

A Review of Grass Carp Use for Aquatic Weed Control and its Impact on Water Bodies

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ABSTRACT

The state of knowledge of grass carp (*Ctenopharyngodon idella* Val.) effects on water bodies are summarized based on a review of selected literature and my own experience from South Bohemian ponds. The subjects considered include aquatic plant control using grass carp, fish age and stocking densities, and direct and indirect consequences of its introduction to water bodies including impacts on water and sediment chemistry, phytoplankton, zooplankton, zoobenthos, fish, amphibian and water birds communities. Lastly, longevity of plant control by the grass carp is addressed. An attempt has also been made to identify weaknesses in the available information.

Key words: *Ctenopharyngodon idella*, biological control, aquatic macrophytes, herbivorous fish, feeding selectivity

INTRODUCTION

The ideal aquatic plant management tool should provide cost effective control with long-term impact, a high level of selectivity, and if possible have minimal or no negative side effects. Fish used for aquatic weed control include several species of tilapia (*Tilapia* spp.), silver dollars (*Metynnis roosevelti* Eig. and *Mylossoma argenteum* E. Ahl.), common carp (*Cyprinus carpio* L.), silver carp (*Hypophthalmichthys molitrix* Val.), and the grass carp (*Ctenopharyngodon idella* Val.) (Shell 1962, Yeo 1967, NAS 1976). Of these fish, only the grass carp is able to consume large quantities of aquatic macrophytes (van der Zwerde 1990). Under suitable conditions, adult grass carp will eat more than its own weight of plant material on a daily basis (Cross 1969). However the grass carp is not an exclusively herbivorous fish species, as it also needs food of animal origin. Grass carp that were bred under laboratory conditions and provided both plant and animal food consumed about 76% of animal food and 24% plants (Fischer 1973). This paper reviews the characteristics of grass carp with emphasis on the relationships between stocking density, grazing impact, feeding selectivity (direct effects) and alteration of water habitat, water quality and sediment chemistry (indirect effects).

RESULTS AND DISCUSSION

Grass Carp Natural Habitat and Introductions

Grass carp (white amur) belongs to the minnow (carp) family (Cyprinidae). Several reviews have been written on its basic biology (e.g., Cross 1969, Michewicz et al. 1972, Krupauer 1989). The grass carp is a native to larger coastal East Asian rivers with Pacific drainage from latitudes 20° to 50° north and from longitudes 100° to 140° east (Fischer and Lyakhnovich, 1973).

It was introduced to Europe for aquatic weed control and to improve fish production through polyculture (van Zon 1977). After the first successful artificial breeding in the former USSR in 1961, many introductions were made to eastern and central European countries: Czechoslovakia (1961), Hungary (1963), Poland (1964), Bulgaria and former East Germany (both in 1965) (van Zon 1977). Since 1965 the grass carp has been slowly introduced to other parts of Europe, mainly in small quantities from Hungary (van Zon 1977). The reason for grass carp introduction to some western European countries (e.g., Austria, Belgium, Denmark, England, France, Switzerland, Sweden, The Netherlands and West Germany) was almost exclusively for weed control (van Zon 1977, Müller 1995).

Grass carp have also been successfully introduced for weed control to North (in 1963 into USA, Guillory and Gasaway 1978) and South America, other parts of Asia (Malaysia, Singapore, Borneo, Indonesia, Thailand, Hong Kong and the Philippines), Africa (e.g., Egypt) and Australia (Opuszyński and Shireman 1995). In some countries (especially in tropical region), the grass carp is an integral part of fish culture, as fish flesh forms an important source of protein for human consumption.

Risk of Grass Carp Introduction

Most of the controversy with grass carp introductions was related to its possible natural reproduction (Sutton 1977) and introduction of parasites, diseases and other fish species. Grass carp spawn and reproduce in large, swift, and turbid rivers with connected vegetated lagoons, lakes or impoundments under very exacting water temperature. Temperature limits to natural breeding of grass carp is set by the mean annual air isotherm of 10 C, which goes approximately over latitude 45° north in east Europe to latitude 50° north in west Europe (Opuszyński and Shireman 1995). Temperatures required for stimulation of sexual maturation, egg incubation, and survival of young range from 19 to 30 C, with an optimum of about 23 C (Stanley et al. 1978). Many other condi-

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tions (especially rapid change in water level of at least 1 m and flowing water with minimal velocity of 0.8 m s⁻¹ and flow of the water volume roughly 400 m³ s⁻¹) must be fulfilled to enable mating, egg laying and egg development of the grass carp (Stanley et al. 1978, Gangstad 1986). Therefore, the likelihood of natural grass carp reproduction is limited to few water bodies according to these data.

The grass carp is tolerant of a wide range of environmental conditions and is capable of extensive migrations once it is released or escapes into an open system. In 1990 to 1995 evidence of grass carp reproduction (juveniles less than 2 cm long and some diploid adults) was noticed in the Illinois and Mississippi Rivers (Raibley et al. 1995). Natural reproduction has been also documented in the Trinity River (Elder and Murphy 1997) and even in Red and Washita Rivers, which form Lake Texoma (Texas) (Hargrave and Gido 2004). Sutton (1977) reported that Canada and over one half of the states (26) in the United States had banned introduction of the diploid grass carp, with the remainder regulating the fish by permits. In the 1980s, triploid ("sterile", i.e., fish can produce gametes but viable offspring are extremely unlikely (Schultz et al. 2001)) grass carp were developed (Leslie et al. 1987). In 12 states in the U.S.A. breeding and stocking of diploid grass carp is permitted and in 19 states only triploid grass carp are permitted for stocking. Use of triploid grass carp is prohibited in another 19 states of the U.S.A. (Allen and Wattendorf 1987 in Müller 1995).

Natural reproduction of grass carp has also been recorded also in Europe (Danube River) (Holčík 1976, Jankovic 1998). Stocking of diploid grass carp is allowed only into small, artificial water bodies with special permission in most of the western European countries (e.g., Germany, Switzerland) (Müller 1995). Diploid grass carp is a minor component of closed polycultural fishponds systems (<5%) in most of the eastern European countries. Its production (aquaculture + capture) was 202 metric tons, which is about 1% of total fish production (21183 metric tons) in the Czech Republic in 1998 (Holá 2001).

Currently sterile triploid grass carp are used for aquatic weed control and fertile diploid grass carp are maintained in small numbers in closed polyculture pond systems. Documentation of some fertile grass carp and their reproductive success in the wild does not prove formation of self-sustaining and harmful populations of grass carp. Based on the limited distribution to date there is no clear reason to consider diploid grass carp as an invasive species.

Direct and Indirect Consequences of Grass Carp Stocking

Stocking of grass carp can both directly and indirectly influence the water body. Primary consequences of grass carp feeding include a selective decrease or elimination of aquatic plant biomass and the release of nutrient-rich excrements into the water. Many authors (e.g., Verigin et al. 1963, Cross 1969, Pine and Anderson 1991) published an approximate order of aquatic plant preferences by grass carp. In general, grass carp prefer soft-tissue aquatic plants, filamentous algae (e.g., *Cladophora* and *Pithophora*) and duckweeds (Lemnaceae). The more fibrous emergent plants and plants with toxic or other compounds, which make them more difficult for

utilization as food, are disliked by the fish (van der Zweerde 1990). The most comprehensive study divided the aquatic and also some of terrestrial plants species (overall about 140) into 3 groups according to their selective uptake by the grass carp at the age of 2, 3 and 4 years (Krupauer 1967, 1968). Nearly all parts of preferred plants were consumed. The grass carp consumes only the leaf edges or the youngest parts of less preferred species, and finally there were plants, which were not eaten but only tasted by the grass carp. This third group comprises especially natant plants with large leaves and plants containing toxic compounds. There was no difference in consumption of aquatic and terrestrial plants (Krupauer 1967). Grass carp preferred the aquatic macrophytes with the highest biomass within each of the 3 Krupauer's groups (Pípalová 2002).

The amount of aquatic plants consumed by grass carp and its selectivity depends on many factors, but especially on grass carp stocking density, grass carp age, temperature conditions, the length of time the fish have been in the pond, and on the quantity and quality of food present. In temperate climates grass carp prefer submersed and floating aquatic plants, although it will eat almost any type of vegetation when its preferred food is not available (Stroganov 1963, Fischer 1968, Sutton 1977, Lembi et al. 1978).

Indirect consequences of grass carp feeding depend on the intensity of the direct changes. Undigested plant material released in the fish faeces can cause changes of water quality, sediment chemistry and thus also changes in communities of producers including aquatic macrophytes and phytoplankton and consumers (i.e., zooplankton, zoobenthos, fish, amphibians and water birds). It is assumed that increased phytoplankton abundance will increase the abundance of zooplankton and zoobenthos, from which planktonivorous fish can profit (e.g., Bettoli et al. 1990). However, reduction or especially elimination of aquatic plants, which serve as spawning and feeding habitat, as well as shelter for the community of producers (especially phytophilous animals), can negatively influence these communities.

Despite the extensive use of grass carp and the existence of several models of the response of water bodies to aquatic macrophyte control by grass carp (Bettoli et al. 1990, Santha et al. 1991, Spencer 1994), the probability of accurate prediction of changes following grass carp stocking is often very low. The reasons relate to differences in such dynamic processes as mineral nutrient loading of water bodies, macrophyte seasonality, and climate variation among water bodies. Although literature on studies devoted to consequences of grass carp stocking is quite abundant, definitive data are scarce.

Most of the experimental studies (Terrell 1975, Fowler and Robson 1978, Lembi et al. 1978, Mitzner 1978, Small et al. 1985, Maceina et al. 1992) were carried out in a single or a few ponds/lakes stocked with grass carp. Unfortunately none of these studies used real control pond(s)/lake(s), indicating changes both in time, caused by weather, water level fluctuations or fish stocking, and space such as the initial difference between the experimental and control treatments. Only Terrell and Terrell (1975) placed enclosures protected from grass carp grazing as a control into the ponds prior to their stocking. Unfortunately, the enclosures are subject to problems caused by the establishment of peculiar

microclimatic conditions inside them (e.g., protection against waves). For evaluating the changes following grass carp stocking, the analysis of variance (if any statistical method) is used, with the time (before and after grass carp stocking) as the only explanatory variable. If possible, a replicated BACI design (before and after control impact), which eliminates both initial variability between experimental treatments (space variability) and also variability caused by time (e.g., climatic conditions during experimental years) should be used (Ter Braak and Šmilauer 1998). In the case of studies carried out in one large lake/pond it is necessary to use a much longer time series to study the impact of grass carp stocking. Real controls were used in the experiments conducted in mesocosm scale and in outdoor plastic pools (Michewicz et al. 1972, Buck et al. 1975). A poor description of the analytical methods used has created difficulties with comparing changes in water chemistry following grass carp stocking.

Stocking Density of Grass Carp

The most favourable stocking density depends on various factors such as climate, fish size, expected weed growth, required level of control and other biotic and abiotic environmental conditions (van Zon et al. 1976). "Overstocking" is followed by complete removal of all vegetation while "understocking" of a water body causes either selective reduction of vegetation (Blackwell and Murphy 1996, Bonar et al. 2002) or it can also result in no control (Bonar et al. 2002). Low stocking densities can maintain intermediate weed control but plants rejected by the grass carp are left and may grow vigorously (van Zon 1977).

The required stocking density of herbivorous fish is estimated mostly from the total biomass of vegetation in a water body (e.g., Cassani et al. 1995). Stocking rates of 3 grass carp (25-30 cm) per metric ton of vegetation (wet weight) significantly reduced macrophyte biomass of two Florida urban impoundments but did not decline to zero during the 4 or 5 years they were monitored after stocking. These two impoundments were dominated with *Chara* sp. or *Najas guadalupensis*. Stocking rates of 4-8.4 grass carp (per metric ton of vegetation wet weight) reduced macrophyte biomass in the impoundments with similar aquatic macrophyte species to zero in 8-17 months (Cassani et al. 1995). Santha et al. (1991) designed a model that involves alternatively stocking and harvesting of grass carp in order to achieve 40% of aquatic plant cover in 1.5 years with respect to the initial carrying capacity of the environment; this was about 28,000 kg ha⁻¹ of plants in the control (ungrazed) pens in Texas ponds. The authors recommended a stocking density of 79-130 individuals per hectare (i.e., about 12-20 kg ha⁻¹). Krupauer (1971) made a table of recommended stocking densities that are effective in aquatic weed control in the fishponds of South Bohemia (both kg ha⁻¹ and ind. ha⁻¹) for grass carp of various ages (1-4 years). Kokord'ák (1983) recommended stocking densities of 2-5 year old grass carp (individual weight of 0.2-3 kg) according to biomass of aquatic macrophytes (e.g., 20-60 kg ha⁻¹ for 500-1000 g m⁻²) for biocontrol of water canals in the Slovak Republic. On average, in temperate regions efficient biocontrol was obtained in the

first year after stocking 150-250 kg ha⁻¹ of one-two year grass carp with an individual weight of 250-400 g (Krupauer 1971, Jähnichen 1973, van Zon et al. 1976). A stocking density of 300 kg ha⁻¹ of 2-year-old grass carp was required to reduce aquatic plant growth to about 50% of its potential in 5 months in England (Robson 1970). The recommended stocking density in tropic regions is lower: 90-120 kg ha⁻¹ (individual fish weight 20-40 g) (Khatab and El-Gharably 1986). Some authors, e.g., Hanlon et al. (2000) recommend a stocking density of grass carp of 25-30 fish ha⁻¹ for problem aquatic plants (such as hydrilla (*Hydrilla verticillata* (L.f.) Royle)) while maintaining a small population of predominantly unpalatable aquatic plants.

Initial plant density is as important as grass carp stocking density. Biocontrol is effective if grass carp is stocked prior to the beginning of the rapid growth of vegetation when it is able to manage or reduce the vegetation. Water level fluctuation should be also predicted and taken into the consideration. Dramatic decrease of water level could cause overstocking of the water body with the grass carp and it is extremely difficult to remove fish from lakes. Stocking density of grass carp should be rather calculated for the lowest water level (acreage) and then subsequently supply some additional fish.

Grass Carp Age

The share of plant food in the grass carp diet increases with fish age, but animal food is also important (Fischer 1973), with zooplankton being partially replaced by benthos and especially, phytophilous fauna (Shireman and Smith 1983, Adámek et al. 1996). The first consumption of plant food, filamentous algae, was observed in grass carp of 25 mm (TL) (Krupauer 1974). Krupauer (1967, 1974) recorded intake of young soft leaves of submersed aquatic plants by individuals sized 35-40 mm (TL) aged 1-1.5 months in South Bohemian ponds. Grass carp sized 33 mm feeds on filamentous algae whereas plants were consumed by grass carp sized 47 mm in ponds of South Moravia (Adámek 1980).

Feeding selectivity of adult grass carp decrease with its age and size (Krupauer 1968, Opuszyński 1972, Catarino et al. 1997). Young grass carp have weak and small pharyngeal teeth and thus the most preferred food are soft and immature plants (Fischer 1968, Opuszyński 1972, van Zon 1977). The fish tend to avoid plants with rough or tough leaves (like *Stratiotes aloides* L. and various monocotyledons), big floating leaves (e.g., *Nymphaea* and *Nuphar* spp.), plants with a strong taste (as *Polygonum hydropiper* L.) (van Zon 1977) and or poisonous plants (*Ranunculus* spp.) (Murphy et al. 2002). Similarly Sutton (1977) reported that fish smaller than 1 kg preferred the roots while larger fish fed also on the leaves and bulbous petioles of water hyacinth (*Eichhornia crassipes* (Mart.) Solms). Older (larger) fishes do not refuse these plants but they only consume them when other plants are not available (van Zon 1977).

Grass carp age (size) is also important due to the possible predation on them, which can markedly reduce their initial stocking density. Grass carp should be larger than 30 cm when stocked, otherwise they are very vulnerable to predations by fish, birds and otter. In some areas otter can capture

grass carp of about 2.7 kg (length 60 cm), causing serious problems for fishpond management (Adámek et al. 2003).

Temperature Conditions

Optimum water temperature for food consumption by the grass carp is 20 to 28 C under the condition of South Bohemian ponds (Krupauer 1989). Stroganov (1963) and Opuszyński (1972) reported similar ranges of optimum water temperature: 21 to 26 C and 25 to 28 C, respectively. Steady plant consumption begins at 10 to 16 C (Stroganov 1963, Kokordák 1978, Adámek and Sanh 1981, Krupauer 1989) and intensive feeding occurs when the water temperature reaches 20 C or higher. At 20 C, daily food intake by grass carp was 50% of its body weight, whereas at 22 C the consumption increased up to 120% of body weight. The upper temperature limit of the consumption of plants is about 35 C (Opuszyński 1972).

Food consumption by the grass carp depends not only on absolute water temperature but also on its changes. A sudden temperature drop may disrupt feeding (Stroganov 1963, Hickling 1966, Krupauer 1989). This is the reason for a wide temperature range at which grass carp either stops or starts feeding. Shireman et al. (1983) reported that feeding stopped at temperatures below 16 C, while other authors reported feeding cessation at 14 C (Colle et al. 1978) or even at 12 C (Opuszyński 1972). A sudden water temperature drop by 4-5 C from 20 C or less decreases or even stops foraging for food. In contrast, a gradual decrease of water temperature (even below 15 C) increased feeding selectivity of grass carp but its food consumption did not decrease (Krupauer 1989).

Changes in the Aquatic Macrophyte Community

Once an aquatic plant is consumed, a niche becomes available for other plants. What species, if any, will replace the species removed by the grass carp depends mostly on grazing pressure (stocking density and temperature) and its duration. Spread of species not eaten by the grass carp (Kogan 1974, Vinogradov and Zolotova 1974, Fowler and Robson 1978, Madsen and Beck 1997, Li 1998), or regrowth of a preferred species (Cassani et al. 1995, Fowler and Robson 1978) can occur following grass carp stocking. Grass carp feeding, if selective for the indigenous plants, might also further support spreading of alien species (Catarino et al. 1997).

When lower stocking densities of grass carp are used in lakes, grass carp can continuously control a preferred aquatic plant species. At higher stocking rates their impacts have been noted for 15 to 20 years. Van Dyke et al. (1984) reported that grass carp (50 to ha) eliminated troublemaking hydrilla in 3 central Florida lakes. The hydrilla remained absent for 6 years and the only remaining vegetation grew in very shallow water and included woody plants and unpalatable species such as spatterdock (*Nuphar lutea* L.). Stocking rates (24 to 74 grass carp per hectare of lake area) often resulted in the total loss of all submerged vegetation (Hanlon et al. 2000).

It is assumed, that elimination of aquatic plant species preferred by the grass carp or in contrast spreading of invasive alien species result in reduction of the diversity of the aquatic macrophyte community (Catarino et al. 1997). Vino-

gradov and Zolotova (1974) reported the disappearance of 36 plant species out of 58 species two years after grass carp stocking. The number of plant species was reduced by half after six and eight years in Florida lakes (50 ind. ha⁻¹) and reservoirs (61 ind. ha⁻¹), respectively (Van Dyke et al. 1984). Diversity does not only mean the number of species, but also their relative abundance (biomass). These data are very limited. Low stocking density of grass carp (30 kg ha⁻¹) has reduced the biomass of aquatic macrophytes (from 109 g DW m⁻² to 33 g DW m⁻²) but species diversity (Shannon-Weaver index) of aquatic macrophytes did not significantly change in a small pond during a one-year study. Grass carp preferred the filamentous alga (*Cladophora*) to other macrophyte species and thus it prevented the filamentous algae from overgrowing a water body. Filamentous algae could not suppress other aquatic macrophytes as it did in the control pond without grass carp (Pípalová 2002). When grass carp were removed from the pond the mean biomass of aquatic macrophytes remained the same during the following 2 years (37 g DW m⁻²), but the species diversity decreased. Non-preferred *Myriophyllum spicatum* L. constituted 81% of the aquatic macrophytes species biomass present (Pípalová not published). The effect of the grass carp on diversity in aquatic systems depends upon density and size of fish stocked, presence/absence of preferred and non-preferred species, duration of fish impact and certainly upon grass carp survival/movement from the system.

Eutrophication and Water Quality Changes

Approximately one half of the nutrients in ingested plant material are used and digested by the grass carp, the other half passes the gut as partly digested, partly fragmented material (Stroganov 1963, Hickling 1966, Stanley 1974a, Stanley 1974b). Hickling (1966) reported about 43 to 47% assimilation of nitrogen in an experiment with grass carp feeding on the aquatic plant *Enhydryas angustipeala* Gagnep. and tapioca leaves (manioc, *Manihot utilissima* Pohl.). Hajra (1987) reported the excretion of nitrogen through faeces representing 24% and 27% of the daily mean nitrogen intake for small and large grass carp fingerlings, respectively, when they were feeding exclusively on coontail (*Ceratophyllum demersum* L.).

While it is naturally assumed that this nutrient release could accelerate eutrophication of waters (Hansson et al. 1987), this has not been clearly demonstrated under field conditions. Venter and Schoonbee (1991) did not record any significant changes in water chemistry even though the biomass of aquatic plants decreased from 193 g m⁻² to 34 g m⁻² during a one-year study. On the contrary, Li (1998) maintained that in some cases binding of nutrients into the fish bodies could inhibit eutrophication. Lembi et al. (1978) reported as much as 54% of the phosphorus and 42% of the nitrogen in the plants was incorporated into fish tissue. The values are fairly consistent with the general statement that the grass carp consumes approximately 50% of the nutrients in ingested foods.

The data presented in Table 1 lists the physical and chemical water parameters reported before and after grass carp stocking (Mitzner 1978, Small et al. 1985, Maceina et al. 1992, Tomajka 1995) or in ponds (lakes, plastic pools)

TABLE 1. CHANGES OF PHYSICAL AND CHEMICAL WATER PARAMETERS FOLLOWING GRASS CARP STOCKING.

Author(s) study site	Buck et al. (1975)				Fowler and Robson (1978)			Mitzner (1978)			
	pools (no flow)				pools (no flow)			lake (29 ha)	4 m depth	8 m depth	
Stocking density [kg ha ⁻¹]	87 ^c	0	87 ^c	0	150	450	0	water surface	4 m depth	8 m depth	
		n = 4, V _{pool} 4 m ³			n = 4, V _{pool} 2.4 m ³			7 (in 1973) and 10 (in 1974)			
Ind. weight [g]	31.6		31.6						380		
Age [years]/ length [cm]	-/10		-/10		2/-				-/31		
Vegetation species	macrophytes: <i>P. fol.</i> , <i>P. pus.</i> , <i>N. fle.</i> , <i>N. gra.</i> and <i>C. dem.</i>		algae: <i>Oscillatoria</i> sp.		<i>P. nat.</i> , <i>P. pec.</i> , <i>M. spi.</i> , <i>E. can.</i> and <i>Ch.</i> sp.			<i>E. can.</i> , <i>N. fle.</i> , <i>C. dem.</i> , <i>P. pec.</i> and <i>P. nod.</i>			
Vegetation biomass [kg DW ha ⁻¹]	B							25 000			
	A	374	473	8	1036			21 000			
Vegetation cover [%]	B					84	90	90			
	A					68	46	92			
Length of experiment		2.5 month (6 th July-18 th -19 th September 1973)				1 month (4 th August-4 th September 1975)			4 years (mid-July 1973-1976)		
Temperature [°C]		23.9	23.7	23.9	24.1	21.5 (1 st week); 25 (2 nd and 3 rd week); 6 (4 th week)			south-central Iowa		
Transparency [cm]	B	in 30 cm depth									
	A										
Turbidity [FTU]	B								7.3	5.5	10.5
	A	15.4 ^{↑*}	10.5 [↓]	35.1 ^{↑*}	12.7 [↓]				10.5 ^{↑*}	6.3 ^{↑*}	12.5 ^{↑*}
pH	B										
	A	8.4	9.3	8.6	9.6	8.7	7.7	9.3			
Alkalinity [mg l ⁻¹]	B								108	108	128
	A	67.2	49.4	71.5	53.6				125 ^{↑*}	129 ^{↑*}	143 ^{↑*}
Water hardness [mg l ⁻¹ CaCO ₃]	B										
	A	33.4 ^{↑*}	24.7	33.0 ^{↑*}	25.2						
O ₂ [mg l ⁻¹]	B										
	A	4.8	6.0	5.3	7.1						
BOD [mg l ⁻¹]	B								4.3	3.6	7.0
	A								2.9 ^{↓*}	3.3 ^{↓*}	4.1 ^{↓*}
TP [mg l ⁻¹];	B										
	A										
PO ₄ -P [mg l ⁻¹]	B					n. d.	n. d.	n. d.			
	A	0.593 ^{↑*}	0.560	0.472 ^{↑*}	0.415	1.0 [↑]	1.4 [↑]	0.6 [↑]			
Porg. [mg l ⁻¹]	B								0.24	0.26	0.32
	A								0.45	0.23	0.24
Pinorg. [mg l ⁻¹]	B								0.28	0.29	1.00
	A								0.40	0.43	0.95
TN [mg l ⁻¹]	B										
	A										
NO ₃ -N [mg l ⁻¹]	B					1.9	2.4	2.5	1.12	1.03	0.77
	A					0.5 [↓]	0.5 [↓]	1.3 [↓]	0.32 ^{↓*}	0.33 ^{↓*}	0.26 ^{↓*}
NO ₂ -N [mg l ⁻¹]	B								0.021	0.025	0.016
	A								0.006 ^{↓*}	0.006 ^{↓*}	0.009 ^{↓*}
NH ₄ -N [mg l ⁻¹]	B										
	A										
Norg. [mg l ⁻¹]	B										
	A										

Note: after (A) or before (B) grass carp stocking, b: bottom, c: calculated, n: number of repetitions, n.d.: not detectable, s: surface, ^{↑*} significant increase, ^{↓*} significant decrease, 1: in JTU (Jacobson turbidity units), 2: [NO₃-N + NO₂-N], *C. dem.*: *Ceratophyllum demersum* L. (coontail), *Ch. sp.*: *Chara* sp. (musk-grass), *H. ver.*: *Hydrilla verticillata* (L.f.) Royle (hydrilla), *E. can.*: *Elodea canadensis* Michx. (Canadian waterweed), *M. spi.*: *M. spicatum* (Eurasian watermilfoil), *M. ver.*: *Myriophyllum verticillatum* L. (whorled leaf watermilfoil), *N. fle.*: *Najas flexilis* (Willd.) Rostk. and Schmidt (slender naiad), *N. gra.*: *N. gracillima* (A. Braun ex Engelm.) Magnus (spring naiad), *N. alb.*: *Nymphaea alba* L. (white water-lily), *P. cri.*: *Potamogeton crispus* L. (curlyleaf pondweed), *P. fol.*: *P. foliosus* Raf. (leafy pondweed), *P. nat.*: *P. natans* L. (broad-leaved pondweed), *P. nod.*: *P. nodosus* Poir. (American pondweed), *P. pec.*: *P. pectinatus* L. (sago pondweed), *P. pus.*: *P. pusillus* (L.) Fernald (small pondweed), *R. cir.*: *Ranunculus circinatus* Sibth. (buttercup).

TABLE 1. (CONTINUED) CHANGES OF PHYSICAL AND CHEMICAL WATER PARAMETERS FOLLOWING GRASS CARP STOCKING.

Author(s) study site	Lembi et al. (1978) ponds (0.21-0.30 ha)				Small et al. (1985) lakes		Maccina et al. (1992) lake ^(6,100 ha)	Tomajka (1995) river
Stocking density [kg ha ⁻¹]	11	20	69	0	52 ha 42 ^c	137 ha 39 ^c	33 fish ha ⁻¹	77 (1982) 37 (1983) 33 (1984)
Ind. weight [g]	n = 3	n = 2	n = 1	n = 2	680	880		1571 (1982) 142 (1983) 702 (1984)
Age [years]/ length [cm]							-/> 20	
Vegetation species	<i>P. fol.</i> , <i>P. cri.</i> , <i>M. ver.</i> , <i>Ch. sp.</i> and <i>Spirogyra sp.</i>				<i>H. ver.</i>		<i>H. ver.</i> , <i>M. spi.</i> , <i>C. dem.</i> and <i>E. can.</i>	<i>C. dem.</i> , <i>M. spi.</i> , <i>R. cir.</i> and <i>N. alb.</i>
Vegetation biomass [kg DW ha ⁻¹]	B 481; 165; 34	523; 170	1405	130; 40	5000 (FW)	3000 (FW)		
	A 0; 3; 9	0; 0	334	493; 876	0 (in 14 months)	0 (in 6 months)		
Vegetation cover [%]	B						44	45
	A						0 (already in 1984)	0 (already in 1984)
Length of experiment	4 months (13 rd June-13 th October 1975)				4 years (March 1979-February 1982)		7 years (1979-1987)	6 years (1982-1987)
Parameter T [°C]	Indiana ponds depth = 0.7-1.2 m				summer: 29.2-30.8, autumn: 25.8-27.2, spring: 21.5-23		Lake Conroe Texas	Danube branch Slovakia
Transparency [cm]	B				282	158	150	77
	A				109↓*	96↓*	90	57
Turbidity [FTU]	B				1.85 ^s	2.19 ^s		
	A	9.9↑*	6.6 ↑	3.9 ↑	4.5	6.50↑*	7.26↑*	
pH	B				6.47 ^b ↑*	7.40 ^b ↑*		7.9
	A	7.8	7.1	8.4	7.7	8.52 ^s	7.42 ^s	
Alkalinity [mg l ⁻¹]	B				8.16 ^s	7.32 ^s		
	A	47.6	58.0	52.3	58.8	8.53 ^s	8.52 ^s ↑*	8.1↑*
water hardness [mg l ⁻¹ CaCO ₃]	B				8.38 ^s	8.48 ^s ↑*		
	A	64.1	76.9	70.1	68.4	20.8 ^c	14.9 ^c	
O ₂ [mg l ⁻¹]	B				39.0 ^c ↑*	19.0 ^c ↑*		
	A				8.67 ^s	8.38 ^s		
TP [mg l ⁻¹]	B				5.18 ^b	6.09 ^b	0.05	0.13
	A	0.036	0.056	0.023	0.034		0.08↑*	0.10
PO ₄ -P [mg l ⁻¹]	B				0.010	0.009	0.04	0.026
	A	0.013	0.016	0.007	0.008	0.007	0.012	0.014
TN [mg l ⁻¹]	B						0.06↑*	0.63
	A							0.81
NO ₃ -N [mg l ⁻¹]	B				0.013	0.015	0.03 ²	0.13
	A	0.071	0.055	0.060	0.026	0.030	0.05 ²	0.29
NH ₄ -N [mg l ⁻¹]	B						0.32	0.034
	A	0.224↑*	0.011	0.040	0.022		0.57↑*	0.066
Norg. [mg l ⁻¹]	B							0.44
	A	0.652	0.912	0.804	0.749			0.46

Note: after (A) or before (B) grass carp stocking, b: bottom, c: calculated, n: number of repetitions, n.d.: not detectable, s: surface, ↑* significant increase, ↓* significant decrease, l: in JTU (Jacobson turbidity units), 2: [NO₃-N + NO₂-N], *C. dem.*: *Ceratophyllum demersum* L. (coontail), *Ch. sp.*: *Chara* sp. (musk-grass), *H. ver.*: *Hydrilla verticillata* (L.f.) Royle (hydrilla), *E. can.*: *Elodea canadensis* Michx. (Canadian waterweed), *M. spi.*: *M. spicatum* (Eurasian watermilfoil), *M. ver.*: *Myriophyllum verticillatum* L. (whorled leaf watermilfoil), *N. fle.*: *Najas flexilis* (Willd.) Rostk. and Schmidt (slender naiad), *N. gra.*: *N. gracillima* (A. Braun ex Engelm.) Magnus (spring naiad), *N. alb.*: *Nymphaea alba* L. (white water-lily), *P. cri.*: *Potamogeton crispus* L. (curlyleaf pondweed), *P. fol.*: *P. foliosus* Raf. (leafy pondweed), *P. nat.*: *P. natans* L. (broad-leaved pondweed), *P. nod.*: *P. nodosus* Poir. (American pondweed), *P. pec.*: *P. pectinatus* L. (sago pondweed), *P. pus.*: *P. pusillus* (L.) Fernald (small pondweed), *R. cir.*: *Ranunculus circinatus* Sibth. (buttercup).

stocked with grass carp and controls without fish (Buck et al. 1975, Fowler and Robson 1978, Lembi et al. 1978). Two short-lasting studies (Buck et al. 1975, Fowler and Robson 1978) were carried out in the small plastic pools without water flow. Grass carp eliminated filamentous algae rapidly and more than vascular plants. This probably corresponds with the greater turbidity increase (by 64%) in the pools with filamentous algae than in pools with vascular plants (by 32%). The significant increases of soluble phosphate (about 9%) and carbonate hardness were comparable in pools with filamentous algae and vascular plants. Fowler and Robson (1978) used higher stocking densities (150 and 450 kg ha⁻¹) and found an increase in phosphate of about 40% and 57%, respectively during a 1-month study. Only water turbidity clearly increased in the small ponds with 3 different low stocking densities of grass carp (11-69 kg ha⁻¹) (Lembi et al. 1978). Most of the significant changes in water quality were reported from the long-lasting experiments (time series) in American lakes (Mitzner 1978, Small et al. 1985, Maceina et al. 1992), especially when the macrophytes were completely eliminated. It seems there are two boundary situations; either increase of nutrients concentrations in the water (increase in N-NH₄, total phosphorus (TP) and soluble reactive phosphorus (SRP) reported by Maceina et al. (1992)) or development of phytoplankton (changes in concentration of oxygen, pH, alkalinity and transparency reported by Small et al. (1985) and or even decrease of nitrites and nitrates concentrations (Mitzner 1978)). Tomajka (1995) reported on the effects of grass carp in a Danube River branch with the area of about 3 ha. The period when the branch was connected to the river ranged between 7 to 112 days during the study years (1981-1986). The hydrological regime had influenced the results more than grass carp stocking.

A decrease of oxygen concentration in the water after grass carp stocking is related to the disappearance of macrophytes (Michewicz et al. 1972, Lembi et al. 1978, Fowler and Robson 1978, Opuszyński 1997). In contrast, production of oxygen during photosynthesis of subsequent phytoplankton blooms increased its concentration in the water after grass carp stocking in some studies (Small et al. 1985, Tomajka 1995). Disappearance of filamentous algae after grass carp stocking reduced wide oxygen fluctuations in the water (van Zon 1977).

Primary producers i.e., phytoplankton and aquatic macrophytes not only release oxygen but also consume CO₂ during photosynthesis, which results in an increase in water pH. Changes in oxygen concentrations following grass carp stocking were positively correlated with changes in pH (Leslie et al. 1983). Uptake of CO₂ by plants also disrupts the HCO₃⁻/CO₃²⁻ equilibrium, affecting water alkalinity (Mitzner 1978, Small et al. 1985). Lembi et al. (1978) and Leslie et al. (1983) however mentioned stable alkalinity after the introduction of grass carp.

The trophic state of the lakes (and thus also result of complete vegetation removal in the lakes) depends on the total phosphorus content of the water column estimated as the sum of the phosphorus content of the water and the phosphorus content of the macrophytes (both in mg m⁻³). When macrophyte biomass contains less than 25% of the total phosphorus in the water column and the mean macrophyte

concentration in the lake is less than 1 g DW m⁻³, vegetation removal will have little effect on lake trophic state (open-water nutrient, chlorophyll-a concentration and water transparency) (Canfield et al. 1983). This statement is limited by the complete phosphorus release from the plants to the overlying water and no phosphorus mobilizing from the sediment. Hydrochemistry is strongly affected by hydrology and morphology of water bodies, weather conditions, and thus proving of statistically significant changes in water chemistry caused by other factors (e.g., grass carp) is difficult. Water quality change as a result of plant removal by the grass carp is most affected in small, non-flowing water bodies and least affected when only small proportion of plants is removed from large, relatively deep, flowing reservoirs. The effects of grass carp on plants and water quality (Table 1) are highly variable and often inconclusive due to the lack of proper control sites. The proportion and rate of plant removal by the grass carp is crucial. The majority of published work suggests, that the stocking density of grass carp up to 30 kg ha⁻¹ causes only negligible changes in water chemistry with visible reduction of preferred aquatic plants, when used only for one growing season (possible only in small ponds). Higher stocking densities of grass carp or its longer impact can increase concentrations of nutrients (especially nitrogen and phosphorus) in the water, but these increases are mainly dependent on the water body characteristics.

Changes in Sediment Chemistry

Only Terrell (1975) and Hestand and Carter (1978) studied both water and sediment chemistry, and both suggest that nutrients from macrophytes were trapped into the sediment (precipitated either by or with organic acids) and thus were not available to phytoplankton. In ponds stocked with grass carp, a significant increase in Fe, Mg and P-PO₄³⁻ concentrations was reported in the sediment (Terrell 1975).

Changes in Phytoplankton

The stocking density and area of weeds controlled affects the extent of phytoplankton production. If weed control by grass carp is slow and some aquatic macrophytes are left in a water body, the indirect consequences of grass carp stocking on phytoplankton are negligible. At a low stocking density (30 kg ha⁻¹) changes in the concentration of chlorophyll-a in the water was non-significant (Pípalová 2002). Cassani et al. (1995) also found that annual mean chlorophyll-a concentration remained stable in lakes, where macrophytes were only suppressed. Phytoplankton growth in pools or mesocosms containing grass carp with vascular macrophytes may have been limited because one or more essential nutrients had been taken up by the remaining stand of coontail not preferred by the grass carp (Buck et al. 1975) or by their immobilization in the sediment (Terrell 1975, Hestand and Carter 1978). These are likely reasons that several studies have shown minimal effect on phytoplankton (Terrell 1975, van Zon et al. 1976, Hestand and Carter 1978, Lembi et al. 1978, Mitzner 1978, Terrell 1982, Leslie et al. 1983, Bonar et al. 2002).

However, a high stocking density (e.g., Small et al. 1985: 55 kg ha⁻¹ for 3 years in Clear Lake) of grass carp which can

eliminates all aquatic macrophytes and the nutrients released produces increased phytoplankton. As a result of the shading effect of higher phytoplankton biomass, remaining aquatic macrophytes are often further suppressed. In this case, wind action can also increase water turbidity due to sediment movement, especially in the shallow water bodies (Bonar et al. 2002). Other studies also mentioned increased turbidity (Buck et al. 1975, Small et al. 1985) or concentration of chlorophyll-a (Gasaway and Drda 1978, Small et al. 1985, Maceina et al. 1992, for stocking densities and duration of experiment see Table 1) as indicators of phytoplankton development following grass carp stocking. Elimination of *Hydrilla verticillata* (L.f.) Royle by the grass carp within 14 months caused a gradual increase of phytoplankton density from an initial 24-month mean of 165000 cells l⁻¹ to a mean level of 787900 cells l⁻¹ in the third year following grass carp stocking (55 kg ha⁻¹) (Richard et al. 1984).

Elimination of macrophytes increased blue-green algae abundance in the phytoplankton community almost 9 times (from 7000 units per ml to 61000 units within 6 years). However the blue-green algae dominated only during the peak phytoplankton season (June-October) in Lake Conroe (8,100 ha) in the southern U.S. (Maceina et al. 1992). Kogan (1974) likewise reported the dominance of the blue-green alga *Microcystis aeruginosa* Kütz. after grass carp had eliminated *Myriophyllum spicatum* L. Three years after grass carp introduction into Clear Lake, the concentration of Chlorophyta (almost 27 times, from 7% to 30%) and Bacillariophyta (almost 3 times, from 3% to 14%) increased. Blue-green algae were dominant, but decreased from 81% to 65% in Florida lakes (Richard et al. 1984). Holdren and Porter (1986) reported shifts in dominant taxa and relative abundances of green and blue-green algae and diatoms, with a general shift to smaller species occurring after grass carp stocking.

In summary, primary production of each of the water bodies depends on light and nutrient availability. These two factors influence unstable equilibrium between macrophytes and phytoplankton and thus both the speed and extent of macrophyte removal by the grass carp influence production of phytoplankton.

Changes in Zooplankton

Consumption of zooplankton is essential both for juvenile and adult grass carp, but the amounts consumed are negligible if the stocking density is not extremely high (Greenfield 1971, Kilgen and Smitherman 1971, Opuszyński 1972, Terrell and Terrell 1975). Most influences on zooplankton tend to be indirect. In lakes stocked with herbivorous fish the growth of zooplankton and zoobenthos is enhanced through consumption of macrophytes by the fish and subsequently increased rates of nutrient remineralization. The overall result can be also demonstrated in an increase of fish production (Zhang and Chang 1994). The zooplankton communities shifted from copepod and copepod-cladoceran dominated to rotifer and small cladocerans. Changes in zooplankton abundance and community structure were due to an increase in phytoplankton and shifts in planktivore predation on zooplankton by fish after macrophyte removal (Hrbáček et al. 1961, Richard et al. 1985). As a result of the repeated stock-

ing of grass carp (77 kg ha⁻¹, 37 kg ha⁻¹, 33 kg ha⁻¹) into a Danube side arm (3 ha, mean water depth 80 cm, Slovakia), the biomass of submersed macrophytes decreased and they were completely eliminated in 2 years. The zooplankton originally dominated by phytophilous crustaceans was gradually replaced by a limnetic assemblage where rotifers dominated. The increase in rotifer biomass was accompanied by a decrease in crustacean biomass. The replacement of crustaceans by rotifers was primarily due to the fact that crustaceans had lost shelter from size-selective predation by fish. Thus, the opened niche could be occupied by euplanktonic rotifers (Vranovský 1991). Increase in zooplankton numbers and biomass have been also observed by Grygierek (1973), van Zon et al. (1976) and Mitchell et al. (1984). Yet studies of some authors show that zooplankton was unaffected by the grass carp (Terrell 1975, Fowler and Robson 1978, Maceina et al. 1992). Unfortunately detailed zooplankton community structure and dynamics in waters stocked with grass carp are not well studied but also varies between water bodies and amount of weeds controlled by the grass carp.

Changes of Zoobenthos

Grass carp do not markedly affect zoobenthos directly by feeding (Terrell and Terrell 1975). However, it can be inferred that grass carp feeding on aquatic macrophytes also ingest phytophilous zoobenthos. For example, George (1982) reported that in canals stocked with grass carp, the snails (*Bulinus* sp. and *Biomphalaria* sp.) that adhere to the leaves of *Potamogeton* spp. were eaten along with the leaves.

Changes in benthos corresponded most closely to changes in aquatic vegetation (Gasaway 1979, van der Zwerde 1982), which stabilize sediments and provide additional substrate in the form of root masses and decaying material (Schramm and Jirka 1989). Zoobenthos also responded to changes in water quality following removal of aquatic macrophytes (Gasaway 1979). Zoobenthos became more than twice as abundant as it had been before grass carp introduction in the reservoirs of Amudarja River (Turkmenistan), because the annual die-off of vegetation was prevented by the presence of grass carp, and oxygen content and water quality were improved (Aliev 1976). Most of the authors (Hickling 1966, Tölg 1967, Greenfield 1971, Prowse 1971, Stott et al. 1971, Grygierek 1973, Buck et al. 1975, Völlmann-Schipper 1975, van Zon et al. 1976, Zwerde van der 1982) reported increased growth of macrofauna (especially bottom dwellers and detritivores) in the presence of grass carp.

The disappearance of aquatic macrophytes reduces phytophilous fauna (van Zon 1977) because of a decrease in number and size of hiding places (Opuszyński 1972). Three years after grass carp stocking (143.3 kg ha⁻¹) phytophilous species were substituted by periphytophagous species (especially by Chironomidae) in the littoral zone with submersed macrophytes in a Danube branch (depth = 77 cm) (Nagy and Šporka 1990). Unfortunately, from this type of study (the impact of grass carp in one Danube branch without any similar branch) it cannot be determined whether any differences were caused by grass carp stocking or by other factors. Nagy and Šporka (1990) also reported changes in the abundance of benthophagous fish and in hydrological conditions dur-

ing the experiment. Kovalkova (1975) and Zweerde van der (1982) found that phytophilous and herbivorous species were replaced (or decreased) by mud-dwelling and detritivorous species in one year when high stocking density of grass carp (360 kg ha⁻¹) was used. No changes in macroinvertebrates community were recorded at lower stocking density (180 kg ha⁻¹) (Zweerde van der 1982).

It seems clear that the grass carp does not influence zoobenthos directly. Indirect changes at the primary level i.e., phytoplankton is still not appropriately quantified and thus changes at the secondary level i.e., zoobenthos are not easy to prove. The same seems true for changes in zooplankton. Since no correlation could be found between the abundances of zooplankton and phytoplankton (Hasler and Jones 1949), it seems that grass carp faeces or attached bacteria may serve as a food source for zooplankton and zoobenthos. Based upon existing literature it is difficult to generalize on the effects of grass carp on the zoobenthos/zooplankton communities.

Changes in Fish Communities

Petr (2000) reviewed the biological control of aquatic plants using fish and its impact on other fish. The feeding activity of grass carp reduces the spawning substrate for phytophilous fish or shelters for predatory fish and their prey. It can also indirectly influence the life of some other fish that are dependent on phytophilous animals (van Zon 1977). In one lake, perch (*Perca fluviatilis* L.) and pike (*Esox lucius* L.) were eliminated after grass carp introduction (Stanley et al. 1978). Vinogradov and Zolotova (1974) also reported the disappearance of perch and pike and the decline of crucian carp (*Carassius carassius* L.) and roach (*Rutilus rutilus* L.). The probable reason was that grass carp removed all vegetation on which these fish species deposit their eggs. There are two other reasons for decline of pike. First, pike seek cover in macrophytes from where it attacks smaller fish in open water, and second, it locates its prey visually and does not like water of low transparency, resulting from increased phytoplankton (Petr 2002, pers. comm.). The reason for perch elimination, which is indifferent in respect to spawning substrate, is not clear. Krzywosz et al. (1980) also reported major reduction of phytophilous fish species (i.e., rudd *Scardinius erythrophthalmus* L., roach and tench *Tinca tinca* L.) during the long-lasting influence of grass carp stocking with average stocking density of 43 kg ha⁻¹ in Lake Dgał Wielki (Poland) in 1966 to 1978. The few remaining aquatic macrophytes were not sufficient and the grass carp began to compete with benthophagous bream (*Abramis brama* L.) in this lake by 1975. Food competition between grass carp and other fish can occur in natural water bodies when aquatic macrophytes are eliminated. In pond polyculture grass carp prefers commercial food to aquatic plants, which cause competition and reduced growth with common carp (*Cyprinus carpio* L.) (Krupauer 1968).

Some fish species increased growth, production and survival in the presence of grass carp because of increased food availability due to increased planktonivorous fish (Prowse 1971, George 1982, Bettoli et al. 1990) or due to the fish feeding on faecal pellets (Hickling 1966, Stott et al. 1971, Edwards 1973, Takamura et al. 1993). Takamura et al. (1993) suggested that planktonivorous fish did not utilize the faeces

of grass carp, but utilize the attached nutritive microorganisms, which are too small to be consumed directly. This is probably the mechanism, which has been employed in Chinese mixed cyprinid culture systems for centuries. Unfortunately numerous authors reported increased fish production in the presence of grass carp, without any substantiation (Tölg 1967, Greenfield 1971, Stott et al. 1971, Grygierek 1973, Völlmann-Schipper 1975, van Zon et al. 1976).

Lower stocking densities of grass carp (75-150 kg ha⁻¹) did not affect other fish three years after stocking (Moore and Spillett 1982). In another study, grass carp reduced hydrilla in Lake Marion and its effect on the fish assemblage during the seven-year study was minimal. Monospecific stands of hydrilla shifted to intermediate levels of structural complexity and thus a major decline of littoral populations did not occur (Killgore et al. 1998).

Macrophytes serve as a spawning substrate (especially for phytophilous fish species), food (phytophilous animals attached to them) and shelter for fish. The number of especially phytophilous fish species decreased when plants were completely eliminated or their biomass decreased significantly. Nevertheless fish spawn mostly during the early summer, when the impact of grass carp on aquatic macrophytes in temperate region is still small (van Zon 1977). Therefore one-year impact of grass carp on other fish breeding is negligible. Food competition between grass carp and other fish species was also reported especially when macrophytes was eliminated. In contrast, nutrient rich faecal pellets can be eaten by other fish and thus increase their productivity.

Changes in Amphibian and Water Birds Communities

Use of grass carp to control nuisance aquatic vegetation may reduce habitat quality for waterfowl especially because the food requirements of the grass carp and some species of water birds overlap (Venter and Schoonbee 1991, McKnight and Hepp 1995, Benedict and Hepp 2000). Massive plant removal and associated habitat simplification and thus degradation contributed to amphibian declines (Murphy et al. 2002).

Longevity of Grass Carp Control

Intensity of aquatic macrophyte control using grass carp depend on many factors i.e. stocking density, grass carp age (size), duration of their stocking, temperature conditions, aquatic macrophyte species present and type of water reservoir. There are two typical scenarios when using grass carp for reduction of aquatic macrophytes. Moreover there is a difference in the stocking densities between lakes and ponds. In ponds about 300 kg ha⁻¹ and 30 kg ha⁻¹ are common weights for high and low stocking densities, respectively. The values range between 12 kg ha⁻¹ and 37 kg ha⁻¹ in lakes. This discrepancy is caused especially by the extent of eutrophication, water depth (volume) and by the percentage of littoral zones, which are preferred by the grass carp for feeding.

Grass carp feeding reduces biomass especially of preferred plant species. When grass carp were stocked in lakes containing 30-50% vegetation cover at levels of approximately 25 to 30 fish per hectare of vegetation (about 10 to 15 grass carp per hectare of water body, i.e., about 13-15 kg ha⁻¹) the com-

plete control of submerged aquatic vegetation has been achieved, while a small community of unpalatable emergent aquatic macrophytes was maintained (Hanlon et al. 2000). Indirect impact is mostly negligible, because the release of nutrients originally bound in the aquatic macrophytes is gradual and remaining plants prevent excessive phytoplankton development. Removal of grass carp from lakes and reservoirs is impossible and thus feeding of grass carp can last as long as they live i.e., 15 or more years according to Opuszyński and Shireman (1995). However, according to other reports triploid grass carp do not survive to age 10 and their mean annual mortality rate estimated in the Santee Cooper reservoirs (South Carolina) was 33% (Kirk et al. 2000).

When lower stocking densities of grass carp (30 kg ha⁻¹) are used in ponds for at least 2 growing seasons, the biomass of preferred aquatic macrophytes is reduced. However in the next year or years either non-preferred, originally present aquatic plants species or "new" often non-native plant species can occupy the new niche. Low stocking densities have resulted in short-term effects in the ponds.

Submerged macrophytes were often eliminated completely when 24 to 74 grass carp per hectare of lake area (i.e., about 12-37 kg ha⁻¹) was stocked (Hanlon et al. 2000). The same results were achieved in ponds in a temperate region when stocking densities of 210-263 kg ha⁻¹ (150 to 750 grass carp per hectare of pond area) was used for one growing season (Krupauer 1971). However the majority of nutrients released through grass carp excrement in non-flowing ponds are utilized by phytoplankton due to its short turnover time. Excessive growth of phytoplankton causes shading of aquatic macrophytes and together with pH fluctuations (which brings in ammonium toxicity) can lead to collapse of the plant community. Decomposing plant tissues causes anoxia in the water and sediment, increasing nutrient release from the hydrosol.

Neither grass carp stocking nor other types of aquatic plant control remove the factors that cause excessive growth of aquatic plants, which often coincides with human activities. Shallow water reservoirs, the warm climate and long growing season in the tropical and subtropical regions, and introduction of exotic species such as hydrilla in the southern U.S. can favour submersed macrophyte growth. While excess plant production has been tied to long-term nutrient loading of our water bodies, grass carp can partly help to convert these nutrients that are tied up in aquatic plants and recycle them into fish flesh and phytoplankton.

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