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Reproduction and survival of the calanoid copepod *Eurytemora affinis* fed with toxic and non-toxic cyanobacteria

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ABSTRACT: Reproduction (egg production and hatching success) and maintenance (mortality and carbon and nitrogen content) of the calanoid copepod *Eurytemora affinis* were measured at 5 concentrations (ca 50, 100, 200, 400 and 600 µg C l^{-1}) of toxic and non-toxic strains of the cyanobacterium *Nodularia* sp. and the green alga *Brachiomonas submarina*, and in 3 different mixtures of these species (1:1, 8:1 and 1:8). In addition, females with egg-sacs were collected from the sea and exposed to different concentrations of *Nodularia* sp., to find out whether cyanobacterial exudates disturb hatching of eggs produced in natural food conditions. With the *B. submarina* diet copepod egg production was high (maximum ca 7 eggs $female^{-1}$ d^{-1}), and increased with increasing food concentration, whereas with both toxic and non-toxic *Nodularia* sp. diet egg production was comparable to that in filtered sea water (0 to 2 eggs $female^{-1}$ d^{-1}), irrespective of food concentration. With both toxic and non-toxic *Nodularia* sp., copepods produced deformed egg-sacs, and hatching success was low, while eggs produced in natural food conditions hatched well, with the exception of those exposed to a high concentration of toxic *Nodularia* sp. Mortality of *E. affinis* fed with toxic *Nodularia* sp. was high, whereas high concentrations of non-toxic *Nodularia* sp. kept copepods alive. No beneficial effects of *Nodularia* sp. in mixtures with *B. submarina* were observed. However, mortality in mixtures with toxic *Nodularia* sp. was low, hatching success generally high and no deformed egg-sacs were produced, which indicated that copepods were able to avoid feeding on toxic algae. Our results suggest that, in addition to its toxic effect, *Nodularia* sp. lacks certain essential elements needed for copepod reproduction. However, the non-toxic strain is sufficiently high in food quality to sustain maintenance of *E. affinis*, if offered in large quantities.

KEY WORDS: Copepod · Cyanobacteria · *Eurytemora affinis* · *Nodularia* sp. · Toxicity · Egg production · Hatching success · Survival

INTRODUCTION

Cyanobacteria are generally assumed to be poor food for aquatic crustaceans (Porter & Orcutt 1980). The negative effects of these may be due to mechanical interference with feeding (Infante & Abella 1985) or toxic substances (DeMott et al. 1991, Reinikainen et al. 1995). Further, the nutritional value of cyanobacteria is low, for instance, because they contain low amounts of long-chain polyunsaturated fatty acids that are essential for growth of aquatic invertebrates (Ahlgren et al. 1992, Müller-Navarra 1995). Poor growth and reproduction of crustaceans fed on a cyanobacterial diet has been observed, e.g. by Arnold (1971), Lampert (1981, 1987), Nizan et al. (1986) and Xu & Burns (1991).

However, certain copepod species feed actively on cyanobacteria (Burns & Xu 1990a, Burns & Hegarty 1994), and some species of cyanobacteria have been shown to sustain egg production and growth of copepods (Burns & Xu 1990b, Xu & Burns 1991, respectively) and crustaceans (Repka 1996, 1997). Further, increased reproduction is sometimes observed in mixtures of cyanobacteria and other food species (Schmidt & Jónasdóttir 1997, DeMott 1998, Twombly et al. 1998). These effects may be due to the high energy content and low C:N ratio of cyanobacteria (Burns & Xu 1990a, Sterner & Robinson 1994) or the substantial amount of

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certain amino acids (Schmidt & Jónasdóttir 1997), which may be beneficial for copepods, especially if other food sources with other essential elements are available (Burns & Hegarty 1994). Thus, cyanobacteria may complement diet if offered in mixtures with other species (DeMott 1998).

Species- and age-specific differences in the response of crustaceans to cyanobacteria are likely to occur (Gilbert 1990, Xu & Burns 1991). The sensitivity of crustacean zooplankton to harmful or toxic cyanobacteria depends on their ability to select food particles (avoiding cyanobacteria) and on their sensitivity to toxins (DeMott & Moxter 1991, DeMott et al. 1991, Kirk & Gilbert 1992). In general, cladocerans are less selective, but also less sensitive, while copepods are often highly sensitive to toxins, but able to avoid ingesting toxic cells (DeMott & Moxter 1991, DeMott et al. 1991). Further, different species and development stages have different nutritional requirements (Xu & Burns 1991), and different nutritional qualities are needed for reproduction, growth and maintenance (Sterner & Robinson 1994). These factors are likely to make responses of zooplankton to cyanobacteria species-specific and complicated (Turner & Tester 1997).

Most of the previous studies on zooplankton-cyanobacterium interactions have been made in fresh water, with cladocerans and cyanobacterial taxa such as *Microcystis*, *Anabaena* and *Oscillatoria*. However, cyanobacteria are also typical for certain brackish water areas and enclosed seas (Richardson 1997, Sellner 1997). In the Baltic Sea, blooms of the cyanobacteria *Nodularia* sp. and *Aphanizomenon flos-aquae* are common in late summer and autumn (Kononen et al. 1996), when the highest mesozooplankton biomass and production also occur (Viitasalo et al. 1995, Koski et al. 1999). Most of the *Nodularia* sp. strains isolated from the Baltic are hepatotoxic, containing the cyclic pentapeptide nodularin, while blooms dominated by *A. flos-aquae* are generally not toxic (Sivonen et al. 1989). Toxicity of blooms may also fluctuate rapidly (Carmichael & Gorham 1981), due to, for example, changing environmental conditions (Rapala et al. 1993).

According to previous studies conducted in the Baltic Sea (Sellner et al. 1994, 1996) copepod ingestion and egg production rates were strongly reduced during cyanobacterial blooms. However, it was not clear if copepods suffered from toxic substances or were simply not able to gather enough high-quality food to reproduce. We investigated this by offering the calanoid copepod *Eurytemora affinis* both toxic (nodularin producing) and non-toxic strains of the cyanobacterium *Nodularia* sp. and measuring their effect on copepod reproduction (egg production and hatching success) and maintenance (survival and C:N content). The aims of the study were to reveal (1) if copepods are able either to reproduce or to survive on a *Nodularia* sp. diet, (2) if the negative effects of *Nodularia* sp. are due to toxicity or poor nutritional quality and (3) if *Nodularia* sp. can supplement the diet if mixed with other food sources.

MATERIAL AND METHODS

Algae. Experiments were conducted with the green alga *Brachiomonas submarina* and 2 different strains of the cyanobacterium *Nodularia* sp., cultured in aerated batch cultures of ca 3 l, at 18°C and in an 18 h light:6 h dark cycle. *B. submarina* culture was obtained from the culture collection of S. and G. Hällfors at Tvärminne Zoological Station (Hällfors & Hällfors 1992). The 2 *Nodularia* sp. strains were isolated from the Baltic Sea (Lehtimäki et al. 1994) and belonged to the culture collection of K. Sivonen (Department of Applied Chemistry and Microbiology, University of Helsinki). Tv2 medium (Hällfors & Hällfors 1992) and modified Z8 medium (Lehtimäki et al. 1994) were used as culture media for *B. submarina* and *Nodularia* sp., respectively. The nodularin content in the toxic *Nodularia* sp. strain (HKVV) was 0.58 ± 0.566 µg mg^{-1} dry wt^{-1}, whereas the other strain (HEM) did not contain any nodularin. The *Nodularia* sp. strain which did not produce nodularin is referred to as non-toxic, and the one which produced nodularin, as toxic, irrespective of other possibly toxic substances which they may produce. All cultures were unialgal but not free of bacteria.

The cell volume and concentration of *Brachiomonas submarina* in cultures were estimated with an ELZONE electronic particle counter (Particle Data Inc.) before each experiment. To achieve the right food concentration for experiments, the average carbon content of *B. submarina* cells was estimated from the measured average volume of 257 μm^3 and carbon-to-volume regression of Montagnes et al. (1994) (27 pg C $cell^{-1}$). Cyanobacterial concentrations were determined spectrophotometrically using a calibration curve of extinction versus carbon concentration, which was derived from chemical oxygen-demand measurements (Gulati et al. 1991).

Copepods. All experiments were conducted with a calanoid copepod *Eurytemora affinis* (Poppe) collected from an open archipelago area on the SW coast of Finland. Copepods were collected with a 200 µm plankton net, with a single haul from near the bottom to the surface, carefully spooled to 30 l containers together with water from near the bottom and directly transported to the laboratory. Carbon and nitrogen content of the freshly collected females were measured from 3 replicate samples (ca 10 ind. $sample^{-1}$), with a stable isotope analyser (RoboPrep-TracerMass ANCA-MS), after drying for 24 h at 60°C in the oven.

Table 1 Starting date of the experiments, alga species and concentrations used, number of replicates (n), average carbon content of copepods (*Eurytemora affinis*) in the field at the beginning of each experiment (µg C ind.$^{-1}$), and average egg production (Ep) in filtered sea water control of each experiment (eggs female^{-1} d^{-1}). (FW: filtered sea water; N: non-toxic *Nodularia* sp.; Nt: toxic *Nodularia* sp.; Br: *Brachiomonas submarina*.) *Female carbon content or egg production which is significantly different (Tukey HSD; $p < 0.05$) from values in other experiments. Means ± standard deviations are denoted

Date	Experiment			Copepod	
	Algae	Conc.	n	Carbon	Ep in FW
23 Jun	FW	0	2	1.8 ± 0.3*	0.5 ± 0.2
	N	50–600	2		
	Nt	50–600	2		
1 Jul	FW	0	2	3.5 ± 0.5	2.1 ± 1.1
	Br	50–600	2		
	Br + N	200+200	3		
	Br + Nt	200+200	3		
	Br + N	400+50	2		
	Br + Nt	400+50	3		
7 Jul	FW	0	2	3.6 ± 0.3	5.1 ± 2.2*
	Br	50–600	1		
	N	50–600	1		
	Nt	50–600	1		
	Br + N	50+400	3		
	Br + Nt	50+400	3		
21 Aug	FW	0	2	3.0 ± 0.2	1.6 ± 1.4
	Br	50, 200, 400	2		
	N	50, 200, 400	2		
	Nt	50, 200, 400	2		
	Br + N	200+200	3		
	Br + Nt	200+200	3		

Experiments were conducted at 4 different time periods from June to August 1998 (Table 1), and the copepods used in experiments were thus likely to belong to different generations. The copepods used in the first experiment were significantly smaller (in carbon content) than copepods used in later experiments (Tukey HSD; $p < 0.05$). Further, copepods used in the 3rd experiment produced significantly more eggs in filtered sea water (Tukey HSD; $p < 0.05$) than copepods in the other experiments. However, despite the differences in egg production rate between copepod generations, the relative response of copepods to food species remained the same with every generation (e.g. egg production was always low with *Nodularia* sp. diet).

Experiments. Egg production, hatching success, mortality and carbon and nitrogen content of *Eurytemora affinis* were measured at 5 concentrations (ca 50, 100, 200, 400 and 600 µg C l^{-1}) of *Brachiomonas submarina* and toxic and non-toxic *Nodularia* sp., and at 3 different mixtures of *B. submarina* offered together with either toxic or non-toxic *Nodularia* sp. (1:1: ca 200 + 200 µg C l^{-1} of each alga, 8:1: 400 µg C l^{-1} of *B. submarina* + 50 µg C l^{-1} of *Nodularia* sp. and 1:8: 50 µg C l^{-1} of *B. submarina* + 400 µg C l^{-1} of *Nodularia* sp.). In addition, hatching success of eggs produced in natural food conditions in the sampling area, and directly exposed to 3 different concentrations (50, 200 and 400 µg C l^{-1}) of *B. submarina* or toxic or non-toxic *Nodularia* sp., was analysed, to reveal possible effects of phytoplankton exudates on the hatching of eggs. Replicate experiments (2 to 5) were conducted with every diet. Since several copepod generations were used in experiments, a 0.2 µm filtered sea water control was included in every series of experiments. Due to differences in the egg production rate between copepod generations (cf. Table 1), egg production was also considered as a percentage of the egg production in filtered sea water in the corresponding experiment.

For the egg production experiments, females with or without egg-sacs were picked with a small amount of water and transferred to filtered sea water for ca 24 h to adapt to the experimental temperature (13°C). Afterwards, females were placed into 1.15 l bottles (ca 10 females bottle^{-1}) containing the desired food solution, and actuated with a plankton-wheel at a turning speed of ca 1 round min^{-1}. After a 24 to 48 h adaptation period, females were carefully filtered onto a 200 µm net to remove phytoplankton, eggs and nauplii, and changed to a new food solution to start the experiment. After 48 h, females and eggs were filtered onto a 50 µm net, and eggs and dead individuals were counted. Egg production was estimated according to

$$P = N_e / (N_f D)$$

where P is the egg production (eggs female^{-1} d^{-1}), N_e is the number of eggs at the end of the experiment, N_f is the number of females and D is the development time of eggs (in days). Development time of eggs at 13°C was assumed to be 2.2 d (Andersen & Nielsen 1997). Half of the females with egg-sacs were placed in petri dishes with filtered sea water and left at 13°C for ca 5 d after which the number of nauplii was counted. In experiments where a only few eggs were produced, several replicates were combined to achieve >15 eggs per hatching experiment. Remaining females were prepared for C:N analyses as described before. In order to obtain at least 2 replicate C:N analyses per treatment, females from 50 and 100 µg C l^{-1} and 400 and 600 µg C l^{-1} treatments were analysed together. No C:N analyses were obtained in mixture experiments.

For the additional hatching experiment, females with egg-sacs were collected from the sampling area as described before, and placed directly into 1.15 l bottles containing the experimental food solution. Water in these bottles was renewed daily. After 5 d of incubation, females and nauplii were filtered onto a

50 µm net, and eggs and nauplii were counted. This experiment was conducted simultaneously with the last egg production experiment (21 August; Table 1).

Differences in egg production, hatching success, mortality and carbon and nitrogen content of copepods between treatments were tested with 1-way analyses of variance (ANOVA) with the SYSTAT statistical package (SPSS Inc., Chicago). The effects of food concentration and food species on egg production, hatching success and mortality of copepods were tested separately for each food species (FW + 5 food concentrations) and each food concentration (3 food species per concentration), respectively. In contrast, the effect of food concentration and species on copepod carbon and nitrogen content and C:N ratio was tested together for all treatments. Tukey's *a posteriori* HSD test was used for pairwise comparisons.

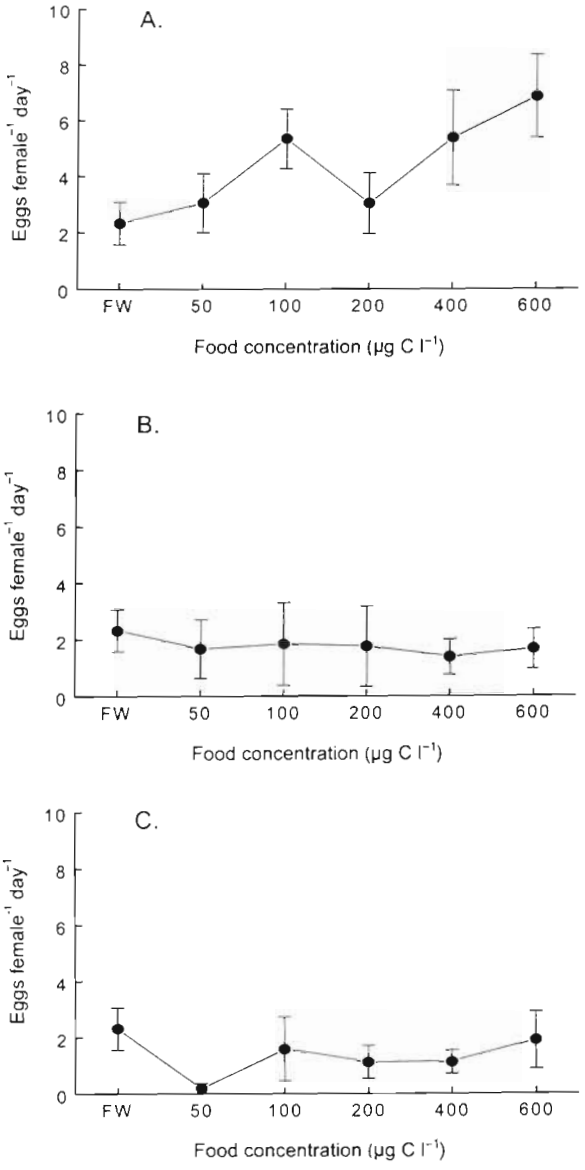

Fig. 1. *Eurytemora affinis*. Mean egg production (eggs female^{-1} d^{-1}) in different concentrations of (A) *Brachiomonas submarina*, (B) non-toxic *Nodularia* sp., and (C) toxic *Nodularia* sp. Data denote means and standard errors; n = 3 to 5 (FW: filtered sea water)

RESULTS

Egg production

Egg production of *Eurytemora affinis* with a *Brachiomonas submarina* diet increased with increasing food concentration, with the exception of unexplained low egg production at the food concentration of 200 µg C l^{-1} (Fig. 1). Egg production with *B. submarina* was always higher than that in filtered sea water; at the lowest food level (ca 50 µg C l^{-1}) egg production corresponded on average to 125% of the egg production in filtered sea water, while at the highest food level the egg production was ca 3 times higher than in filtered sea water in the corresponding experiment (Table 2). At the highest food concentration (600 µg C l^{-1}), egg production was in the range of literature values of maximum egg production of sac-spawning copepods (ca 7 eggs female^{-1} d^{-1} or ca 8% of body weight d^{-1}; Kiørboe & Sabatini 1995) (Table 2), even though higher egg production rates have also been recorded for *E. affinis* (Hirche 1992, Ban 1994). In the same study area the egg production of *E. affinis* in July 1998 was observed to be ca 8 eggs female^{-1} d^{-1} (unpubl. data); thus the lower values in the present study indicated

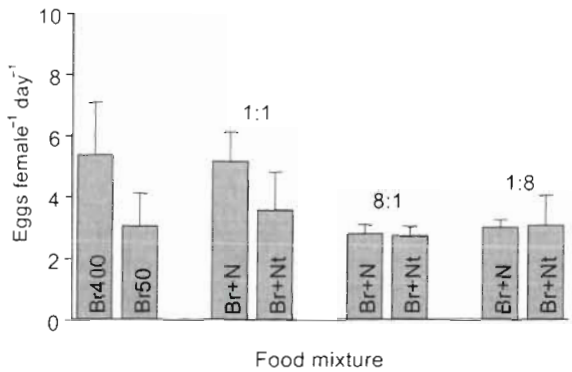

Fig. 2. *Eurytemora affinis*. Mean egg production (eggs female^{-1} d^{-1}) in mixtures of *Brachiomonas submarina* (Br) and non-toxic and toxic *Nodularia* sp. (N and Nt, respectively), and with corresponding concentrations (400 and 50 µg C l^{-1}) of *B. submarina* as a sole food (Br400 and Br50, respectively). Food concentrations used were: 200 + 200 µg C l^{-1} (1:1), 400 + 50 µg C l^{-1} (8:1) and 50 + 400 µg C l^{-1} (1:8) of *B. submarina* and *Nodularia* sp., respectively. Error-bars denote standard errors; n = 2 to 6

Table 2. *Eurytemora affinis*. Average egg production (as eggs female^{-1} d^{-1}, as % of body carbon d^{-1} and as % of the egg production in filtered sea water in corresponding experiment), average percentage of females with deformed egg-sacs (%), average mortality of females (%) in experiments with different food species and concentrations and number of replicate experiments (n). The percentage of egg production from that in filtered sea water is calculated separately for each experiment (cf. Table 1); the values presented in the table are the average of these. Means ± standard deviations are denoted. Abbreviations as in Table 1

Algae	Conc. (µg C l^{-1})	Egg production			Deformed eggs (%)	Mortality (%)	n
		Eggs fem^{-1} d^{-1}	% body weight	% FW			
FW	0	2.3 ± 2.1	2.9 ± 2.6		7.3 ± 8.9	26 ± 33	8
Br	50	3.0 ± 2.4	3.8 ± 2.9	125 ± 107	4.2 ± 5.8	0 ± 0	5
	100	5.3 ± 1.9	6.6 ± 2.3	226 ± 143	0 ± 0	0 ± 0	3
	200	3.0 ± 2.4	3.8 ± 3.0	128 ± 117	0 ± 0	2.5 ± 5.6	5
	400	5.4 ± 3.8	6.7 ± 4.7	226 ± 176	0 ± 0	2.2 ± 5.0	5
	600	6.9 ± 2.6	8.5 ± 3.2	287 ± 180	0 ± 0	0 ± 0	3
N	50	1.7 ± 2.3	2.0 ± 2.8	110 ± 164	13 ± 11	29 ± 44	5
	100	1.8 ± 2.5	2.3 ± 3.1	81 ± 75	15 ± 9.2	20 ± 19	3
	200	1.8 ± 3.2	2.2 ± 3.9	65 ± 71	4 ± 5.5	22 ± 30	5
	400	1.4 ± 1.4	1.7 ± 1.7	145 ± 256	2 ± 4.5	6 ± 8.9	5
	600	1.7 ± 1.2	2.1 ± 1.5	208 ± 276	4.4 ± 7.7	2.2 ± 3.9	3
Nt	50	0.2 ± 0.4	0.2 ± 0.5	3.6 ± 8.0	24 ± 15	72 ± 45	5
	100	1.6 ± 2.0	1.9 ± 2.5	84 ± 90	8.3 ± 14	44 ± 32	3
	200	1.1 ± 1.3	1.4 ± 1.6	67 ± 75	6.7 ± 15	55 ± 35	5
	400	1.1 ± 0.9	1.4 ± 1.1	152 ± 186	13 ± 10	63 ± 29	5
	600	1.9 ± 1.8	2.3 ± 2.2	243 ± 385	3.7 ± 6.4	63 ± 40	3
Br + N	200 + 200	5.2 ± 2.3	6.4 ± 2.9	281 ± 127	0 ± 0	0 ± 0	6
Br + Nt	200 + 200	3.6 ± 3.0	4.4 ± 3.7	183 ± 139	0 ± 0	0 ± 0	6
Br + N	400 + 50	2.8 ± 0.4	3.5 ± 0.5	136 ± 19	0 ± 0	0 ± 0	2
Br + Nt	400 + 50	2.7 ± 0.5	3.4 ± 0.6	133 ± 23	0 ± 0	0 ± 0	3
Br + N	50 + 400	3.0 ± 0.4	3.7 ± 0.5	59 ± 7.9	0 ± 0	0 ± 0	3
Br + Nt	50 + 400	3.1 ± 1.7	3.8 ± 2.1	60 ± 33	0 ± 0	13 ± 23	3

that *B. submarina* may not have been the optimal food for the egg production of *E. affinis*.

The food concentration did not affect egg production with either non-toxic (1-way ANOVA; df = 5, $F = 0.126$, $p > 0.05$) or toxic (1-way ANOVA; df = 5, $F = 1.281$, $p > 0.05$) *Nodularia* sp. as food: egg production was not significantly different from that in filtered sea water (0 to 2 eggs female^{-1} d^{-1} or 0 to 2% of body carbon d^{-1}), irrespective of the toxicity of the strain or food concentration (Fig. 1, Table 2). Further, with both non-toxic and toxic *Nodularia* sp. as food, egg production was always lower than with the *Brachiomonas submarina* diet; in high food concentrations (400 to 600 µg C l^{-1}) this difference was statistically significant (Tukey HSD; $p < 0.05$).

In mixture experiments egg production varied from 3 to 5 eggs female^{-1} d^{-1} (3 to 6% of body weight d^{-1}), which was not significantly different from egg production in the corresponding concentration (ca 400 µg l^{-1}) of *Brachiomonas submarina* (1-way ANOVA; df = 6, $F = 0.811$, $p > 0.05$) (Fig. 2, Table 2). However, *Nodularia* sp. still seemed to interfere with egg production in most of the experiments; only in one mixture (1:1 *B. submarina* + non-toxic *Nodularia* sp.) was the egg production equal to the egg production with *B. submarina* alone. In the 8:1 mixture of *B. submarina* and *Nodularia* sp. the egg production was lower than that in 400 µg C l^{-1} of *B. submarina* alone (Fig. 2), and in the 1:8 *B. submarina* + *Nodularia* sp. the egg production was 60% of that in filtered sea water in the same experiment (Table 2), even though comparable to the average egg production with 50 µg C l^{-1} of *B. submarina* (Fig. 2). This was due to exceptionally high egg production of the copepod generation used in the 1:8 mixture experiment (cf. Table 1).

Eurytemora affinis produced a relatively high percentage of deformed egg-sacs in some of the treatments. These consisted of undeveloped eggs, which were attached together to an undetermined mass, so that the individual eggs could not be separated. Deformed egg-sacs were observed in filtered sea water (ca 7 % of the females with deformed egg-sacs), in low concentrations of non-toxic *Nodularia* sp. (13 to 15 %) and in most concentrations of toxic *Nodularia* sp. (4 to 24 %) (Table 2). The percent of deformed egg-sacs in low concentrations of toxic *Nodularia* sp. was

significantly higher (Tukey HSD; $p < 0.05$) than in other treatments. A few deformed egg-sacs (4 %) were also observed with low concentration of *Brachiomonas submarina*. In contrast, no deformed egg-sacs were produced in any of the mixture diets.

Hatching success

Hatching success of eggs produced at *Brachiomonas submarina* diet was high (>70 %) in most of the food concentrations, with the exception of the food concentrations of 50 and 200 µg C l^{-1}, where hatching success was low and variable (Table 3). Hatching success of the few eggs produced with non-toxic *Nodularia* sp. was generally low (0 to 42 %). However, at the 2 highest food concentrations (400 and 600 µg C l^{-1}) respectively 56 and 87 % of the produced eggs hatched. With the toxic *Nodularia* sp. diet the hatching success was, in general, significantly lower (Tukey HSD; $p < 0.05$) than with the other 2 food species, as none of the eggs produced with toxic *Nodularia* sp. hatched. In food mixtures, hatching success was either comparable or somewhat lower than with a sole *B. submarina* diet. However, hatching success in mixtures was measured only in 1 experiment.

Hatching success of eggs produced in natural food conditions and exposed to experimental food was generally high (73 to 100 %), and always higher than that of eggs produced in experiments (Table 3). With high concentrations of toxic *Nodularia* sp. (200 and 400 µg C l^{-1}) this difference was statistically significant (Tukey HSD; $p < 0.05$). However, high concentrations of toxic *Nodularia* sp. seemed to disturb hatching of *Eurytemora affinis* eggs, irrespective of the food with which they were produced. The hatching success of eggs produced in natural food conditions and exposed to 400 µg C l^{-1} of toxic *Nodularia* sp. was only 36 %, which was significantly different (Tukey HSD; $p < 0.05$) from most other treatments.

Mortality

Mortality of *Eurytemora affinis* in experiments with all concentrations of *Brachiomonas submarina* was low (<2.5 %), and clearly lower than that in filtered sea water (ca 26 %) (Fig. 3, Table 2). With low concentrations of non-toxic *Nodularia* sp., mortality was comparable to that in filtered sea water (20 to 30 %); however, in the 2 highest concentrations mortality was low (2 to 6 %), and not significantly different from mortality with *B. submarina* in corresponding concentrations (Tukey HSD; $p > 0.05$). In contrast, mortality with toxic *Nodularia* sp. was always higher than that in the filtered sea water (40 to 70 %), and significantly different from mortality with *B. submarina* in corresponding concentrations (Tukey HSD; $p < 0.05$). In mixture experiments, almost no mortality was observed; only in the 8:1 toxic *Nodularia* sp. + *B. submarina* treatment was mortality elevated.

Carbon and nitrogen content

Carbon content of copepods measured at the end of the experiments was variable (2 to 4 µg C ind.$^{-1}$); generally carbon content of individuals fed with *Brachiomonas submarina* was higher than that of copepods fed with *Nodularia* sp. or that of starved individu-

Table 3. *Eurytemora affinis*. Hatching success (mean ± standard deviation) of eggs (% per experiment), produced in experiments or produced in natural food conditions and exposed to different concentrations of experimental algae (Field). Number of eggs in hatching experiments and number of replicate experiments (n) are indicated. –: missing values, blanks: no experiments; other abbreviations as in Table 1

Algae	Conc. (µg C l^{-1})	Experiment			Field		
		No. of eggs	Hatching (%)	n	No. of eggs	Hatching (%)	n
FW	0	14–50	41 ± 45	7	109–110	96 ± 3.7	2
Br	50	20–105	29 ± 51	3	111	77 ± 23	2
	100	170	78	1			
	200	20–135	49 ± 69	2	–	100 ± 0	2
	400	62–169	70 ± 0.8	3	141–156	73 ± 2.7	2
	600	216	78	1			
N	50	18–24	42 ± 36	3	77–87	88 ± 10	2
	100	15	0	1			
	200	15–18	34 ± 34	3	93–113	87 ± 13	2
	400	18–67	56 ± 49	3	107	92 ± 6.1	2
	600	94	87	1			
Nt	50	<10	–	–	78–125	100 ± 0	2
	100	18	0	1			
	200	18–20	0 ± 0	3	82	90 ± 9.8	2
	400	30–50	0 ± 0	2	26–47	36 ± 13	2
	600	115	0	1			
Br + N	200 + 200	141	69	1			
Br + Nt	200 + 200	147	58	1			
Br + N	400 + 50	50	51	1			
Br + Nt	400 + 50	57	75	1			
Br + N	50 + 400						
Br + Nt	50 + 400						

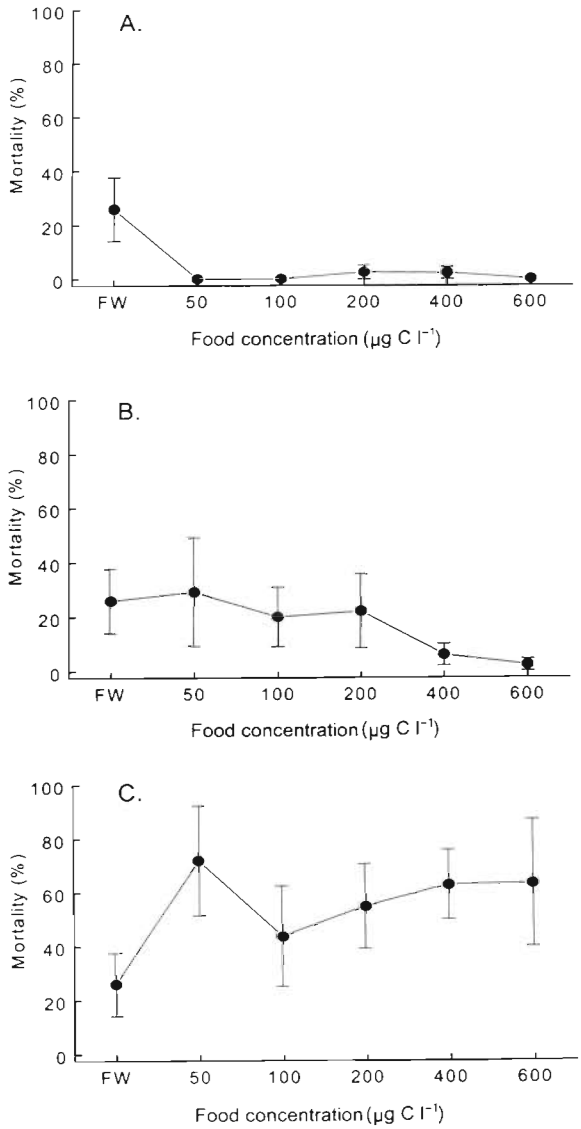

Fig. 3. *Eurytemora affinis*. Mortality (%) in experiments with different concentrations of (A) *Brachiomonas submarina*, (B) non-toxic *Nodularia* sp., and (C) toxic *Nodularia* sp. Data denote means and vertical bars denote standard errors. n = 3 to 5 (FW: filtered sea water)

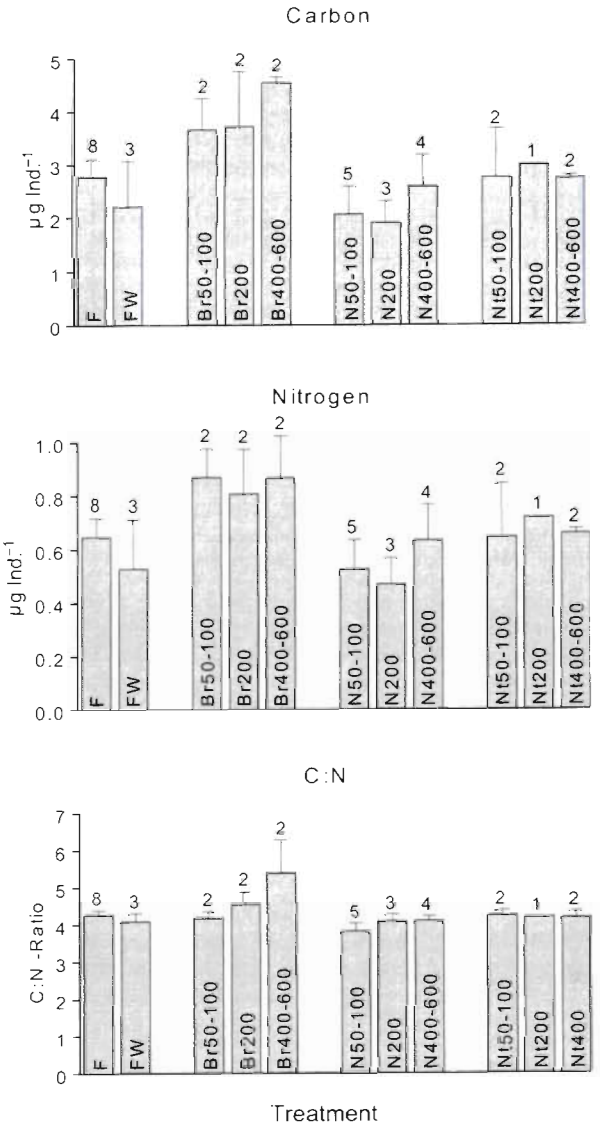

Fig. 4. *Eurytemora affinis*. Mean carbon and nitrogen content (µg ind.$^{-1}$) and C:N ratio of copepods exposed to different concentrations (50–100, 200, 400–600 µg C l^{-1}) of *Brachiomonas submarina* and non-toxic and toxic *Nodularia* sp. Error bars denote standard errors. Number of replicate measurements indicated above each bar. Field (F): individuals collected from the sea at the beginning of each experiment; other abbreviations as in Fig. 2

als (Fig. 4). Also, carbon content of copepods fed with *B. submarina* increased during the experiment if compared to carbon content of field individuals. However, the differences in carbon content between treatments were not statistically significant (1-way ANOVA; df = 10, $F = 1.421$, $p > 0.05$).

Differences in copepod nitrogen content between treatments were generally similar to differences in carbon content, and not significantly different from each other (1-way ANOVA; df = 10, $F = 0.904$, $p > 0.05$). The average nitrogen content of copepods varied between 0.5 and 0.9 µg ind.$^{-1}$ (Fig. 4).

In contrast to variable carbon and nitrogen contents, the C:N ratio of copepods was relatively stable, from 4 to 5 (Fig. 4), and differed significantly between treatments (1-way ANOVA; df = 10, $F = 2.492$, $p < 0.05$). With 400 to 600 µg C l^{-1} of *Brachiomonas submarina* the C:N ratio was significantly higher than that of the field copepods (Tukey HSD; $p < 0.05$). In general, the C:N ratio of *Eurytemora affinis* was lower than what is reported in the literature for high-latitude marine planktonic copepods (Gismervik 1997).

DISCUSSION

The calanoid copepod *Eurytemora affinis* was not able to reproduce on a diet of the cyanobacterium *Nodularia* sp., irrespective of the toxicity of the *Nodularia* sp. strain. Thus, the nutritional quality of *Nodularia* sp. was not high enough to support egg production, which is in agreement with previous findings (Sellner et al. 1996, Schmidt & Jónasdóttir 1997). In contrast, non-toxic *Nodularia* sp. did support maintenance, even though the concentration needed was high (400 to 600 µg C l^{-1}): if compared to *Brachiomonas submarina* as a food source, a similar survival rate was obtained already at the lowest concentration offered, 50 µg C l^{-1}. This is in agreement with the study of Sterner & Robinson (1994), suggesting that the food quality required for maintenance is lower than that needed for growth and that, with low-quality food, threshold food levels are likely to be high. This was also suggested by the increase in carbon and nitrogen content of copepods fed with *B. submarina*, compared to low carbon and nitrogen content of individuals fed with non-toxic *Nodularia* sp. It seemed that individuals fed *B. submarina* had food in excess and were able to build up reserve materials (such as lipids), whereas individuals fed with non-toxic *Nodularia* sp. needed all food to support maintenance. In contrast, the survival of copepods with the toxic *Nodularia* sp. only decreased with increasing food concentration, which indicated a strong toxic effect of nodularin on copepods. Average effects of *Nodularia* sp. and other species of cyanobacteria on growth, reproduction and survival of aquatic crustaceans in the literature and in this study are summarised in Table 4.

The reproductive success of copepods is not only dependent on egg production, but also on egg viability, which may not be affected by food quality in the same manner as egg production is affected (Ianora & Poulet 1993). Since certain food species can induce high egg production, but be detrimental to the hatching success of eggs (e.g. the diatom *Thalassiosira rotula*; Ianora & Poulet 1993, Chaudron et al. 1996), the

Table 4. Summary of the average effects of cyanobacteria on reproduction (egg production and hatching success), growth and survival of aquatic crustaceans from the literature and based on the present study. (+: positive response; –: negative response; 0: no response [in mixtures]. *Species or strains with detected toxins; Ep: egg production)

Cyanobacteria	Ep	Hatching	Growth	Survival	Crustacean	Source
Freshwater studies						
*Microcystis aeruginosa**	–	–	–	–	*Daphnia* spp.	Reinikainen et al. (1994, 1995), Hietala et al. (1995)
M. aeruginosa	–			+	*Achantocyclops robustus*	Vasconcelos (1990)
Aphanizomenon flos-aquae	–		–	–	*D. pulex*	Holm & Shapiro (1984)
Oscillatoria limnetica	+		+		*Daphnia* spp.	Repka (1996, 1997)
Anabaena oscillarioides	+		+	+	*Boeckella* spp.	Xu & Burns (1991), Burns & Xu (1990b)
Anabaena flos-aquae	+		–	+	*Boeckella* spp.	Xu & Burns (1991), Burns & Xu (1990b)
Nostoc sp.	+		–	+	*Boeckella* spp.	Xu & Burns (1991), Burns & Xu (1990b)
Nostoc calcicola	–		–	–	*Boeckella* spp.	Xu & Burns (1991), Burns & Xu (1990b)
Anabaena flos-aquae + *Cryptomonas*	+		–	0	*Boeckella triarticulata*	Twombly et al. (1998)
Synecococcus elongatus + P-limited *Schenedesmus* spp.	+		+		*Daphnia* spp.	DeMott (1998)
Brackish water and marine studies						
Nodularia spumigena	–				*Acartia bifilosa*, *Eurytemora affinis*	Sellner et al. (1996)
Aphanizomenon flos-aquae	–				*A. bifilosa*, *E. affinis*	Sellner et al. (1996)
Nodularia sp.	–	–		+	*E. affinis*	Present study
Nodularia sp.*	–	–		–	*E. affinis*	Present study
Nodularia sp. + *Brachiomonas submarina*	–	0		0	*E. affinis*	Present study
Microcystis aeruginosa	–				*Acartia tonsa*	Schmidt & Jónasdóttir (1997)
Nodularia spumigena	–				*A. tonsa*	Schmidt & Jónasdóttir (1997)
M. aeruginosa + *Thalassiosira weissflogii*	+				*A. tonsa*	Schmidt & Jónasdóttir (1997)
N. spumigena + *T. weissflogii*	0				*A. tonsa*	Schmidt & Jónasdóttir (1997)

quality of alga species as copepod food should not be evaluated based on egg production alone. Food quality may affect the hatching success negatively either by inhibitory compounds or by inadequate nutrition (Poulet et al. 1994, Guisande & Harris 1995, Miralto et al. 1998). In this study we observed both effects. Insufficient food (either quantity or quality) was probably the reason for low hatching success and production of deformed egg-sacs in filtered sea water, and with low concentrations of *Brachiomonas submarina* and non-toxic *Nodularia* sp. In contrast, with toxic *Nodularia* sp. the reproductive success of copepods did not increase with increasing food concentration but hatching success was always zero, suggesting the effect of inhibitory compounds. Thus, beside some diatom species (Poulet et al. 1995, Chaudron et al. 1996), cyanobacteria can also produce compounds which inhibit the hatching success of copepod eggs.

The hatching success of eggs was more dependent on the food conditions during the production of eggs than on the quality of media surrounding the eggs, since the hatching success of eggs produced in natural food conditions was generally high, irrespective of food species or concentrations to which the eggs were exposed. This suggests that the negative effect on egg hatching is mediated via accumulation of toxins in the female, and subsequent inhibition or disturbance of embryogenesis, similar to the studies of inhibitory effects of diatoms on hatching success (e.g. Chaudron et al. 1996). However, very high concentration of toxic *Nodularia* sp. also did decrease hatching success of eggs produced in natural food conditions, probably due to direct toxic effects of cell exudates on eggs. Thus, inhibitory compounds of toxic cyanobacteria may affect hatching success even if copepods would selectively avoid feeding on these species.

Similar to the study of Schmidt & Jónasdóttir (1997), *Nodularia* sp. did not increase reproduction of *Eurytemora affinis* when offered in mixtures with *Brachiomonas submarina*. Generally, if a food species is toxic, resistant to digestion, not ingested or does not add to the nutritional quality of the other food species, no beneficial effect can be expected in mixtures. We assumed that neither toxicity nor low ingestion of *Nodularia* sp. affected the result in mixtures with *B. submarina* and non-toxic *Nodularia* sp. Even though *Nodularia* sp. may produce toxic substances other than nodularin (cf. Nizan et al. 1986, Jungmann 1992), this was not likely to have occurred in our experiments, since mortality of copepods fed with a substantial amount of the non-toxic (nodularin-deficient) *Nodularia* sp. strain was low. Further, since *E. affinis* ingests non-toxic *Nodularia* sp. if it is offered as the sole food (J. Engström, M. Koski, M. Viitasalo, M. Reinikainen, S. Repka, K. Sivonen unpubl.), we assume that it was also ingested in mixtures, especially if the concentration of the other food species was below the saturation level of feeding (as was the case in experiments with 50 or 200 µg C l^{-1}; cf. Kiørboe et al. 1985). We conclude that *Nodularia* sp. did not add to the quality of *B. submarina* as food for *E. affinis*, which is in contrast with the study of Schmidt & Jónasdóttir (1997), who found that the cyanobacterium *Microcystis aeruginosa* did supplement a diatom diet. Possibly the limiting factor for egg production both in green algae and cyanobacteria is the same, e.g. long-chain polyunsaturated fatty acids, which are scarce in both groups of algae (Ahlgren et al. 1992, Dunstan et al. 1994). This could explain why the addition of cyanobacteria did not have a positive effect in our experiments similar to observations by Schmidt & Jónasdóttir (1997). However, *Nodularia* sp. may still have beneficial effects on other life-history parameters, such as number of clutches produced per female or individual age (Twombly et al. 1998), which were not included in the present study.

No increased mortality was observed in most of the mixture experiments, which indicated that *Nodularia* sp. did not excrete a large amount of toxins into the water and that copepods were able to avoid ingesting large amounts of toxic *Nodularia* sp., when offered together with *Brachiomonas submarina*. Also, no deformed egg-sacs were observed in any of the mixture experiments, and hatching success was generally high. However, hatching success was not measured in the mixtures with high concentration of *Nodularia* sp. In contrast, we did observe some inhibitory effects of *Nodularia* sp. on copepod reproduction; the egg production of *Eurytemora affinis* was in most cases (with the unexplained exception of the 1:1 mixture of *B. submarina* and non-toxic *Nodularia* sp.) lower in mixtures than with *B. submarina* alone. It is possible that *Nodularia* sp. filaments decreased copepod feeding efficiency on *B. submarina*, and thus egg production, even though no direct toxic effects were observed.

In conclusion, non-toxic cyanobacteria can be used as an energy source, even though they probably lack some nutritional components essential for growth or reproduction. This is in agreement with previous studies; while there are very few reports on successful reproduction with cyanobacteria as a food source, some studies do show growth or survival on a pure (non-toxic) cyanobacterial diet. In contrast, toxic species induce elevated mortality (at least if ingested), and may have detrimental effects on the hatching success of eggs, and thus generally cannot be used by crustaceans (Table 4).

Our results indicated that *Eurytemora affinis* is able to survive, but not to reproduce, in mono-specific *Nodularia* sp. blooms, if the strain is non-toxic. In contrast, if the bloom is toxic, the mortality rate of *E. affinis*

is likely to be higher than that of starved individuals. However, in more natural conditions, when other food species are also available, *E. affinis* seems to be able to avoid ingesting toxic *Nodularia* sp., and thus survives and produces eggs, the viability of which depends on the concentration of toxic or inhibitory substances in the water. These results indicate that *E. affinis* may be able to survive during cyanobacterial blooms better than the other common copepod species *Acartia bifilosa*, which does not even ingest non-toxic *Nodularia* sp. filaments (J. Engström, M. Koski, M. Viitasalo, M. Reinikainen, S. Repka, K. Sivonen unpubl.) and which has a high mortality rate in the presence of toxins (M. Reinikainen, S. Repka, M. Wahlsten, K. Sivonen unpubl.).

Such differential effects of cyanobacteria on different zooplankton species are well known from freshwater studies (e.g. Gilbert 1990, DeMott et al. 1991). However, for brackish and marine environments data are scarce on the interactions between cyanobacteria and mesozooplankton. In our opinion, more studies are needed to reveal the relationship between different species and life-stages of marine or brackish water copepods and cyanobacteria, to be able to estimate the effect of cyanobacterial blooms on mesozooplankton community structure. Further, more studies are needed to reveal the mechanism behind the negative effect of cyanobacteria on the hatching success of copepod eggs.

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