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# Influence of zooplankton and phytoplankton on the fatty acid composition of digesta and tissue lipids of silver carp: mesocosm experiment

I. Domaizon*, C. Desvilettes, D. Debroas and G. Bourdier

*Laboratoire de Biologie comparée des Protistes, UPRES A CNRS 6023, Université Blaise Pascal Clermont II, 24 avenue des Landais, 63177 Aubière Cedex, France*

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Zooplankton appeared to be the major contributor to the diet of 1+ silver carp, whereas 3+ fishes exhibited a more evenly balanced spectrum between zooplankton and phytoplankton. The fatty acids profiles of digesta were influenced by zooplankton, particularly for 1+ silver carp. Together, fatty acid profiles of tank zooplankton and digesta were characterized by high proportion of 20 : 5$\omega$3 and 20 : 6$\omega$3. The fatty acids composition of the phytoplankton reflected the dominance of cyanobacteria and chlorophycea, with high quantities of 18 : 2$\omega$6 and 18 : 3$\omega$3. Although cyanobacteria accounted for >70% of the phytoplankton biomass ingested by the carp, fatty acids profiles of digesta were not influenced by phytoplankton fatty acids composition. The low digestive and conversion efficiency of *Microcystis aeruginosa* explain this absence of relation. The neutral lipids in silver carp tissues reflected poorly the fatty acids profiles in the diet, the semi-natural conditions and the diet dominated throughout the study by zooplankton, led to little variation in tissues fatty acids. The phospholipids in the muscle, liver and peri-intestinal fat were characterized by a rather low proportion of polyunsaturated fatty acids (PUFA) in both 1+ and 3+ fish. From a qualitative view point, cryptophycea, diatoms, and especially zooplankton are much more valuable food for the silver carp than cyanobacteria and desmid chlorophycea which are poor in long-chain PUFA.



Key words: silver carp; cyanobacteria; feeding behaviour; polyunsaturated fatty acids.

## INTRODUCTION

Recent studies have investigated the influence of pump filter feeding fish, particularly silver carp *Hypophthalmichthys molitrix* (Valenciennes), on plankton community structure and its potential use as a biomanipulation technique to reduce algal biomass (Leventer & Teltsch, 1990; Starling & Rocha, 1990; Starling, 1998). However, the use of silver carp to control excessive phytoplankton growth in eutrophic lacustrine ecosystems remains controversial (Costa-Pierce, 1992; Starling, 1993; Domaizon & Dévaux, 1999*a*). Several key factors could explain successes and failures of these biomanipulations: (1) the level of fish stocking biomass (Starling, 1998); (2) the size structure of the phytoplankton community (Laws & Weisburd, 1990); (3) the size structure of the zooplankton community and the strength of zooplankton grazing on dominant algae (Domaizon & Déveaux, 1996*b*) and (4) the efficiency by which phytoplankton are digested (Vöros *et al*., 1997).

*Author to whom correspondence should be addressed. Fax: 04 73 40 76 70; email: Isabelle.DOMAIZON@lbp.univ-bpclermont.fr



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Studies on food ingestion by silver carp support the hypothesis that food selectivity is a mechanical passive function of the filtering apparatus morphology (Spataru & Gophen, 1985; Smith, 1989). The utilization of food by silver carp has been investigated by several methods, particularly under *in vitro* experiments testing the effects of digestive enzymes on different prey species (Vöros *et al.*, 1997) and quantifying the amino acid release (Bitterlich, 1985). Bitterlich (1985) reported that indirect evidence suggested that zooplankton and amorphous organic detritus are of primary importance in meeting the energy requirements of stomachless filter feeding fish.

The aim of this study was to specify the relative proportion of zooplankton and phytoplankton in silver carp diet, and to evaluate the influence of dietary fatty acids on the lipid composition of digesta and tissues of silver carp. Because the main planktonic classes or genera are characterized by specific fatty acids or ratios of fatty acids, fatty acids can be used as specific natural biomarkers or tracers for studying the transfer of organic matter within the aquatic food web from the primary producers to fish *via* zooplankton (Desvilettes *et al.*, 1994). Moreover, the polyunsaturated fatty acid (PUFA) composition in fish neutral lipids can reflect, under certain conditions, the composition of its main source of food. In order to follow up the fatty acid composition of zooplankton, phytoplankton, digesta and tissues of silver carp, we conducted a mesocosm experiment with immature 1+ silver carp and 3+ silver carp. This study generated information on the digestibility and the food quality of the cyanobacterium *Microcystis aeruginosa* in term of PUFA composition.

## MATERIALS AND METHODS

The experiment was conducted in large fibreglass tanks (5500 l) located near the eutrophic Villerest reservoir, River Loire, France (Domaizon & Dévaux, 1999*a*). During a cyanobacterial bloom, eight tanks equipped with an airlift mixer system were filled with water and plankton pumped from the reservoir.

Silver carp purchased from Les Clouzioux fish farm, Brinon, Cher, France, were acclimated in four holding tanks prior to their introduction to eight experimental tanks. Twelve immature 1+ silver carp (22·2 ± 4·9 g; 15 months old) were put into four tanks and 12 3+ silver carp (126·3 ± 29·5 g; 39 months old) were put into the remaining four tanks. The experiment lasted for 32 days: the relative confinement in mesocosms and the possible periphyton development did not permit a longer experiment. Three times a week nutrients (240 µg N $l^{-1}$; 30 µg P $l^{-1}$) were added to the tanks to sustain phytoplankton production.

### PLANKTON SAMPLING

At the start and at the end of the experiment, 1 l of water was sampled using a Van Dorn type bottle and divided into two fractions. The first fraction (200 ml) was fixed with Lugol's iodine for phytoplankton species identification, counting and determination of specific biovolumes. The second fraction (500 ml) was filtered on pre-combusted Whatman GF/C glass-fibre filters and frozen for determination of fatty acid composition. Zooplankton was sampled using a vertical haul net of 60 µm mesh size. One part of the sample was frozen immediately for further fatty acid analysis and the other part was preserved in 5% sucrose formalin for species identification and counting.

### FISH SAMPLING

On day 32 all the silver carp were collected, killed by a blow on the head and weighed. White muscle (4–12 g) and liver (0·5–3 g) were collected, frozen immediately on dry ice

and kept at $-40^{\circ}$ C until lipid extraction. The digestive tracts were dissected out and the intestinal fat (100–250 mg) removed and frozen. The digesta were extruded from the anterior two-thirds of the gut length. The anterior third was preserved for plankton species counts and the central third of the digesta was pooled and kept frozen until analysed for fatty acid composition.

### LIPID ANALYSIS

Moisture (%) determinations were carried out on muscle, liver and intestinal fat according to standardized methods as described by Horowitz (1980). Total lipids (% DW) in muscle, liver and intestinal fat were determined gravimetrically after extraction with chloroform/methanol according to Folch *et al.* (1957). The Folch *et al.*, method was also used to extract total lipid from the digesta and total lipid from phytoplankton and zooplankton. For fatty acid analysis, neutral lipids and phospholipids from white muscle, liver and intestinal fat were separated by thin layer chromatography on silica gel G60 plates ($20 \times 20$ cm). Chromatograms were developed in hexane : diethylether : methanol : glacial acetic acid (90 : 20 : 3 : 2, by volume). Fatty acid analyses of digesta, phytoplankton and zooplankton were performed on the total lipid extract. Fatty acid methyl esters (FAME) were prepared by hydrolysis in methanolic NaOH and esterification in methanolic $H_2SO_4$, as described previously (Desvilettes *et al.*, 1994). The analyses of FAME were carried out on a Chrompack CP 9001 gas chromatograph equipped with a fused silica capillary column coated with FFAP (Chrompack France, Paris) and a split-splitless injection system, using helium as the carrier gas (column length 25 m, ID 0·32 mm). The oven was programmed to rise from an initial temperature of 150 to 230° C at a rate of 2·5° C $min^{-1}$. Peaks were recorded in a computer equipped with Mosaic® software (Chrompack France, Paris) and identified by comparison with known commercial standards (Supelco FAME Mix; Supelco Bacterial Acid Methyl Esther : BAME) and with our own well characterized standard.

### STATISTICAL ANALYSIS

The differences for each fatty acid between 1+ treatments and 3+ treatments were tested using the Mann–Whitney U-test. The data from analysis of fatty acids on zooplankton, phytoplankton and neutral lipids of silver carp were submitted to a normalized principal component analysis (PCA). To compare the effect of silver carp (1+ and 3+) on zooplankton and phytoplankton biomass in mesocosms, a two-way analysis of variance (ANOVA, model I) was used (time × silver carp). The normality assumption of the error terms was verified by the Shapiro–Wilk test. Statistics were computed using the Minitab package.

## RESULTS

### PLANKTON

On day 0, there were no significant differences between the proportions of zooplankton and phytoplankton sampled in 1+ fish tanks and the proportions of zooplankton and phytoplankton sampled in 3+ fish tanks (Fig. 1). Zooplankton biomass represented 50·1% ± 3·9 (mean of four replicates ± S.D.) in 1+ treatments and 56·7% ± 4·5 (mean of four replicates ± S.D.) in 3+ treatments. At the end of the study, zooplankton accounted for 68·6% ± 2·8 of the biomass encountered in 3+ fish tanks, but only for 30·9% ± 10·0 of the biomass found in 1+ fish tanks. Zooplankton appears as the major contributor to the diet of 1+ silver carp (90·3% of ingested biomass) (Fig. 1), whereas 3+ silver carp exhibited a more evenly balanced food spectrum between zooplankton (44·8% of ingested biomass) and phytoplankton (55·2% of ingested biomass). Further examination of the temporal changes in the phytoplankton species in tanks and digesta

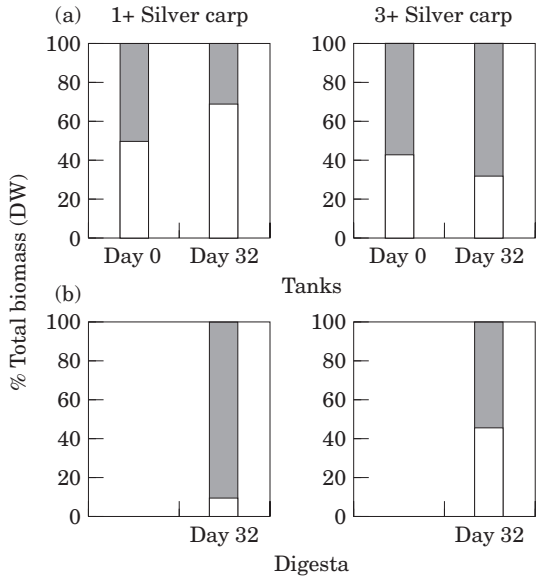


FIG. 1. Relative biomass of zooplankton (▨) and phytoplankton (□) in 1+ and 3+ tanks on day 0 and day 32 (a) and in 1+ and 3+ silver carp digesta on day 32 (b). Data represent the mean for the four replicates of treatment. For clarity standard deviation bars are omitted.

(Fig. 2) shows that cyanobacteria (*Microcystis aeruginosa*) dominated phytoplankton biomass on day 0 in both trials. By day 32, cyanobacteria had decreased significantly (ANOVA, $P<0{\cdot}001$) in both trials, and other algal species had increased significantly e.g., Chlorophyceae ($P<0{\cdot}001$), diatoms ($P=0{\cdot}005$) and Cryptophyceae ($P=0{\cdot}002$). The proportion of cyanobacteria in the digesta (Fig. 2) was significantly higher ($P=0{\cdot}014$) in 1+ silver carp ($87{\cdot}6\% \pm 7{\cdot}3$ of total phytoplankton biomass) than in 3+ silver carp ($71{\cdot}7\% \pm 4{\cdot}6$). Diatoms occurred in the digesta as secondary items but accounted for a higher percentage of total biomass in 3+ silver carp ($18{\cdot}5\% \pm 5{\cdot}7$; $P=0{\cdot}005$). In terms of the relative proportions of cladocera, copepods and rotifers among zooplankton species (Fig. 2), cladocera (mainly *Ceriodaphnia*) dominated, accounting for >70%DW of the total zooplankton biomass in the tanks and for >90%DW of the ingested zooplankton biomass. At the start of the experiment, copepods accounted for $17{\cdot}6\% \pm 5{\cdot}6$DW of the biomass in 1+ tanks and for $28{\cdot}0\% \pm 2{\cdot}8$DW in 3+ tanks. Copepods then decreased markedly ($P<0{\cdot}001$) in both trials reaching percentages <6% of total zooplankton biomass on day 32. Copepods and rotifers represented a negligible proportion of digesta biomass.

## SILVER CARP

Silver carp gained no weight between days 0 and 32 in either trial although sufficient food was present (mean of plankton biomass on day 32 in 1+ treatments: $431{\cdot}0\ \mu g\ l^{-1}$, in 3+ treatments: $807{\cdot}5\ \mu g\ l^{-1}$). There were no significant differences in the moisture contents of liver, muscle and intestinal fat between 1+ fish and 3+ fish. Liver and muscles contained *c.* 77·5%DW of moisture, and intestinal fat contained *c.* 32·2% of moisture. The lipid contents of muscles and intestinal fat of 1+ silver carp and 3+ silver carp were not

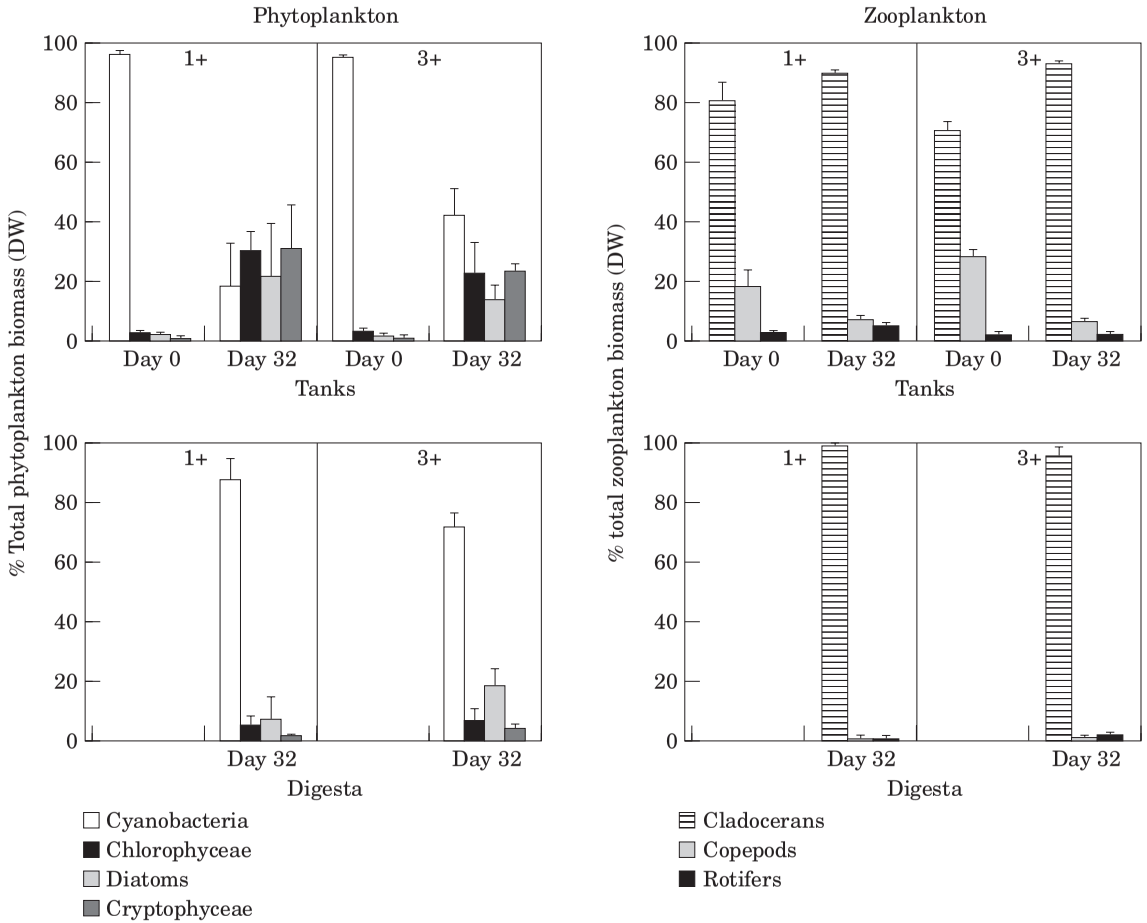


FIG. 2. Relative composition of phytoplankton (a) and zooplankton (b) in 1+ and 3+ tanks on day 0 and day 32 and in silver carp digesta. Data represent the mean ± the analytical S.D. ($n$=4).

TABLE I. Fatty acid composition of *Microcystis*, tank phytoplankton, tank zooplankton and digesta from 1+ and 3+ silver carp

| Fatty acid | *Microcystis* | Phytoplankton | | Zooplankton | | Digesta | |
|---|---|---|---|---|---|---|---|
| | | 1+ | 3+ | 1+ | 3+ | 1+ | 3+ |
| 12 : 0 | 2·90 | 0·56 ± 0·68 | — | — | — | TR | 0·32 ± 0·21 |
| 13 : 0 | 1·76 | — | — | — | — | — | TR |
| 14 : 0 | 5·24 | 2·61 ± 0·48 | 2·80 ± 1·31 | 2·29 ± 0·83 | 2·94 ± 0·96 | 0·83 ± 0·49 | 5·01 ± 3·41 |
| ΣBrFA | 0·91 | 5·47 ± 1·71 | 6·59 ± 3·93 | 3·45 ± 3·99 | 2·78 ± 2·31 | 2·38 ± 0·38 | 2·49 ± 1·15 |
| 15 : 0 | — | 0·61 ± 0·20 | 0·60 ± 0·24 | 0·79 ± 0·55 | 0·71 ± 0·26 | 0·46 ± 0·05* | 0·63 ± 0·12* |
| 16 : 0 | 45·61 | 26·45 ± 7·42 | 27·06 ± 13·57 | 20·45 ± 7·04 | 18·02 ± 5·01 | 21·52 ± 3·61 | 17·59 ± 1·00 |
| 16 : 1ω9 | 3·32 | 6·08 ± 0·78 | 3·79 ± 2·19 | 1·97 ± 1·06 | 1·43 ± 0·45 | 1·55 ± 0·40* | 0·84 ± 0·25* |
| 16 : 1ω7c | 2·58 | 4·75 ± 1·69 | 3·53 ± 1·87 | 6·98 ± 4·14 | 3·92 ± 1·88 | 3·37 ± 0·60* | 4·95 ± 1·25* |
| 16 : 1ω7t | 1·22 | 1·66 ± 0·32 | 1·60 ± 0·64 | — | — | 0·77 ± 0·56 | TR |
| 16 : 2ω6 | — | 0·50 ± 0·61 | 0·75 ± 0·48 | 0·74 ± 0·89 | TR | 1·00 ± 0·67 | 0·77 ± 0·16 |
| 17 : 0 | TR | 1·27 ± 0·52 | 0·72 ± 0·28 | 1·20 ± 1·03 | 2·61 ± 1·62 | 1·42 ± 0·29* | 0·74 ± 0·10* |
| 17 : 1ω7 | TR | 0·40 ± 0·51 | 1·24 ± 0·72 | 0·33 ± 0·65 | — | 0·62 ± 0·12* | — |
| 16 : 3ω3 | TR | 1·76 ± 1·01 | 1·61 ± 1·57 | 0·79 ± 1·04 | 0·66 ± 0·80 | 0·57 ± 0·74 | 0·40 ± 0·12 |
| 18 : 0 | 4·37 | 9·31 ± 4·51 | 4·75 ± 1·41 | 10·89 ± 7·44 | 17·52 ± 10·21 | 8·27 ± 0·57* | 4·87 ± 1·21* |
| 18 : 1ω9 | 5·40 | 5·31 ± 1·59 | 4·24 ± 1·97 | 7·61 ± 1·27 | 5·91 ± 1·70 | 4·42 ± 0·47* | 11·55 ± 2·11* |
| 18 : 1ω7 | 0·96 | 3·23 ± 0·88 | 1·65 ± 0·87 | 5·55 ± 2·94 | 3·41 ± 2·49 | 5·81 ± 1·15* | 2·67 ± 0·37* |
| 18 : 2ω6 | 8·07 | 2·78 ± 1·18 | 3·37 ± 1·81 | 3·33 ± 0·64 | 2·98 ± 0·91 | 2·31 ± 1·17* | 4·92 ± 0·57* |
| 18 : 3ω3 | 5·93 | 9·16 ± 1·73 | 8·85 ± 4·98 | 7·74 ± 2·51 | 7·05 ± 3·62 | 6·37 ± 1·21* | 4·60 ± 0·39* |
| 18 : 4ω3 | 3·28 | 4·66 ± 1·34 | 4·37 ± 2·20 | 2·41 ± 1·70 | 3·41 ± 1·33 | 2·73 ± 0·66* | 5·14 ± 0·80* |

TABLE I. *Continued*

| Fatty acid | *Microcystis* | Phytoplankton | | Zooplankton | | Digesta | |
|---|---|---|---|---|---|---|---|
| | | 1+ | 3+ | 1+ | 3+ | 1+ | 3+ |
| 20 : 0 | TR | 2·19 ± 2·41* | TR | 0·60 ± 1·19 | TR | TR | TR |
| 20 : 1$\omega$9 | — | TR | TR | — | — | 1·59 ± 2·65 | 0·45 ± 0·30 |
| 20 : 2$\omega$6 | — | — | TR | — | — | TR | 1·55 ± 2·19* |
| 20 : 3$\omega$6 | 0·38 | TR | — | — | — | 1·14 ± 0·40 | 1·45 ± 2·27 |
| 20 : 4$\omega$6 | — | — | 0·54 ± 0·26* | 2·11 ± 2·93 | 1·59 ± 1·82 | 5·37 ± 0·77 | 3·44 ± 2·14 |
| 20 : 3$\omega$3 | TR | TR | — | 0·68 ± 1·35 | TR | 0·98 ± 0·17 | 1·07 ± 1·20 |
| 20 : 4$\omega$3 | — | 0·39 ± 0·47 | 0·65 ± 0·36 | 1·52 ± 1·95 | 1·80 ± 1·86 | 1·50 ± 0·21* | 2·81 ± 0·27* |
| 20 : 5$\omega$3 | — | 2·81 ± 1·71 | 1·81 ± 0·69 | 7·25 ± 3·80 | 6·39 ± 4·12 | 7·66 ± 2·24 | 6·03 ± 0·88 |
| 22 : 0 | — | 1·22 ± 1·10* | — | — | — | TR | TR |
| 22 : 4$\omega$6 | — | — | — | — | — | 0·99 ± 0·25 | 0·61 ± 0·45 |
| 22 : 5$\omega$6 | — | — | — | — | — | 1·03 ± 0·39 | 1·65 ± 0·91 |
| 22 : 5$\omega$3 | — | — | TR | — | 0·76 ± 0·81 | 2·28 ± 1·55 | 1·33 ± 0·23 |
| 22 : 6$\omega$3 | TR | 1·52 ± 1·22 | 1·10 ± 0·61 | 1·89 ± 1·68 | 4·07 ± 1·98 | 6·20 ± 3·11 | 8·44 ± 2·12 |
| Others | 7·01 | 3·35 ± 0·91 | 2·58 ± 1·67 | 9·16 ± 12·32 | 2·60 ± 1·91 | 5·04 ± 4·03 | 2·83 ± 1·53 |
| ΣSAFA | 59·88 | 44·22 ± 7·13 | 35·93 ± 11·38 | 36·23 ± 17·23 | 41·80 ± 19·34 | 32·50 ± 4·26 | 29·16 ± 2·88 |
| ΣMUFA | 13·48 | 21·43 ± 3·02 | 16·06 ± 4·19 | 22·44 ± 7·26 | 14·68 ± 5·94 | 18·13 ± 1·19 | 20·46 ± 3·11 |
| ΣPUFA | 17·66 | 23·57 ± 5·41 | 23·05 ± 3·74 | 28·46 ± 6·92 | 28·71 ± 11·68 | 40·13 ± 4·18 | 44·20 ± 5·19 |
| Σ$\omega$3 | 9·21 | 20·29 ± 5·16 | 18·39 ± 3·85 | 22·28 ± 5·07 | 24·15 ± 10·28 | 28·29 ± 3·91 | 29·81 ± 3·09 |
| Σ$\omega$6 | 8·45 | 3·28 ± 1·36 | 4·66 ± 1·18 | 6·18 ± 2·66 | 4·57 ± 1·85 | 11·84 ± 1·53 | 14·39 ± 6·24 |

Data are weight per cent of total fatty acids and represent the mean ± analytical S.D. ($n$=4). BrFA, Branched fatty acids; SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; Σ$\omega$3 and Σ$\omega$6, total fatty acids of ($n$-3) and ($n$-6) series; TR, trace <0·3%.

*Indicates significant difference between 1+ and 3+ treatments ($U$ test).

significantly different, ranging from 4·51 to 6·71%DW for muscles and from 42·3 to 53·7%DW for intestinal fat. On the other hand the liver of 3+ silver carp (12·5%DW ± 0·4) contained higher amounts of lipids than did the liver of 1+ silver carp (7·3%DW ± 0·8).

## FATTY ACID ANALYSIS

There were no differences (*U*-test; $P>0{\cdot}05$) between the fatty acid profiles of phytoplankton sampled in 1+ tanks and the fatty acid profiles of phytoplankton sampled in 3+ tanks (Table I). They contained low levels of highly unsaturated fatty acids (HUFA) and high levels of 18 : 3$\omega$3 and 18 : 4$\omega$3. Although dominated by *Microcystis aeruginosa*, the tank phytoplankton had a fatty acid composition not exactly the same as that of the *Microcystis* culture. Fatty acids such as 16 : 0 and 18 : 2$\omega$6 were present in higher percentages in the laboratory culture.

As with phytoplankton, no significant differences were detected between the fatty acid composition of 1+ and 3+ zooplankton. The major saturated fatty acids present in zooplankton were 16 : 0 and 18 : 0. Mono-unsaturated fatty acids (MUFA) were dominated by 16 : 1$\omega$7, 18 : 1$\omega$7 and 18 : 1$\omega$9. In contrast to phytoplankton, there were high levels of HUFA in zooplankton, for example 20 : 5$\omega$3 and to a lesser extent 22 : 6$\omega$3 and 20 : 4$\omega$6. Other polyunsaturated fatty acids (PUFA) like 18 : 3$\omega$3, 18 : 4$\omega$3 and 18 : 2$\omega$6 were also present in large proportions. Finally, the general pattern of zooplankton fatty acids was not closely related to that of phytoplankton.

The fatty acid composition of the digesta showed several differences between 1+ and 3+ silver carp ($P<0{\cdot}05$), concerning eleven fatty acids the most important of which were 16 : 1$\omega$7, 18 : 0, 18 : 1$\omega$7, 18 : 1$\omega$9, 18 : 2$\omega$6, 18 : 3$\omega$3, 18 : 4$\omega$3 and 20 : 4$\omega$3. In both trials, digesta were rich in PUFA (28·3–29·8% of total fatty acids) and contained notable percentages of 20 : 5$\omega$3 and 22 : 6$\omega$3. The general pattern of these digesta fatty acids seemed to be more closely related to that of tank zooplankton than to that of phytoplankton (Table I).

The statistical analysis of neutral lipid fatty acids (*U*-test; $P<0{\cdot}05$) reveals that there were significant differences between intestinal fat of 1+ and 3+ silver carp and between the white muscles of 1+ and 3+ silver carp (Table II). These differences concern more particularly the proportions of fatty acids with 16 and 18 carbon atoms, for example, 16 : 0, 18 : 0, 18 : 1$\omega$7, 18 : 1$\omega$9, 18 : 2$\omega$6 and 18 : 4$\omega$3. The level of PUFA in the neutral lipids of intestinal fat and in the neutral lipids of muscles was significantly higher in 3+ fish ($P<0{\cdot}05$) due to the high percentages of 18 : 4$\omega$3 and 22 : 6$\omega$3 detected in older silver carp. In contrast, the liver tissues of both fish groups exhibited similar profiles of neutral lipid fatty acids (Table II).

In contrast with neutral lipids, there were few significant differences in the fatty acid composition of phospholipids between 1+ and 3+ silver carp (Table III). In the three tissues examined, PUFA were detected in higher percentages in the 3+ fish. Curiously, these proportions of PUFA were lower than those found in the neutral lipids (Table II). The opposite was found for 22 : 6$\omega$3, which was higher in the carp phospholipids, except in 1+ liver and muscles. The very large proportion of 16 : 0 found in the phospholipids reflects the high levels of

TABLE II. Fatty acid composition of neutral lipids in muscles, liver, and intestinal fat from 1+ and 3+ silver carp

| Fatty acid | Intestinal fat | | Liver | | White muscle | |
|---|---|---|---|---|---|---|
| | 1+ | 3+ | 1+ | 3+ | 1+ | 3+ |
| 12 : 0 | 0·50 ± 0·67 | 0·76 ± 0·26 | 0·37 ± 0·45 | 0·36 ± 0·08 | TR | 0·51 ± 0·06 |
| 13 : 0 | — | TR | TR | TR | TR | TR |
| 14 : 0 | 5·78 ± 3·48 | 9·70 ± 2·34 | 3·83 ± 1·64 | 5·23 ± 1·45 | 4·25 ± 1·01* | 7·38 ± 0·29* |
| ΣBrFA | 2·53 ± 0·88 | 4·18 ± 3·56 | 2·25 ± 0·66 | 2·53 ± 0·44 | 4·06 ± 2·86 | 5·02 ± 4·30 |
| 15 : 0 | 2·45 ± 1·82* | 0·75 ± 0·02* | 0·54 ± 0·30 | 0·83 ± 0·36 | 1·06 ± 0·26 | 0·70 ± 0·12 |
| 16 : 0 | 22·95 ± 4·34 | 14·93 ± 1·68* | 25·18 ± 6·32 | 18·64 ± 8·50 | 20·50 ± 3·73* | 15·25 ± 1·23* |
| 16 : 1ω9 | 1·57 ± 0·29* | 0·99 ± 0·06* | 0·82 ± 0·11* | 2·06 ± 1·18* | 1·10 ± 0·20 | 0·92 ± 0·18 |
| 16 : 1ω7c | 7·04 ± 1·49 | 6·29 ± 0·16 | 4·20 ± 0·68 | 5·13 ± 1·82 | 6·60 ± 2·71 | 5·91 ± 0·85 |
| 16 : 1ω7t | — | — | — | — | — | — |
| 16 : 2ω6 | 1·34 ± 0·82 | 0·73 ± 0·09 | 1·76 ± 0·67 | 2·41 ± 0·37 | 1·26 ± 0·36 | 0·81 ± 0·13 |
| 17 : 0 | 3·70 ± 3·51* | 0·83 ± 0·42* | 0·99 ± 0·28 | 1·16 ± 0·48 | 2·32 ± 1·15* | 0·94 ± 0·22* |
| 17 : 1ω7 | — | 0·40 ± 0·30 | TR | 0·51 ± 0·05 | 0·52 ± 0·54 | 0·61 ± 0·13 |
| 16 : 3ω3 | TR | 0·37 ± 0·21 | 0·30 ± 0·22 | 0·50 ± 0·59 | 0·34 ± 0·44 | TR |
| 18 : 0 | 9·34 ± 3·14* | 2·95 ± 0·58* | 5·26 ± 1·19 | 5·96 ± 2·73 | 8·98 ± 7·28* | 3·34 ± 0·21* |
| 18 : 1ω9 | 10·75 ± 4·94 | 14·52 ± 0·85 | 10·37 ± 3·47 | 10·54 ± 4·39 | 10·60 ± 2·25* | 14·13 ± 0·44* |
| 18 : 1ω7 | 4·99 ± 1·84* | 2·32 ± 0·62* | 3·36 ± 0·87 | 5·73 ± 1·74 | 5·98 ± 1·92* | 2·65 ± 0·44* |
| 18 : 2ω6 | 3·78 ± 0·86* | 6·68 ± 0·31* | 3·64 ± 1·34 | 3·86 ± 1·35 | 4·13 ± 1·00* | 5·87 ± 0·15* |
| 18 : 3ω3 | 6·38 ± 3·35 | 5·11 ± 0·32 | 2·92 ± 0·78* | 5·18 ± 3·37* | 6·25 ± 1·94 | 4·85 ± 0·015 |
| 18 : 4ω3 | 1·80 ± 0·70* | 6·13 ± 1·38* | 2·70 ± 1·53 | 2·58 ± 0·46 | 1·28 ± 1·02* | 5·57 ± 0·85* |
| 20 : 0 | TR | TR | TR | TR | 0·54 ± 0·73 | TR |
| 20 : 1ω9 | TR | 0·61 ± 0·32 | 0·33 ± 0·23 | TR | 1·20 ± 1·81 | 0·83 ± 0·10 |
| 20 : 2ω6 | — | TR | 0·48 ± 0·33 | TR | 0·30 ± 0·35 | 0·40 ± 0·09 |
| 20 : 3ω6 | TR | 0·32 ± 0·22 | TR | 0·40 ± 0·28 | 0·36 ± 0·41 | 0·46 ± 0·06 |
| 20 : 4ω6 | 2·07 ± 0·74 | 2·36 ± 0·53 | 4·82 ± 1·48 | 3·47 ± 1·38 | 4·37 ± 2·87 | 3·33 ± 0·23 |
| 20 : 3ω3 | TR ± 0·28 | TR | 0·91 ± 1·18 | 0·55 ± 0·30 | 0·32 ± 0·37 | TR |
| 20 : 4ω3 | 0·86 ± 0·64* | 3·12 ± 0·40* | 2·20 ± 0·75 | 1·63 ± 0·42 | 1·17 ± 0·92 | 2·59 ± 1·19 |
| 20 : 5ω3 | 4·88 ± 2·50 | 5·26 ± 0·32 | 5·81 ± 0·27* | 7·71 ± 2·55* | 5·80 ± 1·55 | 6·56 ± 0·54 |
| 22 : 0 | — | — | TR | — | — | TR |
| 22 : 4ω6 | — | TR | TR | TR | TR | 0·33 ± 0·16 |
| 22 : 5ω6 | 0·30 ± 0·61 | 1·37 ± 0·41 | 1·84 ± 0·24* | 0·32 ± 0·12* | TR | 1·77 ± 0·30 |
| 22 : 5ω3 | — | 0·77 ± 0·34* | 0·72 ± 0·48 | 1·29 ± 0·94 | 0·61 ± 0·59 | 1·20 ± 0·13 |
| 22 : 6ω3 | 3·40 ± 1·66 | 5·76 ± 0·68 | 12·15 ± 2·14 | 7·60 ± 5·41 | 2·56 ± 2·48* | 7·76 ± 0·70* |
| Others | 2·12 ± 0·29 | 4·13 ± 1·12 | 1·99 ± 2·14 | 2·71 ± 1·95 | 2·83 ± 2·62 | 4·13 ± 0·90 |
| ΣSAFA | 44·72 ± 5·32* | 29·91 ± 2·27* | 36·30 ± 6·19 | 32·17 ± 14·80 | 37·65 ± 11·27 | 28·13 ± 2·06 |
| ΣMUFA | 24·35 ± 4·94 | 25·11 ± 1·13 | 19·28 ± 2·61* | 23·96 ± 11·62* | 26·00 ± 5·05 | 25·04 ± 1·08 |
| ΣPUFA | 24·81 ± 6·60* | 37·98 ± 2·80* | 40·62 ± 2·76 | 37·51 ± 15·91 | 28·74 ± 7·45* | 41·50 ± 1·26* |
| Σω3 | 17·32 ± 5·89 | 26·52 ± 2·14 | 27·72 ± 2·57 | 27·04 ± 11·03 | 18·33 ± 5·77* | 28·53 ± 1·09* |
| Σω6 | 7·49 ± 0·99* | 11·45 ± 1·75* | 12·90 ± 1·28 | 10·47 ± 4·65 | 10·41 ± 3·06 | 12·97 ± 0·71 |

Data are weight per cent of total fatty acids and represent the mean ± analytical S.D. ($n$=4). BrFA, Branched fatty acids; SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; Σω3 and Σω6, total fatty acids of ($n$-3) and ($n$-6) series; TR, trace <0·3%.

*Indicates significant difference between 1+ and 3+ treatments ($U$ test).

saturated fatty acids (SAFA) occurring in the phospholipids from all the tissues. Finally, in all the tissues the proportion of mono-unsaturated fatty acids was lower in the phospholipids than in the neutral lipids (Tables II and III).

TABLE III. Fatty acid composition of polar lipids in muscles, liver, and intestinal fat from 1+ and 3+ silver carp

| Fatty acid | Intestinal fat | | Liver | | White muscle | |
|---|---|---|---|---|---|---|
| | 1+ | 3+ | 1+ | 3+ | 1+ | 3+ |
| 12 : 0 | 0·61 ± 0·62 | — | — | — | 0·34 ± 0·68 | TR |
| 13 : 0 | — | — | — | — | — | — |
| 14 : 0 | 6·53 ± 4·72 | 12·77 ± 6·61 | 1·90 ± 1·56 | 4·26 ± 2·22 | 3·61 ± 4·22 | 4·40 ± 2·56 |
| ΣBrFA | 0·48 ± 0·84 | 1·00 ± 0·69 | 1·16 ± 0·71 | 1·15 ± 0·97 | 1·64 ± 0·59 | 3·60 ± 1·40 |
| 15 : 0 | 0·68 ± 0·59 | 0·68 ± 0·64 | 0·68 ± 0·39 | 0·88 ± 0·22 | 1·30 ± 0·28* | 0·81 ± 0·19* |
| 16 : 0 | 26·49 ± 2·93 | 17·05 ± 9·44 | 18·17 ± 11·14 | 28·90 ± 3·59 | 26·05 ± 4·25 | 20·62 ± 5·47 |
| 16 : 1$\omega$9 | 1·55 ± 1·40 | 1·88 ± 1·22 | 1·16 ± 0·46 | 1·52 ± 0·76 | 1·42 ± 0·41 | 1·18 ± 0·45 |
| 16 : 1$\omega$7c | 3·69 ± 0·96 | 2·91 ± 1·51 | 2·65 ± 2·11 | 3·43 ± 1·20 | 4·05 ± 1·21 | 4·11 ± 1·03 |
| 16 : 1$\omega$7t | — | — | — | — | — | — |
| 16 : 2$\omega$6 | 1·03 ± 0·90 | 0·49 ± 0·36 | 1·44 ± 0·96* | 0·98 ± 0·67* | 1·02 ± 0·74 | 1·13 ± 0·51 |
| 17 : 0 | 3·69 ± 1·48* | 1·27 ± 0·57* | 2·73 ± 1·59 | 2·85 ± 1·12 | 2·65 ± 1·43 | 1·32 ± 0·29 |
| 17 : 1$\omega$7 | — | — | — | — | TR | 0·59 ± 0·63 |
| 16 : 3$\omega$3 | — | TR | — | — | 1·18 ± 2·36 | 0·52 ± 0·40 |
| 18 : 0 | 14·91 ± 7·60 | 7·11 ± 3·61 | 9·34 ± 6·09 | 13·31 ± 4·75 | 13·77 ± 10·59 | 8·21 ± 4·48 |
| 18 : 1$\omega$9 | 9·70 ± 5·83 | 7·43 ± 4·33 | 5·38 ± 2·44 | 9·58 ± 3·80 | 9·38 ± 3·40 | 14·47 ± 2·72 |
| 18 : 1$\omega$7 | 3·63 ± 0·48 | 9·42 ± 7·25 | 4·22 ± 3·10* | 3·32 ± 0·54* | 4·04 ± 1·02 | 2·94 ± 0·80 |
| 18 : 2$\omega$6 | 2·62 ± 2·20 | 2·22 ± 1·32 | 2·00 ± 1·51 | 2·21 ± 0·81 | 7·28 ± 8·47 | 3·58 ± 2·03 |
| 18 : 3$\omega$3 | 2·02 ± 0·13 | 8·74 ± 6·69 | 3·32 ± 1·55 | 1·29 ± 1·23 | 2·48 ± 0·62 | 2·45 ± 2·06 |
| 18 : 4$\omega$3 | 0·91 ± 0·79 | 1·36 ± 0·62 | TR | — | 1·25 ± 1·71 | 2·57 ± 3·28 |
| 20 : 0 | 1·23 ± 0·58* | TR | 0·53 ± 0·46 | 1·11 ± 0·81 | 0·70 ± 0·96 | 0·44 ± 0·39 |
| 20 : 1$\omega$9 | — | TR | — | TR | 0·39 ± 0·79 | 0·98 ± 0·14 |
| 20 : 2$\omega$6 | 0·33 ± 0·57 | TR | — | — | TR | 0·35 ± 0·33 |
| 20 : 3$\omega$6 | 0·43 ± 0·75 | — | TR | TR | TR | TR |
| 20 : 4$\omega$6 | 3·15 ± 1·18 | 2·12 ± 1·59 | 4·17 ± 1·85 | 2·84 ± 1·22 | 2·59 ± 0·73 | 4·34 ± 1·30 |
| 20 : 3$\omega$3 | — | TR | TR | — | TR | TR |
| 20 : 4$\omega$3 | 0·39 ± 0·68 | 0·37 ± 0·47 | 0·32 ± 0·31 | — | 0·75 ± 0·91 | 1·93 ± 1·65 |
| 20 : 5$\omega$3 | 3·51 ± 1·05 | 2·88 ± 0·99 | 6·80 ± 2·83 | 2·61 ± 1·34 | 3·21 ± 0·62 | 4·34 ± 2·19 |
| 22 : 0 | — | TR | 0·88 ± 0·77 | 1·14 ± 0·85 | 0·82 ± 0·95 | TR |
| 22 : 4$\omega$6 | — | TR | 0·44 ± 0·42 | — | — | 0·53 ± 0·47 |
| 22 : 5$\omega$6 | 0·50 ± 0·86 | 0·87 ± 1·02 | — | 0·59 ± 1·18 | 0·69 ± 0·85* | 2·21 ± 0·47* |
| 22 : 5$\omega$3 | 0·62 ± 1·08 | TR | 0·51 ± 0·49 | 0·33 ± 0·66 | TR | 0·99 ± 0·17 |
| 22 : 6$\omega$3 | 11·39 ± 2·96 | 10·21 ± 5·44 | 2·90 ± 1·61 | 13·73 ± 5·89 | 4·52 ± 3·21 | 10·72 ± 4·26 |
| Others | 0·52 ± 0·51 | 1·48 ± 1·00 | 5·24 ± 2·91 | 3·66 ± 3·96 | 4·14 ± 3·09 | 4·33 ± 1·47 |
| ΣSAFA | 54·15 ± 10·76 | 38·88 ± 14·24 | 34·23 ± 24·33 | 52·45 ± 5·51 | 49·25 ± 14·07 | 35·79 ± 8·30 |
| ΣMUFA | 18·57 ± 8·47 | 21·65 ± 6·36 | 13·41 ± 10·87 | 17·85 ± 5·70 | 19·28 ± 4·14 | 21·27 ± 2·51 |
| ΣPUFA | 26·91 ± 3·49 | 29·25 ± 16·28 | 21·90 ± 15·96 | 24·58 ± 7·57 | 24·98 ± 8·01 | 35·65 ± 5·62 |
| Σ$\omega$3 | 18·84 ± 1·75 | 23·55 ± 11·91 | 13·85 ± 8·62 | 17·97 ± 6·51 | 13·40 ± 7·17 | 23·51 ± 6·20 |
| Σ$\omega$6 | 8·07 ± 3·17 | 5·70 ± 5·83 | 8·05 ± 6·72 | 6·61 ± 1·70 | 11·57 ± 9·31 | 12·14 ± 0·70 |

Data are weight per cent of total fatty acids and represent the mean ± analytical S.D. ($n$=4). BrFA, Branched fatty acids; SFA, saturated fatty acids; MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; Σ$\omega$3 and Σ$\omega$6, total fatty acids of ($n$-3) and ($n$-6) series; TR, trace <0·3%.

*Indicates significant difference between 1+ and 3+ treatments ($U$ test).

## DISCUSSION

At the end of the experimental period (day 32), the fatty acid composition of the phytoplankton reflected that of the species composition of the microalgae in

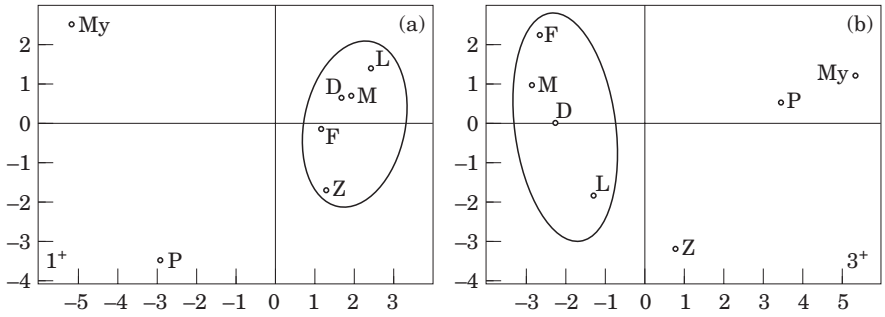


FIG. 3. Principal component plot of fatty acids extracted from *Microcystis aeruginosa* laboratory culture, tank phytoplankton and tank zooplankton computed together with neutral fatty acids extracted from digesta and tissues of silver carp. The analysis is presented for 1+ treatments (a) and 3+ treatments (b). My, *Microcystis aeruginosa*; P, tank phytoplankton; Z, zooplankton; D, digesta of silver carp; F, peri-intestinal fat; L, live; M, white muscle.

the tanks. For example, the high quantities of 18 : 2$\omega$6 and 18 : 3$\omega$3 were representative of a community dominated by cyanobacteria and chlorophyceae (Sargent *et al.*, 1995; Desvilettes *et al.*, 1997). Nevertheless, the development of diatoms and Cryptophyceae within the algal biomass influenced the fatty acid composition, as shown by the presence of small quantities of PUFA characteristic of these algae, such as 18 : 4$\omega$3, 20 : 5$\omega$3 and 22 : 6$\omega$3 (Ahlgren *et al.*, 1992; Groth-Nard & Robert, 1993). This is one of the main reasons explaining the difference in fatty acid composition between the pure culture of *Microcystis aeruginosa* and the phytoplankton sampled in the tanks.

The zooplankton biomass showed all the characteristics of a community dominated by cladocera, with in particular higher proportions of 20 : 5$\omega$3 than 22 : 6$\omega$3. 20 : 5$\omega$3 is a fatty acid that is reported to be typical of cladocera (Weers & Gulati, 1997), whereas 22 : 6$\omega$3 is more abundant in copepoda (Farkas & Csengeri, 1981).

The fatty acid profiles of the digesta were similar to those of the zooplankton, in which high quantities of 20 : 5$\omega$3 were found. However, levels of 22 : 6$\omega$3 and 20 : 4$\omega$6 were much higher in the digestive tract of the carp than in the zooplankton total lipid. The origin of these PUFA in the digesta remain partially unclear. A certain quantity originated probably from ingested zooplankton, but the influence of the intestinal microfauna should not be neglected. Certain strains of marine bacteria can biosynthesize 20 : 5$\omega$3 (Yasawa *et al.*, 1988) and the intestinal liquor of both marine and freshwater fish can contain colonies of *Vibrio* spp. producing 20 : 5$\omega$3 (Ringø *et al.*, 1992). Furthermore, bacterial strains with the ability to produce 22 : 6$\omega$3 have been isolated by Hamamoto *et al.* (1995). This indicates that a proportion of the 22 : 6$\omega$3 detected in the carp digesta could have been synthesized by intestinal bacteria. Nevertheless, it is suggested that the influence of the zooplankton on the digesta is of major importance, which is confirmed by the principal components analysis (PCA). With this analysis, the zooplankton, digesta and neutral lipids of 1+ carp were grouped together, whereas the phytoplankton and *Microcystis aeruginosa* were separated from them (Fig. 3). This is undoubtedly caused by the high consumption of zooplankton by the 1+ carp. On the other hand, in the

3+ carp, the PCA revealed that the zooplankton had a much smaller influence on the fatty acid composition of the digesta (Fig. 3). One of the possible explanations for this difference between the 1+ and 3+ carp could be a greater ingestion of phytoplankton by the 3+ carp. Shapiro (1985) showed also that mature carp tended to consume more phytoplankton than 1+ carp. However, in the present study the impact of the phytoplankton on the fatty acid composition of the digesta was not very pronounced in either 1+ or 3+ carp, probably because it was masked by the influence of the zooplankton. It is certain that the action of lipases and the processes of intestinal absorption changed the assemblage of fatty acids in the digesta. The digesta used in these fatty acid analyses were extruded from the second third of the alimentary tract, where absorption occurs in silver carp and lipase activity decreases (Kirilenko & Chigrinzkaya, 1984; Bitterlich, 1985). The question of the digestibility of the phytoplankton consumed by the carp in this study is also important. Although zooplankton and cladocera are ingested in 20 min (Bitterlich & Gnaiger, 1984), the same is not the case for cyanobacteria and certain Chlorophyceae. These authors reported that the digestive efficiency of *Microcystis aeruginosa* in the silver carp was 32·6% and the conversion efficiency was as low as 4·6%. More recently, Beveridge *et al.* (1993) found that the same species of cyanobacteria was digested poorly by the silver carp. Similarly, Chlorophyceae belonging to the genera *Scenedesmus*, *Tetraedron*, *Pediastrum* and *Coelastrum* seem to be digested very poorly (Vörös *et al.*, 1997). In contrast, the same authors reported an excellent digestibility for Cryptophyceae, diatoms and the cyanobacterian *Aphanizomenon flos-aquae*. Kirilenko & Chigrinzkaya (1984) studied the assimilation of algal neutral fatty acids by the silver carp, and found that it varied from 50·5 to 67·3% when the algae were assimilable by this fish. Therefore, it is probable that the cyanobacterian *Microcystis aeruginosa*, which accounted for >70% of the phytoplankton biomass ingested by the carp in this study, was assimilated poorly. Its decrease throughout the experiment could still be explained partly by carp grazing, even if assimilation was very low, as the carp could still ingest the cyanobacterian, which then would be found in the faeces trapped in mucus, probably in a non-viable state, and would be eliminated from the phytoplankton. However, it seems likely that grazing by zooplankton or competition for nutrients by Chlorophyceae could also have played a role.

It was difficult to show any evidence for the influence of diet on the fatty acid composition of carp tissues. With PCA results, the influence was pronounced only in the case of 1+ carp. The fatty acid profiles in the digesta and the neutral lipid in the muscles were similar in both groups of carp, whereas the neutral lipids of the liver and the peri-intestinal fat had very different fatty acid compositions. In cyprinids the liver is the main organ where fatty acids are synthesized, these being mainly saturated fatty acids of the type 14 : 0 and 16 : 0 (Corraze, 1999). For example in the common carp *Cyprinus carpio* L., the liver is the site of 16 : 0 synthesis (Farkas, 1984) and Δ9 and Δ6 desaturase activity (Schünhe & Wodtke, 1983). In the carp in the present study, it is likely that the fatty acids were rearranged in the liver, with in particular a major synthesis of 16 : 0 and 18 : 0. The fact that the neutral lipids in other tissues reflected poorly the fatty acid profiles in the diet is not surprising in a natural environment. For example, in steelhead trout smolts *Oncorhynchus mykiss* (Walbaum), Sheridan

*et al*. (1985) found that the diet had little influence on the fatty acid composition of body tissues. Similar observations have been made on the Atlantic salmon *Salmo salar* L. (Viga & Grahl-Nielsen, 1990) and between the herring *Clupea harengus* L. and its planktonic food (Linko *et al*., 1985). Viga & Grahl-Nielsen (1990) thought that only very pronounced variations in dietary fatty acids would have an influence on fish tissues, and would be most perceptible in aquaculture with a marked change in feed. In the carp in the present study, the semi-natural conditions and the diet which was dominated quantitatively, throughout the study, by zooplankton would lead to little variation in tissue fatty acids. Alternatively, the duration of the survey, one month, could be considered too short to detect any changes in fatty acid profiles. Literature data are ambiguous on this subject. For instance, a 3-week experiment is sufficient to enhance lipid variations in *Channa punctata* (Bloch) exposed to cold or warm water temperatures (Dutta *et al*., 1984) but Lie *et al*. (1992) fed small cod *Gadus morhua* L. during one year on three different diets to analyse their influence on phospholipid composition in organs. In contrast to this latter experiment, Anderson & Arthington (1989) detected influence of dietary lipid on the fatty acid composition of young silver perch *Leiopotherapon bidyanus* after 16 days. It seems, as stated above, that the degree of variation induced in the experiments, for example the difference between diets, and temperatures, is more important than a long time period in promoting changes in the fatty acid composition of fish.

The phospholipids in the muscle, liver and peri-intestinal fat were characterized in the silver carp by a rather low proportion of PUFA in both 1+ and 3+ fish. These phospholipids contained from 21·90 to 36·65% of PUFA, whereas other cyprinids such as the roach *Rutilus rutilus* (L.) contain 56·5% PUFA (Gunstone *et al*., 1978). In various cyprinids of temperate waters, for example bream *Scardinius erythrophthalmus* (L.) and tench *Tinca tinca* (L.), the dorsal muscles contain from 41·8 to 53·7% of PUFA (Ahlgren *et al*., 1994). The low proportion of PUFA found in the silver carp make this fish similar to the crucian carp *Carassius carassius* (L.), also of Asiatic origin, which contains 36·5% of PUFA in its dorsal muscles (Ahlgren *et al*., 1994). On the other hand, the fatty acid profiles of these phospholipids are not very different from those recorded in other fish, the main PUFA being 22 : 6$\omega$3, 20 : 5$\omega$3, 18 : 3$\omega$3 and 18 : 2$\omega$3. The essential PUFA in the silver carp are probably the same as in the common carp or in the grass carp *Ctenopharyngodon idella* (Valenciennes), namely 18 : 3$\omega$3 and 18 : 2$\omega$6 (Corraze, 1999). Irrespective of whether the type of food ingested was phytoplankton or zooplankton, these fatty acids were present in the silver carp in this study. Nevertheless, it is important to note that cladocera provide high proportions of 20 : 5$\omega$3 PUFA whose incorporation in the diet increases growth in the common and grass carp more than a diet containing only 18 : 3$\omega$3 (Watanabe, 1982; Henderson & Tocher, 1987). Finally, mucilaginous cyanobacteria and desmid Chlorophyceae, which are of uncertain digestibility, are a food that is poor in long-chain PUFA for the silver carp. From a qualitative viewpoint, Cryptophyceae, diatoms and especially zooplankton are much more valuable. The latter is particularly valuable since it represents a quantitatively more abundant supply than the phytoplankton.

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