Marine Biology (2006) 149: 1417–1429
DOI 10.1007/s00227-006-0290-8

RESEARCH ARTICLE

Janna Peters · Jasmin Renz · Justus van Beusekom
Maarten Boersma · Wilhelm Hagen

Trophodynamics and seasonal cycle of the copepod *Pseudocalanus acuspes* in the Central Baltic Sea (Bornholm Basin): evidence from lipid composition

Received: 15 November 2005 / Accepted: 20 February 2006 / Published online: 14 April 2006

Abstract Seasonal lipid dynamics of the copepod *Pseudocalanus acuspes* were studied in the Bornholm Basin (Central Baltic Sea) on a monthly basis from March 2002 until March 2003 and were interpreted in light of life cycle strategies and diet selection. The individual total lipid content of females ranged from 0.9 to 1.8 µg, with relative wax ester content reaching a significant maximum in May (44% of total lipids) and minimum (17% of total lipids) in April and November. Significant changes in size, lipid content, lipid classes and fatty acid composition of structural as well as storage lipids suggested five characteristic seasonal phases that were induced by different feeding histories and environmental conditions. Storage lipids were characterized by 18:1($n-9$) as major component, which ranged between 44% of total fatty acids in June and 23% in February. The strong coherence between 18:1($n-9$) in the seston lipids and the occurrence of ciliates emphasized the importance of ciliates in the diet of *P. acuspes*. As indicated by changes in the amounts of fatty acid markers, other food sources varied over the year, suggesting an opportunistic feeding behavior. The spring period was characterized by an increase in typical diatom and dinoflagellate markers, whereas other sources, potentially cyanobacteria, became more important during summer. The life cycle strategy is discussed with respect to extant adaptations to high latitudinal habitats.

Communicated by O. Kinne, Oldendorf/Luhe

J. Peters (✉) · W. Hagen
Marine Zoology, University of Bremen, P.O. Box 330440, 28334 Bremen, Germany
E-mail: janna.peters@uni-bremen.de
Tel.: +49-421-2189508
Fax: +49-421-2182285

J. Renz · J. van Beusekom · M. Boersma
Alfred Wegener Institute for Polar and Marine Research, P.O. Box 120161, 27515 Bremerhaven, Germany

Introduction

Pseudocalanus acuspes is a key species in the Central Baltic Sea, as it serves as a major food organism for larval as well as for adult planktivorous fish (Hinrichsen et al. 2002, 2003; Möllmann and Köster 1999, 2002; Möllmann et al. 2003). Knowledge about the processes regulating population dynamics of *P. acuspes* in the Baltic Sea is essential to understand the principal mechanisms accounting for the high variability of copepod production and reproductive success of fish, which is a main focus of the German GLOBEC project.

Pseudocalanus acuspes mainly inhabits high latitudes (Frost 1989; Runge and Ingram 1991; Siferd and Conover 1992; Norrbin 1996) and due to its absence in the adjacent North Sea (Bucklin et al. 2003) and wide distribution in the Arctic, it is most likely a member of the Baltic glacial relict fauna. Different life cycles were described for *Pseudocalanus* spp. in high Arctic regions: from biennial (Cairns 1967) and annual cycles (Davis 1976; Conover and Siferd 1993; Lischka and Hagen 2005) up to cycles with two or more generations per year (Pertsova 1981; McLaren et al. 1989; Norrbin 1992). In temperate regions several generations per year are commonly observed (Marshall 1949; Digby 1950).

As a characteristic of the Baltic Sea, adult females of *P. acuspes* are more abundant in water layers below the thermocline and often concentrate near the halocline, presumably induced by the strong vertical stratification of the water column (Hernroth and Ackefors 1979; Henroth 1985; Renz and Hirche 2006). Hence, sinking algae, detritus or microzooplankton are most likely the only available food sources. Feeding and growth conditions might therefore be suboptimal for this originally marine species (Renz and Hirche 2006) in the temperate brackish environment, with seasonal cycle and diet differing from those of other habitats. Valuable information on the life cycle and overwintering strategy of *P. acuspes* in the Baltic Sea can be derived from seasonal dynamics in storage lipid content and fatty acid

composition of polar, i.e. structural lipids as well as from size variations, as these attributes reflect environmental conditions and food supply during growth of different cohorts.

Studies on in situ grazing rates and food selection of *Pseudocalanus* spp. are scarce. It has been described that *Pseudocalanus* spp. exhibits a primarily herbivorous feeding behavior (e.g. Schnack 1975; Corkett and McLaren 1978; Fraser et al. 1989; Cotonnec et al. 2001), whereas other studies suggested a more omnivorous feeding mode (Båmstedt et al. 1990; Norrbin et al. 1990; Peters et al. 2004). To elucidate seasonal dynamics in diet we applied signature fatty acids to identify trophic relationships. We specifically focused on the fatty acid composition of storage, i.e. neutral lipids, in order to obtain unambiguous signals.

The use of specific fatty acids to characterize feeding on different taxonomic groups is well established, e.g. the assignment of 16:1($n-7$) and 20:5($n-3$) to diatoms (Nichols et al. 1993; Dunstan et al. 1994; Skerrat et al. 1997) and 18:4($n-3$) and 22:6($n-3$) to dinoflagellates (Sargent et al. 1987; Graeve et al. 1994). However, it is essential to validate those results in the studied ecosystem by comparing fatty acid profiles of the seston with its taxonomic composition. Beside the fatty acid dynamics in the neutral lipids of the copepods, we therefore provide data on the seasonal variation of the seston composition to reveal seasonal changes in the diet of *P. acuspes*.

Materials and methods

Sampling and experiments

Zooplankton and seston samples were collected in approximately monthly intervals from March 2002 until March 2003 (except for October and December) on 11 cruises in the Bornholm Basin (Fig. 1). To provide representative data for the whole basin, both stations in central and in marginal areas were sampled on each cruise and combined in average values for each month, except for January and February 2003, where only samples from the central basin were available.

Zooplankton was sampled using a WP-2 net with a 10-l bucket end (vertically towed with 0.2 m/s, mesh size 200 µm, 0.26 m^2 opening). Sampling depths were adjusted to hydrography covering the water column from the lower halocline up to the surface. Copepods were sorted on board under ambient temperature conditions into −80°C precooled glass vials. Depending on availability each sample consisted of 20–150 adult females of *P. acuspes* or copepodite stages V (CV), respectively. On three stations of each cruise prosoma lengths of 30 females were measured using formalin preserved samples (4% in seawater).

Seston samples from five depths were taken with 10 l water sampler bottles. Vertical resolution was adapted to the hydrographic structure of the water column, with samples taken from the upper water layer (5 m), from above the thermocline (10 m), from the midwater layer, from above the halocline and in the halocline. Depending on seston concentrations 2–6 l of water were filtered with low pressure (−200 mbar) on precombusted (12 h at 400°C) GF/C filters. All zooplankton organisms were carefully removed under the stereomicroscope immediately after filtration and prior to freezing, so that they did not bias the seston data. Zooplankton samples and filters were permanently stored at −80°C until further analysis.

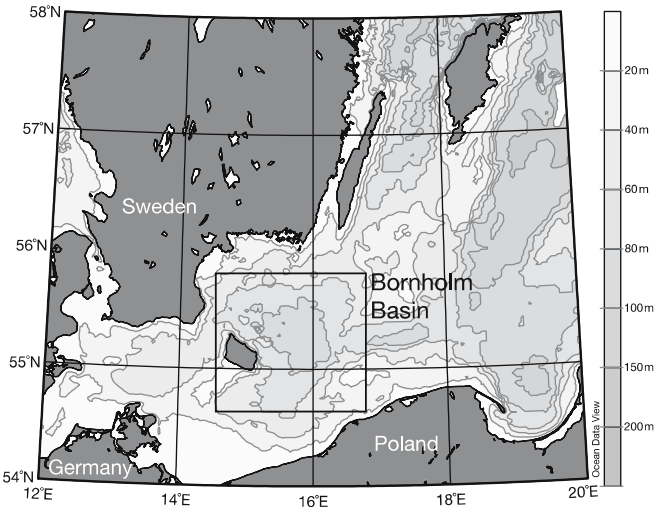

Fig. 1 Map of investigation area, generated with ODV software (Schlitzer 2005)

For analyses of taxonomic seston composition aliquots of 100 ml were taken from water sampler bottles, preserved with 2% acid Lugol's solution and stored cool and dark until further investigation. Samples were analyzed using Uthermöhl microscopy and phytoplankton as well as protozooplankton cell size was converted to biomass according to Edler (1979) and Putt and Stoecker (1989), respectively.

Analytics

After lyophilization dry mass of copepods was determined using a Sartorius micro-balance (±2 µg). During weighing procedure, samples were temporarily stored in a vacuum desiccator to prevent unequal condensation on the tissue. Lipid extraction was performed with minor modifications as described in Folch et al. (1957) using ultrasonic disruption in dichloromethane:methanol (2:1/v:v) and a washing procedure with aqueous KCl solution (0.88%). For quantification of fatty acids, tricosanoic acid was added as an internal standard prior to extraction.

Lipid classes were separated by solid phase extraction, using 1 ml SiOH glass columns (CHROMABOND®, Macherey-Nagel) on a vacuum manifold. To remove residues the columns were washed with a solvent sequence of acetone, diethylether, and hexane:diethylether-mixtures, prior to sample load. After column conditioning with

4 ml of hexane, 4 µl of lipid extract (lipid concentration approx. 5 µg/µl) were added. The neutral lipid fraction was washed out with 2.5 ml hexane:diethylether (95:5/v:v) and 2.5 ml hexane:diethylether (1:1/v:v). Polar lipids were eluted with 2.5 ml methanol and subsequently 5 ml of dichloromethane were added. The polar fraction was then washed with 2 ml aqueous KCl solution (0.88%).

For fatty acid analyses a subsample of total lipids as well as the total neutral and polar lipid fraction were hydrolyzed and fatty acids were converted to their methyl ester derivatives (FAME) in methanol containing 3% concentrated sulfuric acid at 80°C for 4 h (Kattner and Fricke 1986). After cooling, 2 ml of Aqua bidest. were added, and FAMEs were extracted three times with 1 ml hexane. Samples were analyzed using a gas chromatograph (HP 6890A) equipped with a DB-FFAP column (30 m length, 0.25 mm inner diameter, 0.25 µm film thickness) operated with a temperature program and helium as carrier gas. Samples were injected using a hot split/splitless inlet (250°C, split mode 1:20) or a programmable temperature vaporizer injector (solvent vent mode). The FAMEs and fatty alcohols were detected by flame ionization and identified by comparing retention times with those derived from standards of known composition. The accurate identification of the substances was checked for selected peaks using GC-MS.

Calculations and statistical analyses

The proportions of wax esters (WE), triacylglycerols (TAG) and polar lipids (PL) were estimated based on comparisons of the relative fatty acid and alcohol composition of the neutral lipid fraction and the total lipid extract, whereas the composition of the polar lipid fraction was used to verify the results. Taking the non-fatty acid components into account, the usually dominating phosphatidylcholine was assumed to be the only polar lipid component and the corresponding mass ratio was used. However, this method does not account for sterol esters and cholesterol. Furthermore, the WE content was calculated based on the alcohol content in the total lipid extract.

All statistical analyses were performed using the software SPSS. For all statistical operations that require normal distribution, percentage data (e.g. relative fatty acid composition) were transformed using an arc sine square root transformation. Normal distribution and homogeneity of variances were checked using the Shapiro-Wilk- and the Leverne-test, respectively, according to sample size. For identification of coherences between fatty acid markers and seston taxa, as well as within the fatty acids of seston and storage lipids of *P. acuspes* females, principal component analyses (PCAs) were performed on the correlation matrix, extracting non-rotated components with eigenvalues >1. Relevant variables (i.e. length, biomass, total and storage lipid content) were analyzed using one-way ANOVA followed by a Tukey's HSD test for post hoc comparisons with time as independent variable.

To detect seasonal changes between fatty acid compositions in the neutral and the polar lipid fraction of females, the relative amount of each fatty acid was tested between two adjacent months using a Student's *t*-test. If the difference between 2 months was only due to one fatty acid on a significance level of $P<0.01$ or two fatty acids on a significance level of $P<0.05$, the months were fused to one group. Afterwards, these groups were tested against each other. For months with less than three replicates, i.e. January and February, the months were assigned to the group with the highest similarity in a cluster analysis using the PRIMER software (based on Bray-Curtis similarity and complete linkage cluster mode, data not presented). Selectivity, here understood as ratio between availability of individual fatty acids in the seston and the incorporation into the storage lipids of *P. acuspes*, was calculated as ratio between their relative content in the seston and in the neutral lipids of the copepods using a logarithmic scale.

Results

Pseudocalanus acuspes

Females of *P. acuspes* differed substantially in size between succeeding months (Fig. 2a), with a highly significant increase of prosoma length as well as biomass in May up to an average of 966 µm (significant difference to April and June $P<0.001$) and 12.5 µg/individual, respectively. Over the summer their size decreased, reaching a minimum of 870–880 µm in length in November (significant difference to September $P<0.01$) and January (significant difference to February $P<0.001$). From February on, females increased in size again. Dry mass-length ratios, based on monthly averages of variables, basically followed the relationship established by Hay et al. (1988) (Fig. 2b).

The lipid content in terms of total fatty acids and alcohols of the females ranged from 0.9 to 1.8 µg/individual and from 9 to 14% of dry mass, respectively (Fig. 2c), with a maximum in May (significant difference to April $P<0.05$). There was no significant difference in May between the total individual lipid content of the females and the copepodite stage V (mean 2.6 µg/individual). In all other months examined, the lipid amount of CV was clearly higher than that of the females, with an average individual lipid content between 4.7 µg in September and 1.6 µg in January.

In both stages, females and CV, wax esters (WE) as well as triacylglycerols (TAG) served as storage lipids throughout the year. Neutral lipids of females (WE and TAG) comprised about two-thirds of total lipids in May and January, respectively, and one-third of total lipids in November (Fig. 2d, e).

The relative amount of TAG ranged between 15 and 35% of total lipids, but due to a high variability no seasonal trends could be identified, neither for

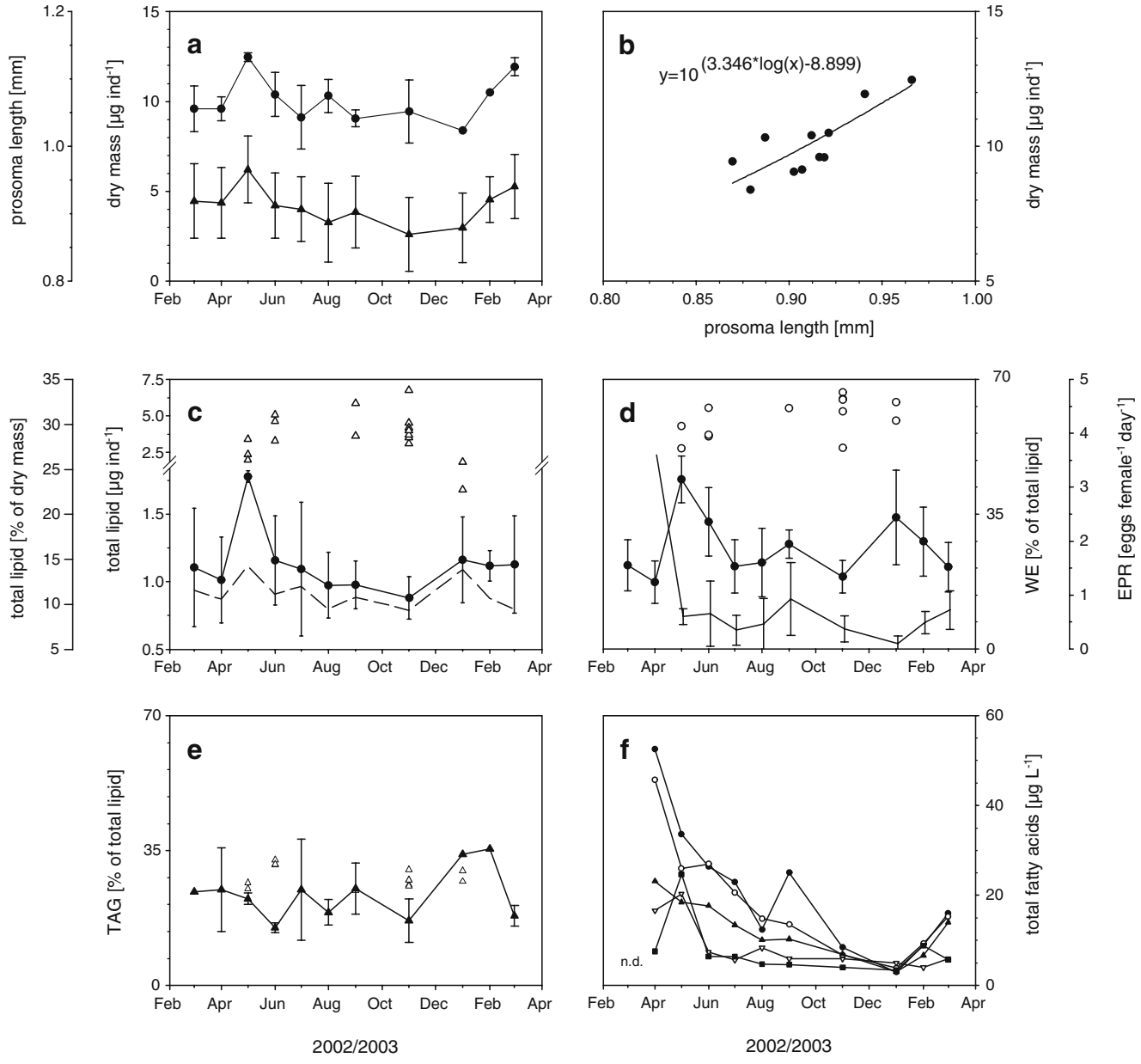

Fig. 2 **a** Prosoma length and dry mass of adult females of *Pseudocalanus acuspes*: *triangles* monthly average of length, *circles* monthly average of dry mass, *error bars* standard deviation. **b** Length dry mass relationship of adult females of *P. acuspes*: *circles* monthly average of dry mass versus monthly average of prosoma length, *line* length dry mass relationship determined by Hay et al. (1988). **c** Total lipid content of *P. acuspes*: *circles* monthly average of total fatty acids and alcohols (TL) per female, *error bars* standard deviation, *open triangles* TL per copepodite stage V (*data points* stations, please note axis break), *dashed line* monthly average of TL in percent of dry mass in adult females. **d** Wax ester (WE) content and egg production rates (EPR) of *P. acuspes*: *filled circles* monthly average of WE [% TL] in adult females, *open circles* WE [% TL] in copepodite stage V (*data points* stations), *line without symbols* monthly average of daily individual egg production, EPR modified from J. Renz et al. (submitted), *error bars* standard deviation. **e** Triacylglycerol (TAG) content of *P. acuspes*: *filled triangles* monthly average of TAG [% TL] in adult females, *open triangles* TAG [% TL] in copepodite stage V (*data points* stations), *error bars* standard deviation. **f** Monthly average of lipid concentration in the seston: *filled circles* upper water layer (5 m), *open circles* above thermocline (10 m), *filled triangles* midwater layer (20–30 m), *open triangles* above halocline (30–40 m), *filled squares* in halocline (40–60 m), *n.d.* no data

females nor CV. In contrast, the relative WE content of the females changed over the year, reaching a maximum of 44% of total lipids in May (significant difference to April $P<0.001$) and lowest values of 17% in April and November. From November the wax ester content increased until January, afterwards it declined again until March. The WE content of CV was significantly higher during all months, except for May, when values were in the same range as for the females.

Egg production data were adopted from J. Renz et al. (submitted). Daily egg production rates (EPR) showed

an overall high variability in the Bornholm Basin (Fig. 2d), reaching a minimum of 0.1 eggs per female per day in January and increasing again in February. The highest EPR was measured in April, but was based only on data from one station, i.e. on the average EPR of 30 females. Whereas in summer mean EPR and WE content paralleled, EPR increased with decreasing WE content in spring 2003.

The total fatty acid composition of females was characterized by high amounts of the typical membrane components 16:0, 20:5($n-3$), 22:6($n-3$), as well as by elevated levels of 18:1($n-9$). Alcohols were dominated by 14:0 and 16:0, while 18:0 and 18:1 were found in much lower quantities (Table).1

Within the neutral lipid fraction ten important fatty acids (i.e. maximum values $\geq$2% of total fatty acids) were identified (Table 2). The fatty acid 18:1($n-9$) dominated during all seasons, ranging between 44% of total fatty acids in June and 23% in February. Based on their relative fatty acid composition, females were merged into five seasonal groups, which exhibited highly significant differences (Table 2). The first group included females from March and April 2002 as well as from February and March 2003. This spring season was characterized by elevated amounts of the dinoflagellate marker 18:4($n-3$), whereas the diatom marker 16:1($n-7$) peaked in May. Both groups showed high percentages of 20:5($n-3$) and 22:6($n-3$), also indicating diatom- and dinoflagellate-based diets, respectively. In May, 18:1($n-9$) strongly increased, reaching maximum values in June. From June to September fatty acids were characterized by rising levels of 18:2($n-6$) and 18:3($n-3$), reaching up to 12 and 8%, respectively. In winter higher amounts of the unspecific fatty acids 16:0, 16:1($n-9$) and 18:0 prevailed.

The neutral lipids of CV showed a very similar fatty acid composition to those of the females (Fig. 3). Especially in May and June there was no significant difference between the fatty acids of both stages, whereas in autumn and winter the fatty acids 18:1($n-9$), 18:2($n-6$), 18:4($n-3$) and 20:5($n-3$) of CV showed higher percentages.

Principal component analysis on the storage lipid composition of females extracted three components with eigenvalues >1. Only the major two, together explaining 68% of the variance, are presented (Fig. 4). The PCA revealed a strong coupling between the fatty acids 18:2($n-6$) and 18:3($n-3$), as well as between 22:6($n-3$), 20:5($n-3$) and 16:1($n-7$). The fatty acids 16:1($n-9$), 18:0 and 18:4($n-3$) were important moieties to distinguish samples along component one, whereas 18:1($n-9$), 22:6($n-3$) and 16:1($n-7$) mostly affected samples influenced by component two. Other fatty acids, like 18:3($n-3$) and 18:2($n-6$) had a high impact on both

Table 1 Relative composition of fatty acids [percentage of total fatty acids] and fatty alcohols [percentage of total fatty alcohols] in total lipids of adult females and copepodite stage V (CV) of *Pseudocalanus acuspes*, values are calculated on basis of monthly averages, values below 1% not shown

	Females				CV			
	Min	Max	Mean	SD	Min	Max	Mean	SD
Fatty acids								
14:0	<1	1.6	1.0	0.3	<1	<1	<1	–
15:0	<1	1.2	<1	–	<1	<1	<1	–
16:0	10.3	20.7	15.0	2.9	6.0	8.3	7.1	1.0
17:0	<1	1.0	<1	–	<1	<1	<1	–
18:0	<1	3.7	2.5	0.6	<1	1.3	<1	–
16:1($n-7$)	1.1	6.5	2.4	1.5	3.3	7.6	4.9	1.6
16:1($n-9$)	<1	2.6	<1	–	<1	<1	<1	–
18:1($n-5$)	1.6	4.1	2.8	0.9	<1	2.1	1.3	0.6
18:1($n-7$)	1.4	2.9	2.0	0.4	1.3	1.6	1.5	0.1
18:1($n-9$)	10.1	26.1	18.9	5.2	28.9	39.6	34.8	4.4
24:1	1.3	3.3	2.2	0.7	<1	<1	<1	–
16:2($n-4$)	<1	1.2	<1	–	<1	<1	<1	–
18:2($n-6$)	2.9	8.5	5.6	1.9	4.2	10.7	7.1	2.8
16:3($n-4$)	<1	1.0	<1	–	<1	<1	<1	–
18:3($n-3$)	1.7	4.8	3.3	1.1	2.2	6.9	5.1	1.9
18:3($n-6$)	<1	1.0	<1	–	<1	<1	<1	–
18:4($n-3$)	1.3	5.8	3.6	1.4	4.1	7.2	6.1	1.2
20:4($n-3$)	<1	1.6	1.1	0.4	1.0	2.9	2.1	0.7
20:5($n-3$)	12.4	19.5	15.2	2.4	9.8	14.3	12.0	2.1
22:6($n-3$)	16.6	26.2	22.0	3.1	10.6	20.5	15.2	4.0
Fatty alcohols								
14:0	21.4	33.2	26.7	3.7	22.9	30.0	27.2	2.7
16:0	55.2	70.2	62.7	5.1	59.5	69.6	65.6	3.9
18:0	<1	11.5	5.1	3.7	1.5	2.6	2.0	0.4
18:1	2.8	8.2	5.2	1.6	3.5	9.6	5.2	2.5
20:1	<1	1.6	<1	–	<1	<1	<1	–

Min Minimum, *Max* maximum, *SD* standard deviation, – SD not calculated

Table 2 Relative fatty acid composition of neutral lipids of females of *Pseudocalanus acuspes*

	I Feb–Apr ($n=11$)		II May ($n=3$)		III June ($n=4$)		IV July–Sept ($n=14$)		V Nov–Jan ($n=4$)		Level of significance (Student's *t*-test)									
											Adjacent groups					Distant groups				
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	I:II	II:III	III:IV	IV:V	I:V	I:III	I:IV	II:IV	II:V	III:V
16:0	13.3	2.5	8.2	1.3	9.4	3.1	14.8	2.8	17.7	4.4	**		**		*	*		***	**	*
18:0	3.0	1.1	1.8	0.6	2.6	1.1	3.0	0.8	6.5	1.9				***	***			*	**	**
16:1($n-7$)	5.0	1.3	9.2	1.0	5.0	0.4	2.5	0.5	3.8	1.1	***	***	***				***	***	**	
16:1($n-9$)	1.6	1.1	1.3	1.4	1.3	0.5	1.6	1.2	7.3	2.8				***	***				**	**
18:1($n-9$)	26.7	5.0	39.1	1.4	43.8	0.5	35.9	4.5	35.7	5.0	***	**	**		**	***	***			*
18:2($n-6$)	8.2	1.3	8.2	0.6	11.6	2.0	12.4	2.2	5.7	1.6		*		***	**	**	***	**		**
18:3($n-3$)	5.7	0.9	3.0	0.3	5.2	1.5	7.9	2.2	2.7	1.0	***	*	*	***	***		**	***		*
18:4($n-3$)	8.3	1.9	3.8	0.3	3.7	1.8	4.3	1.7	1.6	0.6	***			**	***	***	***		**	*
20:5($n-3$)	9.4	2.2	8.5	0.5	6.6	0.4	5.6	0.8	4.7	1.4		**	*		**	**	***	***	*	
22:6($n-3$)	6.3	3.3	8.6	0.9	5.5	0.6	3.6	1.3	3.7	0.9		**	*				**	***	**	*

I–V Seasonal groups, *SD* standard deviation
$^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$

components and could not be assigned clearly. Samples from different months were separated, demonstrating seasonal changes in the fatty acid compositions of storage lipids.

Although polar lipids remained rather uniform throughout the year, with 16:0, 20:5($n-3$) and 22:6($n-3$) contributing between 50 and 73% of total fatty acids (Table 3), their fatty acid profiles divided into the same seasonal groups as the storage lipids. Small but significant differences were mainly due to changes of the 18:1 isomers, as well as of 18:3($n-3$) and 18:4($n-3$), with largest changes between early (March–April) and late spring (May).

Seston

Maximum lipid concentrations in the seston were always found above the thermocline during spring and summer, whereas from autumn until spring, mixing caused more equally distributed lipid contents over the whole water column (Fig. 2f). In terms of total fatty acids and alcohols, maximal lipid contents with up to 52 µg/l were found in upper water layers in April. This lipid-rich seston reached lower water layers with a time delay of 1 month, resulting in a lipid peak near the halocline of 20–24 µg/l in May.

The PCA revealed a strong coherence within the relative seston composition in terms of biomass of different taxonomic groups and typical signature fatty acids (Fig. 5). There was a distinct correlation between 18:1($n-9$) and ciliates and to a lesser degree flagellates, between 16:1($n-7$), 20:5($n-3$) and diatoms as well as a coherence between 22:6($n-3$), 18:4($n-3$) and dinoflagellates. The strong connection between 18:2($n-6$) and 18:3($n-3$) could not be assigned to a specific algal group, but they both had a very similar impact on component one as cyanobacteria and chlorophytes, whereas component two differentiated them. Due to their relative position on component three 18:2($n-6$) grouped with chlorophytes, whilst 18:3($n-3$) correlated with cyanobacteria.

Ciliates contributed significantly to seston biomass at all seasons (Table 4), maximum proportions of diatoms were found in spring, of ciliates and dinoflagellates in May. In contrast, other flagellates and cyanobacteria increased during the summer. No data were available for the winter season.

Trophic interactions

When compared with seston lipids, some fatty acids of *P. acuspes* females developed with a time lag of 1–2 months at the beginning of 2002, whereas in autumn and winter seston and copepods showed relatively parallel progressions (Fig. 3). Specifically the increase of 18:3($n-3$) and 18:2($n-6$) in May and June was reflected with some delay in the storage lipids of females. In May, the increase of 18:1($n-9$) in females co-occurred with a rise in the seston from lower water layers, whereas the peak in the upper water column in July was not found in the copepods.

As indicated by a selection index (Fig. 6), 16:0 and 18:0 were usually negatively selected during all seasons, whereas 18:1($n-9$), 18:2($n-6$) and 20:5($n-3$) were elevated in the neutral lipids most of the time. Selectivity for all other fatty acids changed with time or depth. In early spring 18:3($n-3$), 18:4($n-3$) and 22:6($n-3$) were accumulated in storage lipids as compared to the seston, as well as 16:1($n-7$) in May and June.

Discussion

Seasonal cycle

The seasonal cycle and condition of *P. acuspes* in the Bornholm Basin were described on the basis of lipid content and composition as well as prosoma length, to relate lipid dynamics and size variations to the life cycle of this originally Arctic copepod in the Baltic Sea. Pronounced changes in body size and fatty acid composition of

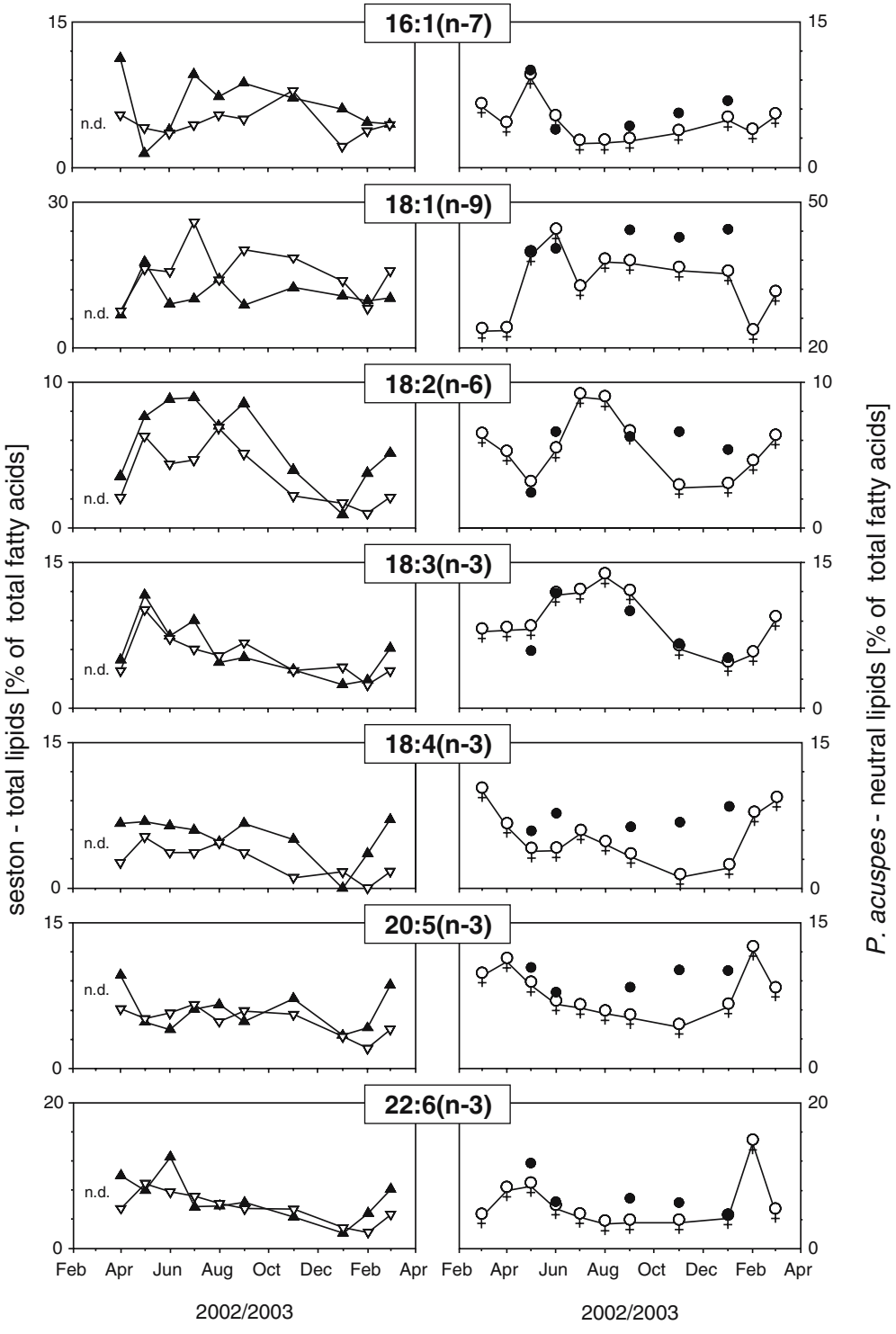

Fig. 3 Seasonal development of mean fatty acid composition of seston (total lipids) and *P. acuspes* (neutral lipids): *n.d.* no data, *filled triangles* seston in upper water layer (5 m), *open triangles* seston in halocline (40–60 m), *filled circles* copepodite stage V, *open circles with cross* adult females

structural lipids of females revealed five "environmental cohorts", which obviously experienced similar biotic and abiotic conditions during development, thus leading to constant attributes of females: early spring (February–April), late spring (May), early summer (June), late summer (July–September) and winter (November–January). Recent studies on stage composition and growth measurements (Renz and Hirche 2006; J. Renz et al., submitted) indicate that *P. acuspes* basically follows an annual cycle in the Bornholm Basin, although the development of a second cohort in summer was also considered possible.

Aligning the "environmental cohorts" in this context, the early spring cohort consisted of females, which successively matured from older overwintering copepodite stages. Their growth was at least partly fueled by storage lipids, as indicated by the decrease in wax ester content. This cohort was followed by females in May, which were

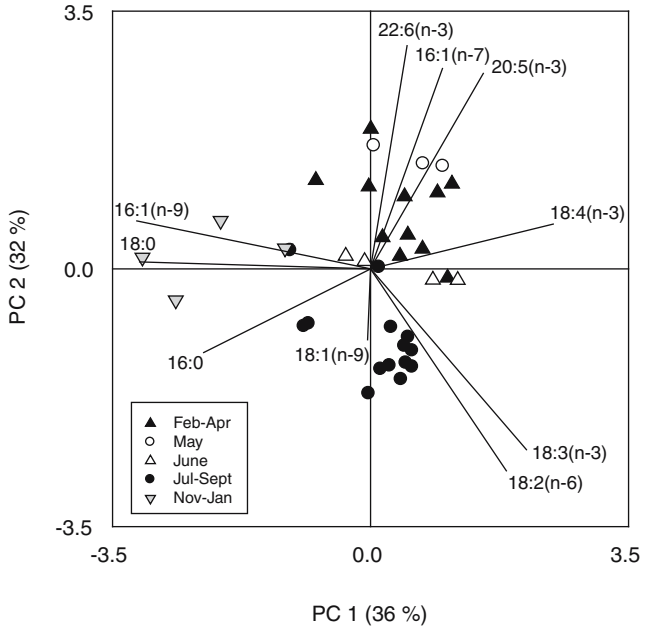

Fig. 4 Principal component analysis on the relative fatty acid composition of neutral lipids of adult females of *P. acuspes*, scales were adjusted to combine plots: scales of principal components (PC) refer to sample plot, scale of variables reaches from −1 to +1 for both PCs

probably larger due to better feeding conditions and lower temperatures (Vidal 1980; Klein Breteler and Gonzalez 1988). Strong changes in size co-occurred with variations in the composition of structural lipids and in storage lipid content, indicating different feeding histories during growth. The May cohort probably derived from younger overwintering copepodids of the previous year, which encountered a high food supply in the upper water column in April. In May lipid-rich seston reached lower water layers, thus providing better feeding conditions for older copepodite stages and females. It remains, however, a matter of conjecture, whether the drastic changes in May were due to successively maturing cohorts or rather to the appearance of a new generation.

To better understand the further progression of the seasonal cycle, valuable information can be derived from comparisons of storage lipid content of CV and females. In May the amounts of storage lipids of females and CV hardly differed, whereas in summer the copepodids were always richer in wax esters. A similar decrease in storage lipids, measured as oil sac volume, was observed by McLaren et al. (1989) in summer females of *P. acuspes* in the Bedford Basin, Nova Scotia. Two, not mutually exclusive mechanisms, causing the pronounced differences between females and copepodids, can be assumed:

1. *Food supply*: The accumulated storage lipids were used up very quickly by the females for metabolic costs of last molt, gonad maturation and egg production. Due to reduced food availability, the depletion of reserves proceeded more quickly during summer than in May, explaining a high wax ester retention of females in late spring. Lipid retention is a direct expression for surplus of food. Apparently, the food supply alone was not sufficient to sustain egg production at ambient temperatures in summer. The pronounced utilization of storage lipids signifies that in summer food limitation might have been an important factor, whereas in May egg production was primarily determined by abiotic factors. Hence, sub-optimum growth conditions might reduce the number of generations per year.
2. *Onset of overwintering*: Only the lipid-poor copepodids accomplished maturation during summer and autumn to produce potentially more successful offspring, whereas the lipid-rich copepodids passed into an "active diapause", with ongoing feeding, suspended development and resting gonads (McLaren et al. 1989). According to this hypothesis, the females found in the Bornholm Basin from summer to winter would represent a still maturing but minor part of the population. This is consistent with the drastic decline

Table 3 Relative fatty acid composition of polar lipids of females of *Pseudocalanus acuspes*

	I		II		III		IV		V				Level of significance (Student's *t*-test)				
	March-Apr ($n=14$)		May ($n=3$)		June ($n=4$)		July–Sept ($n=14$)		Nov ($n=3$)		Jan ($n=1$)	Feb ($n=2$)	Adjacent groups				
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	Mean	I:II	II:III	III:IV	IV:V	I:V
16:0	16.1	1.1	17.6	0.2	17.8	1.5	16.4	1.3	18.5	0.7	22.3	19.7	*			*	**
18:0	3.3	1.9	2.8	0.1	5.0	3.3	3.2	0.4	4.4	1.0	6.5	4.9				**	
18:1($n-5$)	5.1	0.8	3.3	0.1	3.2	0.5	3.5	0.3	3.7	0.1	3.5	4.0	**				**
18:1($n-7$)	1.9	0.2	1.1	0.0	1.3	0.3	1.6	0.3	1.6	0.1	2.2	2.1	***				*
18:1($n-9$)	3.7	0.9	5.4	1.1	7.5	1.0	5.4	1.6	4.9	0.6	7.4	7.8	*	*	*		*
18:2($n-6$)	3.9	1.6	2.5	0.1	6.3	3.4	5.0	1.5	0.5	1.4	1.7	6.4		*		***	***
18:3($n-3$)	1.4	0.3	0.9	0.0	1.8	0.2	2.6	0.8	0.7	0.1	0.6	1.6	**	***	*	***	***
18:4($n-3$)	3.3	0.9	1.6	0.1	2.1	0.6	2.9	1.1	1.0	0.2	1.0	3.4	**			**	***
20:5($n-3$)	21.0	3.1	20.0	1.1	16.8	3.0	20.2	2.0	17.7	0.7	12.9	12.6			**	*	
22:6($n-3$)	33.4	4.9	40.9	0.4	33.0	5.2	34.0	2.9	37.4	2.6	29.0	29.3	*	*			

I–V Seasonal groups, *SD* standard deviation
$^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$

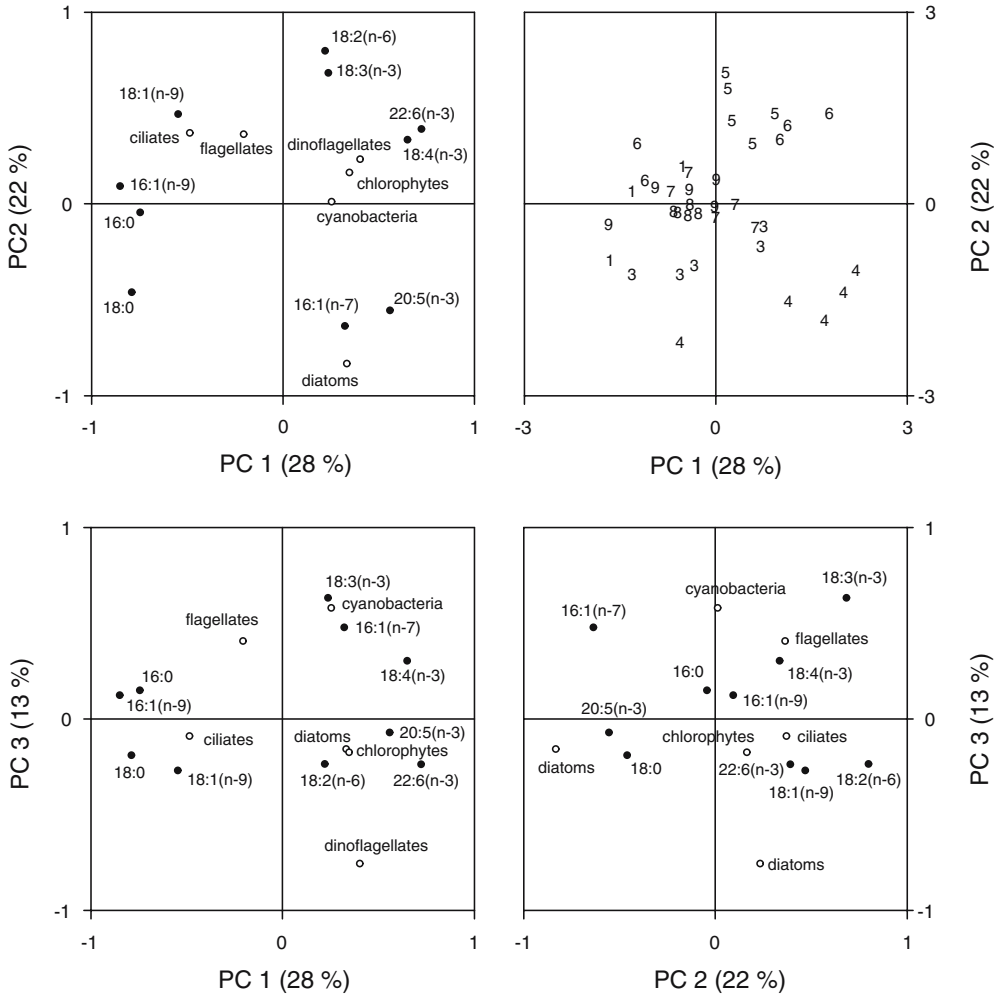

Fig. 5 Principal component analysis on the relative taxonomic (in terms of biomass) and fatty acid composition of the seston: loading plots for the extracted principal components (PC) 1–3 (*open circles* seston taxa, *filled circles* fatty acids) and sample plot for the extracted PCs 1 and 2 (*numbers* months of the year)

of female and nauplii abundance in the water column in July and August (Renz and Hirche 2006) and the slow developmental rates in late spring and summer (J. Renz et al., submitted). Such a continued development of only a minor part of the generation of *Pseudocalanus* sp. was also observed in the White Sea (Pertsova 1981). Norrbin (Norrbin et al. 1990; Norrbin 1996) suggested that it is less a continuous process, triggered by the physiological state as proposed by McLaren et al. (1989), but rather a specific switching date, at which *P. acuspes* copepodids stop maturation but proceed to accumulate lipids. Klein Breteler and Gonzalez (1988) suspected that changes to poor food conditions are necessary to induce hormonal cessation of development in favor of lipid production. Still, it remains unclear, how an external trigger, which would be effective early in the year, should function in the Bornholm Basin, with higher temperatures and longer periods of high food abundance as compared to high latitudinal habitats.

In conclusion, we found evidence that the life cycle of *P. acuspes* in the Baltic Sea resembles that of *Pseudocalanus* spp. in Arctic regions (e.g. Pertsova 1981; McLaren et al. 1989; Norrbin et al. 1990; Norrbin 1991; Conover and Siferd 1993), with highest reproductive activities in spring, a successive accumulation of resting copepodite stages starting in early summer and a potential interposition of minor summer generations. This is supported by the corresponding lipid-storing strategies of *P. acuspes*. Wax ester levels in the Baltic were similar to those found for CIV and CV of *P. acuspes* in Arctic regions (Båmstedt et al. 1990; Norrbin et al. 1990), with values reaching 72% of total lipids in autumn and around 55% in summer. To our knowledge, there are no data available on the wax ester content of *P. acuspes* females.

Based on these fundamental analogies, we hypothesize that life cycle and lipid-storing strategies of *P. acuspes* in the central Baltic Sea originate from extant adaptations to high latitudinal habitats.

Table 4 Relative seston composition [percentage of total biomass]

	Depth (m)	Din	Dia	Chl	Cya	Div fl	Cil
Feb–Apr							
Upper water layer	5	24	18	0	3	9	45
Above thermocline	10	20	23	1	1	14	41
Midwater layer	20–30	7	38	1	2	11	42
Above halocline	30–40	15	45	1	1	5	33
In halocline	40–60	20	45	1	1	3	30
May							
Upper water layer	5	24	1	0	2	7	66
Above thermocline	10	20	0	0	1	8	71
Midwater layer	20–30	50	4	2	11	6	27
Above halocline	30–40	23	1	1	0	2	73
In halocline	40–60	29	0	8	0	7	55
June							
Upper water layer	5	43	1	1	19	17	19
Above thermocline	10	23	1	17	17	15	27
Midwater layer	20–30	25	3	1	11	29	30
Above halocline	30–40	17	2	0	1	10	70
In halocline	40–60	13	2	0	7	9	69
July–Sept							
Upper water layer	5	5	4	0	19	17	56
Above thermocline	10	3	11	2	9	17	57
Midwater layer	20–30	3	5	1	55	14	22
Above halocline	30–40	6	0	2	18	30	42
In halocline	40–60	14	11	1	0	15	59

Din Dinoflagellates, *Dia* diatoms, *Chl* chlorophytes, *Cya* cyanobacteria, *Div fl* all flagellates except dinoflagellates, *Cil* ciliates

Trophodynamics

The five different phases of the seasonal cycle were also reflected in the fatty acid dynamics of neutral lipids, although they are less conservative than structural lipid composition and body size. We applied signature fatty acids (Lee et al. 1971; Sargent and Whittle 1981; Sargent et al. 1987; Graeve et al. 1994; Daalsgard et al. 2003) to identify feeding preferences and food selection of *P. acuspes*. Due to parallel analyses of the seston, we were able to assign the fatty acid markers to specific food sources.

Similar to all other studies dealing with the fatty acid composition of *Pseudocalanus* spp. (e.g. Kattner et al. 1981; Kattner and Krause 1989; Fraser et al. 1989; Norrbin et al. 1990; Cotonnec et al. 2001), we found 18:1($n-9$) to be one of the most abundant fatty acids throughout the year. Apparently, this does not inevitably indicate similar feeding habits in different habitats, but rather a species-specific attribute, probably affected by metabolic processes. This fatty acid is not only known to be characteristic for carnivorous or detritivorous feeding (Sargent and Falk-Petersen 1981; Falk-Petersen et al. 1990), it is also synthesized de novo by copepods (Pascal and Ackman 1976; Sargent and Henderson 1986; Kattner et al. 1994; Kattner and Hagen 1998). Thus, a trophic assignment of 18:1($n-9$) remains problematic. Nevertheless, as revealed by principal component analysis we found a strong coherence between 18:1($n-9$) levels in the seston lipids and the occurrence of ciliates. Lipid profiles of ciliates have been reported to reflect, at least within species-specific ranges, the fatty acid composition of their diet (Ederington et al. 1995; Harvey et al. 1997; Broglio et al. 2003). Therefore, a comparison of field data with fatty acid profiles derived in laboratory studies is rather difficult. However, our data emphasize a high relevance of ciliates in the food spectrum of *P. acuspes*. The apparently intense use of heterotrophic organisms and/or detritus might be explained by the vertically stratified environment in the Baltic Sea. Due to the concentration of older copepodite stages of *P. acuspes* in deeper water

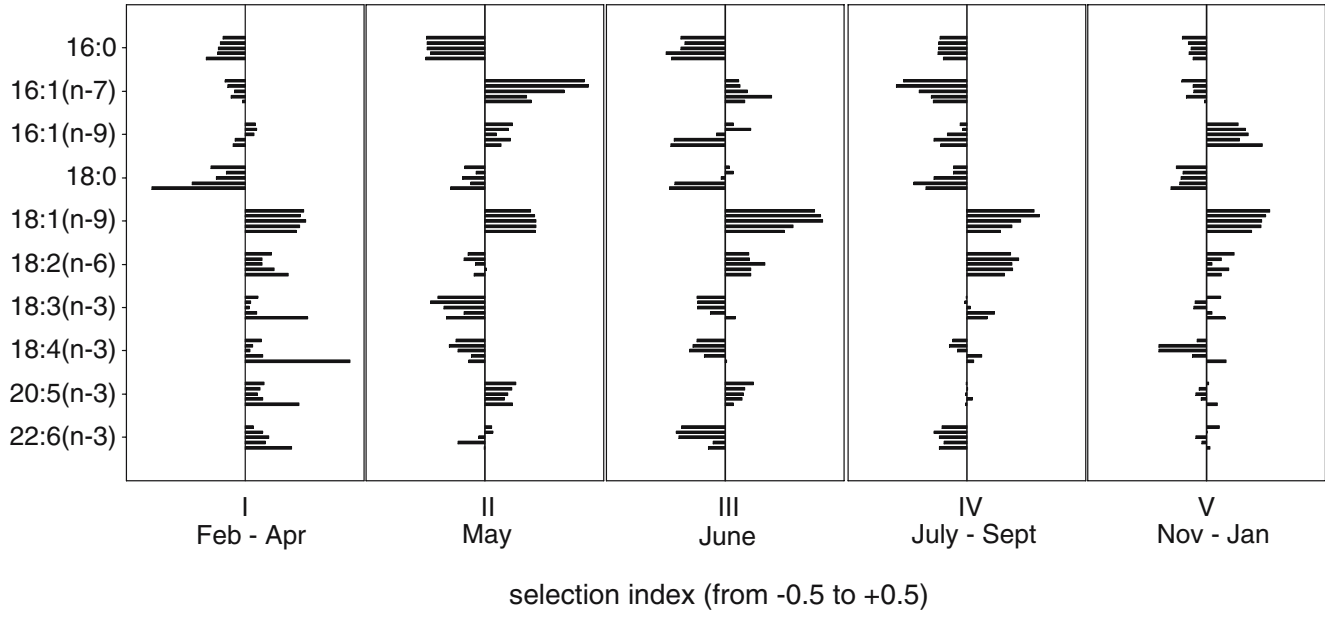

Fig. 6 Selection index for fatty acids with vertical resolution [sorted top-down: upper water layer (5 m), above thermocline (10 m), midwater layer (20–30 m), above halocline (30–40 m), in halocline (40–60 m)]

layers (Hernroth and Ackefors 1979; Renz and Hirche 2006), their potential food mainly consisted of sinking material from the surface and organisms inhabiting the lower stratum of the water column. At least in May and June, those were mainly ciliates, representing approximately 75% of living biomass, co-occurring with very high 18:1($n-9$) levels in the females. Feeding of *Pseudocalanus* spp. on ciliates (Klein Breteler et al. 2004) and heterogeneous particulate matter was documented in laboratory studies (Poulet 1974, 1976; Pavlovskaya and Pechen′-Finenko 1975 as cited by Corkett and McLaren 1978). We did not quantify detritus, although an accumulation of degraded material on the halocline is to be expected.

A comparison between the fatty acid and taxonomic composition of seston revealed a relationship between 18:4($n-3$), 22:6($n-3$) and the biomass of dinoflagellates, as well as coherence between 18:4($n-3$) and other flagellates. Those fatty acids are known to reach high levels in dinoflagellates and cryptophytes (Sargent et al. 1987; Graeve et al. 1994, 2001 and references therein; Daalsgard et al. 2003). In our study, the biomarker 18:4($n-3$) was found in significantly higher amounts in early spring, and 22:6($n-3$) was also more abundant from February until May. This indicates a preferential ingestion of flagellates or dinoflagellates in spring time, although dinoflagellates showed a rather constant portion of total biomass during all seasons examined, whereas other flagellates increased later in the year. *Pseudocalanus* spp. selectively feeds on flagellates such as cryptophytes and dinoflagellates (e.g. Geen and Hargrave 1966; Zagorodnyaya 1974). This high quality food (Brown et al. 1997) enhances growth, egg production and lipid accumulation and also decreases mortality (Klein Breteler et al. 1990; Koski et al. 1998; Koski and Klein Breteler 2003).

Diatom blooms, which have reappeared in the Bornholm Basin since 1999, were mainly restricted to early spring (February–April) (Wasmund et al. 2003, present study). However, the diatom marker 16:1($n-7$) reached its maximum in *P. acuspes* not until May, when diatoms were of only marginal importance in the water column and their fatty acid markers in the seston had already decreased significantly. This suggests that lipids observed in the new females in May probably derived from lipid reserves built up during earlier copepodite stages. This time shift between fatty acid levels in seston and copepods related to the period of higher lipid accumulation or retention by females. Low lipid levels reflect changes much quicker, probably causing the more synchronous progression of fatty acid composition of seston and storage lipids later in the season. Alternatively, in spite of low standing stocks of diatoms, their production rates may have been high, as the production potential of diatoms was evident from a small diatom bloom during July.

Diatom marker levels were rather low in the Baltic. Especially in Polar Regions with more pronounced diatom and ice algal blooms 16:1($n-7$) may reach values of up to 20% of total fatty acids in CIV and CV of *P. acuspes* in the Arctic summer (Norrbin et al. 1990), thus exceeding twice the maximum value found for CV in the present study. Very similar results, indicating diatom-based feeding, were found for other *Pseudocalanus* species in Polar Regions with 16:1($n-7$) levels reaching up to 40% of total fatty acids (Peters et al. 2004, S. Lischka and W. Hagen, submitted).

The rather limited ingestion of diatoms seems to be characteristic for temperate regions, as all studies show similarly low marker amounts (Kattner et al. 1981; Kattner and Krause 1989; Fraser et al. 1989; Cotonnec et al. 2001). Still, the levels of 16:1($n-7$) found in our study belong to the lowest ever measured for *Pseudocalanus* spp., indicating a more intense use of other food sources. Especially cyanobacteria have to be considered as potential diet in the Baltic Sea, as they usually bloom intensively during summer, except for 2002, when only a minor bloom was registered (Wasmund et al. 2003). However, in our study cyanobacteria values reached up to 55% of seston biomass.

Cyanobacteria are very variable in their fatty acid compositions, with marked differences occurring even in the same genus (Gugger et al. 2002). Due to the coexistence of different cyanobacteria species in the Baltic Sea, it is not easy to identify a clear trophic signal. Many studies reported that a characteristic fatty acid pattern of cyanobacteria consists of 16:0, 16:1, 18:2($n-6$) and 18:3($n-3$) (e.g. Murata and Nishida 1987 and references therein, Vargas et al. 1998; Gugger et al. 2002). The simultaneous occurrence of 18:3($n-3$) and 18:2($n-6$) with cyanobacteria and chlorophytes in the seston, indicated that elevated amounts of these fatty acids in *P. acuspes* were due to an augmented use of cyanobacteria in summer, since chlorophytes were only of minor importance. Hoppe (1981) showed that cyanobacteria and microzooplankton often build up agglomerates especially in the late bloom phase, which might improve food quality and attractiveness for copepods, leading to a more intensive use in the later phases (Meyer-Harms et al. 1999). This might explain why cyanobacteria were reflected in the storage lipids with a delay of some months.

We conclude that *P. acuspes* displays a basically opportunistic feeding behavior in the Baltic Sea. Five different seasonal fatty acid profiles were determined in the neutral lipids with high levels of 18:1($n-9$) at all times, indicating a species-specific storage pattern as well as a ciliate-dominated diet. Other food sources varied over the year. In early spring dinoflagellates were increasingly utilized, whereas in late spring diatom markers were most strongly reflected in the fatty acid composition. During summer, cyanobacteria, and probably to a lesser degree chlorophytes, seemed to contribute substantially to the diet of *P. acuspes*.

Acknowledgements The study was funded by the German Federal Ministry for Education and Research within the GLOBEC GERMANY project (03F0320C). We wish to thank the crews and scientific parties of the RV *Alkor*, *Heincke* and *A. v. Humboldt* for the excellent support during the field phase. We also thank M. Graeve

for GC-MS measurements. The critical revision and improvement of the manuscript by H. Auel, D. Stübing and three anonymous reviewers are gratefully acknowledged.

References

Båmstedt U, Håkanson JL, Brenner-Larsen J, Björnsen PK, Geertz-Hansen O, Tiselius P (1990) Copepod nutritional condition and pelagic production during autumn in Kosterfjorden, western Sweden. Mar Biol 104:197–208

Broglio E, Jónasdóttir SH, Calbet A, Jakobsen HH, Saiz E (2003) Effect of heterotrophic versus autotrophic food on feeding and reproduction of the calanoid copepod *Acartia tonsa*: relationship with prey fatty acid composition. Aquat Microb Ecol 31:267–278

Brown MR, Jeffrey SW, Volkman JK, Dunstan GA (1997) Nutritional properties of microalgae for mariculture. Aquaculture 151:315–331

Bucklin A, Frost BW, Bradford-Grieve J, Allen LD, Copley NJ (2003) Molecular systematic and phylogenetic assessment of 34 calanoid copepod species of the Calanidae and Clausocalanidae. Mar Biol 142:333–343

Cairns AA (1967) The zooplankton of Tanquary Fjord, Ellesmere Island, with special reference to the calanoid copepods. J Fish Res Board Can 24:555–568

Conover RJ, Siferd TD (1993) Dark-season survival strategies of coastal zone zooplankton in the Canadian Arctic. Arctic 46:303–311

Corkett CJ, McLaren IA (1978) The biology of *Pseudocalanus*. Adv Mar Biol 15:1–231

Cotonnec G, Brunet C, Sautour N, Thoumelin G (2001) Nutritive value and selection of food particles by copepods during a spring bloom of *Phaeocystis* sp. in the English Channel, as determined by pigment and fatty acid analyses. J Plankton Res 23:693–703

Daalsgard J, St. John M, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225–340

Davis CC (1976) Overwintering strategies of common planktic copepods in some north Norway fjords and sounds. Astarte 9:37–42

Digby PSB (1950) The biology of the small planktonic copepods of Plymouth. J Mar Biol Assoc UK 29:393–438

Dunstan GA, Volkman JK, Barrett SM, LeRoi J-M, Jeffrey SW (1994) Essential polyunsaturated fatty acids from 14 species of diatoms (Bacillariophyceae). Phytochemistry 35:155–161

Ederington MC, McManus GB, Harvey HR (1995) Trophic transfer of fatty acids, sterols, and triterpenoid alcohol between bacteria, a ciliate, and the copepod *Acartia tonsa*. Limnol Oceanogr 40:860–867

Edler L (1979) Recommendations on methods for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. Baltic Mar Biol Publ 5:1–38

Falk-Petersen S, Hopkins CCE, Sargent JR (1990) Trophic relationships in the pelagic, Arctic food web. In: Barnes M, Gibson RN (eds) Trophic relationships in the marine environment. Proceedings of the 24th European marine biological symposium. Aberdeen University Press, Aberdeen, pp 315–333

Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for isolation and purification of total lipids from animal tissues. J Biol Chem 226:497–509

Fraser AJ, Sargent JR, Gamble JC (1989) Lipid class and fatty acid composition of *Calanus finmarchicus* (Gunnerus), *Pseudocalanus* sp. and *Temora longicornis* Muller from nutrient-enriched seawater enclosure. J Exp Mar Biol Ecol 130:81–92

Frost BW (1989) A taxonomy of the marine calanoid copepod genus *Pseudocalanus*. Can J Zool 67:525–551

Geen GH, Hargrave BT (1966) Primary and secondary production in Bras d´Or Lake, Nova Scotia, Canada. Verh Int Ver Theor 16:333–340

Graeve M, Kattner G, Hagen W (1994) Diet-induced changes in the fatty acid composition of Arctic herbivorous copepods: experimental evidence of trophic markers. J Exp Mar Biol Ecol 182:97–110

Graeve M, Dauby P, Scailteur Y (2001) Combined lipid, fatty acid and digestive tract content analyses: a penetrating approach to estimate feeding modes in Antarctic amphipods. Polar Biol 24:853–862

Gugger M, Lyra C, Suominen I, Tsitko I, Humbert J-F, Salkinoja-Salonen MS, Sivonen K (2002) Cellular fatty acids as chemotaxonomic markers of the genera *Anabaena, Aphanizomenon, Microcystis, Nostoc* and *Planktothrix* (cyanobacteria). Int J Syst Evol Microbiol 52:1007–1015

Harvey HR, Ederington MC, McManus GB (1997) Lipid composition of the marine ciliates *Pleuronema* sp. and *Fabrea salina*: shifts in response to changes in diet. J Euk Microbiol 44:189–193

Hay SJ, Evans GT, Gamble JC (1988) Birth, growth and death rates for enclosed populations of calanoid copepods. J Plankton Res 10:431–454

Henroth L (1985) Recommendations on methods for marine biological studies in the Baltic Sea: Mesozooplankton biomass assessment. Baltic Mar Biol Publ 10:1–32

Henroth L, Ackefors H (1979) The zooplankton of the Baltic proper: a long-term investigation of the fauna, its biology and ecology. Rep Fish Bd Sweden Inst Mar Res 2:1–160

Hinrichsen H-H, Möllmann C, Voss R, Köster FW, Kornilovs G (2002) Biophysical modeling of larval Baltic cod (*Gadus morhua*) growth and survival. Can J Fish Aquat Sci 12:1858–1873

Hinrichsen H-H, Lehmann A, Möllmann C, Schmidt J (2003) Dependency of larval fish survival on retention/dispersion in food limited environments: the Baltic as a case study. Fish Oceanogr 12:425–433

Hoppe HG (1981) Blue-green algae agglomeration in surface water: a microbiotop of high bacterial activity. Kieler Meeresforschung Sonderhefte 5:291–303

Kattner G, Fricke HSG (1986) Simple gas–liquid chromatography method for simultaneous determination of fatty acids and alcohols in wax esters of marine organisms. J Chromatogr 361:263–268

Kattner G, Hagen W (1998) Lipid metabolism of the Antarctic euphausiid *Euphausia crystallorophias* and its ecological implications. Mar Ecol Prog Ser 170:203–212

Kattner G, Krause M (1989) Seasonal variations of lipids (wax esters, fatty acids and alcohols) in calanoid copepods from the North Sea. Mar Chem 26:261–275

Kattner G, Krause M, Trahms J (1981) Lipid composition of some typical North Sea copepods. Mar Ecol Prog Ser 4:69–74

Kattner G, Graeve M, Hagen W (1994) Ontogenetic and seasonal changes in lipid and fatty acid/alcohol compositions of the dominant Antarctic copepod *Calanus propinquus, Calanoides acutus* and *Rhincalanus gigas*. Mar Biol 118:637–644

Klein Breteler WCM, Gonzalez SR (1988) Influence of temperature and food concentration on body size, weight and lipid content of two Calanoid copepod species. In: Boxshall GA, Schminke HK (eds) Biology of copepods. Kluwer, Dordrecht, pp 201–210

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

Klein Breteler WCM, Koski M, Rampen S (2004) Role of essential lipids in copepod nutrition: no evidence for trophic upgrading of food quality by a marine ciliate. Mar Ecol Prog Ser 274:199–208

Koski M, Klein Breteler WCM (2003) Influence of diet on copepod survival in the laboratory. Mar Ecol Prog Ser 264:73–82

Koski M, Klein Breteler W, Schogt N (1998) Effect of food quality on the rate of growth development of the pelagic copepod *Pseudocalanus elongatus* (Copepoda: Calanoida). Mar Ecol Prog Ser 170:169–187

Lee RF, Nevenzel JC, Paffenhöfer G-A (1971) Importance of wax esters and other lipids in the marine food chain: phytoplankton and copepods. Mar Biol 9:99–108

Lischka S, Hagen W (2005) Life histories of the copepods *Pseudocalanus minutus, P. acuspes* (Calanoida) and *Oithona similis*

(Cyclopoida) in the Arctic Kongsfjorden (Svalbard). Polar Biol 28:910–921
Marshall SM (1949) On the biology of the small copepods in Loch Striven. J Mar Biol Assoc UK 28:45–122
McLaren IA, Laberge E, Corkett CJ, Sévigny J-M (1989) Life cycles of four species of *Pseudocalanus* in Nova Scotia. Can J Zool 67:552–558
Meyer-Harms B, Reckermann M, Voß M, Siegmund H, Bodungen Bv (1999) Food selection by calanoid copepods in the eutrophic layer of the Gotland Sea (Baltic Proper) during mass occurrence of N_2-fixing cyanobacteria. Mar Ecol Prog Ser 191:243–250
Möllmann C, Köster FW (1999) Food consumption by clupeids in the Central Baltic: evidence for top-down control? ICES J Mar Sci 56:100–113
Möllmann C, Köster FW (2002) Population dynamics of calanoid copepods and the implications of their predation by clupeid fish in the Central Baltic Sea. J Plankton Res 24:959–978
Möllmann C, Kornilovs G, Fetter M, Köster FW, Hinrichsen H-H (2003) The marine copepod *Pseudocalanus elongatus* as a mediator between climate variability and fisheries in the Central Baltic Sea. Fish Oceanogr 12:360–368
Murata N, Nishida I (1987) Lipids of blue-green algae (cyanobacteria). In: Stumpf PK (ed) The biochemistry of plants. Academic, New York, pp 315–347
Nichols DS, Nichols PD, Sullivan CW (1993) Fatty acid, sterol and hydrocarbon composition of Antarctic sea ice diatom communities during the spring bloom in McMurdo Sound. Antarct Sci 5:271–278
Norrbin MF (1991) Gonad maturation as an indication of seasonal cycles for several species of small copepods in the Barents Sea. In: Sakshaug E, Hopkins CCE, Øritsland NA (eds) Proceedings of the pro mare symposium on polar marine ecology, pp 421–432
Norrbin F (1992) Overwintering strategies of small copepods in high latitude marine environments. Dissertation, Faculty of Natural Sciences, Göteborg
Norrbin MF (1996) Timing of diapause in relation to the onset of winter in the high-latitude copepods *Pseudocalanus acuspes* and *Acartia longiremis*. Mar Ecol Prog Ser 142:99–109
Norrbin MF, Olsen R-E, Tande KS (1990) Seasonal variation in lipid class and fatty acid composition of two small copepods in Balsfjorden, northern Norway. Mar Biol 105:205–211
Pascal JC, Ackman RG (1976) Long chain monoethylenic alcohol and acid isomers in lipids of copepods and capelin. Chem Phys Lipids 16:219–223
Pavlovskaya TV, Pechen´-Finenko GA (1975) Comparison of the relative role of living and non-living organic matter in the nutrition of *Pseudocalanus elongatus* (Boeck) (in Russian). Biol Morya Kiev 34:65–70
Pertsova NM (1981) Number of generations and their span in *Pseudocalanus elongatus* (Copepoda, Calanoida) in the White Sea (in Russian). J Zool 60:673–684
Peters J, Tuschling K, Brandt A (2004) Zooplankton in the arctic Laptev Sea - feeding ecology as indicated by fatty acid composition. J Plankton Res 26:227–234
Poulet SA (1974) Seasonal grazing of *Pseudocalanus minutus* on particles. Mar Biol 25:109–123
Poulet SA (1976) Feeding of *Pseudocalanus minutus* on living and non-living particles. Mar Biol 34:117–125
Putt D, Stoecker DK (1989) An experimentally determined carbon:volume ratio for marine "oligotrichous" ciliates from estuarine and coastal waters. Limnol Oceanogr 34:1097–1103
Renz J, Hirche H-J (2006) Life cycle of *Pseudocalanus acuspes* Giesbrecht (Copepoda, Calanoida) in the Central Baltic Sea: I. Seasonal and spatial distribution. Mar Biol 148:567–580
Runge JA, Ingram RG (1991) Under-ice feeding and diel migration by the planktonic copepods *Calanus glacialis* and *Pseudocalanus minutus* in relation to the ice algal production cycle in southeastern Hudson Bay, Canada. Mar Biol 108:217–225
Sargent JR, Falk-Petersen S (1981) Ecological investigations on the zooplankton community in Balsfjorden, Northern Norway: lipids and fatty acids in *Meganyctiphanes norvegica*, *Thysanoessa raschi* and *T. inermis* during mid-winter. Mar Biol 62:131–137
Sargent JR, Henderson RJ (1986) Lipids. In: Corner EDS, O´Hara SCM (eds) The biological chemistry of marine copepods. Clarendon Press, Oxford, pp 59–108
Sargent JR, Whittle KJ (1981) Lipids and hydrocarbons in the marine food web. In: Longhurst AR (ed) Analysis of marine ecosystems. Academic, San Diego, pp 491–533
Sargent JR, Parkes RJ, Mueller-Harvey I, Henderson RJ (1987) Lipid biomarkers in marine ecology. In: Sleigh MA (ed) Microbes in the sea. Ellis Horwood, Chichester, pp 119–138
Schlitzer R (2005) Ocean data view. http://www.awi-bremerhaven.de/GEO/ODV
Schnack S (1975) Studies on the feeding biology of copepods (Crustacea) in the Kiel Bight (in German). Doctoral Thesis, Kiel University
Siferd TD, Conover RJ (1992) Natural history of ctenophores in the Resolute Passage area of the Canadian High Arctic with special reference to *Mertensia ovum*. Mar Ecol Prog Ser 86:133–144
Skerratt JH, Nichols PD, McMeekin TA, Burton HR (1997) Identification of dominant taxa in coastal Antarctic water and ice core samples using lipid signatures. In: Battaglia B, Valencia J, Walton DWH (eds) Antarctic communities. Species, structure and survival. Cambridge University Press, Cambridge, pp 79–85
Vargas MA, Rodríguez H, Moreno J, Olivares H, Del Campo JA, Rivas J, Guerrero MG (1998) Biochemical composition and fatty acid content of filamentous nitrogen-fixing cyanobacteria. J Phycol 34:812–817
Vidal J (1980) 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
Wasmund N, Pollehne F, Postel L, Siegel H, Zettler ML (2003) Assessment of the biological state of the Baltic Sea in 2002 (in German). Meereswiss Ber 56:1–78
Zagorodnyaya YA (1974) Nutrition and migration of Black Sea *Pseudocalanus elongatus* (Boeck) in the winter period (in Russian). Gidrobiol Zhurnal 10:49–56