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Seasonal and long-term variations in the body size of planktonic copepods in the northern Baltic Sea

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Abstract Seasonal and long-term variations in the body size of planktonic copepods were studied in the northern Baltic Sea. The influence of temperature, salinity and phytoplankton concentration to the body size of *Eurytemora affinis*, *Acartia bifilosa* and *Limnocalanus macrurus* (Calanoida) was examined at three sea areas, differing in their hydrographical and trophic conditions (an archipelago area and an enclosed bay on the SW coast of Finland in 1992 and at an open sea station in the Gulf of Bothnia in 1991). There was an inverse relationship between copepod body length and temperature, while there was a direct effect of phytoplankton concentration. According to multiple regression analysis, the relative importance of these factors varied according to species, developmental stage and study area. In the archipelago area, copepod body size was mainly determined by temperature, while in the open Gulf of Bothnia, phytoplankton concentration was usually more important. Interannual variation in the summer body length of *E. affinis* and *A. bifilosa* was examined using samples collected over 18 years (1967 to 1984) in the archipelago area. In this analysis, the inverse relationship between water temperature and copepod body size disappeared; in *E. affinis* the average female length correlated positively with summer temperature. We suggest that the length and timing of the study period greatly influence the investigator's view of the factors regulating copepod body size.

Introduction

Copepods attain a larger size during the cold water season than during summer in both fresh water and marine environments (Coker 1933; Comita and Anderson 1959; Deevey 1960). Experimental work has also confirmed the inverse relationship between copepod body length and temperature during development (e.g. McLaren 1965; Lock and McLaren 1970; Escribano and McLaren 1992), and several hypotheses have been offered to explain this. When temperature increases, respiration and general metabolic demand increase disproportionally more rapidly than ingestion and assimilation (e.g. Lehman 1988), which sets the upper limits for the body size in each temperature. Also, copepods may attain a greater body size at low temperature because the stage duration is markedly prolonged in cold water, while growth proceeds at a relatively more steady rate (Vidal 1980a).

Several investigators have proposed that temperature is the most important factor determining final size in marine copepods, at least in food-satiated conditions (McLaren 1963; McLaren et al. 1989; Hirche 1992; Christou and Verriopoulos 1993). However, separation of the effects of temperature and food supply is problematic in field studies. For instance, Evans (1981), Klein Breteler and Gonzalez (1982) and Ban (1994) have shown that differences in food concentration or quality explained most of the size variation in many coastal calanoid species. It is notable that the majority of the studies on seasonal changes in copepod body size have analysed the size variation over one or a few years

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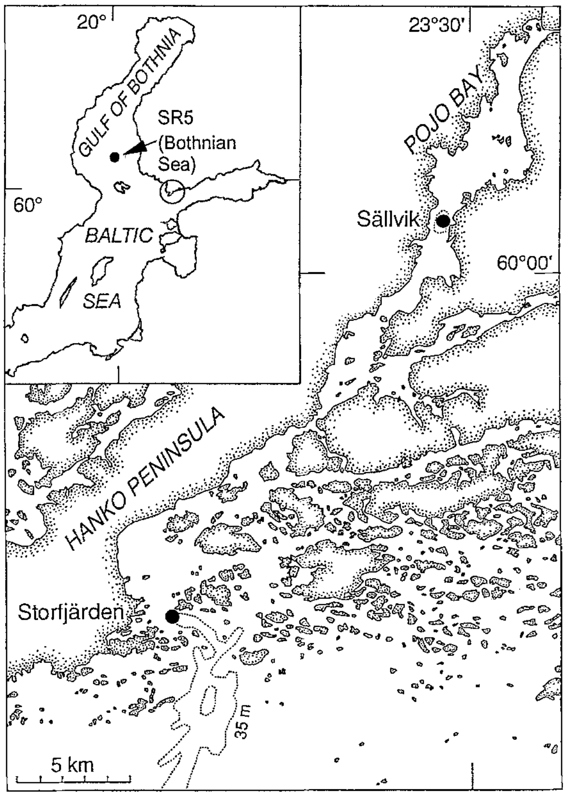

Fig. 1 Study areas on SW coast of Finland and in Bothnian Sea, southern Gulf of Bothnia. Area encircled in the insert is shown in enlargement. Dotted line in the enlargement denotes 35-m isobath.

only; only Evans (1981) has analysed copepod size variation using field data covering more than five years. Examining the more subtle long-term variations could give new insight into this phenomenon.

The present study is the first detailed analysis of the seasonal variation in planktonic copepod body size in the Baltic Sea. Our examples come from the northern Baltic, where the annual temperature range is large (up to ca. 20 °C in the surface layer) and where temperature and plankton development vary between years and areas. To reveal which factor is most responsible for the seasonal change in copepod body size, we first applied a multiple regression analysis on one year of data collected at three sea areas differing in their hydrographical and trophic conditions. We then analysed an 18-year zooplankton time series collected at one of these areas, to investigate whether the interannual variation in copepod body size is controlled by processes similar to those causing seasonal change.

Materials and methods

Study areas

The seasonal variation in copepod size was followed at two coastal areas and one open-sea station during one year (Fig. 1). The coastal study areas are on the eastern side of the Hanko Peninsula, on the SW coast of Finland. The first sampling station, Storfjärden (depth 33 m), was in the relatively open archipelago zone, where the hydrography and the development of the thermocline depend on meteorological factors and on landward movements of the deep saline Baltic water, which periodically reaches the study area along a furrow stretching from the open Baltic proper (Niemi 1975). The long-term data also originated from this station. The second sampling station, Sällvik (depth 42 m), was in a sheltered firth, Pojo Bay, 22 km NE of Storfjärden. There is a 7 m deep sill between Pojo Bay and the archipelago that partly prevents the renewal of the water in the Sällvik deep. Runoff from a river at the head of the bay separates the water above and below the pycnocline (Niemi 1978). The third sampling station, SR5, was in the middle of the Bothnian Sea, in the southern Gulf of Bothnia [Station BMPC4 in the Baltic Monitoring Programme, depth 125 m].

Environmental variables

During 1991 and 1992, temperature and salinity were measured with CTD-probe (conductivity, temperature and depth measurements) at all stations, and means were calculated for the layers above and below 10 m (the deep-water layer was 10 to 30 m at Storfjärden, 10 to 37 m at Sällvik, and 10 to 100 m in the Bothnian Sea). The daily air temperature at the coastal stations in 1992 was taken from the database of the Finnish Meteorological Institute (unpublished) using data from Hanko Tvärminne (1.5 km SW of Storfjärden) and Pohja Pohjankuru (11 km NE of Sällvik). The air temperature in the Bothnian Sea area was calculated as an average of the air temperatures measured at weather stations in Maarianhamina and Vaasa, ca. 100 and 260 km, respectively, from the open sea sampling station (Anonymous 1993). Chlorophyll *a* concentration (Chl *a*) at the coastal stations was measured with a fluorometer from water samples taken at 0, 2.5, 5, 7.5, 10 and 12.5 m depths and an average was calculated for the 0- to 12.5-m layer. At the Bothnian Sea sampling station, Chl *a* measurements were not made throughout the year and the Chl *a* concentration was estimated from phytoplankton samples as follows: phytoplankton species were counted from water samples taken in the 0- to 20-m layer, and the total phytoplankton carbon biomass was calculated using the species-specific carbon content values recommended by the Helsinki Commission (BMEPC 1988). The phytoplankton carbon biomass was then transformed to Chl *a* by using a C:Chl *a* ratio of 40, which was measured from a sample taken on 14 May 1991. This value corresponds to the commonly used C:Chl *a* ratios (between 40 and 50; e.g. Malone and Chervin 1979; Durbin et al. 1983). In addition to momentary values, averages were calculated for the 30-d periods preceding each zooplankton sampling.

During the long-term survey at Storfjärden, the water samples for determination of temperature and salinity were taken three times a month from 1967 to 1984, inclusive, at depths of 0, 5, 10, 15, 20 and 30 m; averages were calculated for the 0- to 10- and 10- to 30-m layers. No Chl *a* or phytoplankton samples were taken.

Zooplankton sampling and analysis

During 1991 and 1992, zooplankton samples were taken using a 100-μm mesh net with a single haul from depths of 30, 35 and 115 m to the surface at both Storfjärden, Sällvik and in the Bothnian Sea. At the coastal stations, zooplankton samples were usually taken twice a month from March to November 1992. In the Bothnian Sea, samples were taken at more irregular intervals from January to December 1991. The samples were preserved in 4% buffered formalin.

The calanoid copepod species studied were *Eurytemora affinis* (Poppe) and *Acartia bifilosa* Giesbrecht at Storfjärden, *E. affinis* and

Limnocalanus macrurus Sars at Sällvik, and *E. affinis*, *A. bifilosa* and *L. macrurus* in the Bothnian Sea. They were counted and measured with a Wild M8 dissecting microscope equipped with a micrometer eye-piece. At each study area, the prosome length was measured from ca. 40 ind of females, males and, in some cases, copepodite stages (C1, 3 or 5). In the Bothnian Sea, only 20 ind were measured for *A. bifilosa* and *E. affinis* copepodite Stage 5. In a few samples, the numbers of a particular copepodite stage were low, and only 5 to 30 ind were measured.

The individual carbon contents for the female calanoid copepods were estimated using length-carbon regressions (shown in Table 1). The carbon contents were analysed using a high temperature combustion method (Salonen 1979). The regressions for *Acartia bifilosa* in the late summer and *Eurytemora affinis* at the coastal stations in spring and summer were determined from samples taken on 26 August 1992, at Storfjärden. The regressions represented both copepodites and adults. The spring carbon weights of *A. bifilosa* at Storfjärden and in the Bothnian Sea were calculated according to the regressions presented by Tanskanen (1994) for copepodites in the Tvärminne region (the archipelago area of the present study) for 15 May 1991. The carbon contents of *E. affinis* females in the Bothnian Sea and *Limnocalanus macrurus* females at Sällvik and in the Bothnian Sea were calculated according to regressions presented by Kankaala and Johansson (1986) for the Bothnian Bay (northern Gulf of Bothnia).

For the analysis of the long-term data, we used samples collected during a long-term survey of mesozooplankton at Storfjärden, from 1967 to 1984, inclusive. Zooplankton samples were collected around noon, simultaneously with water samples for temperature and salinity, usually three times a month during the ice-free period, and one to three times a month during winter. A single haul from a depth of 25 m to the surface was drawn with a Hensen net of 150-μm mesh. The samples were preserved in 4% buffered formalin. Twenty adult *Eurytemora affinis* and *Acartia bifilosa* females were measured from each sample; the months considered were June to September for *E. affinis* and May to September for *A. bifilosa* (one sample per month was analysed). The preserved samples were in very good condition; long-term storage in buffered formalin does not influence the body length of copepods (Kuhlmann et al. 1982).

Statistical analyses

The relative influence of the hydrographical variables and Chl *a* on copepod body size was analysed by multiple regression analysis. The independent variables for the linear regression models were chosen with an interactive forward stepping procedure (provided by the statistical package SYSTAT), by first including the variable with which the coefficient of determination (r^2) was highest; then other statistically significant variables were added into the model if they increased the amount of variance explained. For *Eurytemora affinis* and *Acartia bifilosa*, the equations typically contained one temperature variable and Chl *a*. In some cases, including a second variable did not have a great effect on the r^2, and in other cases, adding more variables (such as temperature, salinity or Chl *a* calculated as an average for other depths or periods) would have increased the r^2. However, since the aim of this analysis was to rank the effects of temperature and phytoplankton concentration on copepod body size, only the most important hydrographical variable and Chl *a* were retained in the equations. To estimate how large a fraction of the variance could be explained by the environmental factors alone, simple regressions were calculated between copepod body size and the variables included in the multiple regression models.

In the long-term analysis, Chl *a* data was not available and multiple regressions were not calculated. The relationship between the hydrographical variables and the average copepod length was analysed with a non-parametric Spearman rank correlation analysis.

Results

Environmental conditions during 1991 and 1992

During May 1992, the air temperature at the coastal stations increased from ca. 7 to 18 °C, which caused relatively early and rapid warming of the water. In June, the weather turned colder; at Storfjärden, the average water temperature (in the 0- to 30-m layer) fell from 12.7 °C (10 June) to 6.1 °C (24 June). This was probably caused by the upwelling of cold water from deeper layers. The salinity at Storfjärden varied from 5.3 to 6.4‰. At Storfjärden there was a strong phytoplankton spring bloom which peaked at the end of April (max. Chl *a* concentration 23.7 $\mu g\ l^{-1}$). In September and October, Chl *a* values were slightly higher than during the summer, but a clear autumnal phytoplankton bloom did not occur (Fig. 2a).

At Sällvik, the water layers were clearly separate entities, as can be seen in the seasonal development of temperature (Fig. 2b). The surface-water temperature declined only slightly in June. The spring bloom at Sällvik was much smaller than at Storfjärden (max. Chl *a* 13.6 $\mu g\ l^{-1}$), and there was a distinct autumnal bloom (max. Chl *a* 14.1 $\mu g\ l^{-1}$).

The air temperature increased much more slowly in the Bothnian Sea in 1991 than at the coastal stations in 1992, and the surface-water temperature only began to increase in June (Fig. 2c). The period when the surface-water temperature was above 10 °C was only 2 mo, while the similar period lasted for more than 4 mo at the coastal stations in 1992. There was practically no halocline in the Bothnian Sea: salinity in the whole water column varied between 5.6 and 6‰. There was much less phytoplankton in the Bothnian Sea than at the coastal stations. Phytoplankton biomass peaked in the middle of May (max. Chl *a* 4.2 $\mu g\ l^{-1}$) and there was no autumnal bloom.

Seasonal changes in copepod body size

In the coastal study areas, *Eurytemora affinis* adults were large in late April and in May, small during June to September, and again relatively large in October and November (Fig. 3a). At Storfjärden, *E. affinis* size responded to the abrupt temperature decline in early summer: when the water temperature declined (between 10 June and 24 June), slightly larger C1 copepodites occurred on 24 June, larger C3 copepodites on 8 July and larger adults on 22 July. The increase in *E. affinis* adult length between 8 July and 22 July was statistically significant (Mann–Whitney *U*-test statistics for females 244, $p < 0.001$, and for males 486, $p < 0.01$). The subsequent decline in size between 22 July and 18 August was also significant in females (Mann–Whitney *U*-test statistic 1216, $p < 0.001$). *E. affinis* adults were considerably larger at Sällvik than at

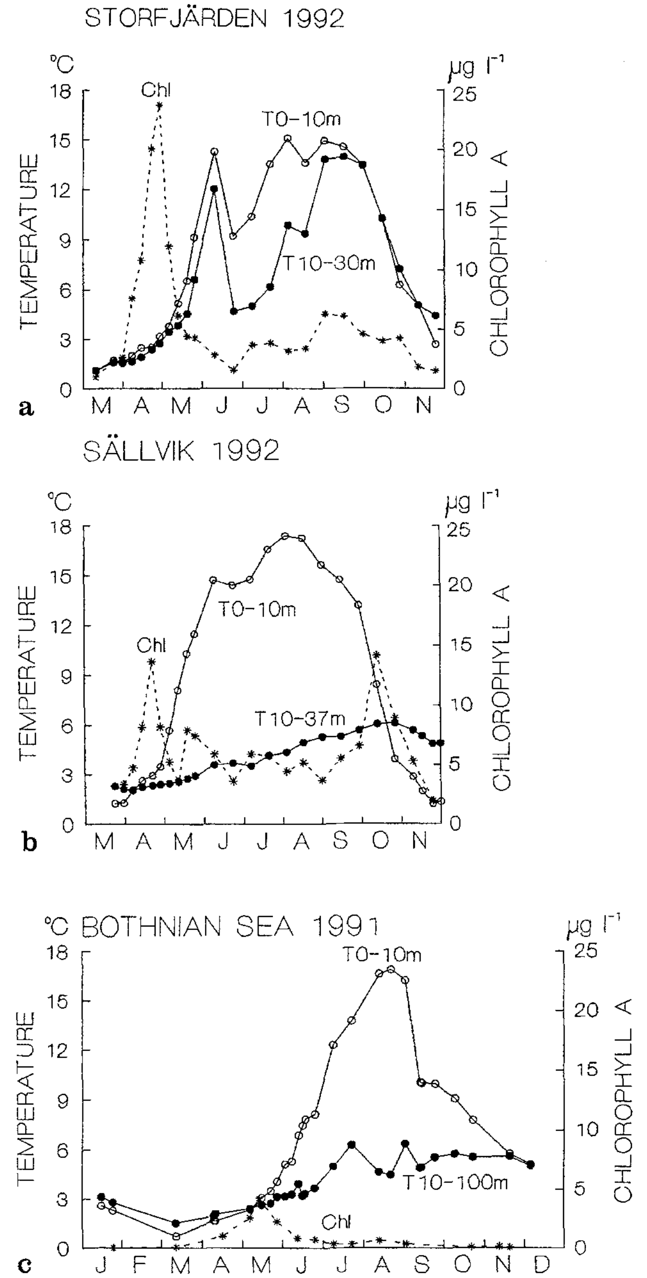

Fig. 2 Seasonal development of temperature and phytoplankton biomass **a** at Storfjärden in 1992, **b** at Sällvik in 1992 and **c** in the Bothnian Sea in 1991. Temperature (*T*) in the surface-water layer (0 to 10 m) denoted by open circles; temperature in the deep-water layer (10 to 30, 10 to 37 and 10 to 100 m at Storfjärden, Sällvik and Bothnian Sea, respectively) denoted by filled circles. Concentration of chlorophyll *a* (*Chl*) in the 0- to 12.5-m layer (Storfjärden and Sällvik) or in the 0- to 20-m layer (Bothnian Sea) denoted by asterisks

the other study areas. In the Bothnian Sea, the largest *E. affinis* females occurred in June, i.e., about a month later than at the coastal stations.

At Storfjärden in 1992, the range and timing of the seasonal variations in body length of *Acartia bifilosa* (Fig. 3b) were very similar to those in *Eurytemora affinis*. In contrast, the response to the June water temperature decline was not as clear. A few larger adults occurred on 8 July, but the body size change over the whole population was not statistically significant. This suggests that only a part of the *A. bifilosa* population responded to the temporary decline in temperature. As in *E. affinis*, the largest *A. bifilosa* adults occurred about a month later in the Bothnian Sea than at Storfjärden.

The summer decline in the body length of *Limnocalanus macrurus* (Fig. 3c) at Sällvik did not occur as early as that of the decline in body length of *Eurytemora affinis*: *L. macrurus* females remained relatively large until July. *L. macrurus* females were much larger in the Bothnian Sea than at Sällvik, and the size variation did not follow the same pattern as at Sällvik.

The average body lengths and the corresponding individual carbon content of copepod females in spring and summer are presented in Table 1. In *Eurytemora affinis* at Storfjärden, the individual carbon weight of the summer females was about half of that of the spring females (CW% column in Table 1). In *Acartia bifilosa* at Storfjärden and in the Bothnian Sea, the carbon content of the summer females was only one third of that of the spring females. In *Limnocalanus macrurus* at Sällvik, the seasonal change in body size was not as large as in the other calanoids: the carbon content of the summer females corresponded to 80% of that of the spring females.

Relationships between copepod body lengths and environmental factors in 1991 and 1992

In *Eurytemora affinis* at Storfjärden, surface-water temperature and Chl *a* concentration together explained 30 to 50% of the variation in copepod body length, depending on developmental stage (Table 2a). Temperature was a more important factor than Chl *a* for all stages except C3. This was verified by the higher coefficients of determination (r^2) in the simple regressions and by the higher standardized coefficients for temperature (scT) in the multiple regressions. At Sällvik (where only adults were measured), water salinity explained a slightly larger fraction of the variation than temperature; however, together with Chl *a*, salinity only explained 16 to 19% of the variation in adult *E. affinis* body size. In the Bothnian Sea, temperature and Chl *a* together explained 40 to 59% of the variation in body length. In copepodites, Chl *a* was a more important variable than temperature, while the opposite was true for females.

In *Acartia bifilosa* at Storfjärden, the temperature of the surface-water layer and Chl *a* together explained 54 to 66% of the variation in the body length; in females Chl *a* had a slightly larger influence, while in copepodites and males, temperature was a more important factor. In the Bothnian Sea, in contrast, Chl *a* was the most important variable affecting body length at all developmental stages (Table 2b).

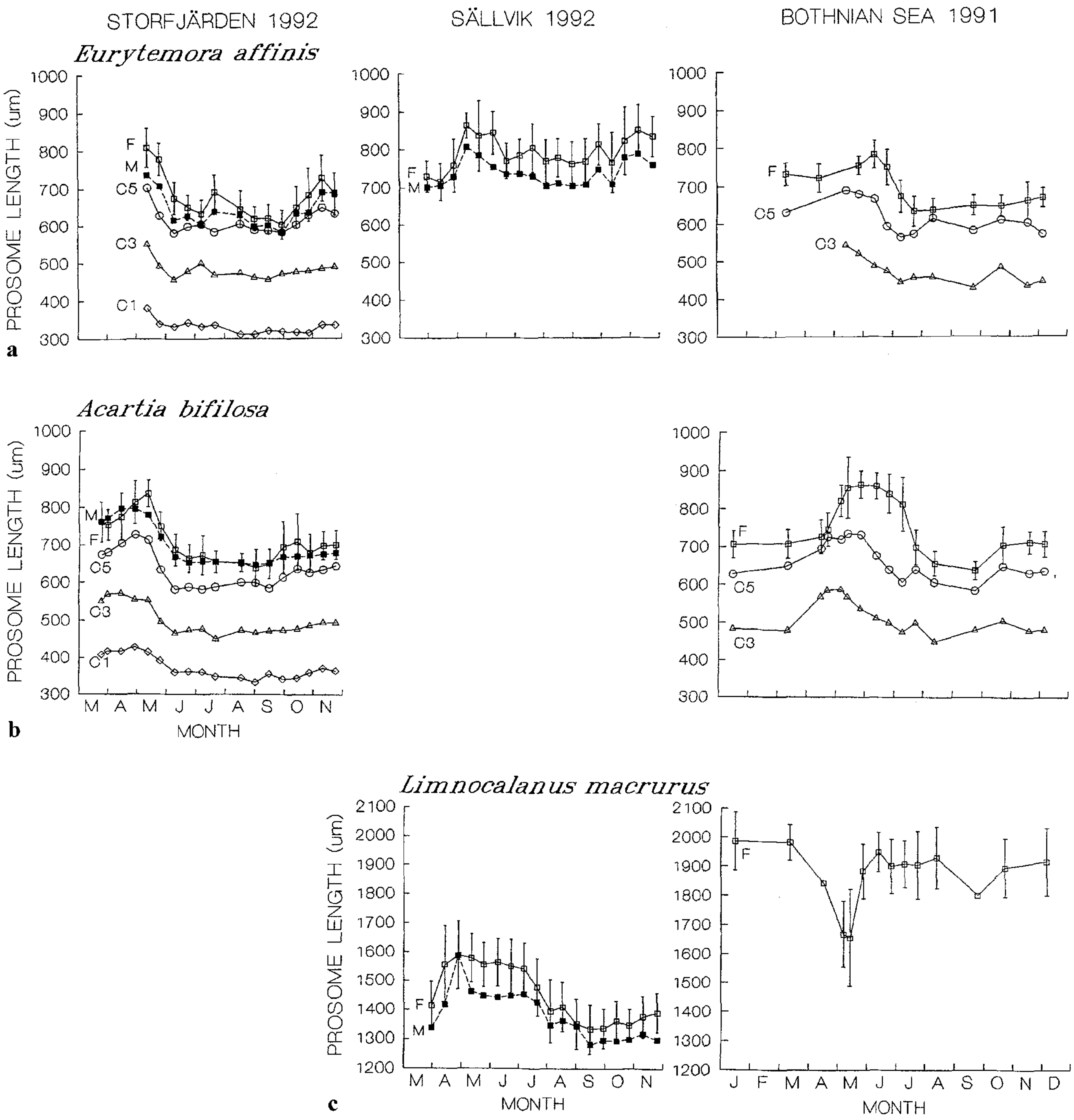

Fig. 3 **a** *Eurytemora affinis*; **b** *Acartia bifilosa*; **c** *Limnocalanus macrurus*. Seasonal variation in prosome length of copepods at Storfjärden and Sällvik (SW coast of Finland) and in the Bothnian Sea. (*F* Females; *M* Males; *C*1, *C*3, *C*5 copepodite Stages 1, 3 and 5, respectively) SD bars shown only for females

In *Limnocalanus macrurus*, only adults were measured. At Sällvik, the temperature of the deep-water layer was the only significant variable in the regression equations: it explained about 40% of the variation in adult body length (Table 2c). This is consistent with the later increase in deep-water temperature and the delayed seasonal decline in the body size of *L. macrurus*, compared to *Acartia bifilosa* and *Eurytemora affinis* (Fig. 3). In the Bothnian Sea, Chl *a* seemed to have a negative influence on *L. macrurus* length, but this was largely due to the exceptionally small body size of *L. macrurus* females just during the phytoplankton spring bloom in May (Fig. 3c); the variance explained was only 25%.

Table 1 *Eurytemora affinis*, *Acartia bifilosa* and *Limnocalanus macrurus*. Mean length (*L*) and corresponding individual carbon weight (*CW*) of spring and summer females at Storfjärden and Sällvik, SW coast of Finland in 1992 and Bothnian Sea, southern Gulf of Bothnia, in 1991. Carbon weights calculated from carbon-length regressions; sources: *ps* present study, *KJ* Kankaala and Johansson (1986), *T* Tanskanen (1994). *L*% and *CW*% denote ratios between lengths and carbon contents, respectively, of smallest summer females and largest spring females

Species Area	Season (dates)	L (mm)	CW (μg)	Regression	Source	Summer:spring ratio Area	L %	CW %
Eurytemora affinis								
Storfjärden	spring (13–26 May 1992)	0.793	2.5	$y = e^{3.904x-2.181}$	ps			
	summer (2–30 Sep 1992)	0.614	1.2	$y = e^{3.904x-2.181}$	ps	Storfjärden	77	50
Sällvik	spring (12 May–9 Jun 1992)	0.848	3.1	$y = e^{3.904x-2.181}$	ps			
	summer (4 Aug–15 Sep 1992)	0.769	2.3	$y = e^{3.904x-2.181}$	ps	Sällvik	91	74
Bothnian Sea	spring (28 May–26 Jun 1991)	0.762	3.0	$y = 0.28e^{3.13x}$	KJ			
	summer (24 Jul–23 Oct 1991)	0.640	2.1	$y = 0.28e^{3.13x}$	KJ	Bothnian Sea	84	68
Acartia bifilosa								
Storfjärden	spring (29 Apr–13 May 1992)	0.825	3.3	$y = 5.873x^{2.92}$	T			
	summer (18 Aug–16 Sep 1992)	0.648	1.2	$y = e^{3.793x-2.285}$	ps	Storfjärden	79	36
Bothnian Sea	spring (7 May–10 Jul 1991)	0.844	3.6	$y = 5.873x^{2.92}$	T			
	summer (13 Aug–24 Sep 1991)	0.648	1.2	$y = e^{3.793x-2.285}$	ps	Bothnian Sea	77	33
Limnocalanus macrurus								
Sällvik	spring (14 Apr–7 Jul 1992)	1.564	6.9	$y = 3.51x^{1.52}$	KJ			
	summer (1 Sep–27 Oct 1992)	1.347	5.5	$y = 3.51x^{1.52}$	KJ	Sällvik	86	80

Long-term variations

There was considerable variation in the body size of *Eurytemora affinis* and *Acartia bifilosa* females over the period 1967 to 1984 (Fig. 4). Both the average body size and the timing of its seasonal decline varied from year to year. When only July, August and September observations (the period when adults are most abundant; Viitasalo 1992) are considered, the average female size varied from 650 to 730 μm in *E. affinis* (Fig. 5a) and from 650 to 770 μm in *A. bifilosa* (Fig. 5b). Thus, in 1992 the summer adults of these species were relatively small (cf. Fig. 3).

The correlations calculated for the overall long-term data revealed that the average sizes of the two species were positively correlated (Spearman correlation coefficient r_S 0.65, $p < 0.001$), which suggests that similar factors caused their variation. There was a very significant negative correlation ($p < 0.001$) between water temperature during development and average body size of *Eurytemora affinis* and *Acartia bifilosa* females (Table 3a). This indicates that temperature controlled the timing of the seasonal decline of copepod body size in spring and early summer. In contrast, when only the interannual differences between the main productive periods (July to September) were analysed, the sizes of the two species were not intercorrelated (r_S 0.45, $p > 0.05$). In *A. bifilosa* the average female size showed an increasing trend from 1967 to 1984 (correlation with time r_S 0.65, $p < 0.01$), while *E. affinis* body length varied more irregularly (Fig. 5). In the correlation analysis of the summer females (Table 3b), the negative correlation with temperature disappeared: *A. bifilosa* length was not statistically significantly correlated with any of the environmental factors studied, and *E. affinis* female length was positively correlated with the average deep-water temperature ($p < 0.01$; see also Fig. 5a).

Discussion and conclusions

Both temperature and phytoplankton concentration influenced the body size of copepods in the study areas. The differences in the relative importance of temperature and Chl *a* were generally more evident between sites than between species, and the various developmental stages also showed different responses to these factors. In the archipelago area, the role of temperature was greater than that of phytoplankton. The important role of temperature at this station was evidenced by the regression analyses and by the increase of *Eurytemora affinis* body size after a short cool period in early summer. Also, the long-term data (consisting of spring, summer and autumn observations) confirmed the inverse relationship between temperature and copepod body size. In the bay area, only deep-water temperature influenced *Limnocalanus macrurus* body size. The lack of correlation with the surface parameters is plausible because the species mainly dwells below the thermocline in the Baltic Sea (Lindquist 1961).

Table 2 **a** *Eurytemora affinis*, **b** *Acartia bifilosa* and **c** *Limnocalanus macrurus*. Regression analyses of copepod length against hydrographical variables and phytoplankton concentration. Simple regressions: $r^2 : T$ (or S) and $r^2 : Chl$ coefficients of determination calculated with each of the independent variables of the multiple regressions as the only independent variable (equations not shown for *E. affinis* and *A. bifilosa*). Multiple regressions: L copepod length (μm); T0–10 temperature (°C) of surface-water layer (0 to 10 m); T'0–10 temperature of surface-water layer: average for the month preceding zooplankton sampling; T'10–37 temperature of deep-water layer (10 to 37 m): average for the month preceding zooplankton sampling; S10–37 salinity (‰) of deep-water layer; S0–37 salinity of whole water layer (0 to 37 m); Chl chlorophyll a concentration (μg l^{-1}) in surface-water layer; Chl' chlorophyll a in surface-water layer: average for the month preceding zooplankton sampling [$scT(S)$ and $scChl$ standardized coefficients for independent variables in multiple regressions, i.e., T temperature (or S salinity) and chlorophyll a; r^2 coefficient of determination; n number of cases (ind. measured); $C1$, $C3$, $C5$ copepodite stages 1, 3 and 5, respectively] All regressions and their coefficients were statistically very significant ($p < 0.001$)

(a) *Eurytemora affinis*

Area	Month/year	Stage	Simple regression		Multiple regression				
			$r^2 : T(S)$	$r^2 : Chl$	Equation	$scT(S)$	$scChl$	r^2	n
Storfjärden	5–11/1992	females	0.44	0.27	$L = 756.10–10.975T'0–10 + 6.015Chl'$	−0.54	0.27	0.50	541
		males	0.44	0.18	$L = 726.07–9.683T'0–10 + 2.662Chl'$	−0.59	0.15	0.45	540
		C5	0.25	0.16	$L = 646.80–5.815T0–10 + 4.702Chl'$	−0.44	0.31	0.34	563
		C3	0.21	0.22	$L = 493.85–3.249T0–10 + 3.858Chl'$	−0.38	0.39	0.36	559
		C1	0.28	0.13	$L = 352.44–2.840T'0–10 + 1.199Chl'$	−0.46	0.17	0.30	553
Sällvik	3–11/1992	females	0.09	0.08	$L = 1331.47–134.715S10–37 + 7.127Chl'$	−0.30	0.19	0.16	616
		males	0.10	0.13	$L = 998.60–82.676S0–37 + 8.205Chl'$	−0.24	0.31	0.19	605
Bothnian Sea	3–11/1991	females	0.41	0.33	$L = 724.42–8.044T'0–10 + 36.701Chl'$	−0.53	0.45	0.59	395
	3–11/1991	C5	0.20	0.32	$L = 618.01–3.537T0–10 + 25.710Chl'$	−0.30	0.48	0.40	201
	5–11/1991	C3	0.12	0.44	$L = 469.67–1.697T0–10 + 22.135Chl$	−0.19	0.57	0.47	332

(b) *Acartia bifilosa*

Area	Month/year	Stage	Simple regression		Multiple regression				
			$r : T$	$r^2 : Chl$	Equation	scT	$scChl$	r^2	n
Storfjärden	4–11/1992	females	0.41	0.43	$L = 717.35–6.706T'0–10 + 8.621Chl'$	−0.39	0.43	0.54	640
		males	0.49	0.41	$L = 722.53–7.202T'0–10 + 5.957Chl'$	−0.50	0.35	0.57	641
		C5	0.43	0.35	$L = 653.55–6.577T0–10 + 6.366Chl'$	−0.51	0.42	0.58	643
		C3	0.50	0.31	$L = 530.92–5.519T'0–10 + 2.330Chl$	−0.57	0.29	0.57	643
		C1	0.60	0.41	$L = 395.48–4.565T'0–10 + 2.576Chl'$	−0.61	0.29	0.66	656
Bothnian Sea	3–11/1991	females	0.28	0.52	$L = 738.12–5.350T'0–10 + 56.495Chl'$	−0.24	0.61	0.57	457
		C5	0.29	0.37	$L = 666.96–4.570T0–10 + 26.085Chl'$	−0.42	0.51	0.53	210
		C3	0.31	0.43	$L = 512.10–3.527T'0–10 + 15.739Chl$	−0.36	0.48	0.53	339

(c) *Limnocalanus macrurus*

Area	Month/year	Stage	Simple regression		
			Equation	r^2	n
Sällvik	3–11/1992	females	$L = 1701.67–61.342T'10–37$	0.40	710
		males	$L = 1591.98–51.277T'10–37$	0.39	705
Bothnian Sea	3–11/1991	females	$L = 1946.62–56.107Chl$	0.25	300

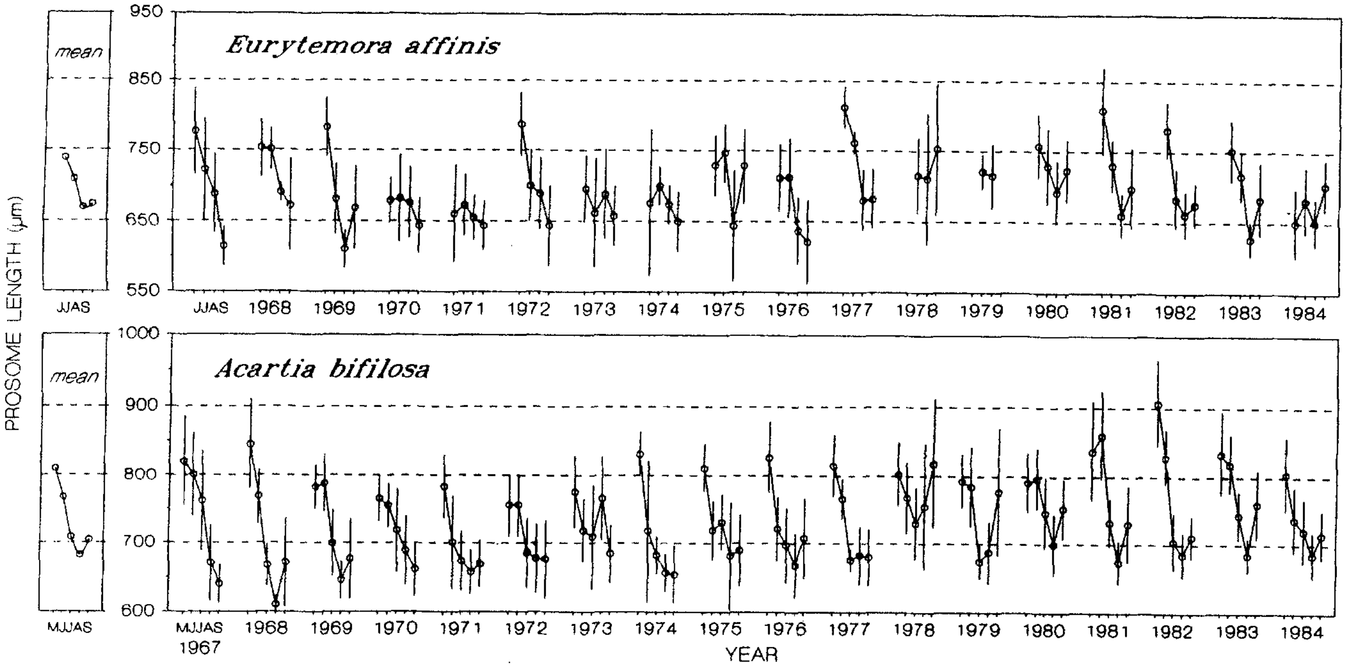

Fig. 4 *Eurytemora affinis* and *Acartia bifilosa*. Long-term changes in prosome length of females at Storfjärden, SW coast of Finland, in June to September (*E. affinis*) or May to September (*A. bifilosa*), 1967 to 1984. Average seasonal development of body size in corresponding months is shown in small panels at the left. Vertical bars indicate SD

In the bay area and in the open Bothnian Sea, the influence of phytoplankton was greater than in the archipelago area. This could be the result of limitation of copepod growth by food availability. The phytoplankton biomass was very low in the Bothnian Sea, and, at Sällvik, the autochtonous production is, due to high turbidity and low phosphorus level, also relatively low (H. Kuosa, Finnish Institute of Marine Research, personal communication). If the copepods were food limited, one may wonder why *Eurytemora affinis* and *Limnocalanus macrurus* adults grew to such a large size at Sällvik and in the Bothnian Sea. According to Vidal (1980b), as water temperature increases, larger species and individuals cannot maintain a positive energy balance, because the energetic costs of large body size increase relatively more rapidly than those of small body size. However, for reasons that are not dependent on food conditions, different sized ecotypes may occur in different areas of the Baltic Sea; according to Kankaala and Johansson (1986) the body length of *L. macrurus* females may vary from 1100 to 2500 µm. Thus, if the Bothnian Sea and Sällvik copepods were genetically determined to be large, they could be food limited in summer. Unfortunately, these considerations are hampered by the fact that the total food availability for copepods is not known. In addition to phytoplankton, *E. affinis* feeds on detritus (Heinle et al. 1977), *Acartia* spp. prey on ciliates and rotifers (Stoecker and Egloff 1987), and *L. macrurus* eats rotifers and crustacean zooplankton (Warren 1985).

The time period during which the copepod size was monitored influenced the view of the relationship between copepod body size and the environmental factors. When only the interannual variations in the summers 1967 to 1984 were examined, the inverse relationship between copepod size and temperature disappeared. In this case, it is possible that high summer temperature is linked with other factors favouring large body size. For instance, small auto- and heterotrophic flagellates proliferate during the warm season in the study region (Kuuppo 1994), and, since *Eurytemora affinis* is able to suspension feed on small particles (Schnack 1982), it might be able to grow to an exceptionally large size during the warmest summers. These hypotheses cannot be verified however, since no data on food conditions during 1967 to 1984 were available.

The seasonal change in body size evidently has consequences for copepods and possibly also for other trophic levels. First, size change affects the production of copepods. Although temperature and food availability basically determine the egg production rate (e.g. Durbin et al. 1983; Kiørboe and Nielsen 1994), female size also plays a role: in many copepod species, e.g. *Pseudocalanus* sp. (McLaren 1965) and *Eurytemora affinis* (Hirche 1992; Ban 1994), larger females produce larger clutches of eggs. This could contribute to a more rapid increase in the copepod population in spring, when the initial female density is very low. Second, larger copepod individuals are able to ingest larger

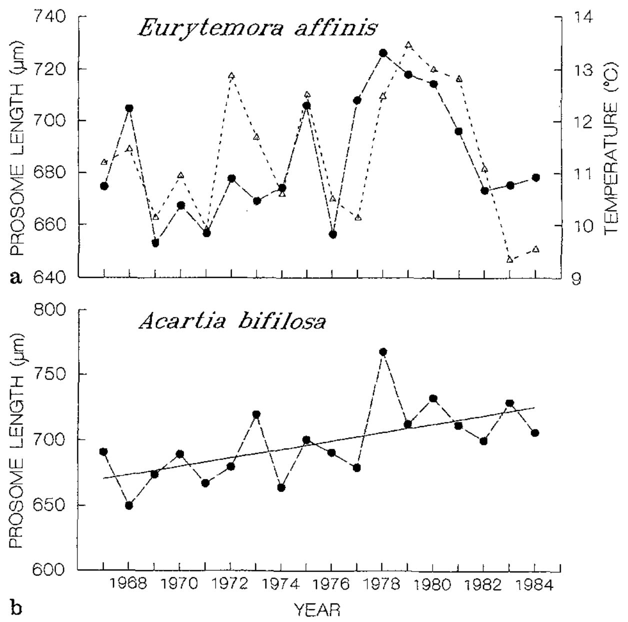

Fig. 5 **a** *Eurytemora affinis*; **b** *Acartia bifilosa*. Interannual variation in prosome length of females at Storfjärden, SW coast of Finland, during late summer 1967 to 1984. Average body length for July, August and September denoted with filled circles; average temperature for the deep-water layer (10 to 30 m) during the same period denoted with open triangles in **a**. The statistically significant increasing trend in *A. bifilosa* body size indicated with a regression line (drawn with least squares method) in **b**

Table 3 *Eurytemora affinis* and *Acartia bifilosa*. Long-term analysis. Spearman rank correlations between average body length of females and temperature at Storfjärden, SW coast of Finland, from 1967 to 1984. **a** Correlations for monthly data; **b** correlations for annual data (averages for July, August and September). T_{0-10} Spearman correlation coefficients (r_S) between copepod body length and temperature of surface layer (0 to 10 m); T_{10-30} r_S between copepod body length and temperature of deep-water layer (10 to 30m); T'_{0-10} r_S between copepod body length and average temperature of surface layer during the month preceding zooplankton sampling; T'_{10-30} r_S between copepod body length and temperature of deep-water layer during the month preceding zooplankton sampling. AT_{0-10} and AT_{10-30} r_S between average copepod body length in July to September and average water temperature in the same period, in the two water layers. Statistical significance: $*0.05 < p < 0.01$; $**0.001 < p < 0.01$; $***p < 0.001$; *ns* not significant

	E. affinis	*A. bifilosa*
(a)		
Months	6,7,8,9	5,6,7,8,9
n	69	90
T_{0-10}	$-0.27*$	$-0.58***$
T_{10-30}	$-0.36**$	$-0.58***$
T'_{0-10}	$-0.41***$	$-0.65***$
T'_{10-30}	$-0.37**$	$-0.62***$
(b)		
Period	average for 7, 8, 9	average for 7, 8, 9
n	18	18
AT_{0-10}	0.44^{ns}	0.31^{ns}
AT_{10-30}	$0.64**$	0.43^{ns}

food particles than small copepods (Berggreen et al. 1988). Large phytoplankton cells dominate the spring bloom in the Baltic Sea, which could favour the largest individuals during this period. Third, seasonal changes in predation pressure might also influence the average body size in copepod populations. In lakes, fish predation modifies the size structure and the demography of the copepod community (Warren et al. 1986). In the Baltic Sea, the predation by the Baltic herring is more intense during summer than during spring (Rudstam et al. 1992) and, as herring preys selectively on the most conspicuous items (Flinkman et al. 1992), predation could influence the average body size of preferred prey species. In the present study this was not likely because the selective predation would have influenced mainly the relative abundance of the largest individuals, and the copepodite Stages C1 and C3 also showed a clear seasonal variation in size. However, even if predation did not cause the phenomenon, it could have other food-web consequences: the ca. 20% decline in average body length (and the 50 to 65% decline in carbon content) observed in *E. affinis* and *Acartia bifilosa* might lead the fish to seek other prey, such as cladocerans or larger copepod species.

Our results indicate that the effects of temperature and food conditions on copepod body size vary according to species, developmental stage and study area. Deevey (1960) proposed that the seasonal temperature range determines which factor is the most important: when the annual mean temperature range was 14 °C or more, copepod body size correlated negatively with temperature; when this temperature range was smaller, phytoplankton concentration was more important. This underlines the importance of the relative ranges of the influencing environmental variables. When only one year is analysed, the strongest explanatory factor is often temperature, but when long-term data are investigated, other variables can be more important. It may not be a coincidence that many of the studies that have stressed the importance of food on the size variation of copepods have examined long-term data in the laboratory (Klein Breteler et al. 1990) or in the field (Evans 1981). In conclusion, we suggest that the timing of the spring decline of copepod body size is mostly controlled by temperature but that food concentration influences the average body size within each season. Therefore, the length and timing of the study period greatly influence the investigator's view of the factors regulating copepod body size.

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References

Anonymous (1993) Meteorological yearbook of Finland 1991. Finnish Meteorological Institute, Helsinki

Ban S (1994) Effect of temperature and food concentration on post-embryonic development, egg production and adult body size of calanoid copepod *Eurytemora affinis*. J Plankton Res 16: 721–735

Berggreen U, Hansen B, Kiørboe T (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. Mar Biol 99: 341–352

BMEPC (1988) Baltic Marine Environment Protection Commission, Helsinki Commission 1988. Guidelines for the Baltic Monitoring Programme for the Third Stage; Part D. Biological determinands. Baltic Sea Environment Proceedings 27D, Helsinki

Christou ED, Verriopoulos GC (1993) Length, weight and condition factor of *Acartia clausi* (Copepoda) in the eastern Mediterranean. J mar biol Ass UK 73: 343–353

Coker RE (1933) Influence of temperature on size of freshwater copepods (*Cyclops*). Int Rev ges Hydrobiol 29: 406–436

Comita GW, Anderson GC (1959) The seasonal development of a population of *Diaptomus ashlandi* Marsh, and related phytoplankton cycles in Lake Washington. Limnol Oceanogr 4: 37–52

Deevey GB (1960) Relative effects of temperature and food on seasonal variations in length of marine copepods in some eastern American and western European waters. Bull Bingham oceanogr Coll 17: 54–85

Durbin EG, Durbin AG, Smayda J, Verity PG (1983) Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island. Limnol Oceanogr 28: 1199–1213

Escribano R, McLaren IA (1992) Influence of food and temperature on lengths and weights of two marine copepods. J exp mar Biol Ecol 159: 77–88

Evans F (1981) An investigation into the relationship of sea temperature and food supply to the size of the planktonic copepod *Temora longicornis* Müller in the North Sea. Estuar cstl Shelf Sci 13: 145–158

Flinkman J, Vuorinen I, Aro E (1992) Planktivorous Baltic herring (*Clupea harengus*) prey selectively on reproducing copepods and cladocerans. Can J Fish aquat Sciences 49: 73–77

Heinle DR, Harris RP, Ustach JF, Flemer DA (1977) Detritus as food for estuarine copepods. Mar Biol 40: 341–353

Hirche H-J (1992). Egg production of *Eurytemora affinis* – effect of k-strategy. Estuar cstl Shelf Sci 35: 395–407

Kankaala P, Johansson S (1986) The influence of individual variation on length–biomass regressions in three crustacean zooplankton species. J Plankton Res 8: 1027–1038

Kiørboe T, Nielsen TG (1994) Regulation of zooplankton biomass and production in a temperate, coastal ecosystem. 1. Copepods. Limnol Oceanogr 39: 493–507

Klein Breteler WCM, Gonzalez SR (1982) Influence of cultivation and food concentration on body length of calanoid copepods. Mar Biol 71: 157–161

Klein Breteler WCM, Schogt N, Gonzalez SR (1990) On the role of food quality in grazing and development of life stages, and genetic change of body size during cultivation of pelagic copepods. J exp mar Biol Ecol 135: 177–189

Kuhlmann D, Fukuhara O, Rosenthal H (1982) Shrinkage and weight loss of marine fish food organisms preserved in formalin. Bull Nansei natn Fish Res Lab 14: 13–18

Kuuppo P (1994) Annual variation in the abundance and size of heterotrophic nanoflagellates on the SW coast of Finland, the Baltic Sea. J Plankton Res 16: 1525–1542

Lehman JT (1988) Ecological principles affecting community structure and secondary production by zooplankton in marine and freshwater environments. Limnol Oceanogr 33: 931–945

Lindquist A (1961) Untersuchungen an *Limnocalanus* (Copepoda, Calanoida). Inst mar Res Lysekil Ser Biol 13: 1–94

Lock AR, McLaren IA (1970) The effect of varying and constant temperatures on the size of a marine copepod. Limnol Oceanogr 15: 638–640

Malone TC, Chervin MB (1979) The production and fate of phytoplankton size fractions in the plume of the Hudson River, New York Bight. Limnol Oceanogr 24: 683–696

McLaren IA (1963) Effects of temperature on growth of zooplankton, and the adaptive value of vertical migration. J Fish Res Bd Can 20: 685–727

McLaren IA (1965) Some relationships between temperature and egg size, body size, development rate, and fecundity, of the copepod *Pseudocalanus*. Limnol Oceanogr 10: 528–538

McLaren IA, Sévigny J-M, Corkett CJ (1989) Temperature-dependent development in *Pseudocalanus* species. Can J Zool 67: 559–564

Niemi Å (1975) Ecology of phytoplankton in the Tvärminne area, SW coast of Finland. II. Primary production and environmental conditions in the archipelago and the sea-zone. Acta bot fenn 105: 1–73

Niemi Å (1978) Ecology of phytoplankton in the Tvärminne area, SW coast of Finland. III. Environmental conditions and primary production in Pojoviken in the 1970s. Acta bot fenn 106: 1–28

Rudstam LG, Hansson S, Johansson S, Larsson U (1992) Dynamics of planktivory in a coastal area of the northern Baltic Sea. Mar Ecol Prog Ser 80: 159–173

Salonen K (1979) A versatile method for rapid and accurate determination of carbon by high temperature combustion. Limnol Oceanogr 24: 177–183

Schnack SB (1982) The structure of the mouth parts of copepods in Kiel Bay. Meeresforsch Rep mar Res 29: 89–101

Stoecker DK, Egloff DA (1987) Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. J exp mar Biol Ecol 110: 53–68

Tanskanen S (1994) Seasonal variability in the individual carbon content of the calanoid copepod *Acartia bifilosa* from the northern Baltic Sea. In: Ferrari FD, Bradley BP (eds) Ecology and morphology of copepods. Proc. 5th Internat. Conf. on Copepoda, Baltimore, USA, 6–13 June 1993. Hydrobiologia 292/293: 397–404

Vidal J (1980 a) Physioecology of zooplankton. II. Effects of phytoplankton concentration, temperature, and body size on the development and molting rates of *Calanus pacificus* and *Pseudocalanus* sp. Mar Biol 56: 135–146

Vidal J (1980 b) Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Mar Biol 56: 111–134

Viitasalo M (1992) Mesozooplankton of the Gulf of Finland and northern Baltic proper. A review of monitoring data. Ophelia 35: 147–168

Warren GJ (1985) Predaceous feeding habits of *Limnocalanus macrurus*. J Plankton Res 7: 537–552

Warren GJ, Evans MS, Jude DJ, Ayers JC (1986) Seasonal variations in copepod size: effects of temperature, food abundance, and vertebrate predation. J Plankton Res 8: 841–853