Impact of introduced carp (*Cyprinus carpio*) in subtropical shallow ponds in Central Mexico

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Abstract

In Mexico, as in many other subtropical and tropical countries, there has been a recent trend towards stocking non-native carp (*Cyprinus carpio*) in lakes and ponds as a source of food in rural areas. However, the results of a study in a series of small (1–8 ha), shallow (<2 m), semi-natural ponds in Acambay, a high altitude valley in the basin of the Lerma river in the volcanic belt in central west Mexico, illustrate that the stocking of carp over a threshold value may have a detrimental ecological impact at several trophic levels. Ponds with carp tended to be turbid with high levels of suspended solids, and with few rooted macrophytes and epibenthic invertebrates. In contrast, ponds without carp had clear water and abundant rooted macrophytes and associated invertebrates, particularly gastropod molluscs. The direct uprooting of macrophytes by benthic foraging carp appeared to be the most important mechanism in switching the ponds from a clear macrophyte-dominated to a turbid state. The subtropical study ponds thus appear to confirm the alternative stable-state hypothesis developed in temperate lakes, although the importance of benthic rather than pelagic interactions was emphasised. The implications of stocking carp for native fauna of high intrinsic conservation value and as a food supply for local people are outlined.

Introduction

It is now widely accepted that shallow lakes may exist in either of two alternative stable states, one dominated by phytoplankton and the other by submerged macrophytes, within a range of nutrient concentrations (Irvine et al., 1989; Scheffer et al., 1993). Each state is buffered by a variety of mechanisms, even in the face of an increase or decline in available nutrients (Moss et al., 1996). Theoretical models and practical experience of such dynamics are, however, largely restricted to temperate zones. Subtropical and tropical lakes, in contrast, are relatively poorly understood. Due to their higher light availability and temper-

ature, biological production is intuitively higher in tropical than in temperate lakes, provided that nutrients are not limiting. Consequently, minimum phytoplankton biomass tends to be higher for a given nutrient status in tropical systems (Lewis, 1990), although composition or seasonal dynamics do not appear to differ in any fundamental way between the two types (Kalff & Watson, 1986; Matveev et al., 1992). Because of the a protracted growing season of tropical lakes, submerged macrophytes may also be expected to achieve higher biomass than in temperate systems. The higher macrophyte density, through a variety of mechanisms, may help to buffer a lake from any impact of an increase in nutrient

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loading (see Stansfield et al., 1997). A high primary productivity of phytoplankton may not be manifested as a high density of individuals, or even biomass, of grazing zooplankton (Fernando, 1994) in tropical lakes, because of predation by characteristically abundant, productive, and efficient fish stocks (Gliwicz, 1994).

In temperate shallow lakes, the abundance and biomass of fish may be instrumental in the ultimate dominance of phytoplankton or submerged macrophytes, through two major pathways, either acting individually or in combination. Firstly, fish may exert top-down control of zooplankton, which has a positive potential subsequent impact upon phytoplankton and, therefore, a negative effect on water clarity (the trophic cascade-Carpenter et al., 1987). Secondly, there may be a variety of direct and indirect mechanisms as a result of benthic foraging by the fish. These include the re-suspension of suspended solids (Szumiec, 1989; Breukelaar et al., 1994), promotion of nutrient release (Tatrai & Istvanovics, 1986; Tatrai et al., 1990; Cline et al., 1994), and uprooting of macrophytes (Ten Winkel & Meulemans, 1984). The presence or absence of submerged macrophytes has a major feedback effect on fish community structure, especially the ratio of piscivores to zooplanktivores/benthivores (Bronmark & Weisner, 1992). The impact of foraging fish in tropical waters, without a cold season, is predicted to be more intense than in temperate lakes, although little quantitative information is as yet available.

The introduction of fish, particularly members of the Cyprinidae, Cichlidae and Clupeidae, as a source of protein for human consumption, into tropical and subtropical lacustrine systems is continuing apace (Fernando, 1991). Stocking of carp (*Cyprinus carpio*) is prevalent in Mexican rural zones, partly as a result of its high capacity to survive and grow in poor quality waters (Maitland & Campbell, 1992). It has long been known that carp may have a dramatic impact on lake ecology (Cahn, 1929). Introductions of carp and related species such as goldfish (*Carassius auratus*) may have severe negative impacts on native fauna and flora through changes in water quality and disturbance or depletion of shared resources in both temperate (Richardson et al., 1995) and subtropical systems (Brumley, 1991). The current paper reports on the first attempt to assess the trophic impacts of stocking of carp in Mexico. The basic approach was to determine the general pattern of relationships between biological, chemical, and physical parameters and carp biomass in a series of ponds in a valley of the Lerma River. The results of the study are discussed in the light of the alternative stable state hypothesis and its application to subtropical rather than temperate shallow lakes.

Study site

Data were collected from small (0.8–8 ha), shallow (mean ± 1 SE = 0.84 ± 0.21 m) ponds in Acambay in the Alto Lerma zone on the Mexican volcanic belt (altitude 2550 m) in central west Mexico (19° 57' N, 99° 51' E). The region is delimited in the north by the Acambay-Tixmadeje fault system and in the south by the Venta de Bravo fault system. Acambay is in a valley in the basin of the Lerma river identified as being of conservation value because of its high density of endemic species. Some of these, including axolotl (*Ambystoma mexicanum*), crayfish (*Cambarellus montezumae*), and long-finned amarillo (*Girardinichthys multiradiatus*) (Espinoza et al., 1993), a small live-bearing fish of the family Goodeidae, are present in the ponds. Some ponds are natural but most are artificial, created partly to provide irrigation for the surrounding agricultural land and the crops (mainly maize and wheat) it supports. Ponds are dependent on precipitation (903.8 mm per annum – García, 1988) in the wet season beginning in June. The ponds tend to fill in July/August, coinciding with the heaviest rains. The annual average annual temperature is 14.2 °C (maximum 16.8 °C, minimum 10.6 °C – García, 1988). During the sampling season in this study water temperatures ranged from 8 °C at 6.00 in the morning on the coldest day to 24 °C at 13.00 in the afternoon on the hottest day.

In some ponds juvenile carp are stocked at 3–5 cm in length, often in densities >2 m^{-2} (above the governmental recommended stocking level of 0.5–2 m^{-2}), according to availability from the centres of production, and left to grow for one or two years (preferably to a minimum of 20 cm) before being harvested, traditionally around Easter. This coincides with the peak of the dry season, when the ponds partially or even totally dry out. The fish crop is insufficient to be of commercial interest. Relatively wealthy farmers may allow their workers to harvest the carp for their own consumption, which they catch when the water level declines to 20–30 cm, with a simple mesh bag or by hand. Subsistence farmers harvest the fish for their own purposes, although a number of fish are lost to poachers, who may use rifles

to shoot carp where the water is clear. Although native fauna, including amphibians, fish, and especially crayfish, is consumed to a greater or lesser extent by local people, carp is generally welcomed as an additional source of protein.

Methods

A variety of physical, chemical and biological variables across all trophic levels were quantified from the twelve study ponds at the onset of the dry season. Nine ponds were sampled from January to March 1995, and three in February of 1996. Eight ponds were known to be stocked with carp, whereas four were thought to be carp-free. Unfortunately, some of the ponds dried out before data on all variables could be collected. Physical variables included pond morphometry (area in ha and mean depth in m), Secchi depth, and temperature. Water quality parameters were measured from a pooled sample (of three subsamples) of 1 litre of water collected around midday in each pond, according to the standard methods described by APHA (1985). These included total organic nitrogen (TON) and ammonia NH_3 by the Kjeldahl technique; nitrate (NO_3) by the Brusin Sulphate technique (see DGN, 1986), and total phosphorus (TP) and ortho-phosphate (PO_4) by the Stannous chloride method. The concentration (mg l^{-1}) of total suspended solids was obtained by the gravimetric method after ignition to 105 °C.

Chlorophyll a concentration was used as an index of phytoplankton biomass and consequently primary productivity. This was determined using the fluorometric method (Lorenzen, 1966) from 50–500 ml of filtered water from a pooled sample of three subsamples taken at 10 cm under the water surface. As an index of macrophyte abundance, cover of rooted (submerged and emergent) and floating macrophytes was estimated within a 40 cm diameter circular frame (Necchi et al., 1995) at 5 sample points along each of twelve 10 m transects (60 samples per pond in total). Sampling thus encompassed the zone close to the littoral margin, where the majority of any macrophytes occurred. As ponds were generally square, three transects were taken at equal distances along each side, originating from, and perpendicular to, the littoral margin.

Five samples of the entire water column (from 0.5 m to 1.9 m depth and 2–6 litres volume) were taken with a PVC tube (2 m length, 7 cm diameter) for zooplankton. The resulting pooled sample was filtered through a 200 μ mesh plankton net and stored in alcohol. In the laboratory the sample was made up to 200 ml. Five 5 ml subsamples were taken and the number of cladocerans and copepods in each was determined.

The abundance (org. m^{-3}) of epibenthic invertebrates and small native fishes was estimated using a small beam net (Renfro, 1962) along three transects of 12 m in length in each pond. The abundance (org. m^{-3}) of benthic organisms was estimated from a 5 litre pooled sample of mud taken by means of an Ekman grab in a variety of locations. Organisms were separated from the mud in the field by 3 sieves (4 mm, 2 mm and 0.4 mm mesh size) and identified and counted in the laboratory. An overall estimate of abundance of the various groups was provided by combining the estimates obtained by each sampling method.

Two multi-mesh gill-nets of 20 m in length, split into four panels of 5 m each with 1.27 cm, 5.71 cm, 7.62 cm and 8.9 cm (0.5–3.5 inches) mesh, respectively, were used to sample carp from 7–40 cm, covering the entire size range expected in the ponds. The first net was set at 90° to, and from, whereas the second was set in a transverse manner to the first in the middle of the pond. Nets were set in the hours of daylight for between 6–10 hours. The difference in the length of time the nets were set was found to be of little consequence, as subsequent analysis of catch over the time period showed the bulk of captures occurred within 4 hours of the net being set. Data were expressed as catch per unit effort (CPUE) ha^{-1} by abundance and biomass.

The Kendall coefficient of concordance (W; Siegel & Castellan, 1988) was used to test the degree of association of variables within each of three groups, indicative of the likely trophic pathways of the impact of carp. The first group comprised the variables predicted to respond to an increase in nutrients (Carvalho & Moss, 1995). The second group consisted of those variables illustrative of potential top-down control of zooplankton by young carp (Carpenter et al., 1987). The third group was composed of those variables potentially affected by the benthic foraging action of carp. To indicate potential cause and effect, Spearman rank correlation coefficient (r_s) was used to describe the relationships between variables obtained from significant Kendall concordance coefficients (W). The nature of any significant relationships was then further qualified by determining the best-fit curve for the data (SIGMASTAT. Jandel-Scientific, V.1, USA).

Table 1. Parameters of physical, chemical and biological variables in the 12 study ponds sampled

Pond number	Physical and chemical data											Biological data											
	Size	SD	Phosphorous		Nitrogen				Suspended solids			Phyto.	Zooplankton			Macrophytes			Invertebrates		Vertebrates		
			PO$_4$	Tot.	NO$_3$	NH$_3$	Org.	Tot.	In.	Org.	Tot.	C.a	Cla.	Cop.	Tot.	F.F.	Rtd.	Tot.	Epi.	Ben.	Gm	C(n)	C(g)
	(ha)	(m)	(mg l^{-1})		(mg l^{-1})				(mg l^{-1})			(mg l^{-1})	(n l^{-1})			(%)					(n m^{-3})	(CPUE)	(CPUE ha^{-1})
Without carp																							
1	4.96	0.90	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	1.0	9.1	10.6	19.6	n.d.	n.d.	n.d.	62	7000	0.2	0.0	0
2	8.02	0.53	0.06	0.06	0.00	0.05	0.97	1.02	3.0	0.0	3.0	1.8	5.7	17.5	23.2	54	38	93	n.d.	1800	n.d.	0.0	0
3	0.85	n.d.	0.03	0.13	0.03	0.05	2.64	2.72	23.0	7.0	30.0	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	0.0	0
4	2.50	1.27	0.01	0.21	0.07	0.08	0.28	0.43	n.d.	n.d.	11.4	0.3	11.1	9.6	20.7	16	54	85	20	2740	0.5	0.0	0
Mean	4.08	0.90	0.03	0.13	0.03	0.06	1.30	1.39	13.0	3.5	14.8	1.0	8.6	12.6	21.2	35	46	89	41	3847	0.4	0.0	0
se	2.70	0.30	0.02	0.06	0.03	0.01	0.99	0.97	10.0	3.5	11.3	0.6	2.2	3.5	1.5	19	8	4	21	2263	0.1	0.0	0
With carp																							
5	1.56	0.73	0.04	0.30	0.00	0.05	1.19	1.24	3.0	0.0	3.0	10.1	15.3	3.8	19.1	50	48	98	111	7600	0.1	0.2	21
6	2.59	0.29	0.20	0.28	0.02	1.08	2.02	3.12	52.0	12.0	64.0	170.4	2.8	3.4	6.2	0	30	30	9	0	4.4	1.0	86
7	0.81	0.05	0.18	0.23	0.00	0.94	3.76	4.71	168.0	20.0	188.0	0.7	7.9	7.9	15.7	5	6	11	3	1000	0.1	1.0	22
8	1.10	0.14	0.22	0.21	0.04	0.33	0.25	0.62	n.d.	n.d.	24.9	2.8	5.8	4.1	9.8	18	18	36	9	1268	2.5	1.3	n.d.
9	1.19	0.31	0.08	0.48	0.00	0.27	4.03	4.30	50.0	14.0	64.0	0.5	2.3	9.1	11.4	11	14	25	30	8600	3.5	1.7	3623
10	1.20	0.42	0.01	0.22	0.03	0.11	0.51	0.65	n.d.	n.d.	15.1	1.9	2.9	2.7	5.6	5	27	32	18	2200	3.0	1.8	n.d.
11	1.53	0.24	0.03	0.17	0.04	0.17	0.80	1.00	28.0	8.0	36.0	3.6	4.7	11.7	16.4	0	12	12	0	3200	3.1	2.5	532
12	1.41	0.22	0.02	0.21	0.00	0.67	2.29	2.96	58.0	10.0	68.0	4.2	9.3	9.5	18.8	0	4	4	2	400	1.0	4.8	694
Mean	1.42	0.30	0.10	0.26	0.02	0.45	1.85	2.32	59.8	10.7	57.9	24.3	6.38	6.51	12.9	11	20	31	23	3034	2.2	1.8	830
se	0.50	0.19	0.08	0.09	0.02	0.37	1.35	1.55	51.8	6.07	54.2	55.3	4.12	3.19	5.05	16	14	27	35	3081	1.5	1.3	1276
Tot. mean	2.46	0.48	0.07	0.21	0.02	0.30	1.62	1.93	40.8	7.8	41.0	15.3	6.8	8.1	14.6	18	25	43	27	3224	1.6	1.0	415
se	0.54	0.10	0.02	0.03	0.01	0.10	0.35	0.40	15.5	2.0	13.8	12.9	1.1	1.2	1.9	6	5	11	9	777	0.5	0.4	299

Tot. = total, In. = Inorganic, Org. = Organic, Phyto. = Phytoplankton, C.a = Clorophyll *a*, Cla. = Cladocera, Cop. = Copepoda, F.F. = Free floating macrophytes, Rtd. = Rooted macrophytes, Epi. = Epibenthic, Ben. = Benthic, Gm = *G. multiradiatus*, C = *C. carpio*, n.d. = no data

Results

Nutrient concentrations were typically high, with mean TP of 232 μg l^{-1} and mean TON of 1.7 mg l^{-1} (Table 1). All ponds were therefore classed as hypereutrophic (Wetzel, 1983). However, a high nutrient concentration was not necessarily expressed as a high biomass of algae. Chlorophyll *a* concentrations ranged from 0.31 to 170 μg l^{-1} (Table 1) and appeared not to be related to the concentration of nutrients (Table 2).

Total macrophyte cover ranged from 4% to 98% divided between rooted (4–54%) and floating macrophtytes (0–54%; Table 1). The abundance of rooted macrophytes was significantly positively related to Secchi depth (which ranged from 5–127 cm; Tables 1 and 2) and accordingly to the concentration of suspended solids (Table 2). Suspended, mostly organic, solids were of sufficient concentration (to 188 mg l^{-1}) to bestow a brown coloration in some ponds. The concentration of suspended solids was significantly related to the abundance of rooted macrophytes (Tables 1 and 2).

Populations of benthic and epibenthic organisms were variable but often relatively high (Table 1), with the invertebrate orders Malacostraca (the native crayfish *C. montezumae*), Insecta, Gastropoda, Lamellibranchia, Ostracoda, and Turbellaria represented. Insecta was present in all ponds for which data were available, Gastropoda in 64% and Malacostraca in 40%, while the rest of the orders appeared only in one pond.

The density of cladoceran and copepod zooplankton was low (5–23 individuals l^{-1}). The potentially zooplanktivorous native *G. multiradiatus* occurred in all ponds and reached a high density >4 m^{-3} (Table 1). The native amphibian *A. mexicanum* was only present in one pond and is thus unlikely to have had a general functional role in the structure of the trophic web.

Carp had been introduced into eight of the twelve ponds, although density varied from 0 to 4.8 CPUE and biomass ranged from 0 to 3623 g CPUE (Table 1). Because of the seasonal nature of the ponds, carp were generally young and therefore relatively small (i.e. in pond 6 mean (±1 SE) length = 13.3±1.09 cm, mean (±1 SE) weight = 145±46.2 g). However, in pond 9, carp were much larger (mean (±1 SE) length = 44.0±5.26 cm, mean (±1 SE) weight = 2150±362 g), suggesting this pond had retained water for at least two seasons and, probably as a consequence, had not been harvested. Carp biomass was related to the benthic group of variables in the concordance analysis (Table 2), with significant negative correlations between carp and Secchi depth, rooted macrophytes and epibenthic organisms (Table 3). These relationships were nonlinear (Figure 1).

Table 2. Kendall concordance analysis for variables grouped on different type of effects due to carp. 1. enhancing nutrients, 2. decreasing zooplankton abundance and 3. disturbing the bottom

1. Nutrients effects	2. Top-down effects	3. Benthivorous effects
Total suspended solids	Secchi depth	Rooted macrophytes
NO3	Chlorophyll a	Epifauna
NH3	Cladocera	Infauna
Total N	Copepoda	G. multiradiatus
Total P	G. multiradiatus	CPUE (C.carpio)
PO4	CPUE (C.carpio)	Total suspended solids
Chlorophyll a		Secchi depth
Free floaters macrophytes		
CPUE (C.carpio)		
n = 10	n = 10	n = 10
W = 0.12	W = 0.13	W = 0.51
Xi = 9.8	Xi = 10.6	Xi = 32
p = n.s.	p = n.s.	p < 0.001

Table 3. Relationships between selected variables

Factors		n	r_s	p
Carp number	Secchi depth	11	−0.67	0.02
	Suspended solids	11	0.53	n.s.
	Rooted macrophytes	10	−0.79	0.004
	Epibenthic organisms	10	−0.66	0.03
	Benthic organisms	10	−0.22	n.s.
	G.multiradiatus	10	0.51	n.s.
Rooted macrophytes	Secchi depth	10	0.85	0.001
	Suspended solids	10	−0.84	0.001
	Epibenthic organisms	9	0.72	0.03
	Benthic organisms	10	−0.24	n.s.

Discussion

The partial or even total drying out of some ponds may have led to fundamental differences in the structure of the food web, confounding the interpretation of the impact of carp on the ponds. Ponds retaining water may have been expected to have more stable communities of macrophytes and epibenthic invertebrates and native fish than those subject to water loss. However, observations suggest that the speed at which macrophytes and benthos can colonise any pond was less than two months from the onset of the wet season. This suggests adaptations on the part of many of the plants and animals. For example, several of the macrophyte species may have resistant bulbs and seeds. Contrary to other studies on temporary ponds (e.g. Bazzanti et al., 1996), the potential dominance of less mobile, slow to colonise, groups, such as gastropods, in the ponds also suggests some resistance to drying-out.

The live-bearing strategy of the fish G. multiradiatus may be a specific adaptation to exploit temporary waterbodies as they become available. This fish is not thought to be tolerant of drying out, and its ubiquitous presence in the pond system indicates that the pond system is readily connected by the temporary streams that begin to flow at the onset of the wet season. The resistance of several important components of the community to drying coupled with the speed of colonisation of others, and exacerbated by the connection to temporary streams suggests that the temporary status

of some ponds should not be the dominant factor in determining pond community structure.

The ready division of the ponds into those that were clear with a high coverage of rooted macrophytes and those that were turbid with a low coverage of rooted macrophytes within a narrow range of nutrient loading, conforms to the alternative stable state hypothesis proposed for temperate shallow lakes (Irvine et al., 1989; Scheffer et al., 1993). The negative exponential relationships between carp and macrophytes and Secchi depth is also supportive of the view that fish may not only have a critical role in determining the alternative states in subtropical in temperate lakes (Bronmark & Weisner, 1992; Jeppesen et al., 1997), but that a threshold value (around a carp CPUE of 1) operates, above which any buffering mechanism is over-run and the water body rapidly switches from the clear to the turbid state (see Scheffer et al., 1993). Although further experimental work is required, there are also indications of the nature of the fish-induced mechanisms responsible.

The lack of any relationship between carp and nutrients and chlorophyll a suggests that carp did not contribute to the overall nutrient values of the ponds, and thus to algal production, either through physiological processes or release through sediments (Breukelaar et al., 1994; Tatrai & Istvanovics, 1986; Cline et al., 1994). The hypertrophic nature of the ponds is somewhat unexpected given their altitude and seasonal nature. However, Acambay valley is in a tectonic depression and the base volcanic rock is some 200 m below the surface and overlain with soil deposits potentially from the bed of an ancient lake (Ramirez-Herrera et al., 1994). Consequently, the area is favoured for agriculture. Evidence that the general source of nutrients was from run-off
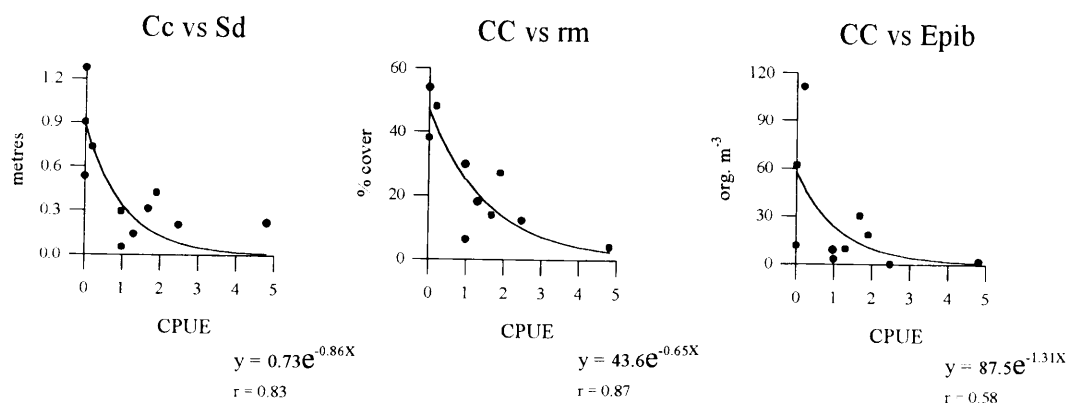
Figure 1. Curve fit relations from carp non parametric significant relations (Table 1). CPUE = Capture per unit of effort, Cc = Cyprinus carpio, Sd = Secchi depth, rm = root macrophytes, and Epib = epibenthic fauna.

from the surrounding crops is provided by the high ammonia: nitrate ratio (>10:1) indicating input of fertilisers (Wetzel, 1983). The high proportion (mean $89.0\pm18.7\%$) of inorganic solids also suggests allochthonous input of chemicals (Table 1). We therefore suggest that the ponds would naturally be of significantly lower nutrient status and therefore most likely to be dominated by macrophytes rather than phytoplankton (Scheffer et al., 1993).

Although nutrients appeared to be abundant in the water, the ponds seem to have a relatively low primary productivity of algae (mean $\pm$ SE = 24.03 ± 20.94 μg l^{-1}). This pattern may be linked to complex water chemical interactions at this level, such as changes in the limited availability of nutrient in a form for algal uptake. For example, the ratio of PO_4:TP varied from pond to pond (mean $\pm$ SE = 4.06 ± 1.04, min. 1.07, max. 9.55) suggesting differences in the P cycle. However, currently it is unknown whether the concentration of nutrients in this type of system should be considered only as an upper limit for chlorophyll a productivity instead of a defined curve-fit between nutrients and algae densities (Scheffer, 1998). Additionally, it is not clear whether this is an effect of an enhanced rate of cycling in the higher temperatures of the subtropics and whether carp have some role in nutrient cycling.

The generally low biomass of algae in the ponds is intuitively likely to limit the size and structure of the zooplankton populations. The lack of a significant concordance correlation between *G. multiradiatus*, carp, zooplankton and chlorophyll a (Table 2), suggests that pelagic interactions were unimportant in these systems. This is further supported by the presence of only a few zooplankton in the diet of a small

number carp (n = 100) taken for analysis. There has been some suggestion that zooplankton populations are generally of insufficient size or lacking in suitable structure (i.e. lacking large grazing Cladoceransalthough this is debated, Dumont, 1994) in subtropical and tropical systems to be of importance in promoting clear water through algal control (Crisman & Beaver, 1990), in contrast with the typical pattern in many temperate shallow lakes (Perrow et al., 1997).

Concordance analysis and subsequent correlations with suspended solids, Secchi depth and rooted macrophytes, suggest that the benthic foraging of carp (digging pits to 10 cm in depth – Ivlev, 1961), exploiting what may be an abundant benthic resource, is responsible for the observed patterns. This is supported by limited dietary samples, which mainly consisted of mud, epibenthic algae and benthic fauna. Values of Secchi depth around 20–30 cm appeared to be the critical threshold value above which the production of a high coverage of rooted macrophytes could occur in the ponds. This in turn appeared to be dependent on the concentration of suspended solids. The latter are less strongly related to carp than to rooted macrophytes. The strong negative relationship between carp and rooted macrophytes may thus be more indicative of direct disturbance (Ten Winkel & Meulemans, 1984; Kolasa & Weber, 1995) than an indirect effect through shading (see Meijer et al., 1990; Breukelaar et al., 1994). Once the macrophytes are lost, the potential for sedimentation of solids may be dramatically reduced (James & Barko, 1990).

The abundance of epibenthic invertebrates also declined rapidly for values of CPUE ha^{-1} of carp >1 (Figure 1), corresponding with the value at which macrophytes declined, suggesting an indirect rather

than direct impact of carp upon invertebrates (Tatrai et al., 1994). Moreover, as there was no relationship between carp and benthic organisms, which normally constitute the bulk of the diet (Lammens & Hoogenboezem, 1991), a strong direct predation effect seemed unlikely. The proportion of gastropods in the community, the group intuitively linked to the abundance of macrophytes, also declined rapidly with macrophytes, from 60% ($\pm$ SE 5.4) in ponds with CPUE ha^{-1} of carp >1 to 2.1% ($\pm$ SE 0.4) in ponds with CPUE ha^{-1} of carp >1.

This preliminary correlational study results suggest that the introduction of a non-native benthivorous fish, carp, to the study ponds, has provoked a detrimental ecological impact, as predicted by other studies in both temperate and subtropical systems (e.g. Cahn, 1929; Szumiec, 1989; Brumley, 1991; Breukelaar et al., 1994; Richardson et al., 1995). The effect appeared stronger than either nutrient enrichment from the surrounding arable land or partial drying-out for some ponds. On one hand, the loss of rooted macrophytes, possibly directly through uprooting during benthic foraging, is intuitively likely to lead to a decline in biological diversity (Crowder & Painter, 1991) in the ponds of this area of high intrinsic conservation, particularly for endemic fish, amphibians, and reptiles. On the other, the lack of a detectable impact upon the native fish (*G. multiradiatus*) suggests otherwise; apparently, this native fish is not affected by changes in the bottom-benthos-macrophyte interactions. Moreover, as *G. multiradiatus* are also exploited as food by local people, at face value, the introduction of carp represents a net gain in the available food resource. However, the impact upon other exploitable natural food resources, such as the native crayfish (*C. montezumae*), and other endemic species of freshwater fish from nearby zones, is also unknown. As such species are consumed by the poorest people of the zone, there may also be sociological implications.

The relative costs and benefits of the introductions of carp clearly depend on a more thorough analysis of the impact upon native species, exploitable natural food resources and social consequences, than was possible in the current study.

The current work has provided a baseline of the potential for trophic interactions within the ponds and some insight into the similarities and differences between subtropical and temperate shallow lakes. For example, benthic interactions may be dominant in subtropical and tropical systems. Further, more detailed experimental work is required to unravel the interactions within the ponds and ultimately to determine whether the introduction of carp can be undertaken in a less detrimental and more sustainable manner, both in ecological and socio-economic terms.

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References

APHA (American Publish Health Association), 1985. Standard Methods for the Examination of Water and Wastewater, 16th edn. Amer. Pub. Health. Assoc., Washington. D.C.

Bazzanti, M., S. Baldoni & M. Seminara, 1996. Invertebrate macrofauna of a temporary pond in central Italy-composition, community parameters and temporal succession. Arch. Hydrobiol. 137: 77–94.

Breukelaar, A., E. Lammens, J.G.P. Klein Breteler & I. Tatrai, 1994. Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspension and concentrations of nutrients and chlorophyll *a*. Freshwat. Biol. 32: 112–121.

Bronmark, C. & S.E.B. Weisner, 1992. Indirect effects of fish community structure on submerged vegetation in shallow, eutrophic lakes: An alternative mechanism. Hydrobiologia 243/244 (Dev. Hydrobiol. 79): 293–301.

Brumley, A.R., 1991. Cyprinids of Australasia. In: Winfield I.J. & J.S. Nelson (eds), Cyprinid Fishes-Systematics, Biology and Exploitation. Fish & Fisheries Series 3. Chapman & Hall, Ltd., London.

Cahn, A.R., 1929. The effect of carp on a small lake: The carp as dominant. Ecology 10: 37–374.

Carvalho, L. & B. Moss, 1995. The current status of a sample of English Sites of Special Scientific Interest subject to eutrophication. Aquat. Conserv: Mar. Freshwat. Ecosyst. 5 (3): 191–204.

Carpenter, S.R., J.F. Kitchell, J.F. Hodgson, P.A. Cocharn, J.J. Elser, M.M. Elser, D.M. Lodge, D. Kretchmer, X. He & C.N. Von Ende, 1987. Regulation of lake primary productivity food web structure. Ecology. 68: 1863–1876.

Cline, J.M., T.L. East & S.T. Threlkeld, 1994. Fish interactions with the sediment–water interface. Hydrobiologia 275/276 (Dev. Hydrobiol. 94): 301–3012.

Crisman, T.L. & R.J. Beaver, 1990. Applicability of planktonic biomanipulation for managing eutrophication in the subtropics. Hydrobiologia 200/201 (Dev. Hydrobiol. 61): 177–183.

Crowder, A. & D.S. Painter, 1991. Submerged macrophytes in Lake Ontario: Current knowledge importance, threats to stability, and needed studies. Can. J. Fish. Aquat. Sci. 48(8): 1539–1545.

DGN, 1986. Método Sulfato Brusina para determinar Nitratos. NMX-AA-79-1986. Dirección General de Normas, SECOFI, México.

Dumont, H.J., 1994. On the diversity of the Cladocera in the tropics. Hydrobiologia 272: 27–38.

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Espinoza, P.H., D. Gaspar & M. P. Fuentes, 1993. Listados faunísticos de México III, los peces dulceacuícolas mexicanos. Instituto de Biología, UNAM, México.

Fernando, C.H., 1991. Impacts of fish introductions in Tropical Asia and America. Can. J. Fish. Aquat. Sci. 48: 24–32.

Fernando, C.H., 1994. Zooplankton, fish and fisheries in tropical fresh-waters. Hydrobiologia 272: 105–123.

García, E., 1988. Modificaciones al sistema de clasificación climática de Köppen. México.

Gliwicz, Z.M., 1994. Relative significance of direct and indirect effects of predation by planktivorous fish on zooplankton. Hydrobiologia 272: 201–210.

James, W.F. & J.W. Barko, 1990. Macrophyte influences on the zonation of sediment accretion and composition in a north-temperate reservoir. Arch. Hydrobiol. 2: 129–142.

Jeppesen, E., J.P. Jensen, M. Søndergaard, T. Laurisdsen, L.J. Pedersen & L. Jensen, 1997. Top down control in freshwater lakes: The role of fish, submerged macrophytes and water depth. Hydrobiologia 342/343 (Dev. Hydrobiol. 119): 151–164.

Irvine, K., B. Moss & H. Balls, 1989. The loss of submerged plants with eutrophication II. Relationships between fish and zooplankton in a set of experimental ponds, and conclusions. Freshwater Biology 22: 89–107.

Ivlev, V.S., 1961. Experimental Ecology of the Feeding of Fishes (Transl. by D. Scott). New Haven, Yale University Press.

Kalff, J. & S. Watson, 1986. Phytoplankton and its dynamics in two tropical lakes: A tropical and temperate zone comparison. Hydrobiologia 138 (Dev. Hydrobiol. 33): 161–176.

Kolasa, J. & L. Weber, 1995. Relationship between the spatial scale an biotic variability in a wetland ecotone. Hydrobiologia 303: 61–67.

Lammens, E.H.R.R. & W. Hoogenboezem, 1991. Diets and feeding behaviour. In: I.J. Winfield & J.S. Nelson (eds), Cyprinid Fishes-Systematics, Biology and Exploitation. Fish and Fisheries Series 3. Chapman & Hall., Ltd., London.

Lewis, W.M. Jr., 1990. Comparisons of phytoplankton biomass in temperate and tropical lakes. Limnol. Oceanogr. 35: 1838–1845.

Lorenzen, C.J., 1966. A method for the continuous measurement of in vivo chlorophyll concentrations. Deep-Sea Research 13: 223–227.

Matveev, V., C.C. Martinez, S.M. Frutos & Y. Zalocar De Domitrovic, 1992. Population control in planktonic crustaceans of a subtropical lake during seasonal succession. Arch. Hydrobiol. 124: 1–18.

Maitland, P.S. & R.N. Campbell, 1992. Freshwater Fishes. Harper Collins Publishers, London.

Meijer, M.-L., M.W. De Hann, A.W. Breukelaar & H. Buitveld, 1990. Is reduction of the benthivorous fish an important case of high transparency following biomanipulation in shallow lakes? Hydrobiologia 200/201 (Dev. Hydrobiol. 61): 303–315.

Moss, B., J. Stansfield, K. Irvine, M.R. Perrow & G.L. Phillips, 1996. Progressive restoration of a shallow lake: A 12-year experiment in isolation, sediment removal and biomanipulation. J. Applied. Ecology 33: 71–86.

Necchi, O. Jr., L.H.Z. Branco & C.C.Z. Branco, 1995. Comparison of three techniques for estimating periphyton abundance in bedrock streams. Arch. Hydrobiol. 134: 393–402.

Perrow, M.R., M.-L. Meijer, P. Dawidowicz & H. Coops, 1997. Biomanipulation in shallow lakes: State of the art. Hydrobiologia 342/343 (Dev. Hydrobiol. 119): 355–365.

Ramirez-Herrera, M.T., M.A. Summerfield & M.A. Ortiz-Pérez, 1994. Tectonic geomorphology of the Acambay graben, Mexican Volcanic Belt. Z. Geomorph. N. F. 38: 151–168.

Renfro, W., 1962. Small beam net for sampling postlarval shrimp. Galveston Biological Lab. June 30. U.S. Fish and Wild. Serv. Circ. 161: 86–87.

Richardson, M.J., F.G. Whoriskey & L.H. Roy, 1995. Turbidity generation and biological impacts of an exotic fish Carassius-auratus, introduced into shallow seasonally anoxic ponds. J. Fish Biol. 47: 576–585.

Scheffer, M., 1998. Ecology of Shallow Lakes. Chapman & Hall, London.

Scheffer, M., S.H. Hosper, M.-L. Meijer, B. Moss & E. Jeppesen, 1993. Alternative equilibria in shallow lakes. TREE 8: 275–279.

Siegel, S. & J.N. Castellan Jr., 1988. Nonparametric Statistic for Behavioral Sciences. McGraw-Hill International Editions, 399 pp.

Stansfield, J.H., M.R. Perrow, L.D. Tench, A.J.D. Jowitt & A.A.L. Taylor, 1997. Submerged macrophytes as refuges for grazing Cladocera against fish predation: Observations on seasonal changes in relation to macrophyte cover and predation pressure. Hydrobiologia 342/343 (Dev. Hydrobiol. 119): 229–240.

Szumiec, M.A., 1989. The role of carp, temperature and morphometry in solar radiation transmission in ponds. Arch. Hydrobiol. Beih. Ergebn. Limnol. 33: 571–577.

Tatrai, I. & V. Istvanovics, 1986. The role of fish in the regulation of nutrient cycling in Lake Balaton, Hungary. Freshwat. Biol. 16: 417–424.

Tatrai, I., G. Toth, J.E. Ponyi, J. Zlinskzky & V. Istvanovics, 1990. Bottom-up effects of bream (Abramis brama L.) in Lake Balaton. Hydrobiologia 200/201 (Dev. Hydrobiol. 61): 167–175.

Tatrai, I., E.H.R.R. Lammens, A.W. Breukelaar & J.G.P. Klein Breteler, 1994. The impact of mature cyprinid fish on the composition and biomass of benthic macroinvertebrates. Arch. Hydrobiol. 131: 309–320.

Ten Winkel, T.E.H. & J.T. Meulemans, 1984. Effects of fish upon submerged vegetation. Hydrobiol. Bull. 18: 157–158.

Wetzel, R.G., 1983. Limnology. Saunders College Publishing, USA.