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Calanoid copepods feed and produce eggs in the presence of toxic cyanobacteria *Nodularia spumigena*

Abstract—Feeding and fecundity of two calanoid copepod species (*Acartia bifilosa* and *Eurytemora affinis*) were studied in a food assemblage dominated by toxic cyanobacteria, to reveal whether mesozooplankton are able to obtain sufficient good quality food in different phases of a cyanobacteria bloom. Bloom conditions were simulated in a mesocosm by adding a high concentration of cultured hepatotoxic *Nodularia spumigena* to 100 μm filtered natural sea water. This seston was fed to copepods at days 1, 7, and 14 from the start of the mesocosm experiment, when it consisted of actively growing cyanobacteria (days 1 and 7) and increasing amounts of heterotrophic organisms and probably detritus (day 14). From bulk changes in chlorophyll and estimated ratios between chlorophyll and accessory pigments, it appears that both copepod species ingested large quantities of cyanobacteria in the first experiment but switched to ciliates when those became more abundant. Egg production of *A. bifilosa* was observed in all experiments, irrespective of the high concentration of nodularin in the mesocosm. The results demonstrate that the dominant copepod species of the Baltic Sea are able to feed, survive, and produce eggs in a plankton community dominated by toxic cyanobacteria.

Most studies of mesozooplankton grazing on natural plankton assemblages show avoidance of cyanobacteria (Meyer-Harms and von Bodungen 1997) and a negative correlation between secondary production and cyanobacteria abundance (Schmidt et al. 1998). Laboratory studies generally agree: even though some zooplankton species may sometimes have relatively high grazing and reproduction rates on cyanobacteria (Burns and Xu 1990; Engström et al. 2000), the majority of studies show low rates of ingestion and/or fecundity (e.g., Lampert 1987; Sellner et al. 1996; Koski et al. 1999). In general, besides often being toxic, cyanobacteria are likely to be poor-quality food for aquatic crustaceans. This is probably due to the lack of the long-chain polyunsaturated fatty acids 20:5ω3 and 22:6ω3 (Ahlgren et al. 1992), which are essential for mesozooplankton growth (Müller-Navarra et al. 2000).

The quality of cyanobacteria as copepod food may change because of aging or accumulation of an active microbial community on the algae (Hoppe 1981). First, toxicity of cyanobacteria blooms may decrease as the bloom ages (Kankaanpää et al. 2001); second, decomposing cyanobacteria filaments have been shown to be better-quality food than actively growing ones, probably because of attached bacteria (Repka et al. 1999). Decaying filaments and associated bacteria may also be consumed by ciliates and heterotrophic flagellates (Rolff 2000), which in turn can be consumed by copepods (Gifford 1991). Some protozoans improve the food quality for mesozooplankton by producing essential food components (e.g., long-chain polyunsaturated fatty acids and sterols) that are low in their algal prey (Klein Breteler et al. 1999). Therefore, aging, decreasing toxicity, colonization by bacteria, and biochemical ''upgrading'' by microzooplankton may improve the quality of cyanobacteria as food for mesozooplankton.

A study of mesozooplankton feeding and production in a cyanobacteria-dominated food assemblage was undertaken to reveal whether mesozooplankton are able to obtain sufficient good-quality food for egg production and survival in different phases of a cyanobacteria bloom and investigate whether the food quality of cyanobacteria improves as blooms age. A mesocosm experiment was conducted in which a natural plankton community was enriched with a high concentration of cultured toxic *Nodularia spumigena.* The development of the plankton community in this bloom

Table 1. Concentration of pigments, particulate organic carbon, nitrogen and phosphorus, ammonia, total nodularin, protein and fatty acids (μg L^{-1}), POC : PON, POC : POP and POC : Chl *a* ratios (μg : μg), bacteria volume (μm^3), and ciliate biomass (μgC L^{-1}) at days 1, 7, and 14 from the start of the mesocosm experiment (mean of the four enclosures ± SD). SAFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; EPA, eicosapentaenoic acid 20 : 5ω3; DHA, docosahexaenoic acid 22 : 6ω3; and —, Missing data.

	Day 1	Day 7	Day 14
NH_4	5.4 ± 9.2	7.6 ± 2.4	48 ± 37
Chl *a* total	53 ± 6.3	56 ± 3.9	36 ± 13
Chl *a* <10 μm	2.3 ± 0.1	3.1 ± 0.9	2.6 ± 0.8
Fucoxanthin	1.2 ± 0.2	0.7 ± 0.2	2.7 ± 0.9
Zeaxanthin	1.1 ± 0.1	2.9 ± 0.7	1.4 ± 1.0
Echinenone	2.5 ± 0.4	3.4 ± 0.7	1.1 ± 0.9
POC	1670 ± 13	3330 ± 93	1740 ± 730
PON	420 ± 5.8	820 ± 45	340 ± 180
POP	44 ± 0.5	49 ± 3.2	28 ± 2.1
POC : PON	4.0 ± 0.03	4.1 ± 0.1	5.8 ± 1.7
POC : POP	38 ± 0.6	68 ± 4.3	64 ± 29
POC : Chl *a*	32 ± 3.7	59 ± 5.2	48 ± 19
Bacteria	0.8 ± 1.3	—	11 ± 11
Ciliates total	6.2 ± 1.5	14 ± 3.6	50 ± 31
Urotricha sp.	0.6 ± 0.1	0.7 ± 0.2	0.2 ± 0.3
Other ciliates <30 μm	3.0 ± 1.1	4.8 ± 1.0	5.1 ± 5.3
Mesodinium spp.	0.1 ± 0.1	1.3 ± 0.7	0.03 ± 0.04
Euplotes sp.	0 ± 0	0.6 ± 0.3	40 ± 31
Other ciliates >30 μm	2.4 ± 0.7	6.4 ± 3.0	5.1 ± 7.0
Proteins	—	8.1 ± 9.5	18 ± 12
Fatty acids total	—	380 ± 40	420 ± 70
SAFA	—	140 ± 10	180 ± 30
MUFA	—	69 ± 4	100 ± 20
PUFA	—	140 ± 20	86 ± 11
ω3 : ω6	—	9.6 ± 0.5	7.0 ± 0.9
EPA	—	6.7 ± 0.3	20 ± 7
DHA	—	11 ± 1.4	13 ± 3.2
Nodularin total	9.2 ± 0.8	13 ± 2.2	11

was followed for 13 d (Engström-Öst et al. in press), and additional laboratory experiments were conducted to study copepod feeding and egg production. This note focuses on the response of the two dominating calanoid copepod species of the northern Baltic Sea (*Acartia bifilosa* and *Eurytemora affinis*) to different phases of the artificially created cyanobacteria bloom. The results demonstrate that these copepod species are able to feed, survive, and produce eggs in a plankton community dominated by toxic cyanobacteria.

The experiments were conducted in July 1999 on the southwestern coast of Finland, Baltic Sea. Four translucent enclosures of 120 liters were filled with 100 μm filtered seawater from an open archipelago area, a high concentration (~460 μgC L^{-1}) of toxic *N. spumigena* added, and the bags placed to float in a rack. The enclosures were monitored weekly for chlorophyll *a* and other pigments, organic and inorganic nutrients, bacteria, ciliates, nodularin, and total protein and fatty acids. The setup of the mesocosms and analyses are described in detail in Engström-Öst et al. (in press).

The hepatotoxin-producing cyanobacterium *N. spumigena* (strain AV1) was obtained from the Division of Microbiology, University of Helsinki (Lehtimäki et al. 2000). The hepatotoxin, nodularin, accounts for most of the toxicity to vertebrates in *N. spumigena* (Sivonen et al. 1989); nodularin concentration of cultures in exponential growth phase approximates 3–4 μg ml^{-1} (~11 μg (mg dry weight)$^{-1}$; Lehtimäki et al. 1994).

Grazing of *A. bifilosa* and *E. affinis* and egg production of *A. bifilosa* were measured in laboratory incubations with use of water from the mesocosm at days 1, 7, and 14 from the start of the mesocosm experiment. After a thorough mixing, an equal proportion of water (~10 liters) was taken from each enclosure, mixed in a container, and transported to the laboratory. The concentrations of phytoplankton pigments, particulate organic matter, protein, fatty acids, and cyanobacteria toxins, as well as the abundance of bacteria and ciliates in the mesocosm water at the start of each experiment, are given in Table 1.

Copepods in the experiments originated from the same area as the mesocosm water. Copepods were collected with a 200-μm plankton net 1 d prior to the experiments, placed into containers with water from below the thermocline, and quickly transported to the laboratory. Adult females were carefully picked out by use of a binocular microscope and placed in filtered seawater for 12–24 h to empty their guts and adapt to the experimental temperature (15°C).

For the grazing experiments, 20 adult females of both copepod species were placed into three–four replicate 1.2-liter bottles. In addition, three replicate control bottles without

animals were set up. All bottles were placed on a plankton wheel that rotated at ~1 rpm (rotor size 0.5 m), for ~24 h. At the beginning and the end of the experiment, two 100-ml water samples were preserved in acid Lugol's solution for microscopic counts, and 200 ml was filtered on GF/F filters (Whatman) and frozen at −20°C for pigment analysis. The concentration of ciliates was estimated from 50-ml samples by use of an inverted microscope. Pigments were analyzed with high-pressure liquid chromatography (HPLC) (Engström-Öst et al. in press).

Copepod filtration and ingestion rates were calculated according to the method of Frost (1972), from the disappearance of pigments and particles in bottles containing copepods compared with the controls without grazers. As a measure of copepod food selectivity, the selection index α was used, comparing the ingestion of ciliates or pigments (in carbon) to their availability (Chesson 1983). According to Chesson (1978) $\alpha > m^{-1}$, where m is number of food types, indicates positive selection. Therefore, in our experiments with seven–eight different food types (Table 2), a selection index >0.14 indicated positive selection.

Ingestion of ciliates was converted to carbon by use of species-specific wet weight values of K. Kivi (unpubl. data) and a wet weight-to-carbon conversion factor of 0.11 (Edler 1979). Chl *a* was converted to carbon with carbon-to-pigment conversion factors of 31, 59, and 47 for days 1, 7, and 14, respectively (*see Table 1*), derived from the measured particulate organic carbon (POC) : Chl *a* ratios in mesocosms, after removal of the contribution of total ciliate biomass from POC values.

To convert other phytoplankton pigments to carbon, a conversion factor for Chl *a* and other pigments was established (e.g., Meyer-Harms and von Bodungen 1997), separately for each experimental day, by use of a multiple-regression analysis of Chl *a* and the respective pigments measured in mesocosm enclosures. The respective equations for days 1, 7, and 14 were

$$\text{Chl } a = 0.7 + 3.6(\text{fuco}) + 4.1(\text{zea}) + 29(\text{Chl } b) + 13(\text{echi}) \quad (1)$$

$$\text{Chl } a = 1.4 + 1.8(\text{fuco}) + 3.5(\text{zea}) + 104(\text{Chl } b) + 4.1(\text{echi}) \quad (2)$$

$$\text{Chl } a = 8.6 + 0.7(\text{fuco}) + 6.3(\text{zea}) + 3.1(\text{hexa}) + 3.1(\text{echi}) \quad (3)$$

The r^2 for these regressions was 0.985, 0.978, and 0.980 for days 1, 7, and 14, respectively, with a significance level of $P < 0.01$ ($n = 10$). Phytoplankton groups and dominant species represented by each pigment are listed in detail in Engström-Öst et al. (in press); generally, echinenone and zeaxanthin represent cyanobacteria, fucoxanthin and 19′-hexanoyloxyfucoxanthin diatoms, prymnesiophytes and chrysophytes, and chlorophyll *b* chlorophytes, euglenophytes, and prasinophytes.

In egg production experiments, female *A. bifilosa* were sampled in a similar way as the copepods used in grazing experiments, but, in addition to the 12–24 h in filtered sea water, females were adapted to experimental food for the next 24 h. After this period, the contents of bottles were carefully filtered on a 200-μm net, and retained animals were flushed into a petri dish that contained filtered seawater. Actively swimming individuals were picked out, by use of a binocular microscope, and placed into three–four replicate 1.2-liter bottles (~20 females per bottle) that contained experimental water. After 24 h, the bottle contents were carefully filtered onto a 50-μm net and flushed into a petri dish, dead females removed, and healthy animals transferred to a new food solution. After 48 h, numbers of eggs and live and dead females were counted by use of a binocular microscope. Egg production of *A. bifilosa* was estimated for the 2 d subsequent to the adaptation period, whereas mortality was calculated cumulatively for the 3 d of incubation (1 d of adaptation + 2 d of experiment).

Filtered seawater and seawater enriched with a high concentration (>400 μg C L^{-1}) of the green flagellate *Brachiomonas submarina* were used as a reference of minimum and near maximum egg production potential of copepods. *B. submarina* was cultured in aerated batch cultures of ~3 liters, at 18°C and in a 18 h light : 6 h dark cycle, with use of Tv2 medium (Hällfors and Hällfors 1992). Cell concentrations and mean cell volumes for *B. submarina* were estimated by use of an ELZONE electronic particle counter (Particle Data Inc.). The carbon content of *B. submarina* cells was ~27 pg $cell^{-1}$ when the volume-carbon regression of Montagnes et al. (1994) was used.

All data were tested for normal distributions, and, if they were not met, data were log-transformed. Differences in copepod feeding (filtration and ingestion) and selection between days and copepod species were tested with a two-way multivariate analysis of variance (MANOVA), with copepod species and day as independent factors and filtration, ingestion, or selection of different foods as dependent variables. The MANOVA was followed by two-way analyses of variance (ANOVAs) on each of the foods. Egg production and mortality of *A. bifilosa* on different prey were tested with a two-way ANOVA that used food type and day as independent variables. In addition, differences in egg production between the 2 subsequent incubation days in the egg production experiments (24 and 48 h) were tested with use of the incubation day and food source as independent variables. Because there were no significant differences in egg production between the 2 d of incubation (two-way ANOVA; $F_{1,47} = 3.3$; $P > 0.05$), the 2-d average was used in further tests and in Fig. 1. The Bonferroni a posteriori test was used for pairwise comparisons. All statistical analyses were conducted by use of the SYSTAT 7.0 statistical package.

During the first week of the mesocosm experiment, cyanobacteria were actively growing, as indicated by an increase in Chl *a*, echinenone, and zeaxanthin concentrations from days 1 to 7 (Table 1). Thereafter, cyanobacteria decayed, as indicated by a decrease in the same pigments, an increase in the ratios of POC : particulate organic nitrogen (PON) and POC : particulate organic phosphorus (POP), and an increase in the concentration of ammonium. In addition, cyanobacteria filament length declined during the mesocosm experiment, from 288 ± 267 μm at day 1 to 158 ± 89 μm at day 14 (mean ± SD), and was visibly deteriorating at day 14. Bacteria volume and ciliate biomass increased between

Table 2. Filtration (F, ml ind^{-1} h^{-1}) and ingestion (I, μgC ind^{-1} d^{-1}) rates of *Acartia bifilosa* and *Eurytemora affinis* for phytoplankton pigments and ciliates at days 1, 7, and 14 from the start of the mesocosm experiment (mean ± SD). (N, No. of replicate experiments; —, missing values; and BD, below detection (concentration of pigment/ciliate too low to detect grazing). Other abbreviations as in Fig. 1.

	Day 1			Day 7			Day 14		
	F	I	N	F	I	N	F	I	N
A. bifilosa									
Chl *a*	0.5 ± 0.1	14 ± 2.5	3	−0.5 ± 0.2	−20 ± 7.2	4	0.01 ± 0.3	−0.02 ± 1.6	4
Chl *b*	−1.6 ± 1.3	−13 ± 14	3	BD	BD		BD	BD	
Fuco	−0.2 ± 0.2	−0.6 ± 0.5	3	−0.2 ± 0.5	−1.2 ± 2.6	4	0.1 ± 0.6	0.1 ± 0.7	4
Echi	1.3 ± 0.7	23 ± 11	3	−0.2 ± 0.2	−2.1 ± 2.1	4	BD	BD	
Zea	0.7 ± 0.6	1.8 ± 1.4	3	−0.1 ± 0.3	−0.7 ± 2.2	4	0.4 ± 0.3	0.6 ± 0.5	4
Cil <30	0.2 ± 0.6	0.02 ± 0.07	3	0.8 ± 0.9	0.1 ± 0.1	4	0.1 ± 0.5	0.01 ± 0.1	4
Cil >30	1.4 ± 1.5	0.09 ± 0.07	3	2.0 ± 0.6	0.2 ± 0.03	4	−1.2 ± 1.9	−0.08 ± 0.1	3
Urot	−0.4 ± 0.1	−0.005 ± 0.001	3	−0.2 ± 0.7	−0.001 ± 0.003	4	−1.4 ± 0.7	−0.02 ± 0.01	4
Mesod	BD	BD		0.2 ± 0.1	0.01 ± 0.003	3	BD	BD	
Eupl	BD	BD		BD	BD		0.3 ± 0.3	0.4 ± 0.4	4
E. affinis									
Chl *a*	0.2 ± 0.02	6.2 ± 0.7	3	−0.3 ± 0.1	−10 ± 4.6	4	−0.1 ± 0.1	−0.5 ± 0.4	3
Chl *b*	−0.4 ± 0.2	−2.1 ± 1.2	3	BD	BD		BD	BD	
Fuco	−0.2 ± 0.3	−0.6 ± 0.9	3	0.6 ± 0.6	2.6 ± 2.4	4	−0.1 ± 0.7	−0.2 ± 0.8	3
Echi	0.5 ± 0.3	10 ± 5.7	3	0.4 ± 0.4	3.7 ± 4.0	4	BD	BD	
Zea	−0.2 ± 0.5	−1.0 ± 1.7	3	0.3 ± 0.4	2.4 ± 2.7	4	0.2 ± 0.03	0.4 ± 0.06	3
Cil <30	5.6 ± 1.6	0.3 ± 0.02	3	1.5 ± 1.4	0.1 ± 0.1	3	−0.5 ± 0.3	−0.1 ± 0.1	3
Cil >30	—	—		−0.1 ± 0.3	−0.01 ± 0.03	3	−0.7 ± 2.0	−0.04 ± 0.1	2
Urot	6.1 ± 2.5	0.03 ± 0.004	3	0.3 ± 0.6	0.001 ± 0.002	3	0.02 ± 0.6	−0.001 ± 0.004	3
Mesod	BD	BD		1.8 ± 1.6	0.03 ± 0.02	3	BD	BD	
Eupl	BD	BD		BD	BD		0.1 ± 0.2	0.1 ± 0.3	3

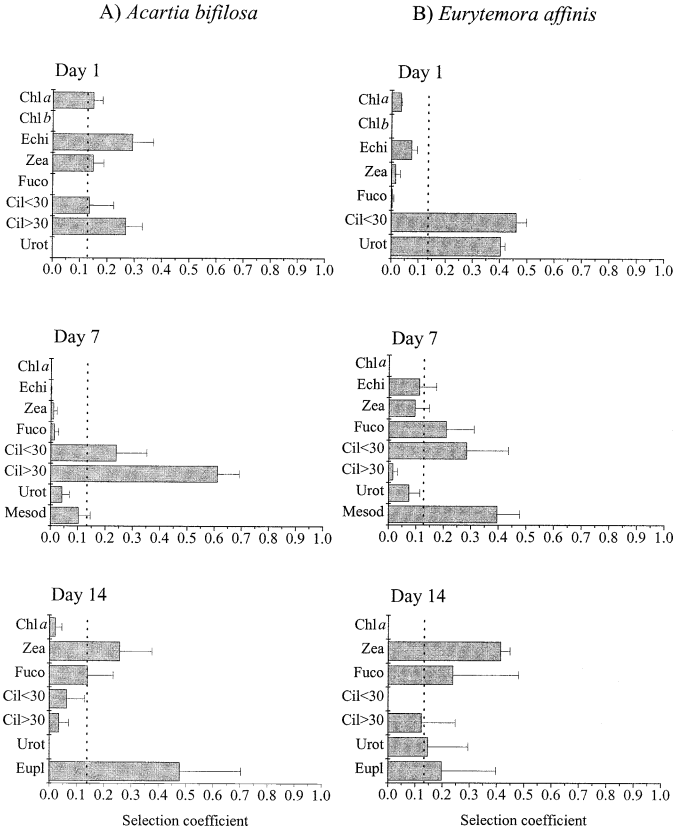

Fig. 1. Selection coefficient (α) for (A) *A. bifilosa* and (B) *E. affinis* grazing on different food items at days 1, 7, and 14 from the start of the mesocosm experiment (mean ± SE). The dotted line indicates the value of α when the food item is eaten in the same proportion as it occurs in the seston (no selection). Echi, echinenone; Zea, zeaxanthin; Fuco, fucoxanthin; Cil <30, Ciliate spp. <30 μm; Cil >30, Ciliate spp. >30 μm; Urot, *Urotricha* sp.; Mesod, *Mesodinium* sp.; and Eupl, *Euplotes* sp.

subsequent experiments (from 0.8 to 11 μm^3 and from 6.2 to 50 μgC L^{-1}, respectively), which suggests that cyanobacteria decay increased the proportion of heterotrophic food items (ciliates and possibly detritus), whereas the availability of autotrophic food declined. Concentrations of total proteins (8.1 at day 7 vs. 18 μg L^{-1} at day 14) and fatty acids (380 vs. 420 μg L^{-1}), as well as saturated (140 vs. 180 μg L^{-1}) and monounsaturated (69 vs. 100 μg L^{-1}) fatty acids, were higher at day 14, whereas the concentration of polyunsaturated fatty acids (140 vs. 86 μg L^{-1}) and the $\varpi 3/\varpi 6$ ratio (9.6 vs. 7) were higher at day 7. The total concentration of nodularin (cell bound + dissolved) remained nearly constant during the experiment, being always >9 μg L^{-1} (Table 1).

Filtration and ingestion rates of the different food items were mostly variable, ranging from negative values to 6.1 ml ind^{-1} h^{-1} and 23 μg C ind^{-1} d^{-1}, respectively (Table 2). Both ingestion and filtration rates were significantly different between days (MANOVA; Pillai's trace: $F_{10,24} = 24$ and 11, respectively; $P < 0.001$) and the two copepod species ($F_{5,11} = 24$ and 7.9, respectively; $P < 0.01$). Furthermore, the copepod × day interaction was significant both for ingestion and filtration ($F_{10,24} = 5.4$ and 3.5, respectively; $P < 0.01$). The differences in ingestion and filtration between days were mainly due to the differences in ingestion−filtration of Chl *a* (two-way ANOVA; $F_{2,15}$ = respectively, 71 and 40; $P < 0.001$), <30 μm ciliates ($F_{2,15} = 9.3$ and 18, respectively; $P < 0.01$), and *Urotricha* sp. ($F_{2,15} = 113$ and 20, respectively; $P < 0.001$), whereas ingestion−filtration of <30 μm ciliates ($F_{1,15} = 9.3$ and 20, respectively; $P < 0.01$) and *Urotricha* sp. ($F_{1,15} = 156$ and 35, respectively; $P < 0.001$) accounted for the differences between copepod species.

At day 1, both copepod species fed on phytoplankton (mainly cyanobacteria; 0.5–1.3 ml ind^{-1} h^{-1}) and ciliates. However, *A. bifilosa* fed predominantly on larger ciliates (1.4 ml ind^{-1} h^{-1}), whereas the filtration rate of *E. affinis* was higher on <30 μm ciliates (including *Urotricha* sp.; ~6 ml ind^{-1} h^{-1}). Still, because of the very high phytoplankton biomass at day 1, ingestion rates of both copepod species were higher on cyanobacteria (23 and 10 μgC ind^{-1} d^{-1} for *A. bifilosa* and *E. affinis*, respectively) than on other food items (<2 μgC ind^{-1} d^{-1}) (Table 2).

At day 7, both copepods fed mostly on heterotrophic food, even though *E. affinis* was also feeding on algae. Filtration of <30 μm ciliates (0.8 and 1.5 ml ind^{-1} h^{-1} for *A. bifilosa* and *E. affinis*, respectively) and *Mesodinium* sp. (respectively, 0.2 and 1.8 ml ind^{-1} h^{-1}) by both copepods, as well as filtration of >30 μm ciliates by *A. bifilosa* (2.0 ml ind^{-1} h^{-1}) were higher than filtration of phytoplankton (<0.6 ml ind^{-1} h^{-1}). Again, *E. affinis* ingested more phytoplankton (>2.4 μgC ind^{-1} d^{-1}) than ciliates (0.1 μgC ind^{-1} d^{-1}). At day 14, there were no differences in filtration or ingestion rates among food species, but observed feeding rates were quite variable (Table 2).

The selection index α was significantly different over the experiment (MANOVA; Pillai's trace: $F_{10,24} = 7.4$; $P < 0.001$) but not between copepods ($F_{5,11} = 2.2$; $P > 0.05$). The copepod × day interaction was not significant ($F_{10,24} = 1.4$; $P > 0.05$). Differences in selectivity between days was mostly due to differences in the selection index for Chl *a* (two-way ANOVA; $F_{2,15} = 36$; $P < 0.001$) and <30 μm ciliates ($F_{2,15} = 8.4$; $P < 0.01$). At day 1, both copepods selected more ciliates than most phytoplankton groups (with the exception of cyanobacteria, indicated by echinenone) and more cyanobacteria than other phytoplankton (fucoxanthin and chlorophyll *b*). *A. bifilosa* selected larger ciliates, whereas *E. affinis* selected small ciliates, including *Urotricha* sp. At day 7, selection coefficients indicated that most ciliates were preferred, even though *E. affinis* also fed on cyanobacteria and other algae. At day 14, selection for some phytoplankton groups (cyanobacteria, chrysophytes, or prymnesiophytes) and/or some ciliates (*Euplotes* sp.) was noted for both copepods (Fig. 2).

Food effects on fecundity were also related to food quality. Egg production in *A. bifilosa* was significantly different between foods (two-way ANOVA; $F_{2,21} = 97$, $P < 0.0001$) and days ($F_{2,21} = 13$, $P < 0.0001$). Egg production of *A. bifilosa* in mesocosm water was 5–8 eggs $female^{-1}$ d^{-1}, which is not significantly different from egg production in the good food control (*B. submarina*, 3–5 eggs $female^{-1}$ d^{-1}; Bonferroni; $P > 0.05$); egg production in filtered sea water was always significantly lower (<2 eggs $female^{-1}$ d^{-1}; Bonferroni; $P < 0.05$). When egg production in mesocosm water

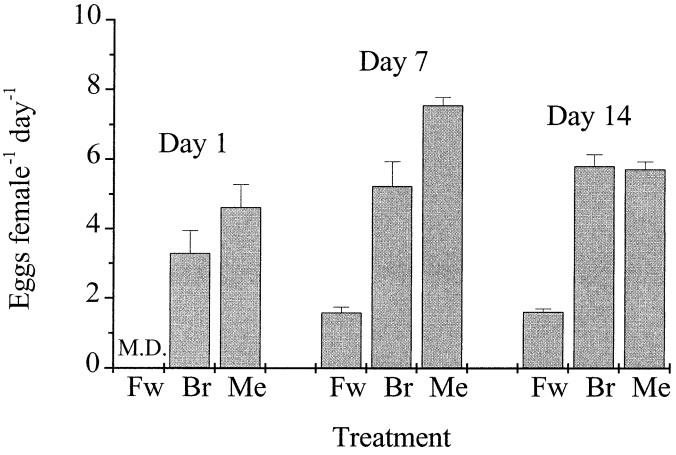

Fig. 2. Egg production (number of eggs female^{-1} d^{-1}) of *A. bifilosa* in filtered seawater, in *B. submarina* control and in mesocosm water at days 1, 7, and 14 from the start of the mesocosm experiment (mean ± SE). FW, filtered sea water; Br, *B. submarina;* Me, mesocosm water; and M.D., missing data.

was expressed as a percentage of that noted in *B. submarina* control of the corresponding day, significantly higher egg production was observed at days 1 and 7 (139 ± 33% and 145 ± 10%, respectively) than at day 14 (97 ± 6%) (Bonferroni; $P < 0.05$), which indicates that relatively more eggs were produced when cyanobacteria were actively growing (Fig. 1).

Egg production in *B. submarina* was significantly lower at day 1 than at days 7 or 14 (Bonferroni; $P < 0.05$), which indicates that copepods were initially in poor condition in this experiment. This was also indicated by the high mortality of *A. bifilosa* at day 1 in all treatments (56 ± 20%, 61 ± 34%, and 59 ± 6% in filtered seawater, *B. submarina*, and mesocosm water, respectively), in contrast with low mortality in all treatments at days 7 and 14 (<8%, irrespective of the treatment). Because of the high mortality at day 1, mortality of *A. bifilosa* was significantly different over the experiment (two-way ANOVA; $F_{2,21} = 61$, $P < 0.0001$) but not between treatments ($F_{2,21} = 1.1$, $P > 0.05$).

Grazing on both phytoplankton and heterotrophic organisms was detected during bloom succession. At day 1, copepods were feeding on phytoplankton. Although the filtration rates on Chl *a* and other pigments were high, they were still in the range of values reported elsewhere (Burns and Hegarty 1994; Engström et al. 2000). However, ingestion rates were extremely high, generally more than three times higher than observed earlier (Meyer-Harms and von Bodungen 1997; Engström et al. 2000). This was probably due to the very high concentrations of cyanobacteria in mesocosm water, which allowed copepods to consume large quantities, possibly to compensate for the low quality of the cyanobacteria diet (*see* Cruz-Rivera and Hay 2000). On the basis of changes in bulk chlorophyll and estimated ratios between chlorophyll and accessory pigments, it therefore appears that Baltic copepods may graze cyanobacteria at higher rates than has been reported elsewhere (Sellner et al. 1996; Meyer-Harms et al. 1999). These differences could be better resolved after future direct measurements of copepod ingestion (gut content).

Despite the high ingestion of cyanobacteria at day 1, copepods generally selected ciliates over phytoplankton, in accord with previous findings (Wiadnyana and Rassoulzadegan 1989). The observed filtration and ingestion rates of ciliates (up to 6 ml ind^{-1} d^{-1} and 0.3 μgC ind^{-1} d^{-1}) were within the range of earlier studies (Tiselius 1989; Wiadnyana and Rassoulzadegan 1989). The contribution of ciliates to the diet of *A. bifilosa* increased from <1% at day 1 to ~22% and 54% at days 7 and 14, respectively. This increase corresponded to a respective increase of ciliate abundance in the seston, from <10 μgC L^{-1} up to 14 and 50 μgC L^{-1}. The increased consumption of ciliates with their increased concentration is consistent with observations in Tiselius (1989) that, at low ciliate concentrations, the ciliate contribution to a copepod's diet is negligible. Because summer ciliate concentrations in the Baltic Sea are generally <5 μgC L^{-1} (Kivi 1986), increased ciliate numbers during cyanobacteria bloom decay may improve possibilities for copepod feeding on heterotrophic organisms.

A. bifilosa was able to produce eggs in mesocosm water throughout the experiment. The maximum egg production was ~8 eggs female^{-1} d^{-1}, which is lower than the maximum egg production of this species reported in previous studies (~20 eggs female^{-1} d^{-1} with *B. submarina* diet; Sellner et al. 1996), which possibly indicates that food quality was not optimal. However, because egg production in mesocosm water was equal or higher than that noted in the *B. submarina* control, the low egg production level was likely related to the condition of the copepods rather than to food quality.

Egg production of *A. bifilosa* in mesocosm water was significantly higher (as a percentage of the *B. submarina* control) at days 1 and 7, when copepods were feeding on actively growing cyanobacteria and ciliates, than at day 14, when the bloom was visibly decaying. These results thus did not fully support the hypothesis of the better food quality of the decaying cyanobacteria bloom: perhaps an actively growing cyanobacteria population with increasing concentrations of ciliates might provide the best nutrition for *A. bifilosa.*

Cyanobacteria biomass or toxins (>9 μg L^{-1}) did not seem to have any negative effect on grazing, egg production, or survival of copepods, similar to observations of M. Reinikainen (pers. comm.). This suggests that the tolerance of *A. bifilosa* and *E. affinis* for cyanobacteria toxins is high. If these copepod species are resistant to cyanobacteria toxins, the cyanobacteria blooms in the Baltic could provide an abundant food source of reasonable quality in otherwise low food conditions of the late summer. For instance, the seston POC : PON and POC : POP ratios in the mesocosm water (<5.8 and <68, respectively) were considerably lower than those in the open Baltic Sea in June–July (respectively, 7–8 and >60; Heiskanen and Tallberg 1999) and the concentration of different polyunsaturated fatty acids high (>80 μg L^{-1}; cf. <12 μg L^{-1} in Jónasdóttir et al. 1995). However, we did not measure the hatching success of eggs, which is likely to be more sensitive to inhibitory compounds than fecundity (Miralto et al. 1999). Therefore, even though the

composition of seston during the growth and decay of the cyanobacteria bloom seemed to have been favorable for copepod egg production, the hatching success of eggs must be measured before the effects of cyanobacteria blooms on copepod recruitment are estimated.

Mass occurrences of the cyanobacteria *Aphanizomenon flos-aquae* and *N. spumigena* are a common phenomenon in the Baltic Sea during late summer and early autumn (Kononen et al. 1996), coinciding with the peak abundance of mesozooplankton (Viitasalo 1992). These cyanobacteria blooms were simulated by the addition of a high concentration of cultured toxic *N. spumigena* to <100-μm filtered natural sea water. Cyanobacteria densities and nodularin concentrations produced in these experiments, comparable to or higher than those observed in the Baltic Sea during naturally occurring blooms (Sivonen et al. 1989; Kononen et al. 1996; Kankaanpää et al. 2001), were far from inhibitory to summer copepod populations. Both copepod species fed on cyanobacteria and the associated fauna, and *A. bifilosa* produced eggs and survived. Hence, the results do not support the general view of detrimental effects of cyanobacteria on copepod feeding and fecundity but show that the dominant calanoid copepod species of the Baltic Sea are able to survive and produce eggs in these blooms and potentially use cyanobacteria as a food source. The results further stress the importance of studies that include the entire plankton community rather than monocultures or mixtures of a few species to reveal effects of cyanobacteria blooms on mesozooplankton.

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Variation in iron(III) solubility and iron concentration in the northwestern North Pacific Ocean

Abstract—Vertical distributions of Fe(III) hydroxide solubilities (<0.025 μm) and dissolved Fe (<0.2 μm) concentrations at 0–250 m depth were studied inside (HP) and outside (LP) a high-production (phytoplankton spring bloom) patch area in the northwestern North Pacific Ocean during May 1999. In the surface mixed layer, the Fe(III) solubility values at HP were much higher (2–4 nM) than those (0.3–0.9 nM) at LP and strongly correlated with chlorophyll *a* and nutrient concentrations. The high Fe(III) solubility observed in the surface mixed layer was probably due to a higher concentration or stronger affinity of natural organic Fe(III) chelators. In the surface waters, the dissolved Fe concentrations were generally