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Published on: 01 Jan 1990 - [Journal of Plankton Research](#) (Oxford University Press)

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Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters

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Abstract. The nutritional value of several planktonic algae was tested by means of feeding trials with three cladoceran zooplankters. The algae were monocultures and included two blue-greens, four greens and four flagellates with a size range of 5–48 μm . The specific growth rates of the zooplankters were chosen as the measure of the nutritional value of the algae. The three cladocerans showed large differences in growth rate in the different algae, but the two cryptomonads were without doubt best suited as food for all. The fatty acid composition for the cryptomonads were different from the other algae. They contained high percentages of the polyunsaturated fatty acids 20:5 ω 3 (EPA) and 22:6 ω 3 (DHA), which also are common in fish. It is suggested that the lipid composition is a probable factor determining the nutritional quality of the algae.

Introduction

Research on the nutritional requirements of zooplankton started in the 1950s and was originally oriented towards marine species (Corner and Cowey, 1968). It was established that certain algal species (e.g. some diatoms, cryptomonads and flagellates) were 'good' feed while others (some green and blue-green algae) were characterized as 'poor' feed (e.g. De Pauw and Pruder, 1986). However, the exact reasons why certain algal species promote better growth and reproduction than others are still poorly known.

There are many aspects which must be considered when determining the nutritional quality of algae for zooplankton, that is acceptable size range, digestible cell wall, non-toxicity and proper chemical composition. A great deal of research has been carried out on the first three aspects (e.g. Burns, 1968; Porter, 1973; Lampert *et al.*, 1986; Skogstad *et al.*, 1987; Burns, 1987; Lampert, 1987). A variety of algae of suitable size may be ingested by a zooplankton species, but only a limited number of algal species will be nutritionally adequate and therefore of importance to zooplankton (Stemberger, 1981).

During early studies of zooplankton nutrition a great interest was paid to the algal amino acid composition, but conflicting results were reported from different studies (e.g. Parsons *et al.*, 1961; Corner and Cowey, 1968). Recently, an increasing interest has been put into the lipid fraction and particularly the content of unsaturated fatty acids of ω 6 and ω 3 type (two families of the polyunsaturated fatty acids, differing by the position of the first double bond in the carbon chain). Interest in fatty acid composition originates to a large degree from the growing interest in aquaculture, which requires nutrient-rich microalgae and/or zooplankton for the diets of larval stages of commercially important fish and shellfish. There is a general lack of knowledge on the nutritional requirements of these organisms, and it is highly probable that the requirements differ between species (Taub, 1970; De Pauw and Pruder, 1986). Natural food seems to be essential for many of these sensitive organisms, and it has been

suggested that the composition of lipids in the diet may be more important than that of the protein or carbohydrate components (De Pauw and Pruder, 1986).

The objective of this study was to determine the utility of several freshwater algae as food for three cladoceran zooplankters with special interest paid to the unsaturated fatty acids. We suggest that the lipid composition is a possible factor determining the nutritional quality of the algae.

Materials and methods

The phytoplankton were chosen to cover a common size range and species composition representative of meso- to eutrophic temperate lakes (Table I). The synthetic medium L16 (Lindström, 1983a) was used for all the experiments which were carried out at a temperature of 15°C and a 14/10 h light/dark cycle. The phytoplankton cultures used were not axenic, but it can hardly give any decisive influence to the main results (see further under Discussion). *Microcystis* and *Scenedesmus*, which are generally colonial in lake plankton, were largely single celled in the monocultures used.

The zooplankter *Chydorus sphaericus* (0.3 mm) was taken from a laboratory monoculture, while *Eubosmina longispina* (0.5 mm) and *Daphnia longispina* (1.2 mm) were isolated from Lake Vallentunasjön just before the start of the experiments. The zooplankters were preconditioned by keeping them in the different food types for 10 days. Since only growth experiments can provide information on the ultimate utilization of a certain food, we chose the specific growth rate of the zooplankters as a measure of the nutritional value of the algae.

The experiments were carried out in 75 ml Erlenmeyer flasks. At the start of the experiments 10 or 20 individuals of the zooplankters were added to each

Table I. Size characteristics of the food algae

	Length		Width	
	µm	(CV)	µm	(CV)
Blue-greens				
<i>Microcystis aeruginosa</i> Kütz.	4.8	(29)	–	
<i>Oscillatoria agardhii</i> Gom.	557	(24)	4.8	(0)
Greens				
<i>Chlamydomonas</i> sp.	10.1	(22)	7.8	(24)
<i>Chlorella homosphaera</i> Skuja	4.6	(17)	–	
<i>Scenedesmus acutus</i> Meyen	13.0	(10)	5.0	(16)
<i>Scenedesmus quadricauda</i> Turp.	11.5	(13)	5.9	(20)
cells with spines	19.7	(15)	11.5	(19)
Flagellates				
<i>Chromulina chinophila</i> Stain	5.5	(9)	–	
<i>Cryptomonas</i> sp.	17.3	(9)	9.1	(11)
<i>Rhodomonas lacustris</i> Pasch. & Ruttn.	11.0	(15)	6.4	(16)
<i>Peridinium cinctum</i> (O.F.Müll.) Ehr.	48.0	(15)	43.7	(11)

CV = coefficient of variation, i.e., SD in % of mean.
n = 10.

algal monoculture. The growth experiments lasted 10 days and had six replicates. In those cases where survival during the preconditioning period was poor, fewer replicates were employed (cf. Table II). In order to avoid food limitation additional algae were added to those assays where a risk for overgrazing was apparent. Supposing exponential growth the instantaneous growth rates (r) of the zooplankters were calculated from the means of change in number of the individuals according to the following equation (e.g. Edmondson and Winberg, 1971, p. 165):

$$r = (\ln N_t - \ln N_0)/t$$

where N_0 = number of individuals at day 0
 N_t = number of individuals at day 10
 t = time (10 days)

The different algae were grouped in three size groups (5, 11 and $\geq 17 \mu\text{m}$) when presenting the estimated growth rates of the zooplankters (Figure 1).

The fatty acid composition of the algae was analysed by means of a Hewlett-Packard GLC-system on chloroform-methanol extracts of freeze-dried algae (Boberg *et al.*, 1985).

Results

The three cladoceran zooplankters showed large differences in growth in the different phytoplankton cultures (Table II and Figure 1). When given the blue-greens, only *Chydorus* was able to increase in some of the replicates in *Oscillatoria*. *Eubosmina* could not even survive for 20 days (the conditioning and

Table II. Means of number of zooplankters (N), standard deviation (SD) and number of replicates (n) after 10 days in the different algal cultures. The number of individuals at the start of the experiments was 10 in all cases. † = all died

Food algae	<i>Chydorus</i>			<i>Eubosmina</i>			<i>Daphnia</i>		
	N	SD	n	N	SD	n	N	SD	n
Blue-greens									
<i>Microcystis</i>	3.4	0.2	6	0.3	0.0	4	2.9	1.0	5
<i>Oscillatoria</i>	11.3	2.3	6	†	–	5	0.8	0.5	4
Greens									
<i>Chlamydomonas</i>	21.2	2.1	6	0.9	0.6	5	16.8	2.2	6
<i>Chlorella</i>	19.2	2.9	6	2.1	0.8	6	3.6	1.3	5
<i>Scenedesmus acutus</i>	20.7	2.4	6	†	–	0	26.2	4.4	6
<i>Scenedesmus quadricauda</i>	4.9	2.1	6	0.6	0.6	4	3.0	1.2	4
Flagellates									
<i>Chromulina</i>	17.0	1.8	6	0.4	0.3	4	3.8	1.9	5
<i>Cryptomonas</i>	24.8	1.5	6	15.1	4.9	5	115	16	5
<i>Rhodomonas</i>	30.3	1.5	6	17.7	9.0	6	146	12	6
<i>Peridinium</i>	–	–	–	†	–	3	2.8	0.5	4

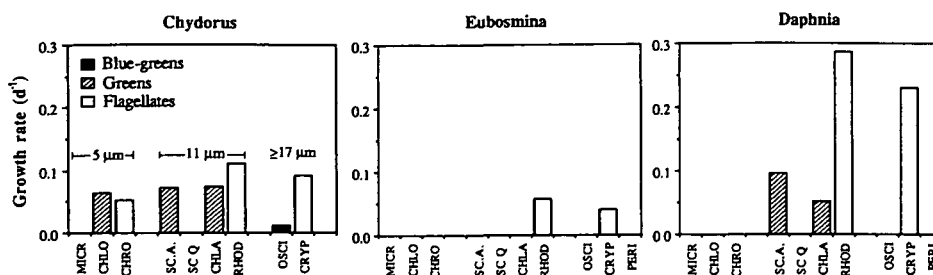


Fig. 1. Estimated growth rates of the three cladocerans fed the different freshwater algae. The algae are grouped in three size groups which are indicated in the figure.

experimental period) in the two blue-greens. Concerning the four green algae (striated bars in Figure 1) all but *Scenedesmus quadricauda* were good food for *Chydorus* whereas *Daphnia* increased only on *Scenedesmus acutus* and *Chlamydomonas*. *Eubosmina* was able to survive in all greens except *S. acutus*, but did not show positive population growth (Table II). *Scenedesmus quadricauda* did not support growth of any of the cladocerans. The two cryptomonads, *Rhodomonas minuta* and *Cryptomonas* sp., despite different sizes, were with no doubt best suited as food for all three cladocerans (Figure 1).

Thus, *Chydorus* survived in all experiments and did very well in *Rhodomonas*, and *Cryptomonas*, and rather well in *Chlamydomonas*, *S. acutus*, *Chlorella* and *Chromulina*. In contrast, *Eubosmina* did not grow in most of the experiments and in three of them (*Oscillatoria*, *S. acutus* and *Peridinium*) they died in all replicates. *Eubosmina* showed a positive growth only in the *Cryptomonas* and *Rhodomonas* cultures. *Daphnia* also survived in all cultures but showed more variation between the algal species than did *Chydorus* (Table II). *Daphnia* had a positive growth rate in four of the algal cultures, that is *Rhodomonas*, *Cryptomonas*, *S. acutus* and *Chlamydomonas* (Figure 1).

The fatty acid composition varied a great deal between the algal species (Table III). Only the flagellates contained long-chained polyunsaturated fatty acids with 20 or 22 carbon. More than 50% of the fatty acids in *Cryptomonas* and *Rhodomonas* consisted of the two ω 3 acids EPA (eicosapentaenoic acid, 20:5 ω 3) and DHA (docosahexaenoic acid, 22:6 ω 3). All the greens and *Oscillatoria* contained instead more of a shorter ω 3-acid, 18:3 ω 3 (α -linolenic acid).

Discussion

There are several reports of blue-greens being poorly utilized as food (e.g. Arnold, 1971; Lampert, 1987). *Daphnia* was found to decrease in size and embryo production when *Oscillatoria* became numerous, which could depend on *Oscillatoria* filaments interfering with the feeding process, and/or a chemical inhibition (Infante and Abella, 1985). Blue-greens are known to produce toxic metabolites, and Porter and Orcutt (1980) showed in their study of *Daphnia magna* that a toxin-producing strain of *Anabaena flos-aquae* promoted indivi-

dual growth but reduced survivorship when ingested. When investigating the gut contents of *Daphnia galeata* and *D. cucullata*, G.-Tóth *et al.* (1987) noticed that although the guts contained blue-greens, it appeared that these were not digested. According to De Bernardi *et al.* (1981) the size of the colonies of *Microcystis* is the major reason for their unsuitability as food rather than their undigestibility. They suggested that *Microcystis* can be efficiently utilized if the algal colonies are small. *Microcystis* was single celled in the present study so that explanation is inconsistent with our results. A more general explanation why the blue-greens so often are found to be of poor quality can be that they simply are nutritionally incomplete.

Studies with *Daphnia* and ciliates have shown low growth rates and reproductive values when fed with the green alga *Chlorella* (Infante and Litt, 1985; Skogstad *et al.*, 1987). The reproduction by *Daphnia pulex* was much lower than normal when fed *Chlorella pyrenoidos* and *Chlamydomonas reinhardtii* (Taub and Dollar, 1968). Many eggs showed an abnormal development or did not develop at all, which can be interpreted as lack of essential substances. There are also examples where green algae (*Scenedesmus*, *Ankistrodesmus* and *Chlorella*) have given good growth for *Daphnia* and *Keratella* (Rees and Oldfather, 1980; Lindström, 1983b, Lundstedt and Brett, unpublished). *Chlamydomonas* has been shown to be suitable food for ciliates (Skogstad *et al.*, 1987) and for *D. magna* (Porter and Orcutt, 1980).

Among the green algae there are, thus, more variable results; related algal species or even the same species could be characterized as 'poor' or 'good' feed in different experiments. It has, however, been demonstrated very early that the nutritional value varies with the growth condition of the algae, for example, Ryther (1954) and McMahon and Rigler (1965) showed that old slow growing *Chlorella vulgaris* was of lower quality as food for *D. magna* than fast growing algae. Marine species of *Chlorella* were more valuable as food for rotifers than freshwater species of this genus (Watanabe *et al.*, 1983). Different growth conditions of the same species can be an explanation to many conflicting results in determining their food value for herbivores.

There are many examples in the literature showing the grazing habits of daphnids on cryptomonads (especially *Rhodomonas*) (see the review of Klaveness, 1988). The cryptomonads were also shown to be important food for other zooplankters for example *Rotifera* and ciliates (Stemberger, 1981; May, 1987; Skogstad *et al.*, 1987). Infante and Litt (1985) found in their study of *Daphnia pulicaria* and *D. thorata* that *Cryptomonas* was the best food for both and suggested that the reasons for that could be their solitary condition, form and size, despite relatively low amounts of carbon and nitrogen. Their favourable size and/or form should, thus, compensate for their low amounts of nutrients. The fact that these flagellates are motile and remain in suspension, could also make it easier for the filtering zooplankters to ingest the cells (May, 1987).

On the other hand, the fatty acid composition for the two cryptomonads is different from the other algae (Table III). They contained high percentages of the long-chained polyunsaturated fatty acids EPA and DHA, which also are

Table III. Fatty acid composition of the feed algae (% of total fatty acids)

Acids <i>x:yωz</i>	Blue-greens		Greens			Flagellates				
	<i>Microcystis</i>	<i>Oscillatoria</i>	<i>Chlamydomonas</i>	<i>Chlorella</i>	<i>Scenedesmus acutus</i>	<i>Scenedesmus quadricauda</i>	<i>Chromulina</i>	<i>Cryptomonas</i>	<i>Rhodomonas</i>	<i>Peridinium</i>
14:0	17.0	2.1	2.2	2.3	0.7	1.4	11.1	1.7	2.0	7.6
16:0	29.1	18.5	9.8	20.4	18.9	12.7	5.0	11.1	12.8	28.8
16:1ω7	1.8	22.6	1.1	0.3	-	-	2.1	0.6	0.3	2.1
Unident	2.7	1.7	21.8	0.9	7.2	14.8	-	-	-	-
18:0	1.9	1.6	0.7	4.2	2.1	0.6	1.5	1.3	0.7	0.4
18:1ω9	3.2	1.9	5.0	5.4	36.5	11.6	-	1.1	1.0	30.0
18:1ω7	2.5	0.5	1.8	0.2	0.4	0.4	2.3	0.6	2.1	0.4
18:2ω6	2.9	11.4	9.0	22.1	6.7	12.9	7.1	1.0	0.9	0.5
18:3ω6	0.3	-	0.2	-	0.4	1.3	3.4	-	-	-
18:3ω3	5.5	24.6	22.8	37.2	14.9	22.2	6.6	9.7	21.3	0.2
18:4ω3	-	-	2.5	-	3.4	3.3	26.6	21.8	23.9	4.3
20:0	-	-	-	0.1	0.1	0.2	-	-	-	-
20:1ω9	-	-	-	-	0.3	0.3	2.4	0.7	-	-
20:3ω6	-	-	-	-	-	-	0.4	-	-	-
20:4ω6	-	-	-	-	-	-	0.6	-	-	-
20:5ω3	0.6	-	-	-	-	-	0.6	20.5	15.8	6.9
22:4ω6	-	-	-	-	-	-	0.4	-	-	-
22:5ω3	-	-	-	-	-	-	-	-	-	-
22:5ω6	-	-	-	-	-	-	9.9	4.7	2.7	-
22:6ω3	-	-	-	-	-	-	2.5	7.2	4.3	12.2
Σω6	3.2	11.4	9.2	22.1	7.1	14.2	21.8	5.7	3.6	0.5
Σω3	6.1	24.6	25.3	37.2	18.3	25.5	36.3	59.2	65.3	23.6
Σω3/Σω6	1.9	2.2	2.8	1.7	2.6	1.8	1.7	10.4	18.1	47.2

The fatty acids are fully described by the three numbers *x:yωz*, where *x* = number of carbon atoms; *y* = number of double bonds; *z* = the position of the first double bond counting from the methyl end of the molecule (- not found or <0.1%).

common in fish and shellfish. Chemical composition of the food particles is probably more important than other factors, for example, cell size or digestibility of cell walls, in determining population growth rates. Bern (1987, 1990) found that the optimum cell classes of *Chydorus sphaericus* was $\sim 10 \mu\text{m}$, and the selectivity coefficient was halved for particles of $19 \mu\text{m}$. In our experiments *Chydorus* showed nearly the same growth rates when fed the larger *Cryptomonas* as when fed *Rhodomonas* (Figure 1). Also the other two cladocerans showed the highest growth rates when fed the two cryptomonads, independent of cell size (Figure 1). Concerning digestibility of cell walls, no difference was found between *S. acutus* and the softwalled *Chlamydomonas* as food for *Chydorus*, and when fed *Daphnia* the hardwalled *Scenedesmus* gave, in fact, a higher growth rate than *Chlamydomonas*. In the smallest cell class, *Chydorus* grew with about the same rate on *Chlorella* and the softwalled *Chromulina*, but the softwalled *Microcystis*-cells could not support growth of any of the cladocerans. If algal particles are nutritionally inadequate, it is irrelevant that they are of a suitable size. Bacteria are considered to contain no long-chained polyunsaturated fatty acids (Kenyon, 1972; Volkman *et al.*, 1989), so the bacteria in the non-axenic cultures could hardly influence the main results or the conclusions.

It has been found that microalgae determine the quality of the marine rotifer *Brachionus plicatus*, which is frequently used as a food organism in industrial hatcheries (Watanabe *et al.*, 1983). That is thought to be due to the essential fatty acids which are only synthesized by algae (De Pauw and Pruder, 1986; Volkman *et al.*, 1989). The dietary value of rotifers for fish has been related to the content of highly unsaturated fatty acids of the $\omega 3$ -type (Watanabe *et al.*, 1983). It is probable that these compounds also are essential for the two larger cladocerans, whereas *Chydorus* can use the shorter $18\omega 3$ acids in the green algae as well as in *Oscillatoria* and *Chromulina*. As a measure of the effects of cell size (Table I) against the fatty acids of $\omega 3$ - and $\omega 6$ -type (Table III) of the food algae on the growth response of the cladocerans (Table II) the Spearman's rank correlation coefficients are calculated (Table IV). The coefficients are highest

Table IV. Effects of cell sizes, the sum of $\omega 3$ -acids and the sum of $\omega 3 + \omega 6$ -acids of the food algae on the growth response of the cladocerans measured as Spearman's correlation coefficients (ρ)

Cladoceran	Variable	ρ	<i>n</i>	Significance
<i>Chydorus</i>	Size	0.49	9	0.185
	$\Sigma\omega 3$	0.65	9	0.058
	$\Sigma\omega 3 + \omega 6$	0.58	9	0.099
<i>Eubosmina</i>	Size	-0.07	10	0.853
	$\Sigma\omega 3$	0.87	10	0.001
	$\Sigma\omega 3 + \omega 6$	0.80	10	0.005
<i>Daphnia</i>	Size	0.30	10	0.403
	$\Sigma\omega 3$	0.59	10	0.074
	$\Sigma\omega 3 + \omega 6$	0.59	10	0.074

for the fatty acids for all cladocerans. The probability is between 0.1 and 10% that the growth response of the zooplankters is independent on the fatty acids, whereas the probability is between 19 and 85% that the growth response is independent of the cell size. In this test the diameter of the *Oscillatoria* filaments was chosen as the size variable. Using the length of the filaments as size variable gave a ρ of only 0.2 for *Chydorus*, which is probably misleading. (*Chydorus* could, in fact, eat those soft filaments.)

The reason why *Chydorus* could not utilize *S.quadricauda* cannot be explained by fatty acid composition, which was very similar to that of the other three green algae. Harder cell walls and resisting spines may be the reason. *Microcystis*, which also was 'poor' food, contained the lowest per cent of $\omega 3$ acids of all species (Table III). It is interesting to note that *Microcystis* contained traces of EPA, which may be an explanation for the fact that *Daphnia* and *Chydorus* showed positive growth on *Microcystis* in another series of experiments (Lundstedt and Brett, unpublished). *Peridinium* also contained some EPA and DHA fatty acids. The difficulties for *Eubosmina* and *Daphnia* to increase or even survive in *Peridinium* could depend on the size (48 μm) and the hard cell wall of the algae. According to Burns' (1968) relationship between carapace length and bead particles ingested, the cladocerans must be at least 1.5 mm to be able to eat particles of 48 μm . Bern (1990) has recently demonstrated that *D.cuculata* (0.75 mm) did not select particles >38 μm . *Peridinium cinctum* has been shown to be an excellent food source for the large rotifer *Asplanchna* (Brett, unpublished).

Conclusions

The two cryptomonads, which contained high percentages of long-chained polyunsaturated fatty acids of $\omega 3$ -type, were the best food for all cladocerans, in spite of the fact that they belonged to different size classes. We suggest that the lipid composition is a probable factor determining the nutritional quality of the algae.

Acknowledgements

We wish to thank S.Tengblad, I.-B.Gustavsson and M.Boberg, Department of Geriatrics, Uppsala, for help with the fatty acid analyses. We also thank L.Bern, Institute of Limnology, Uppsala, for valuable suggestions on the manuscript.

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Lipid composition and food quality of some freshwater phytoplankton

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G.Ahlgren et al.

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Received on June 19, 1989; accepted on March 27, 1990