

# Effects of common carp on nutrient dynamics and littoral community composition: roles of excretion and bioturbation

Shin-ichiro S. Matsuzaki<sup>1</sup>, \*, Nisikawa Usio<sup>2</sup>, Noriko Takamura<sup>2</sup> and Izumi Washitani<sup>1</sup>

With 4 figures and 2 tables

**Abstract:** We manipulated through an enclosure experiment the presence and absence of small common carp (*Cyprinus carpio*, L) and their sediment access using a mesh net. The aims of the experiment were to determine carp effects on nutrient dynamics and community composition, and partially separate bioturbation effects from the remaining carp effects such as excretion and predation. During the two months, carp influenced water quality and nutrient dynamics, altered phytoplankton biomass and composition and decreased submerged macrophyte biomass independently of sediment access, indicating that nutrient excretion was the primary mechanism for the carp effects. However, Secchi depth decreased while the concentration of suspended solids increased when carp access to the sediments was allowed, suggesting that bioturbation by carp influenced water transparency. Increase in phytoplankton (dominated by cyanobacteria) and suspended solids resulted in reduced submerged macrophyte biomass through reduction of light availability. Zooplankton, numerically dominated by rotifers, increased in carp enclosures. In addition, benthic macroinvertebrates decreased in carp enclosures, regardless of the presence and absence of the netting. Because direct predation effects were not evident, carp probably affected benthic macroinvertebrates through reduction of submerged macrophytes. These results indicate that carp can have dramatic direct and indirect impacts on nutrient dynamics and littoral community structure through excretion and bioturbation. Ecosystem engineering by carp may therefore trigger a shift from a clear water state dominated by submerged macrophytes to a turbid water state dominated by phytoplankton.

**Key words:** enclosure experiment, phytoplankton, submerged macrophytes, ecosystem engineers, catastrophic regime shifts.

## Introduction

In freshwater systems, consumers can directly or indirectly affect nutrient dynamics and primary producers in multiple ways, including excretion, bioturbation and predation (Vanni 2002). Many studies have considered excretion by fish to be an important

source of nutrients for phytoplankton production (e. g. Andersson et al. 1988, Brabrand et al. 1990, Carpenter et al. 1992, Schindler et al. 1993, Schaus et al. 1997, Attayde & Hansson 1999, 2001, Schaus & Vanni 2000). For example, Schindler (1992) demonstrated that 95 % of the variations in chlorophyll concentrations were explained by phosphorus excretion

<sup>1</sup> **Authors' addresses:** Department of Ecosystem Studies, Institute of Agricultural and Life Sciences, The University of Tokyo, Bunkyo-ku, Tokyo 113-8657, Japan.

<sup>2</sup> National Institute for Environmental Studies, Tsukuba, Ibaraki 305-8506, Japan.

\* Corresponding author; current address: National Institute for Environmental Studies, Tsukuba, Ibaraki 305-8506, Japan; E-mail: matsuzaki.shinichiro@nies.go.jp

by planktivorous fish (Sockeye salmon; *Oncorhynchus nerka*), while Schaus & Vanni (2000) reported that a low N:P ratio of gizzard shad (*Dorosoma cepedianum*) excreta shifted the phytoplankton structure in favour of cyanobacteria. Thus, both nutrient supply rates and ratios of fish excreta may influence phytoplankton composition and production (Tilman et al. 1982, Smith 1983, Vanni & Layne 1997, Schaus & Vanni 2000).

In addition, many aquatic animals such as fish and invertebrates physically disturb sediments through feeding, walking and/or burrowing activities, a process known as bioturbation (Fukuhara & Sakamoto 1987, Pringle & Blake 1994, Flecker 1996, Moore et al. 2004, Usio & Townsend 2004). For example, detritivores such as fish (Flecker 1996) and decapod crustaceans (Pringle & Blake 1994, Usio & Townsend 2004) reduce the accumulation of fine sediments in streams. As a result, sediment removal by detritivores may positively or negatively influence the distribution patterns of algae and/or invertebrates (Pringle & Blake 1994, Flecker 1996, Usio & Townsend 2004). Furthermore, physical mixing of sediments by benthic invertebrates or fish can increase the rate at which porewater nutrients are released into the water column, permitting nutrient exchanges between sediments and the water column (Fukuhara & Sakamoto 1987, Parkos et al. 2003, Tarvainen et al. 2005).

Predation is also important for the organization of biological communities (e.g. Sih et al. 1985). Fish selectively consume large herbivores and change zooplankton composition (Brooks & Dodson 1965), that in turn affect phytoplankton and primary production (Carpenter et al. 1987). Clearly, nutrient release, bioturbation and predation by consumers are all important in the structure and functioning of freshwater communities (Novales-Flamarique et al. 1993, Mc Collum et al. 1998, Usio & Townsend 2004). When resource availability for other organisms is influenced either positively or negatively through these mechanisms, such effects are considered 'ecosystem engineering' (sensu Jones et al. 1994).

The common carp (*Cyprinus carpio*, L) is an omnivorous, benthic fish species that is relatively long-lived and can attain large size. Unlike planktivorous fish, bottom-feeding fish such as common carp can increase the concentration of lake water nutrients by consuming benthic organisms and excreting nutrients into the water column in dissolved inorganic forms (Schaus et al. 1997, Schaus & Vanni 2000). As bioturbators, carp can enhance sediment resuspension and

release porewater nutrients from sediments to the water column (Qin & Threlkeld 1990, Richardson et al. 1990, Breukelaar et al. 1994, Lougheed et al. 1998, Parkos et al. 2003, Chumchal & Drenner 2004). Shading from disturbed sediments, phytoplankton or periphyton may adversely affect submerged macrophytes (Moss 1976, Meijer et al. 1990, Brönmark & Weisner 1992, Lougheed et al. 1998, Zambrano & Hinojosa 1999, Williams et al. 2002, Parkos et al. 2003). In addition, benthic feeding by carp can directly affect submerged macrophytes through herbivory (King & Hunt 1967) and/or uprooting (sensu Crivelli 1983). As predators, carp can positively or negatively affect the biomasses of zooplankton and benthic macroinvertebrates (Richardson et al. 1990, Tatrai et al. 1994, Lougheed et al. 1998, Parkos et al. 2003). Although carp can potentially affect lake food webs via all of these mechanisms, it is unclear which mechanism is of greater importance. As one of the 100 of the world's worst invasive alien species listed by the IUCN (International Union for Conservation of Nature and Natural Resources, ISSG 2000), the common carp is often referred to as an 'exotic ecosystem engineer' (sensu Crooks 2002). In Japan, the common carp is regarded as a native species (Barus et al. 2001), but is introduced accidentally or intentionally through translocation where the fish had not originally occurred. Subsequently, common carp are widely distributed throughout the Japanese archipelago.

Here we investigated through an enclosure experiment how carp affect water quality, nutrient dynamics and the community members. We experimentally manipulated sediment access using a mesh net in order to separate bioturbation effects from the remaining carp effects such as excretion and predation. Earlier studies have adopted similar experimental designs (Qin & Threlkeld 1990, Havens 1991, 1993, Schaus & Vanni 2000), but no study has reported the impact of benthivorous fish at the ecosystem level (cf. Crooks 2002) that encompasses biological interactions among component species and nutrient dynamics therein in a complex system including submerged macrophytes and benthic macroinvertebrates. Earlier experiments found that when fish had access to the sediments, phytoplankton and total phosphorus in the water column increased by three- to fivefold, that in turn altered phytoplankton composition (Havens 1991, 1993, Schaus & Vanni 2000). When sediment access was prevented, fish had weak or no effects on phytoplankton biomass and water column nutrients (Havens 1991, 1993, Schaus & Vanni 2000). In contrast, Qin & Threlkeld (1990) found that carp

increased phytoplankton even when carp could not access to sediments. Therefore, the increase in phytoplankton biomass following the carp introduction was not due to physical disturbance on the sediments (bioturbation), but to nutrient release in the form of excretion (Qin & Threlkeld 1990, also see Lamarra 1975). Furthermore, Driver et al. (2005) demonstrated that significance in bioturbation and excretion differed between different size classes of common carp. Thus, the relative significance of bioturbation and excretion on nutrient dynamics and phytoplankton composition may vary depending on study systems and/or the ontogenetic stages of carp. The presence of submerged macrophytes may further complicate the ecosystem level impact of carp because macrophytes play key roles in ecosystem functioning (Carpenter & Lodge 1986, Takamura et al. 2003).

In shallow lakes, two stable states (i.e. alternative stable states) are recognized (Scheffer et al. 1993). One is a clear water state characterized by high submerged macrophyte abundance (and low phytoplankton biomass) and the other is a turbid water state characterized by high phytoplankton biomass (and low macrophyte abundance). A sudden change from a clear water state to a turbid water state, referred to as a 'regime shift' (Scheffer et al. 2001a), has been reported to be modulated by excessive nutrient loads (Scheffer 1998), high abundances of planktivorous (Scheffer 1998) or benthivorous fish (Zambrano et al. 2001, Scheffer et al. 2003) and/or climate warming (Scheffer et al. 2001b). Thus, direct and indirect effects of the common carp can potentially initiate a regime shift coupled with extermination of macrophytes from the system.

Based on earlier studies, we hypothesized that if bioturbation is more important than excretion, carp would increase nutrients, phytoplankton and sediment resuspension, and reduce macrophytes only when fish could access to sediments (cf. Havens 1991, 1993, Schaus & Vanni 2000). If excretion is the most important effect, increased algae would shade macrophytes in the presence of fish, regardless of the presence of a net (cf. Qin & Threlkeld 1990). If direct consumption on macrophytes is the most important mechanism (cf. King & Hunt 1967), then macrophytes would be most reduced where fish can directly access the sediments. Because we used small carp in this study, their high excretion rates (cf. Driver et al. 2005) may have significant consequences for the ecosystem functioning.

## Methods

### Study site

Lake Kasumigaura is a shallow eutrophic lake, which has a surface area of 220 km<sup>2</sup>. Although the lake had been associated with large areas of emergent, floating-leaved and submerged macrophytes along the littoral areas until about 1970s, only fragments of emergent or floating-leaved macrophytes now remain in the lake due to eutrophication, concrete bank protection and water regime alterations (Nishihiro et al. 2004). Recently, restoration of lakeshore vegetation using the soil seed bank is being carried out in some shoreline ponds of the lake in order to recover macrophyte assemblages. A group of Kihara experimental ponds (each pond; 65 m × 45 m) is one of the restoration sites. Therefore, submerged macrophytes are abundant in the experimental ponds. These ponds are connected to the lake with small channels that permit water exchange between the lake and ponds. The experimental ponds were not exposed to wave action. We constructed enclosures in the centre pond in June 2004.

### Experiment

An enclosure experiment was performed during the summer between July and September 2004. We crossed the presence or absence of common carp with access/no access to sediments in a 2 × 2 factorial, completely randomized-block design with four replicates each. Thus, the 16 enclosures were randomly assigned to either (1) fishless –net, (2) fishless +net, (3) carp –net or (4) carp +net treatments. Note that “–net” and “+net” indicate the absence and presence of netting, respectively. The enclosures (2 m × 2 m × 1 m height, water depth 0.7–0.8 m) were constructed from nylon-reinforced polyethylene sheeting, with the top and bottom left open. One month before the start of the experiment, we removed macrophytes and replanted equal numbers (40 shoots and about 12 g DW/enclosure) of a submerged macrophyte species (*Potamogeton pectinatus*, L) in each enclosure. After replanting macrophytes, we removed all fish from enclosures using an electroshocker. Eight enclosures were associated with 2.0 cm mesh nets stretched across at the height of about 40 cm from the bottom (approximately 30 cm from the water surface). The mesh opening was coarse enough for submerged macrophytes to go through the net as they grow. The netting prevented carp (if present) from directly disturbing sediments, but allowed other trophic and non-trophic effects (predation and excretion) as well as the sediment-water column nutrient exchanges. Enclosures associated with the netting but without common carp served as controls to quantify the netting effect per se.

Field sampling was carried out four times on days 0 (22 July), 21 (12 August), 42 (2 September) and 67 (28 September) during the experimental period. Enclosures were stocked with common carp on day 15 (6 August). Each carp treatment was stocked with one small common carp (wet mass = 148 ± 13 g, standard length = 16.1 ± 1.3 cm), resulting in a total of 369 ± 32 kg/ha. The carp biomass was within the range observed in natural ponds/lakes (113 – 476 kg/ha; Panek 1987). Water temperature and dissolved oxygen (DO) were measured at water

surface. Water transparency was measured using a Secchi disc. Water samples were collected from the water column using a PVC tube sampler (70 mm diameter, 1.2 m long) to measure  $\text{NH}_4\text{-N}$ ,  $\text{PO}_4\text{-P}$ , total nitrogen (TN), total phosphorus (TP), suspended solids (SS) and chlorophyll *a* (chl-*a*) concentrations. The water samples for nutrient analyses were filtered through a precombusted (at 530 °C for 1 h) Whatman GF/F filter (Whatman International Ltd., Maidstone, UK) and were frozen at -30 °C for later analyses.  $\text{NH}_4\text{-N}$  and  $\text{PO}_4\text{-P}$  were measured using an automatic analyzer (AACS II, Bran + Luebbe K. K., Norderstedt, Germany) (APHA 1998). TP and TN were determined by digesting with persulfate in an autoclave (120 °C, 45 min.) using disposable polycarbonate bottles. Seston samples were collected onto a precombusted GF/F filter and dry mass (70 °C for 2 days) was determined. Phytoplankton samples were filtered onto a GF/F filter and frozen until later spectroscopic analyses; chl-*a* concentrations were determined by extracting with methanol (Marker et al. 1980). At the end of the experiment (day 67), phytoplankton subsamples were preserved with 1% Lugol's iodine solution and abundant taxa were identified and counted with an inverted microscope following Utermöhl (1958).

Zooplankton were sampled using a 40- $\mu\text{m}$  mesh net and preserved in 4% sugar formalin (Haney & Hall 1973). Zooplankton were identified to the lowest possible taxonomic unit and counted using an optic microscope. Benthic macroinvertebrates were collected from each enclosure using a cylindrical PVC core sampler (50 mm diameter). The core samples were washed and filtered through a 0.45-mm sieve, and preserved in 10% formalin. Benthic macroinvertebrates were sorted by eye, counted and identified to family, where possible, under a binocular microscope.

At the end of the experiment, we attempted to collect all of the submerged macrophytes and filamentous green algae from each enclosure. The plant samples were dried at 60 °C for 2 or 3 days and weighed to determine the biomasses of the total submerged macrophyte and total filamentous green algae, separately.

## Statistical analyses

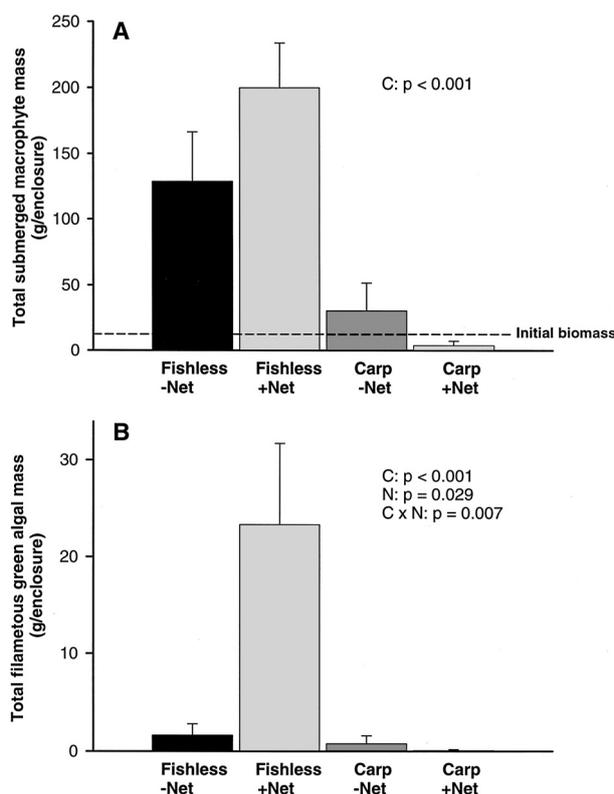
Data were analyzed using  $2 \times 2$  factorial ANOVAs with the presence of carp and the netting as the main factors, and day as repeated measures. Because enclosures were installed in a quasi-natural pond, we tested if the initial conditions (day 0) differed significantly between enclosures with different treatments, using one-way ANOVAs. As a result, one-way ANOVAs did not reveal significant differences between treatments ( $P > 0.08$ , in all cases); we dropped the initial data from the subsequent analyses with two-way repeated measures ANOVAs. When day  $\times$  treatment interactions showed statistical significance ( $P < 0.05$ ), within-day treatment comparisons were performed using post-hoc tests. For submerged macrophytes and filamentous green algae, we compared the final biomasses (on day 67) among treatments using two-way ANOVAs. All data were log-transformed to normalize distributions or to meet the assumption of homogeneity of variances. Statistical significance was evaluated at  $\alpha = 0.05$ . All analyses were conducted using the statistical package SPSS 11.0.

## Results

### Submerged macrophytes and filamentous green algae

Submerged macrophyte biomass decreased significantly in both the carp – net and carp + net treatments (Fig. 1 A). The result from a two-way ANOVA showed a significant carp effect ( $F_{1,12} = 28.57$ ,  $p < 0.001$ ) with no carp  $\times$  net interaction being evident ( $F_{1,12} = 3.145$ ,  $p = 0.101$ ). Although submerged macrophyte biomass was similar among enclosures at the start of the experiment (Fig. 1 A), macrophytes increased in fishless enclosures but decreased in carp enclosures at the end of the experiment.

On the other hand, a carp  $\times$  net interaction was significant for filamentous green algae (*Oedogonium* sp.) (two-way ANOVA,  $F_{1,12} = 10.31$ ,  $p = 0.007$ ), indicating that carp effects on filamentous green algae dif-



**Fig. 1.** Histograms of submerged macrophyte biomass (A) and filamentous green algae biomass (B) on day 67 (the final sampling date) in the four experimental treatments. Carp access to sediments was prevented using a mesh net. “+Net” and “-Net” indicate with and without the netting, respectively. Data are the means of four replicates + 1 SE. *P*-values are given only when main treatment effects (C = Carp and N = Net) and/or an interaction term (C  $\times$  N) were statistically significant ( $p < 0.05$ ). The broken line indicates the initial biomass (day 0) of submerged macrophytes.

ferred depending on the presence and absence of the netting; filamentous green algae increased dramatically only in the fishless + net treatment (Fig. 1B).

### Water quality, nutrient dynamics and phytoplankton

Secchi depth and SS showed significant or marginally significant ( $p < 0.06$ ) day  $\times$  carp  $\times$  net interactions (Table 1). Post-hoc within-day treatment contrasts indicated that carp effects on Secchi depth and SS were evident on day 21. Secchi depth showed the lowest value while SS showed the highest value in the carp – net treatment on day 21 (Fig. 2). The concentration of DO was significantly higher in carp enclosures compared with fishless enclosures, with a significant carp effect (Table 1, Fig. 2). The concentration of chl-*a* increased in carp enclosures (Fig. 2). However, the concentration of chl-*a* was higher in the carp + net relative to the carp – net treatments (Fig. 2), as indicated by a significant carp  $\times$  net effect (Table

1). TN increased in carp enclosures, with a significant carp effect (Fig. 2, Table 1). In contrast, TP did not differ among treatments (Table 1). Although a carp  $\times$  net interaction on NH<sub>4</sub>-N differed over time (Table 1), post-hoc ANOVAs did not reveal any statistical significance on any dates ( $p > 0.05$ ). PO<sub>4</sub>-P was significantly lower in the carp treatments compared with the fishless treatments, as indicated by a significant carp effect (Fig. 2, Table 1).

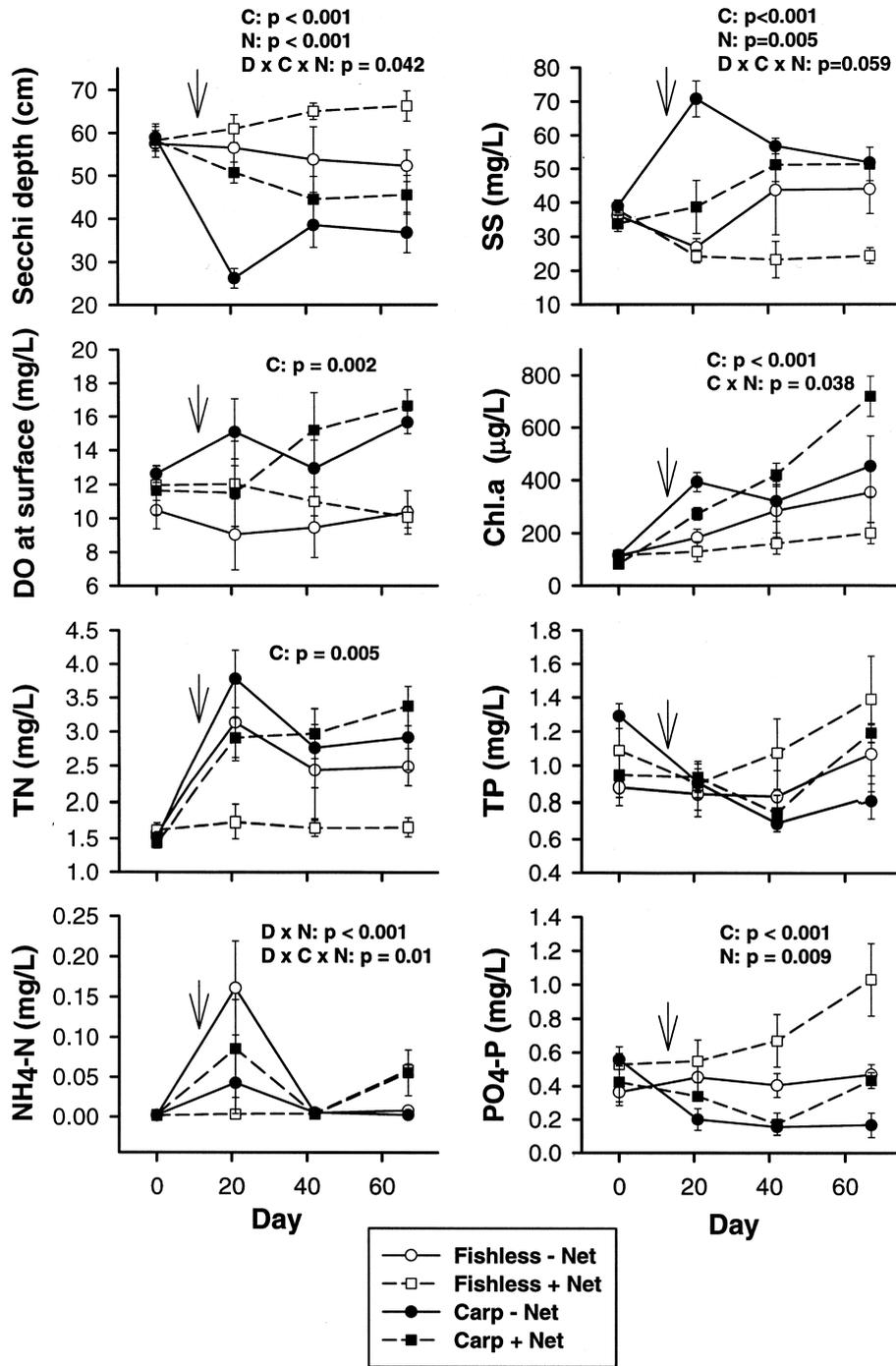
It was noticeable that the most abundant phytoplankton species differed among treatments. On day 67, cryptophyte (*Cryptomonas* spp.) predominated in fishless enclosures, while cyanobacteria (mainly *Anabaenopsis arnoldii*) were most abundant in carp enclosures. On the other hand, Secchi depth and PO<sub>4</sub>-P concentration were higher but chl-*a*, SS and TN concentrations were lower in the fishless + net treatment relative to those in the fishless – net treatment (Fig. 2), probably reflecting the biomasses of filamentous green algae in the respective treatments (Fig. 1B).

**Table 1.** Summary results of repeated-measures ANOVAs on limnological response variables. Bold characters indicate statistical significance ( $p < 0.05$ ). SS = suspended solids, DO = dissolved oxygen, Chl-*a* = chlorophyll-*a*, TN = total nitrogen and TP = total phosphorus.

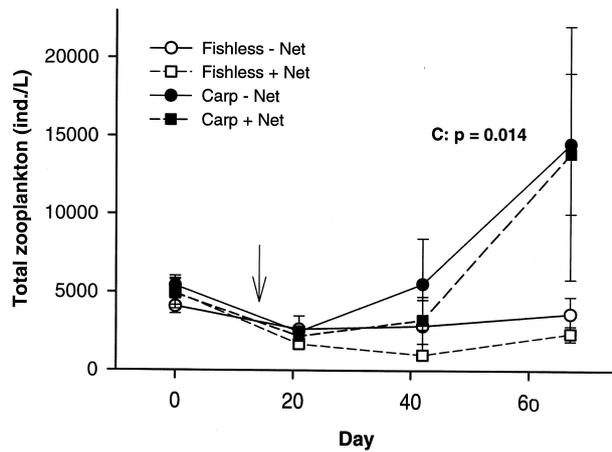
Variable	Carp		Net		Carp $\times$ Net		Day		Day $\times$ Carp		Day $\times$ Net		Day $\times$ Carp $\times$ Net	
	$F_{(1,12)}$	$p$	$F_{(1,12)}$	$p$	$F_{(1,12)}$	$p$	$F_{(2,24)}$	$p$	$F_{(2,24)}$	$p$	$F_{(2,24)}$	$p$	$F_{(2,24)}$	$p$
Secchi depth	48.185	<b>&lt;0.001</b>	18.227	<b>&lt;0.01</b>	1.741	0.212	0.397	0.676	0.383	0.686	1.091	0.352	3.634	<b>0.042</b>
SS	41.189	<b>&lt;0.001</b>	12.076	<b>0.005</b>	1.033	0.330	0.527	0.597	0.406	0.671	0.061	0.941	3.190	0.059
DO	15.257	<b>0.002</b>	0.488	0.498	1.009	0.335	0.978	0.360	0.624	0.479	0.437	0.566	1.624	0.227
Chl- <i>a</i>	31.630	<b>&lt;0.001</b>	0.995	0.338	5.445	<b>0.038</b>	4.538	<b>0.021</b>	0.247	0.783	0.938	0.405	1.084	0.354
TN	11.941	<b>0.005</b>	3.162	0.101	3.554	0.084	2.128	0.141	0.053	0.948	2.494	0.104	0.322	0.728
TP	0.798	0.389	1.954	0.187	<b>0.008</b>	0.930	7.428	<b>0.003</b>	2.183	0.135	1.715	0.201	0.463	0.635
NH <sub>4</sub> -N	0.646	0.437	0.520	0.485	3.280	0.095	6.988	<b>0.004</b>	0.508	0.608	10.790	<b>&lt;0.001</b>	5.586	<b>0.010</b>
PO <sub>4</sub> -P	30.384	<b>&lt;0.001</b>	9.684	<b>0.009</b>	0.429	0.525	2.097	0.145	1.287	0.294	1.366	0.274	0.465	0.634

**Table 2.** Summary results of repeated-measures ANOVAs on zooplankton and benthic macroinvertebrate densities. Bold characters indicate statistical significance ( $p < 0.05$ ).

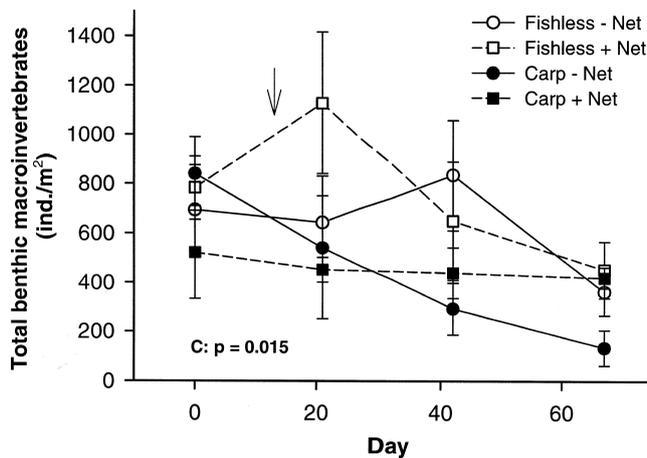
Variable	Carp		Net		Carp $\times$ Net		Day		Day $\times$ Carp		Day $\times$ Net		Day $\times$ Carp $\times$ Net	
	$F_{(1,12)}$	$p$	$F_{(1,12)}$	$p$	$F_{(1,12)}$	$p$	$F_{(2,24)}$	$p$	$F_{(2,24)}$	$p$	$F_{(2,24)}$	$p$	$F_{(2,24)}$	$p$
<b>Zooplankton</b>														
Total zooplankton	8.534	<b>0.014</b>	1.708	0.218	0.213	0.654	11.189	<b>&lt;0.001</b>	2.558	0.100	0.232	0.795	0.288	0.751
Rotifers	11.229	<b>0.006</b>	4.294	0.063	1.111	0.315	17.530	<b>&lt;0.001</b>	1.519	0.241	0.070	0.933	0.274	0.763
Cladocera	0.709	0.418	1.047	0.328	1.482	0.249	5.106	<b>0.015</b>	0.523	0.600	1.225	0.313	<b>0.042</b>	0.959
Adult Copepod	0.301	0.594	<b>0.041</b>	0.844	0.187	0.673	6.213	<b>0.007</b>	1.705	0.205	2.076	0.156	1.466	0.253
Nauplii	1.814	0.205	2.441	0.146	2.790	0.123	28.400	<b>&lt;0.001</b>	0.214	0.709	0.045	0.888	0.414	0.597
<b>Benthic macroinvertebrates</b>														
Total macroinvertebrates	8.022	<b>0.015</b>	3.675	0.079	2.105	0.172	7.070	<b>0.004</b>	<b>0.011</b>	0.989	1.918	0.169	2.388	0.133
Oligochaeta	9.184	<b>0.010</b>	4.677	0.051	3.273	0.096	4.564	<b>0.021</b>	0.264	0.770	1.745	0.196	2.000	0.157
Chironominae	0.174	0.684	1.464	0.250	0.299	0.595	0.580	0.568	<b>0.002</b>	0.998	0.739	0.488	<b>0.030</b>	0.970
Tanypodinae	0.470	0.506	<b>0.030</b>	0.865	<b>0.001</b>	0.970	6.290	<b>0.006</b>	2.315	0.120	0.381	0.687	5.680	<b>0.010</b>



**Fig. 2.** Responses of limnological variables in the experimental treatments over time. Data are means  $\pm$  1 SE- The arrows indicate the carp introduction to enclosures. “-Net” = without netting. “+ Net” = with netting. SS = suspended solids, DO = dissolved oxygen, Chl-*a* = chlorophyll-*a*, TN = total nitrogen and TP = total phosphorus. *P*-values are given only when there were significant ( $p < 0.05$ ) or marginally significant ( $p < 0.06$ ) main treatment (C = Carp and N = Net) and/or interaction effects [C  $\times$  N, Day (D)  $\times$  C, D  $\times$  N and D  $\times$  C  $\times$  N]. Significant “Day” effects were omitted from the graphs because these were not of our interest.



**Fig. 3.** Mean ( $\pm 1$  SE) densities of the total zooplankton in the experimental treatments over time. Rotifers comprised of more than 80% of total zooplankton density. The arrow indicates the addition of carp into enclosures. “-Net” = without netting. “+ Net” = with netting.



**Fig. 4.** The abundance of the total benthic macroinvertebrates in the experimental treatments over time. Oligochaeta comprised of more than 90% of the total benthic macroinvertebrate abundance. Data are means  $\pm 1$  SE. The arrow indicates the carp introduction to enclosures. “-Net” = without netting. “+Net” = with netting.

### Zooplankton and benthic macroinvertebrates

Rotifers (mainly *Keratella* spp., *Brachionus* spp. and *Anuraeopsis* sp.) comprised of more than 80% of total zooplankton abundance. Repeated measures ANOVAs showed that carp effects were significant for the abundances of the total zooplankton and rotifers, which were greater in carp enclosures compared with the fishless treatments (Table 2, Fig. 3). In contrast, the abundances of other zooplankton taxa (Cladocera, Adult Copepods and Nauplii) did not differ among treatments (Table 2).

Benthic macroinvertebrates were dominated by Oligochaeta, which exceeded 90% of the total abundance. Repeated measures ANOVAs showed that a carp  $\times$  net interaction was not significant, but carp effects were significant for the densities of total benthic macroinvertebrates and Oligochaeta (Table 2). The abundance of the total benthic macroinvertebrate declined substantially in the carp treatments compared with the fishless treatments (Fig. 4). Chironominae (mainly *Chironomus plumosus*) abundance was influenced little by experimental treatments (Table 2). For Tanyptodinae, a significant day  $\times$  carp  $\times$  net interaction was evident (Table 2), but individual ANOVAs did not reveal statistical difference on any dates ( $p > 0.05$ ).

### Discussion

Our experiment demonstrated that the introduction of common carp had significant consequences for nutrient dynamics and community structure in a littoral pond food web (Figs 1–4). We will discuss potential mechanisms for these carp effects in the following sections.

### Water quality, nutrient dynamics and phytoplankton

In carp enclosures, the introduction of carp resulted in lower transparency, lower concentration of  $\text{PO}_4\text{-P}$  and higher concentrations of DO, SS and TN compared with the fishless treatments (Fig. 2). Furthermore, carp greatly enhanced phytoplankton biomass (as indicated by chl-*a*) even when sediment access was prevented (Fig. 2). Carp affected phytoplankton biomass and modified phytoplankton species composition. On day 67, cyanobacteria and cryptophyte dominated the total phytoplankton densities in carp enclosures and fishless enclosures, respectively. Some large inedible taxa such as cyanobacteria and dinoflagellates as well as small edible taxa such as cryptomonads have been shown to respond more to excretion than to zooplankton herbivory (Vanni & Layne 1997, Attayde & Hansson 2001). In fact, many studies have shown that nutrient excretion by freshwater fish plays important roles in determining nutrient dynamics and/or the species compositions of primary producers (Lamarra 1975, Andersson et al. 1988, Qin & Threlkeld 1990, Schindler 1992, Schaus et al. 1997, Attayde & Hansson 1999, Schaus & Vanni 2000, Tarvainen et al. 2005, but see Nakashima & Leggett 1980). Likewise, in the present study, excre-

tion by carp may have directly stimulated nutrient dynamics and changed phytoplankton biomass and composition, resulting in a cyanobacteria bloom.

In contrast to earlier studies (Lamarra 1975, Drenner et al. 1998, Parkos et al. 2003), TN but not TP increased in carp enclosures in the present study (Fig. 2). This was probably owing to differences in limited nutrient conditions in the water column. Chumchal & Drenner (2004) experimentally demonstrated that common carp increased TN in mesocosms associated with phosphorus loading but had no effect on TN in mesocosms without phosphorus loading. Our study system was probably at a nitrogen-limited condition because TN:TP (weight ratio) was low, ranging from 2 to 4. Thus, in our experiment, nitrogen excretion by carp resulted in relatively great increase in chl-*a*. Further, PO<sub>4</sub>-P decreased significantly in the carp treatments (Fig. 2). This was probably because of rapid uptake of PO<sub>4</sub>-P through cyanobacteria blooming (see Williams et al. 2002, Figueredo & Giani 2005).

In the carp treatments, responses of some of the limnological parameters differed depending on whether carp could access to the sediments (Fig. 2). For example, SS increased while Secchi depth decreased in the carp – net treatment relative to the carp + net treatment even though chl-*a* concentration was low (Fig. 2). This was likely a result of increased sediment resuspension through bioturbation. Carp have been shown to increase turbidity by enhancing inorganic suspended particles without increasing phytoplankton biomass (Qin & Threlkeld 1990, Breukelaar et al. 1994, Lougheed et al. 1998, Parkos et al. 2003). Breukelaar et al. (1994) also reported that carp densities correlated positively with SS through the mixing of both particulate and dissolved matter in the water column. Driver et al. (2005) showed that large (>2000 g/individual) and small common carp (about 700 g/individual) tended to influence nutrient dynamics and phytoplankton biomass by means of differential mechanisms through bioturbation and excretion, respectively. Similarly, small gizzard shad have been reported to show higher mass-specific excretion rates compared with the equivalent biomass of large gizzard shad (Schaus et al. 1997, Schaus & Vanni 2000). Because the carp used in the present study were small (about 150 g), effects of nutrient excretion were more pronounced than that of bioturbation (see Lamarra 1975, Qin & Threlkeld 1990).

### Submerged macrophytes and filamentous green algae

Carp can negatively affect submerged macrophyte biomass by reducing light availability, enhancing siltation rates, consuming the plant material and/or uprooting (Crivelli 1983, Roberts et al. 1995, Sidorke-wicz et al. 1996, Drenner et al. 1998, Zambrano & Hinojosa 1999, Williams et al. 2002, Parkos et al. 2003). In our experiment, submerged macrophytes were markedly reduced in both the carp – net and carp + net treatments (Fig. 1 A). Earlier studies showed that carp did not consume macrophytes to a significant degree (Crivelli 1983, Roberts et al. 1995, Williams et al. 2002, Parkos et al. 2003). On the other hand, SS increased significantly in the carp – net treatment on day 21, indicated that bioturbation may have contributed at least in part to the disappearance of submerged macrophytes. Because carp reduced macrophyte abundance even when sediment access was prevented, we believe that most powerful mechanism to be excretion; high nutrient loading may have caused cyanobacteria blooming, that in turn limited light availability for submerged macrophytes.

We observed that filamentous green algae increased only in the fishless + net treatment (Fig. 1 B). This may have been an artefact, where the mesh net acting as colonization substrates for the algae. Increase in the biomass of filamentous green algae resulted in high transparency and low chl-*a* concentration (Fig. 2). This was likely a result of filamentous green algae taking up nutrients from the water column at high rates (Planas et al. 1996, Parker & Maberly 2000). The likely reason that filamentous green algae did not increase in the carp + net treatment was because carp directly consumed these algae (Fig. 1 B). Sibbing (1988) documented from gut content analysis that filamentous green algae were one of the major food items of common carp. Further, Drenner et al. (1998) reported from their enclosure experiment that the introduction of common carp was followed by reduction of filamentous green algae.

### Zooplankton and benthic macroinvertebrates

The total zooplankton abundance, mainly dominated (>80%) by rotifers, significantly increased in the two carp treatments (Fig. 3, Table 2). This contradicts from some studies, which showed that common carp had negative or no effects on zooplankton abundance (Qin & Threlkeld 1990, Lougheed et al. 1998). Our result was consistent with other studies (Richardson et al. 1990, Attayde & Hansson 2001, Parkos et al.

2003, Chumchal & Drenner 2004), although the underlying mechanisms were probably different. Richardson et al. (1990) found that juvenile common carp (average standard length = 68.5 mm), by selectively consuming large zooplankton, increased the abundance of small zooplankton such as rotifers and *Bosmina* as a result of reduced competition between zooplankton. Likewise, Parkos et al. (2003) reported that common carp had cascading impacts on zooplankton through reduction of invertebrate predators such as odonates. In the present study, however, both large-bodied zooplankton and macroinvertebrate predators were rare. Attyde & Hansson (2001) hypothesized that nutrient excretion by fish would positively affect zooplankton by indirectly changing the composition and biomass of phytoplankton. Likewise, in our study, modification of the quality and quantity of phytoplankton through carp excretion may have indirectly facilitated zooplankton.

The abundance of the total benthic macroinvertebrates (mainly Oligochaeta) markedly decreased in the carp – net and carp + net treatments (Fig. 4). Earlier studies demonstrated that benthivorous fish directly consume benthic macroinvertebrates (Tatrai et al. 1994, Richardson et al. 1990, Zambrano & Hinojosa 1999). On the other hand, Gido (2003) argued in his experimental study that bioturbation by gizzard shad (*Dorosoma cepedianum*) rather than direct consumption or competition for resources was likely the main mechanism for the decline of Chironomidae. Because carp predation on macroinvertebrates was not evident in our experiment, the reduction of benthic macroinvertebrates was probably owing to the loss of submerged macrophytes (Fig. 1 A), as indicated by Parkos et al. (2003). In fact, Sagova-Mareckova (2002) documented that Oligochaeta were particularly abundant in the vicinity of macrophyte roots. Macrophyte roots release oxygen and thereby change the chemical characteristics of the surrounding sediment (Sorrell & Armstrong 1994, Sagova-Mareckova & Kvet 2002). Such changes in sediment chemistry and generation of exudates may promote bacteria production (Wood & Hayasaka 1981), which serves an important food source for Oligochaeta (McMurtry et al. 1983).

### Carp as ecosystem engineers

Although bioturbation by large carp may have significant consequences for community structure and ecosystem processes (Havens 1991, Loughheed et al. 1998, Zambrano & Hinojosa 1999, Parkos et al. 2003), small carp in the present study increased nutri-

ent concentration and phytoplankton biomass through excretion rather than bioturbation. Dramatic increase in phytoplankton biomass (cyanobacteria bloom) resulted in reduction of submerged macrophytes by indirectly reducing light availability for the aquatic plants. Reduction of submerged macrophytes subsequently led to reduction of benthic macroinvertebrates probably because their microhabitat availability has become limited. These results suggest that excretion by small carp can have a significant consequence for community members in the form of ecosystem engineering.

### Implications for regime shifts

Our experiment demonstrated that carp can increase phytoplankton biomass and reduce submerged macrophytes through a combination of excretion and bioturbation although excretion alone may be sufficient to cause a shift from a clear water state to a turbid state. Likewise, Carlsson et al. (2004) reported that excretion by the golden apple snail (*Pomacea canaliculata*) induced a regime shift by enhancing phytoplankton biomass. Because many studies have shown that submerged macrophytes can decrease turbidity by stabilizing bottom sediments with their roots, provide substrate or refuges for zooplankton and suppress phytoplankton biomass by releasing allelopathic substances (see Scheffer 1998 and the references therein), their disappearance may lead to loss of biodiversity and ecosystem functioning in the entire system. Our study helps to show how a benthivorous fish can initiate a regime shift. Future studies should focus on the effects of other benthivorous fish species because different species can affect ecosystem functioning in differential ways depending on size, foraging modes, densities, nutrient excretion rates/ratios, habitat use and behavioral patterns (Gido 2002, Williams et al. 2002).

In Japan, the common carp is treated as a native fish species so that the fish is being continuously released into rivers, ponds and lakes. We suggest that carp introduction should be carefully scrutinized because such native, non-indigenous fish may cause drastic changes on the structure and functioning of shallow lakes/ponds.

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