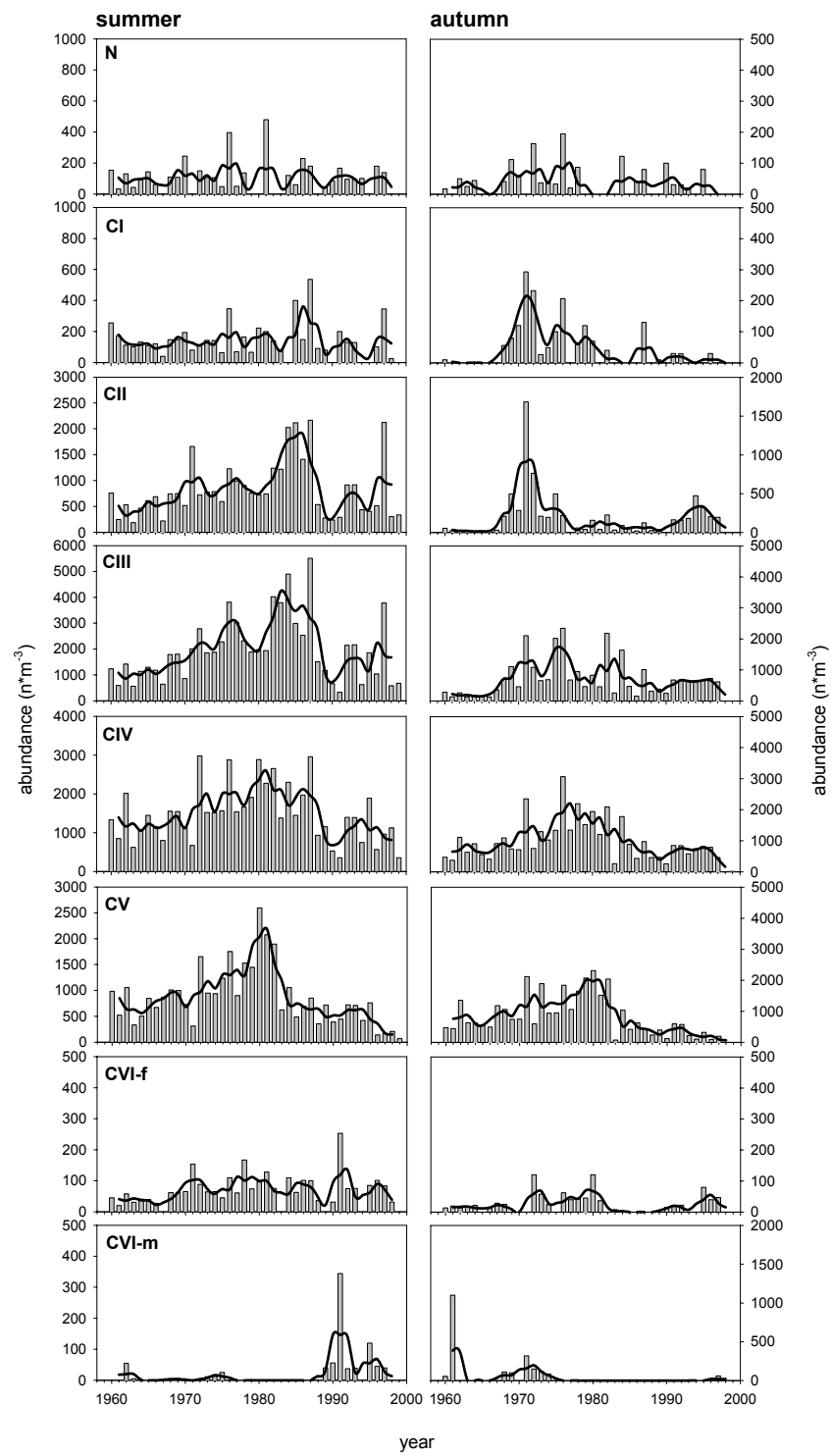


Figure 3b

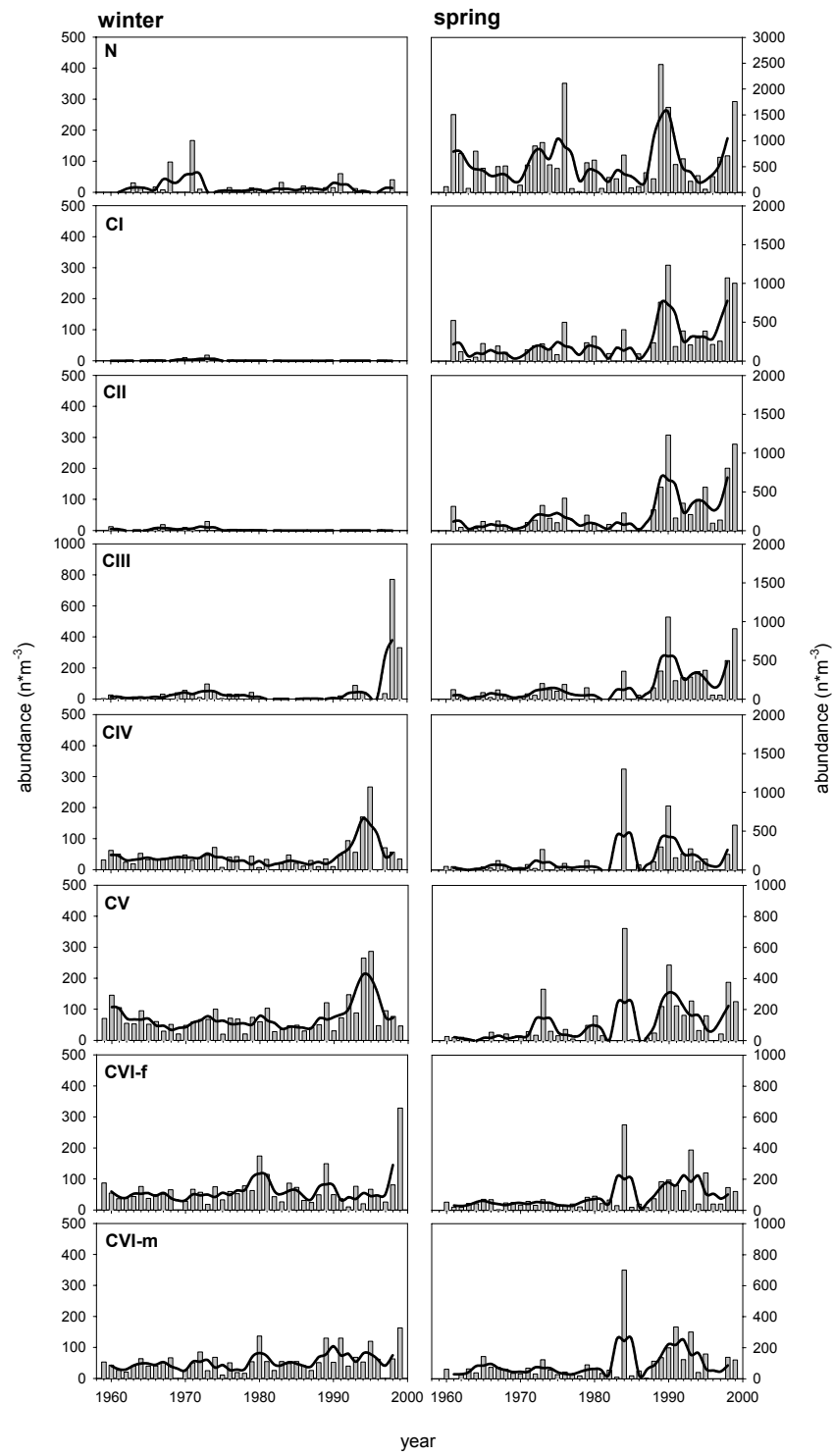


Figure 3b cont.

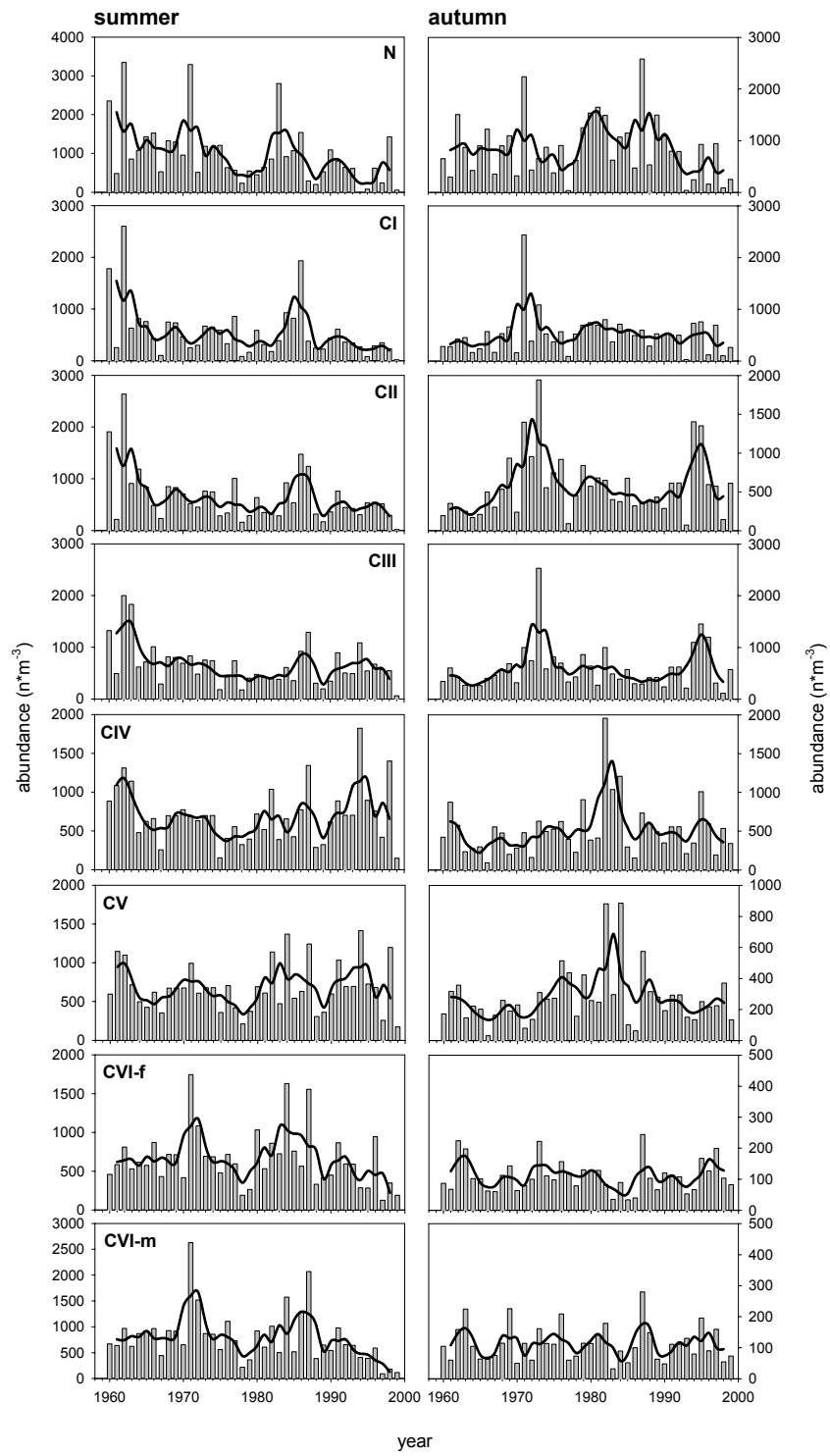


Figure 3c

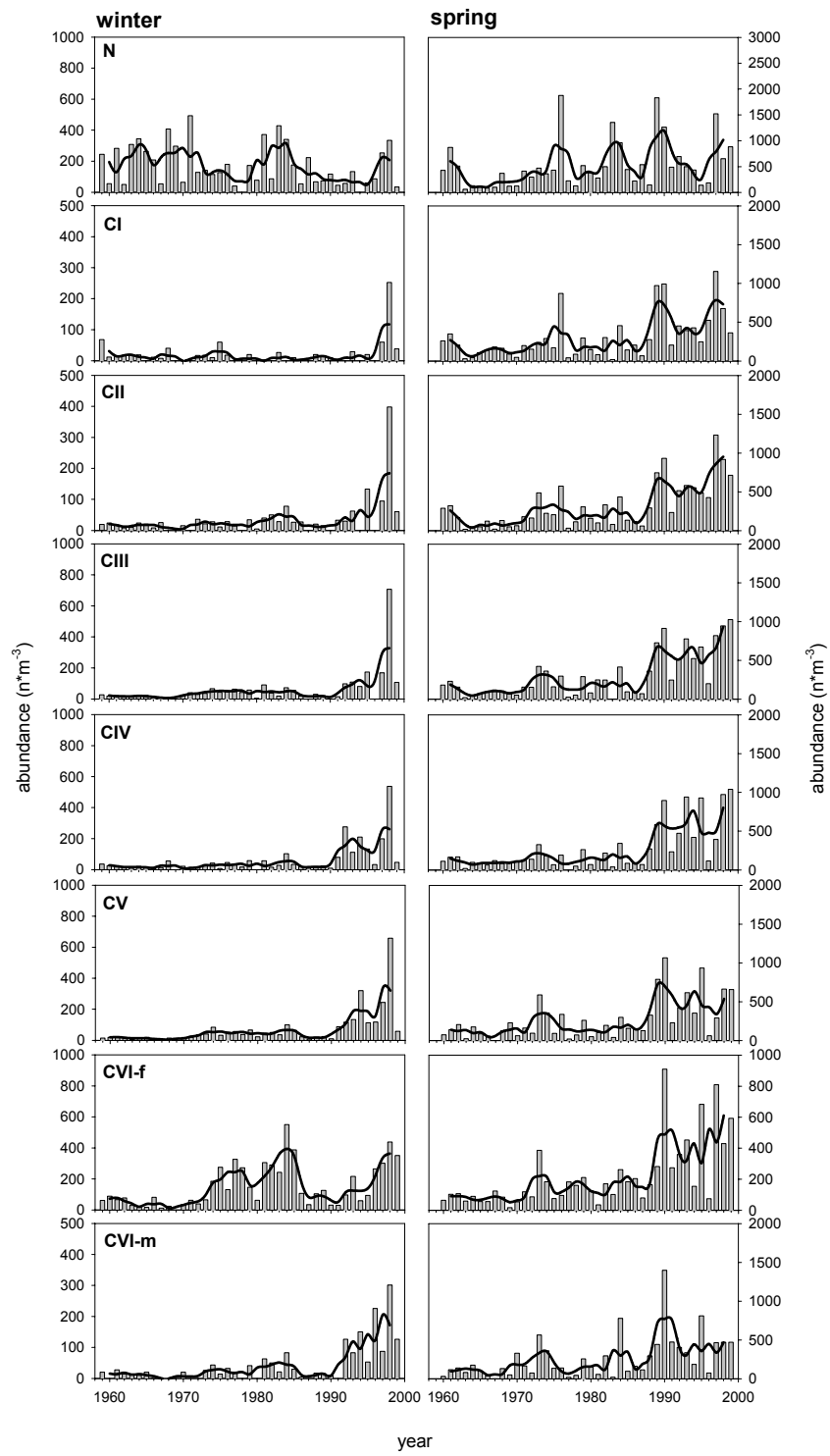


Figure 3c cont.

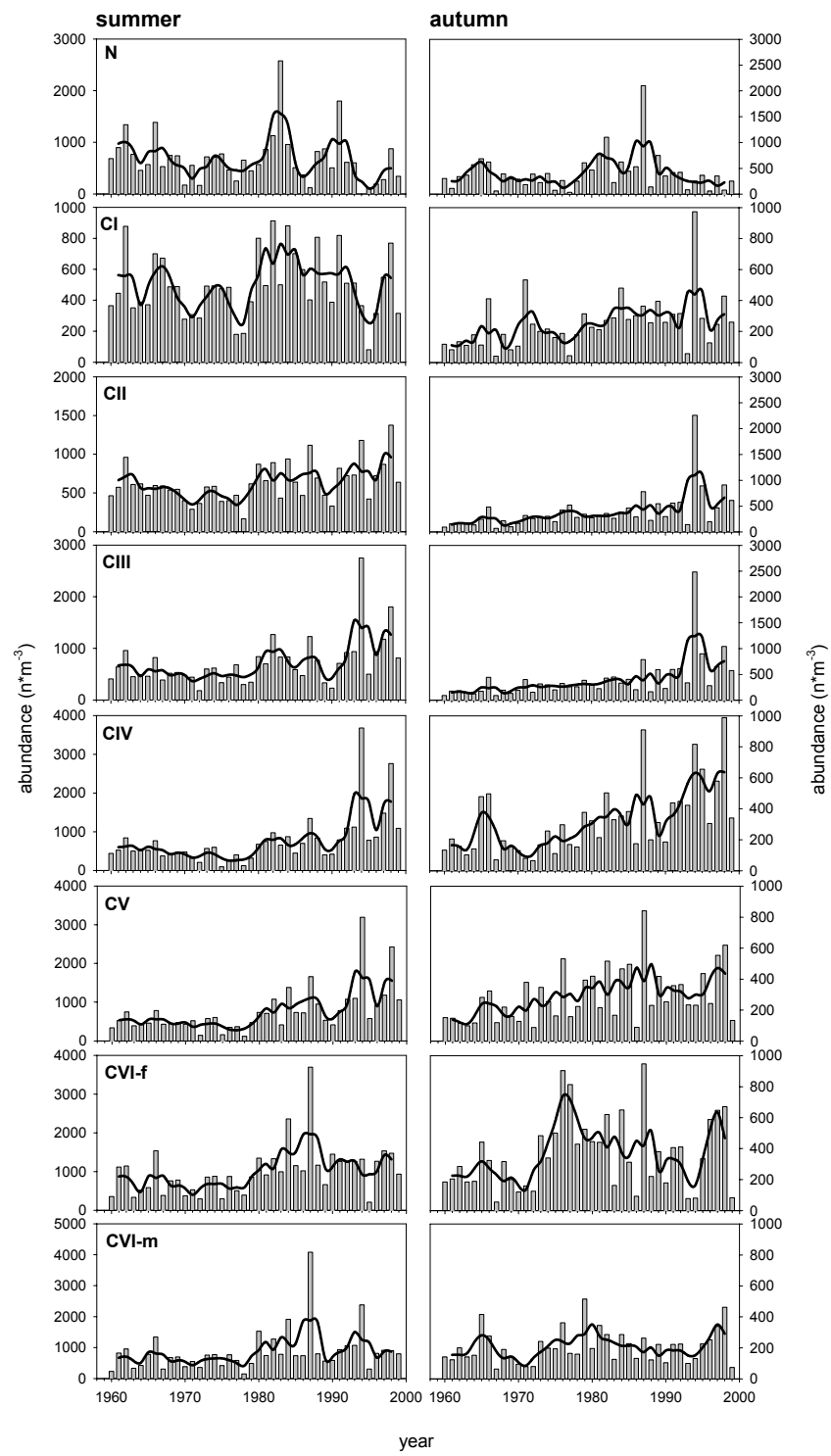


Figure 4

