

Contrasting impacts of invasive engineers on freshwater ecosystems: an experiment and meta-analysis

Shin-ichiro S. Matsuzaki · Nisikawa Usio ·
Noriko Takamura · Izumi Washitani

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Abstract Invasion by common carp (*Cyprinus carpio*) and red swamp crayfish (*Procambarus clarkii*) in shallow lakes have been followed by stable-state changes from a macrophyte-dominated clear water state to a phytoplankton-dominated turbid water state. Both invasive carp and crayfish are, therefore, possible drivers for catastrophic regime shifts. Despite these two species having been introduced into ecosystems world-wide, their relative significance on regime shifts remains largely unexplored. We compared the ecological impacts of carp and crayfish on submerged macrophytes, water quality, phytoplankton, nutrient dynamics, zooplankton and benthic macroinvertebrates by combining an enclosure experiment and a meta-analysis. The experiment was designed to examine how water quality and biological variables responded to increasing carp or crayfish biomass. We found that even at a low biomass, carp had large and positive impacts on suspended solids, phytoplankton and nutrients and negative impacts on benthic macroinvertebrates. In contrast, crayfish had a strong negative impact on submerged macrophytes. The impacts of crayfish on macrophytes were significantly greater than those of carp. The meta-analysis showed that both carp and crayfish have significant effects

on submerged macrophytes, phytoplankton, nutrient dynamics and benthic macroinvertebrates, while zooplankton are affected by carp but not crayfish. It also indicated that crayfish have significantly greater impacts on macrophytes relative to carp. Overall, the meta-analysis largely supported the results of the experiment. Taken as a whole, our results show that both carp and crayfish have profound effects on community composition and ecosystem processes through combined consequences of bioturbation, excretion, consumption and non-consumptive destruction. However, key variables (e.g. macrophytes) relating to stable-state changes responded differently to increasing carp or crayfish biomass, indicating that they have differential ecosystem impacts.

Keywords Common carp · Density manipulation experiment · Ecosystem engineering · Red swamp crayfish · Regime shifts

Introduction

A wide range of ecosystems, including lakes, coral reefs, oceans, forests and arid lands, can shift abruptly to an alternative stable state (Scheffer et al. 2001). These rapid stable-state changes (i.e. regime shifts) in ecosystems are often caused by abiotic factors, such as climate change, nutrient loading and pollution (Scheffer 1998; Scheffer et al. 2001). However, there is an increasing body of evidence suggesting that invasion by invasive species can also be a causative agent for regime shifts (Carlsson et al. 2004; Suding et al. 2004; Byers et al. 2006). Invasive species can alter ecosystems via a number of pathways, but catastrophic ecological impacts are often modulated by

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S. S. Matsuzaki · I. Washitani
Department of Ecosystem Studies, Graduate School
of Agricultural and Life Sciences, The University of Tokyo,
1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan

S. S. Matsuzaki (✉) · N. Usio · N. Takamura
Research Center for Environmental Risk, National Institute
for Environmental Studies, 16-2 Onogawa, Tsukuba,
Ibaraki 305-8506, Japan
e-mail: matsuzaki.shinichiro@nies.go.jp

ecosystem engineering (Jones et al. 1994; Crooks 2002). For example, the Australasian isopod (*Sphaeroma quoyanum* H. Milne Edwards), which has been introduced into American salt marshes, was found to cut into marsh banks by burrowing, resulting in reduced sediment stability and significant alterations of marshes into mudflats (Talley et al. 2001). Other empirical evidence also suggests that introductions of invasive ecosystem engineers, such as earthworms (e.g. *Lumbricus terrestris* L.), zebra mussel (*Dreissena polymorpha* Pallas), Chinese mitten crab (*Eriocheir sinensis* H. Milne Edwards) and North American beaver (*Castor Canadensis* Kuhl), can trigger comparable stable-state changes (Crooks 2002; Bohlen et al. 2004; Rudnick and Resh 2005; Zhu et al. 2006).

The stable states of shallow lakes comprise a clear water phase characterized by abundant submerged macrophytes and a turbid water phase dominated by phytoplankton (Scheffer et al. 1993). Submerged macrophytes have vital roles in freshwater ecosystems in that they influence water clarity and nutrient dynamics and increase the diversity of the physical habitat (see Scheffer 1998 and the references therein). A sudden change to an alternative stable state has previously been shown to be mediated by high nutrient loading and abundant planktivorous fish (Scheffer et al. 1993; Scheffer et al. 2001). A number of researchers have recently reported that the common carp (*Cyprinus carpio* L.) and red swamp crayfish (*Procambarus clarkii* Girard) may also have system-wide impacts freshwater systems. In North America and Australia, the common carp has caused extensive damage to macrophyte communities and increased the frequency of algal blooming (Cahn 1929; Koehn 2004; Miller and Crowl 2006). Likewise, Rodriguez et al. (2003) observed that about 90% of macrophytes disappeared following the introduction of the red swamp crayfish in Spain, which in turn resulted in a dramatic increase in phytoplankton biomass and nutrient concentrations. Feminella and Resh (1989) have also reported that the red swamp crayfish eliminated submerged macrophytes within a few years of its invasion.

The common carp (hereafter termed carp) and red swamp crayfish (crayfish) are large benthic omnivores that have strong impacts on multiple trophic levels in freshwater communities through predation and ecosystem engineering. Both species are common in freshwater systems in Japan as well as in many parts of the world, and they sometimes show high biomass and production rates (Koehn 2004; Maezono et al. 2005). As ecosystem engineers, the two benthic species can have strong direct or indirect impacts on water quality, nutrient dynamics, community compositions and ecosystem processes through bioturbation by increasing sediment resuspension by way of feeding, walking and burrowing activities (Breukelaar et al. 1994; Angeler et al. 2001; Crooks 2002; Parkos et al. 2003; Geiger et al. 2005).

Both species can also alter nutrient dynamics and increase phytoplankton biomass through excretion (Angeler et al. 2001; Matsuzaki et al. 2007). In addition, carp and crayfish have strong negative effects on submerged macrophytes. However, carp and crayfish are expected to have different impacts on ecosystems due to their differential modes of ecosystem engineering. For example, many experimental studies have indicated that carp can indirectly reduce the biomass of submerged macrophytes by disturbing the sediments and enhancing phytoplankton biomass and, thereby, changing the light availability through shading (Lougheed et al. 1998; Zambrano and Hinojosa 1999; Williams et al. 2002; Parkos et al. 2003; Miller and Crowl 2006; Matsuzaki et al. 2007). On the other hand, crayfish, by utilizing chelipeds, can directly reduce macrophyte biomass through both consumptive and non-consumptive destruction (Rodriguez et al. 2003; Anastacio et al. 2005a, b; Gherardi and Acquistapace 2007).

Although the factors that influence the impacts of ecosystem engineers are poorly understood, the population density of the engineer has been suggested as one of the key attributes impacting on the magnitude of ecosystem engineering (Flecker et al. 1999; Cardinale et al. 2004; Moore et al. 2007). For example, Moore et al. (2007) reported that suspended sediments and nutrients associated with nest-digging activities of Pacific salmon (*Oncorhynchus* spp.) increased linearly with increasing salmon densities, while Flecker et al. (1999) documented that bioturbation effects by detritivorous frog tadpoles (*Rana palmipes* Spix) saturated at 5 m^{-2} (a medium density observed in natural tropical streams). Some experimental studies have shown that the ecological impacts of carp or crayfish can change as a function of density (Crivelli 1983; Lougheed et al. 1998; Williams et al. 2002; Parkos et al. 2003; Anastacio et al. 2005a; Chumchal et al. 2005; Driver et al. 2005; Gherardi and Acquistapace 2007). Because carp and crayfish have differential modes of ecosystem engineering, their density-dependent impacts may differ depending on response variables, leading to differential susceptibility to stable-state changes.

Here, we performed a field enclosure experiment that was designed to compare the magnitude of carp and crayfish engineering in a shallow lake ecosystem and to explore whether the impacts of ecosystem engineering differ in proportion to their biomasses. We tested whether each of the response variables showed either a linear (linear model) or non-linear (non-linear model) relationship with increasing animal biomasses. To assess which engineer species had greater impacts on community structure and ecosystem processes, we compared carp and crayfish impacts at relatively low biomasses, which is the likely situation with their arrival in new habitats at the invasion front. Specifically, we focused on the impacts on

submerged macrophytes in both the experiment and meta-analysis because macrophytes are keystone species in aquatic ecosystems and are considered to be an ecosystem indicator for stable-state changes (Scheffer 1998; Scheffer et al. 2001). In addition, we examined the impacts of carp and crayfish on water quality, phytoplankton biomass, nutrient dynamics, zooplankton and benthic macroinvertebrates because these variables can both affect and be affected by the presence or absence of macrophytes. Based on the results of earlier studies, we made the following predictions: (1) both carp and crayfish would reduce the level of submerged macrophytes and benthic macroinvertebrates (Richardson et al. 1990; Parkos et al. 2003; Anastacio et al. 2005b; Rudnick and Resh 2005; Gherardi and Acquistapace 2007) and increase suspended solids, chlorophyll and nutrients in the water column (Qin and Threlkeld 1990; Angeler et al. 2001; Roozen et al. 2007); (2) carp would have positive impacts on zooplankton (Matsuzaki et al. 2007), while crayfish would not have measurable effects on this taxon. Finally, we assessed the generality of our findings by quantitatively summarizing the impacts of carp and crayfish using a meta-analysis (Osenberg et al. 1997; Gurevitch and Hedges 1999).

Materials and methods

Common carp and red swamp crayfish in Japan

The common carp (*Cyprinus carpio*) has been assessed to be among the world's worst 100 invasive alien species by the International Union for the Conservation of Nature and Natural Resources (ISSG 2000). This species is considered native to Japan, but the species has been to consist of two types: a torpedo-shaped wild type and a deep-bodied domesticated type. A recent mitochondrial DNA analysis revealed that the wild type represents the native Japanese population, while the domesticated type has been introduced from the Eurasian continent, including Germany and China, for aquaculture purposes (Mabuchi et al. 2005). However, it remains uncertain when the non-native domesticated carp arrived in Japan. The distribution of the wild type is now limited, but the domesticated type occurs throughout the Japanese archipelago as a result of accidental or intentional translocations. In our study, we consider the domesticated type to be an alien species.

The red swamp crayfish (*Procambarus clarkii* Girard; hereafter termed crayfish) is native to south central USA and northeastern Mexico (Huner 1988). This species was introduced from New Orleans (USA) to Japan in 1927 as a food for the bullfrog (*Rana catesbeiana* Shaw) and were kept at a commercial frog farm in central Honshu (the main island) (Masumoto 1987). After the frog farm was closed,

crayfish escaped from the farm ponds and have since invaded streams, rice fields and ponds throughout the Japanese archipelago (Masumoto 1987).

In Japan, alien species that cause damage to native biodiversity, human safety and/or agriculture are designated as invasive alien species (IAS) in the IAS Act by the Ministry of the Environment of Japan. Under the IAS Act, the releasing, importing, cultivating, keeping, transporting and/or selling of live IAS are strictly regulated. For IAS, control is mandatory to mitigate their ecological impacts. However, neither common carp nor red swamp crayfish are currently designated as IAS because the carp is considered to be a native species and the crayfish has been considered to be too widely distributed to be controlled successfully.

Study site

Lake Kasumigaura is a shallow eutrophic lake with a surface area of 220 km². Although until about the 1970s the lake had large littoral vegetation areas of emergent, floating-leaved and submerged macrophytes, only remnants of vegetation of emergent or floating-leaved macrophytes now remain following a rapid decline due to eutrophication, concrete bank protection and water regime alterations (Nishihiro et al. 2004). The restoration of lakeshore vegetation using the soil seed bank has recently been initiated and is being carried out in some shoreline ponds of the lake with the aim of recovering macrophyte assemblages. A group of experimental ponds (65 × 45 m each) is located at one of the restoration sites in Kihara, where dredged sediments from Lake Kasumigaura containing seeds from the seed bank have been spread thinly over the bottom of the ponds (Nishihiro et al. 2004). These ponds are connected to the lake by small channels that permit water exchange between the lake and ponds. We performed the experiment using 21 enclosures situated in the central pond to minimize effects from wave action.

Experimental design

The enclosure experiment was started on 5 July 2005, immediately before submerged macrophytes began to germinate, and ended on 2 September 2005. The enclosures (2 × 2 × 1 m height, water depth 0.7–0.8 m) were made of nylon-reinforced polyethylene sheeting, with the top and bottom left open.

The biomasses of carp and crayfish were manipulated at three levels each (low, medium and high biomasses). Enclosures containing neither carp nor crayfish served as controls. Each of the seven treatments was replicated three times, and each treatment was randomly assigned to the 21 enclosures. In each crayfish enclosure, metal plates were embedded 15–20 cm in the sediments to prevent crayfish

from escaping. For carp and crayfish enclosures, large (diameter 10 cm, length 20 cm) (carp) or small (diameter 5 cm diameter, length 10 cm) (crayfish) plastic pipes were added as shelters to reduce cannibalism and intraspecific interactions. The number of plastic pipes in each enclosure was equivalent to the number of animals in each enclosure.

We compared biomass-dependent ecological impacts between carp and crayfish using the natural biomasses of each species rather than adjusting the biomasses of the two (Boyer and Fong 2005). Carp enclosures were stocked with one, two or three individuals of juvenile fish (initial 14.5 ± 0.7 cm, 64.5 ± 3.34 g wet mass, $n = 18$) per enclosure (mean total biomass 16.1, 32.3, 48.4 g wet mass m^{-2} , respectively). In contrast, crayfish enclosures were stocked with 12, 24 or 36 individuals per enclosure (mean total biomass 47.0, 93.9, 140.9 g wet mass m^{-2} , respectively), with small adults [initial orbital carapace length (OCL) 20–30 mm] and large adults (initial OCL 30–45 mm) at a ratio of 2:1. The natural biomass or density ranges of carp and crayfish are 0.88–87.2 g wet mass m^{-2} (Crivelli 1983; Panek 1987) and crayfish 0.2–15 ind. m^{-2} , respectively (Rhodes and Avault 1986; Maezono et al. 2005; Gherardi and Acquistapace 2007). Carp (domesticated carp) were obtained from an aquaculture facility, and crayfish were collected from nearby ponds and marshes. On 28 July (day 0), we added carp and crayfish to enclosures, at a time when there was no seedling emergence of submerged macrophytes in the enclosures. One of the low crayfish biomass enclosures was broken during the experimental period, so this enclosure was omitted from further analysis.

Sampling

Sampling from the enclosures was carried out five times—on days –7 (21 July), 4 (1 August), 10 (7 August), 20 (17 August) and 35 (1 September) during the experimental period. The Day –7 sampling was performed 7 days before the carp and crayfish introductions and represents the initial environmental conditions of the enclosures. We collected vertically integrated water samples (6.0–8.0 L) from each enclosure using a PVC tube sampler (diameter 70 mm, length 1.2 m) to measure suspended solids (SS), inorganic suspended solids (ISS), chlorophyll *a* (Chl-*a*), NH_4-N , PO_4-P , total nitrogen (TN) and total phosphorus (TP) concentrations. From each enclosure, 200–300 mL of the water sample was filtered through two precombusted Whatman GF/F filters (pore size 0.7 μm ; Whatman International, Maidstone, UK) in the laboratory. The first filter samples were dried at 70°C for 2 days, weighed, ashed at 530°C for 2 h and reweighed to calculate SS and ISS. The second filter samples were frozen for later spectrophotometric analyses of Chl-*a* concentrations, as

determined by methanol extraction (Marker et al. 1980). The filtered water samples were subsequently used to analyze NH_4-N and PO_4-P using an automatic analyzer (AACS II; Bran+Luebbe K.K., Norderstedt, Germany) (APHA 1998). Total phosphorus and TN were measured in unfiltered water samples, collected in disposable polycarbonate bottles, by digestion with persulfate in an autoclave (120°C, 45 min.). The concentrations of nitrate (NO_3^-) and nitrite (NO_2^-) in all water samples were below the detection limit.

Zooplankton were collected from each enclosure by filtering a 6.0–7.0 L water sample through a 40- μm mesh net. The filtered zooplankton were preserved in 4% sugar formalin. Zooplankton were identified to the lowest possible taxonomic unit using an optical microscope. Benthic macroinvertebrates were collected using a cylindrical PVC core sampler (50-mm diameter). Six core samples were taken from each enclosure on each sampling date. In the laboratory, the six subsamples were pooled and sieved through a 0.45-mm mesh. The macroinvertebrate and detritus retained on the sieve were 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 from each enclosure. The plant samples were dried at 60°C for 3 days and weighed to determine the total submerged macrophyte biomass. Using the core sampler, we also collected the top 10-mm layer of the sediment from each enclosure to determine percent organic matter (ash-free dry mass per dry mass (AFDM/DM), as measures of the biomasses of benthic algae and detritus. The sediment samples were dried at 60°C for 3 days and ashed at 530°C for 2 h to determine DM and AFDM.

Statistical analyses

For each enclosure, a time-weighted average (WA) was calculated for each response variable (Stephen et al. 2004) as follows:

$$WA = [(1 \times V_1) + (2 \times V_2) + (3 \times V_3) + (4 \times V_4)] / (1 + 2 + 3 + 4)$$

where V is a response variable (except for submerged macrophytes and sediment organic matter) at each of the four sampling dates (1–4) weighted by sequential numbers to give increasing emphasis on each date to account for temporal effects. Weighted average has been widely used in recent studies (e.g. Jakobsen et al. 2003; Hansson et al. 2004; Glaholt and Vanni 2005) and is also suitable for a replicated regression design (Cottingham et al. 2005). We performed model selections using linear and non-linear regression with WA variables to assess the relationships

between carp or crayfish biomasses and response variables. Based on the replicated regression design, we used the mean total biomass of each animal-biomass treatment as independent variables. The same three control replicates were used in the statistical analysis for each taxon, but the controls were not used twice in statistical comparisons between taxa. We compared the three candidate models—the linear model (simple linear regression), the non-linear model (exponential curve) and the null model (intercept only)—using the Akaike information criterion corrected for small sample size (AICc; Burnham and Anderson 2002). The best model has the smallest AICc. If there is a very small difference in AICc between the models (less than two), the models are considered to be equivalent (Burnham and Anderson 2002). Therefore, we rejected the non-linear model only when the difference of AICc values between the non-linear model and linear model was less than two ($AICc_{\text{non-linear}} - AICc_{\text{linear}} < 2$). All analyses were performed using the statistical software R version 2.5.1.

When there was no relationship between carp or crayfish biomass and a response variable, we compared the difference between controls and pooled biomass treatments (i.e., controls vs. low + medium + high biomass treatments) using randomization tests.

Meta-analysis

We conducted a meta-analysis (Osenberg et al. 1997; Gurevitch and Hedges 1999) to systematically synthesize the impacts of carp and crayfish reported in previous studies. We searched for suitable studies using the online database ISI Web of Science and the table of contents of the Proceedings of the International Association of Theoretical and Applied Limnology (SIL). We searched for papers published in 1929 and later, because 1929 is when the first paper on this topic was published by Cahn (1929). To be included in the analysis, a study had to meet the following criteria: (1) examined the effects of carp (only *C. carpio*) or crayfish (only *P. clarkii*) on submerged macrophytes (density or biomass), SS (concentration), Chl-*a* (concentration), nutrients (concentration), benthic invertebrates (density or biomass) and/or zooplankton (density) through manipulative experiments and/or field studies (before–after invasions); (2) the experimental treatments had a reference control with no carp or crayfish. Data were obtained from the primary literature or by direct communications with the authors. When data from multiple sampling dates were available, we only used the data from the final sampling date. Because of differences in methodological approaches, only 24 studies met our criteria (Table 1). To compare ecological effects of carp and crayfish, we calculated the effect size (Δr) after Osenberg et al. (1997) and Downing et al. (1999), as follows:

$$\Delta r = \frac{\ln(X_{t,E}/X_{t,C})}{t}$$

where $X_{t,E}$ and $X_{t,C}$ are the means of the experimental and control groups, respectively, at the end of the experiment, and t is the duration of the experiment (days). The use of Δr is advantageous because it is relatively insensitive to sample size, meets the assumptions of parametric analyses and has direct biological interpretation in the form of the proportional change in the response variable per unit time (Osenberg et al. 1997).

We performed fixed-effect model meta-analyses and calculated 95% bootstrap confidence intervals (CI) with 9999 replicates using the statistical software R version 2.5.1. When 95% CI did not include zero, the mean Δr was considered to significantly differ from zero. We also used a randomization test to compare the Δr of carp and crayfish.

To assess the generality of our findings, we also calculated the effect size Δr of each carp or crayfish biomass treatment from our enclosure experiment. The mean Δr and 95% bootstrap CI were subsequently calculated for each species.

Results

Enclosure experiment

Submerged macrophytes

In the control treatment, submerged macrophytes (*Najas oguraensis* Miki and *Potamogeton pectinatus* L.) germinated from the seed bank, and plants had established by the final sampling day (Fig. 1). Both carp and crayfish had negative impacts on the seedling emergence and establishment of submerged macrophytes; the biomass of submerged macrophytes decreased with increasing animal biomasses. However, the relationships between explanatory and response variables were different between carp and crayfish. In the carp treatment, the linear model was the best model. In contrast, in the crayfish treatment, the non-linear model showed a markedly better fit relative to the linear model.

Water quality, phytoplankton and nutrient dynamics

Suspended solids, ISS and Chl-*a* increased significantly with increasing animal biomass in both the carp and crayfish treatments (Fig. 2). For these variables, the non-linear model fit better than the linear model in the carp treatments, while in the crayfish treatments, the linear model fit better than the non-linear model.

Table 1 Published studies that examined the impact of carp or crayfish. Twenty-four studies were used in the meta-analysis

Species	Density/biomass	Effect on	References
<i>Cyprinus carpio</i>	kg ha ⁻¹		
	<17.8 ind. m ⁻² >	Chironomidae	Batzer (1998) ^a
	300, 500	SS	Breukelaar et al. (1994) ^a
	670	Chl- <i>a</i> , TN, TP, Rotifers, Copepods	Chumchal and Drenner (2004) ^a
	330, 570, 650	Chl- <i>a</i> , TN, TP	Driver et al. (2005) ^a
	No data	Macrophytes	Evelsizer and Turner (2006) ^a
	520	Chl- <i>a</i>	Khan et al. (2003) ^a
	162, 365, 1,250	Chl- <i>a</i> , TP	Lamarra (1975) ^a
	369	Macrophyte, SS, Chl- <i>a</i> , TN, TP, NH ₄ -N, PO ₄ -P, Oligochaeta, Rotifers	Matsuzaki et al. (2007) ^a
	163	Macrophytes, Chironomidae, Oligochaeta	Miller and Crowl (2006) ^a
	174, 476	SS, Chl- <i>a</i> , TP, Chironomidae, Oligochaeta, Cladocerans, Copepods	Parkos et al. (2003) ^a
	<1.3 inds. m ⁻² >	PO ₄ -P, Cladocerans, Rotifers, Copepods	Qin and Threlkeld 1990 ^a
	18.2	Chironomidae, Rotifers, Copepods	Richardson et al. (1990) ^a
	2,948	SS, Chl- <i>a</i> , TN, TP, NH ₄ -N, Cladocerans, Rotifers	Roopen et al. (2007) ^a
	163, 210	Macrophytes	Sidorkewicz et al. (1998) ^a
	200, 700	Macrophytes, Chironomidae, Oligochaeta	Williams et al. (2002) ^a
	200, 700	TP	Williams and Moss, (2003) ^a
<i>Procambarus clarkii</i>	Individuals m ⁻²		
	0.8, 4.3	Rice	Anastacio et al. (2005a) ^a
	4.8	Rice	Anastacio et al. (2005b) ^a
	3.8	SS, Chl- <i>a</i> , TN, TP, NH ₄ -N, PO ₄ -P	Angeler et al. (2001) ^a
	4.0, 8.0	Macrophytes	Gherardi and Acquistapace (2007) ^a
	6.0, 13.0	Macrophytes, Chironomidae	Ilheu et al. 2002 ^a
	1.1	Macrophytes	Maezono et al. (2005) ^a
	2.0	Macrophytes, Chl- <i>a</i> , TP	Rodriguez et al. (2003) ^{a,b}
5.0	Macrophytes, Oligochaeta	Rudnick and Resh (2005) ^{a,b}	

SS, suspended solids; Chl-*a* chlorophyll *a*; TN, total nitrogen; TP, total phosphorus

^a Experimental studies using enclosures, mesocosms or experimental ponds

^b Field studies (before–after invasions)

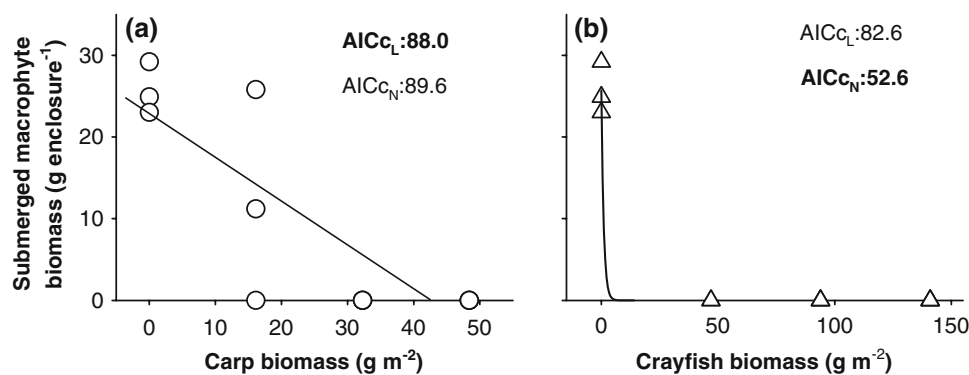
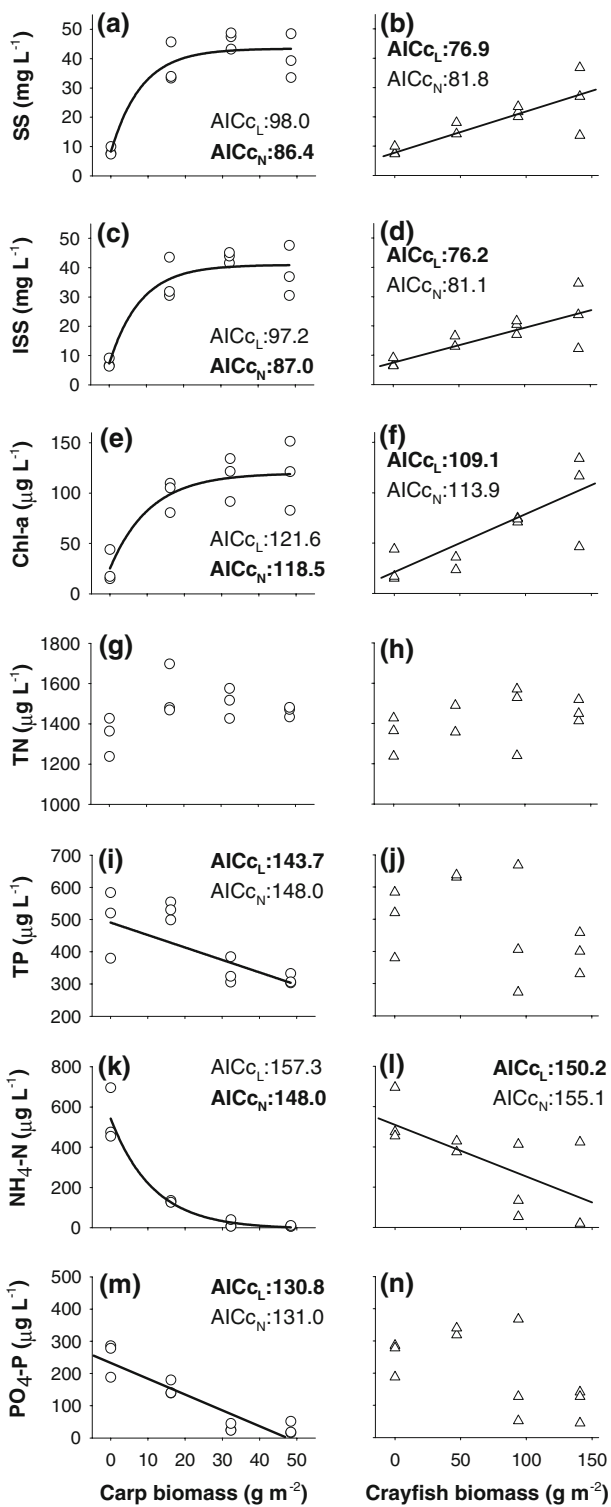


Fig. 1 Relationships between total submerged macrophyte biomass (on the final sampling day, gram dry weight per 4-m³ enclosure) and carp (*Cyprinus carpio*) (a) or crayfish (b) (*Procambarus clarkii*) biomass (grams wet weight per square meter). The Akaike

information criterion corrected for small sample size (*AICc*) of the linear (*L*) and non-linear (*N*) models are shown. *Lines* or *curves* represent the best fit regression for the best model, which is the model with the smallest *AICc* (indicated in **bold**)



Carp reduced the concentrations of TP, NH₄-N and PO₄-P, but the relationships between carp biomasses and the response variables varied (Fig. 2). The linear models best predicted TP and PO₄-P, while for NH₄-N, the non-linear model was the best model. Neither the linear nor non-linear model explained the relationship between carp

Fig. 2 Relationships between seven characteristics of water chemistry and carp (*left panels*) or crayfish (*right panels*) biomass. Data represent the time-weighted averages from each treatment. The AICc of the linear (*L*) and non-linear (*N*) models are shown. *Lines or curves* represent the best fit regression for the best model, which is the model with the smallest AICc (indicated in **bold**). *Graphs without AICc values* indicate that the neither linear nor non-linear model were markedly different from the null model. *SS* Suspended solids, *ISS* inorganic suspended solids, *Chl-a* chlorophyll *a*, *TN* total nitrogen, *TP* total phosphorus

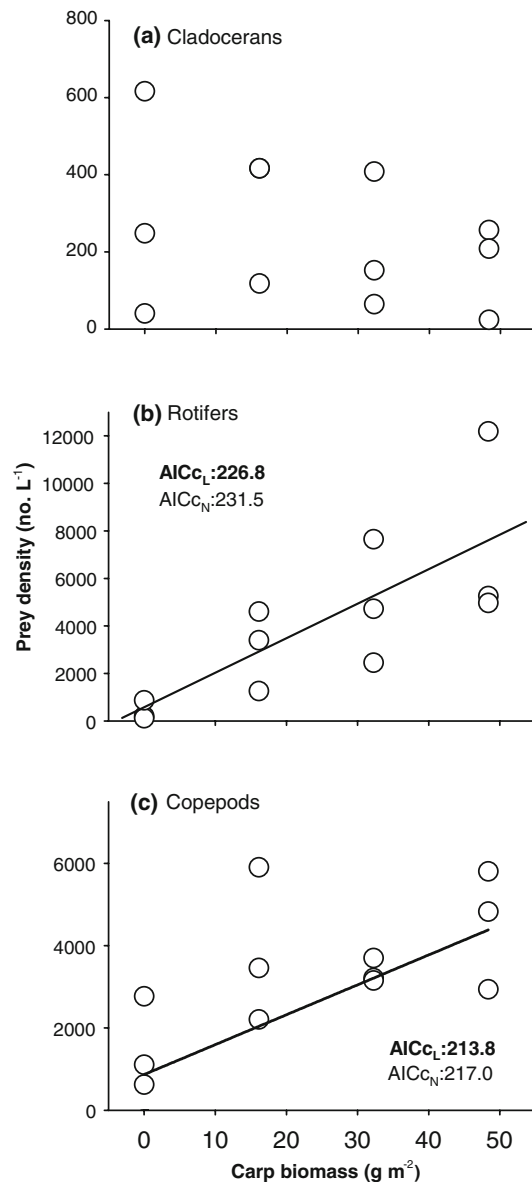


Fig. 3 Relationships between prey density and carp biomass for cladocerans (**a**), rotifers (**b**) and copepods (**c**). Data represent the time-weighted averages from the experimental treatments. There were no significant relationships between crayfish biomass and zooplankton taxa (data not shown). See Fig. 1 for the explanation of AICc

biomass and TN (Fig. 2). When all carp biomass treatments were pooled, TN concentrations were significantly higher in the carp treatments than in the controls (randomization test $P = 0.015$). On the other hand, crayfish influenced $\text{NH}_4\text{-N}$ only, with the concentration lower in the crayfish treatments than in the controls (linear model). Other response variables showed no clear relationships with crayfish biomass (i.e. the null model showed the best fit).

Zooplankton and benthic macroinvertebrates

Carp but not crayfish had significant impacts on zooplankton (Fig. 3). Rotifers (mainly *Keratella* spp. and *Brachionus* spp.) and copepods (mainly cyclopoid and nauplii) were significantly more numerous with increasing carp biomass, and the linear model showed a better fit compared with the exponential model. Neither the linear

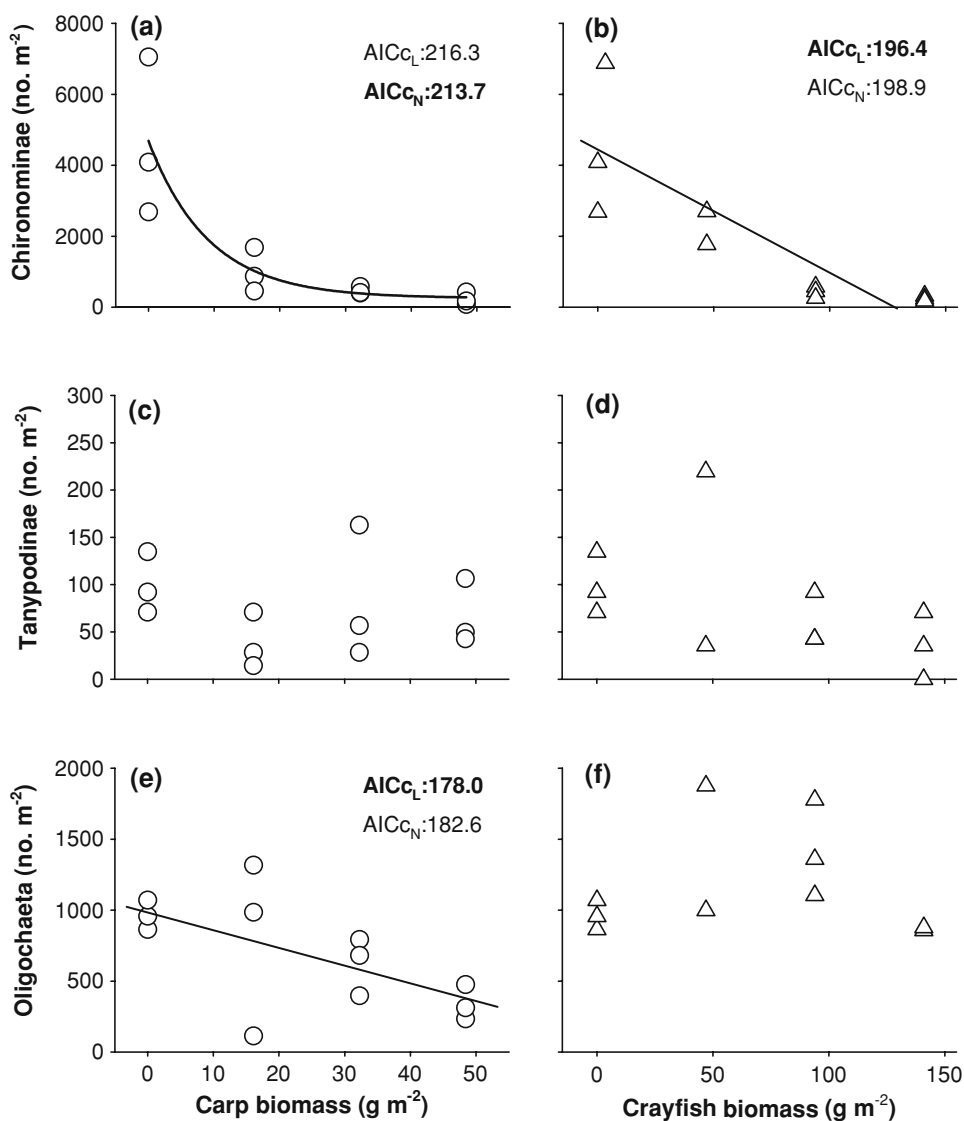
nor the non-linear model explained the relationship between carp biomass and cladocerans.

Carp and crayfish significantly influenced benthic macroinvertebrates (Fig. 4). Both carp and crayfish reduced Chironominae (mainly *Chironomus plumosus* L.), but biomass-dependent relationships were different between the two species. In the carp treatment, the non-linear model showed the best fit. In the crayfish treatment, however, the linear model was the best. Oligochaeta showed a significantly negative linear relationship with carp biomass but not with crayfish. Neither carp nor crayfish significantly affected Tanypodinae.

Sediment organic matter

Neither the linear nor the non-linear model explained the relationship between percentage sediment organic matter (AFDM/DM) and carp or crayfish biomass. When the three

Fig. 4 Relationships between three benthic macroinvertebrates and carp (left panels) or crayfish (right panels) biomass: **a, b** Chironominae, **c, d** Tanypodinae, **e, f** Oligochaeta. Data represent the time-weighted averages from each treatment. See Fig. 1 for the explanation of AICc



carp treatments were pooled, the percentage of sediment organic sediment matter in the carp treatments was significantly higher than that in controls (controls: median 3.3, interquartile range 1.9–3.4; carp treatments: median 5.0, interquartile range 4.7–6.7) (randomization test $P = 0.035$).

Meta-analysis

Carp had significant negative effects on submerged macrophytes, $\text{NH}_4\text{-N}$ and Chironomidae, and significant positive effects on Chl-*a*, SS, TP, rotifers and copepods (Fig. 5). The 95% CI of the carp effect on Oligochaeta included zero because one study (Miller and Crowl 2006) showed a positive impact of carp on the biomass of this taxon. When this study was omitted, significant negative carp impacts were detected for Oligochaeta ($\Delta r = -0.038$, 95% CI = -0.075 , -0.011). Crayfish had significant negative impacts on submerged macrophytes (Fig. 5), and significant positive effects on the concentrations of Chl-*a* and TP.

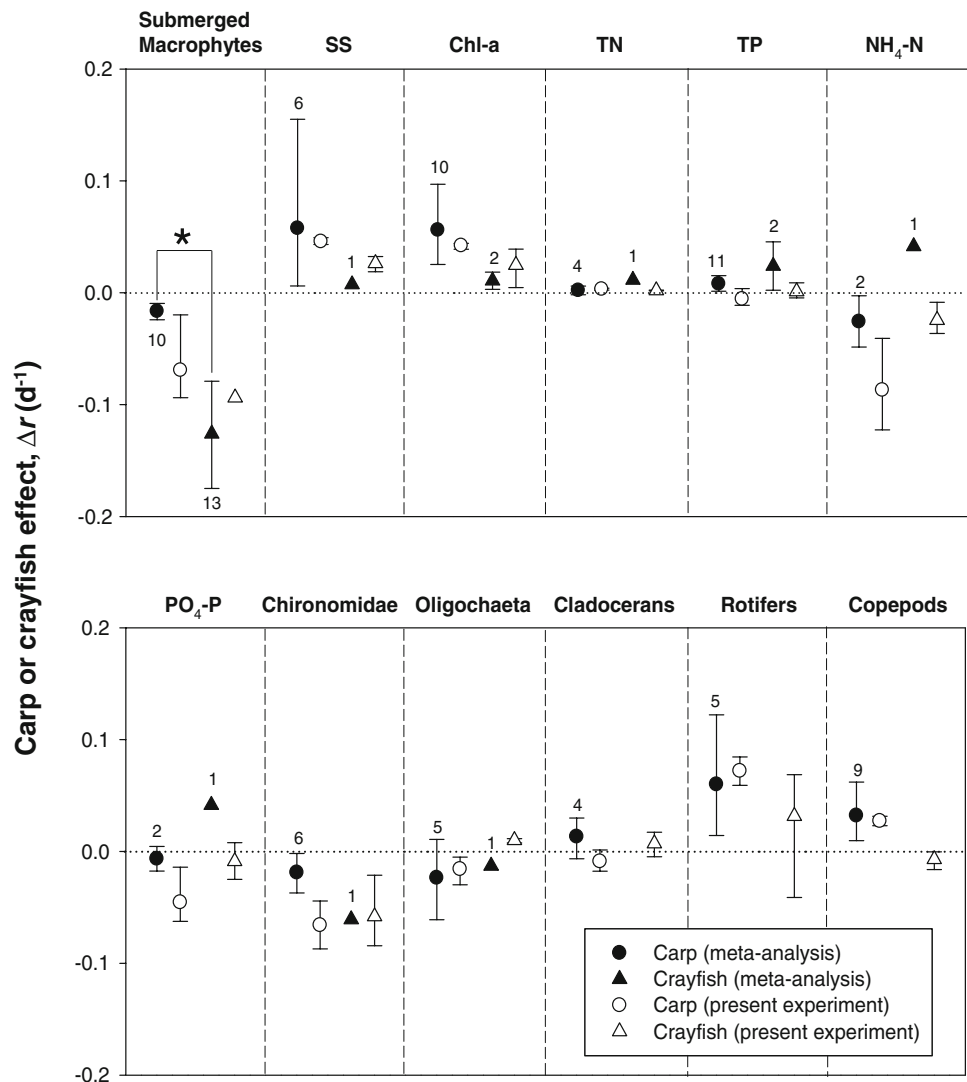
When the effect size of carp and crayfish was compared, crayfish had a significantly greater negative impact on submerged macrophytes than carp (randomization test $P = 0.0013$).

In the enclosure experiment, carp had significant negative effects on submerged macrophytes, $\text{NH}_4\text{-N}$, $\text{PO}_4\text{-P}$, Chironomidae and Oligochaeta, and significant positive effects on Chl-*a*, SS, TN, rotifers and copepods (Fig. 5). In contrast, crayfish had significant negative effects on submerged macrophytes, $\text{NH}_4\text{-N}$ and Chironomidae and significant positive effects on Chl-*a*, SS, TN and Oligochaeta (Fig. 5).

Discussion

The results from our field experiment and meta-analysis suggest that carp and crayfish, as invasive ecosystem engineers, can have profound effects on water quality,

Fig. 5 Results of a meta-analysis (solid symbols) and this experiment (open symbols) showing the mean the effect size (Δr) [$\pm 95\%$ bootstrap confidence interval (CI)] of carp (circles) and crayfish (triangles). Positive and negative values indicate a significant positive and negative effect on the response variables, respectively. The 95% bootstrap CIs that do not include zero are considered to be significant positive or negative impacts. Numbers indicate the number of experiments or studies used in the meta-analysis. An asterisk indicates a significant difference in Δr between carp and crayfish from a randomization test ($P < 0.05$). Note that no published studies have investigated the impacts of *P. clarkii* on zooplankton except for the present experiment. See Fig. 2 for the explanation of the abbreviations



nutrient dynamics and community structure in relation to their biomasses. Most of the observed relationships between the response variables and carp or crayfish biomasses were non-linear (see Figs. 1, 2, 3, 4), indicating that engineering effects saturated at relatively low animal biomasses. We discuss the potential mechanisms for the ecosystem effects of carp and crayfish on community members and ecosystem processes in the following sections.

Effects on submerged macrophytes

As predicted, both carp and crayfish suppressed seedling emergence from seed banks (Fig. 1). Although crayfish are known to inhibit seedling establishment of aquatic plants (Nyström and Strand 1996; Anastacio et al. 2005b), this is the first study to demonstrate a deleterious effect of carp on the regeneration of submerged macrophytes. We found a non-linear relationship between crayfish biomass and submerged macrophyte biomass, suggesting that crayfish can have large impacts on the biomass of submerged macrophytes even at low biomass. These results are consistent with those of earlier studies (Lodge and Lorman 1987; Chambers et al. 1990; Gherardi and Acquistapace 2007). Our meta-analysis supports these experimental results. Both carp and crayfish had negative effects on submerged macrophytes, with the impacts of crayfish being much greater than those of carp (Fig. 5).

A number of researchers have reported that crayfish reduce submerged macrophytes through both consumptive and non-consumptive destruction (i.e. ecosystem engineering) (Lodge and Lorman 1987; Nyström and Strand 1996; Nyström et al. 2001; Gherardi and Acquistapace 2007). Crayfish destroy much more plant tissue than they eat, using chelipads in the established stage of macrophytes, while direct consumption is the main mechanism for macrophyte reduction in the seedling stage (Nyström and Strand 1996). However, Anastacio et al. (2005a, b) showed that even in the seedling stage, crayfish reduced seedling biomass through destruction, including cutting and uprooting. Therefore, in our experiment, the loss of submerged macrophytes in the crayfish treatments was likely due to both consumptive and non-consumptive effects, although the relative importance of these effects remains unclear.

The relationship between carp biomass and submerged macrophyte biomass was linear. Many studies have shown that carp can directly reduce the biomass of submerged macrophyte through herbivory (Sidorkewicz et al. 1996) and uprooting (Crivelli 1983; Sidorkewicz et al. 1996) and indirectly reduce it through bioturbation and excretion (Lougheed et al. 1998; Williams et al. 2002; Parkos et al. 2003; Matsuzaki et al. 2007). In our study, carp may have influenced the water quality and phytoplankton through

bioturbation and/or excretion (Fig. 2), so increased concentrations of SS, ISS and Chl-*a* in the water column may have severely limited the light availability for macrophytes. However, carp also consume the seedlings of macrophytes (Sidorkewicz et al. 1996), so direct consumption can also be another mechanism for the disappearance of submerged macrophytes.

Effects on water quality, phytoplankton and nutrient dynamics

Results from the experiment and meta-analysis are consistent with the prediction that both carp and crayfish increase the concentrations of SS and Chl-*a* (Fig. 2, 5). Bioturbation by carp and crayfish has probably changed water quality and increased phytoplankton biomass because high ISS concentrations in the water column are indicators of sediment resuspension (Parkos et al. 2003; Roozen et al. 2007). It is known that both carp and crayfish can increase sediment resuspension and release nutrients from the sediments to the water column through bioturbation (i.e. ecosystem engineering) (Breukelaar et al. 1994; Angeler et al. 2001; Parkos et al. 2003; Roozen et al. 2007). In contrast to these studies and our prediction, however, carp reduced TP, NH₄-N and PO₄-P concentrations but enhanced TN concentration, and crayfish reduced the NH₄-N concentration (Fig. 2). The reduction of dissolved nutrients, specifically NH₄-N, may have been due to their rapid uptake by phytoplankton, while the increase in TN concentration may have been a consequence of increased phytoplankton biomass because of the nitrogen-limited condition in the study site (Matsuzaki et al. 2007). However, the reduction in TP concentration was likely a result of high nutrient uptake and the storage of phosphorus by periphyton on the sediments (McCormick et al. 2001), as supported by the fact that percentage sediment organic matter increased in the presence of carp. Persson and Svensson (2006a) also reported that benthivorous fish, such as carp, can increase periphyton biomass on the sediments.

In addition, carp likely modified the water quality and increased phytoplankton biomass through excretion because benthivorous fish also feed on benthic organic matter and release a portion of the consumed nutrients via excretion (Schaus and Vanni 2000). In fact, previous studies have demonstrated that carp can influence water quality and phytoplankton biomass even when sediment access was restricted, indicating excretion was the main mechanism (Qin and Threlkeld 1990; Matsuzaki et al. 2007). Furthermore, Driver et al. (2005) demonstrated that small carp with high mass-specific excretion rates tended to influence turbidity and phytoplankton biomass through excretion rather than bioturbation. Crayfish can also influence the availability of nutrients for phytoplankton via

excretion (Evans-White and Lamberti 2005), but their mass-specific excretion rates have been shown to be much lower than those of fish or zooplankton (Kristiansen and Hessen 1992). In our experiment, crayfish had a weak effect on phytoplankton, supporting a weak influence through excretion.

Although there was no significant difference between carp and crayfish in terms of their impacts on SS and Chl-*a* in the meta-analysis, our experiment showed that carp had a greater impact on SS, ISS and Chl-*a* than crayfish. The concentrations of SS, ISS and Chl-*a* increased non-linearly with increasing carp biomass, while the relationship was linear with crayfish biomass. Parkyn et al. (1997) also showed that the removal rate of fine sediments on the gravel substrate by New Zealand crayfish (*Paranephrops planifrons* White) increased linearly with increasing crayfish densities. Earlier studies demonstrated that the concentrations of SS, ISS and/or Chl-*a* increased linearly with increasing carp densities (Breukelaar et al. 1994; Loughheed et al. 1998; Parkos et al. 2003; Chumchal et al. 2005), but these results are inconsistent with those from our experimental study. The differences in the biomass-dependent effects of carp and crayfish on SS, ISS and Chl-*a* may be explained by differential modes of bioturbation between the two species. Benthivorous fish, such as carp, stir up the sediments and increase sediment resuspension when they forage (Breukelaar et al. 1994). In contrast, crayfish disturb the sediments and enhance sediment transport through walking, burrowing and feeding activities (Angeler et al. 2001). Persson and Svensson (2006a) demonstrated that there was no significant difference between the effects of bream (*Abramis brema* L.) and tench (*Tinca tinca* L.) on biogeochemical processes because the two fish species showed similar bioturbation modes. However, Persson and Svensson (2006b) demonstrated that the effects of bream on water quality and benthic organisms were different from those of ruffe (*Gymnocephalus cernuus* L.) because bream forages deeper into the sediment while ruffe searches benthic macroinvertebrates near the sediment surface. In our study, carp reduced both Chironominae and Oligochaeta biomasses, while crayfish reduced Chironominae biomass only (Fig. 4). Because Oligochaeta inhabit deeper in the sediments relative to Chironomidae (James et al. 1998), the impacts of the foraging activities of carp may have been greater than those of the bioturbation activities of crayfish. Indeed, carp influenced on water quality through bioturbation even at low biomass, but the magnitude of crayfish bioturbation was proportional to crayfish biomass.

Effects on zooplankton and benthic macroinvertebrates

As expected, both the experiment and meta-analysis showed that carp enhanced the densities of rotifers and

copepods proportional to their biomass (Figs. 3, 5). Because carp had little impact on cladocerans, selective feeding (Richardson et al. 1990) was not evident in our experiment. Instead, modifications of the quality and/or quantity of phytoplankton through engineering activities (bioturbation and excretion) may have indirectly facilitated zooplankton. Attayde and Hansson (2001) hypothesized that nutrient excretion by fish can positively affect zooplankton by indirectly changing the composition and biomass of phytoplankton. In contrast, there was no evidence that crayfish influenced any of the zooplankton taxa. However, Dorn and Wojdak (2004) demonstrated that crayfish (*Orconectes vivilis* Hagen) had positive effects on zooplankton biomass by indirectly changing phytoplankton composition.

Our experiment and meta-analysis support the prediction that both carp and crayfish have negative impacts on benthic macroinvertebrates, but the effects were different between Chironominae and Oligochaeta (Figs. 4, 5). In our experiments, carp reduced Oligochaeta density. However, the negative impact of crayfish on Oligochaeta, as shown in the meta-analysis, was not evident in the enclosure experiment. Carp and crayfish are known to prey on benthic macroinvertebrates (Richardson et al. 1990; Parkos et al. 2003; Geiger et al. 2005), so direct predation may be a major mechanism for the reduction of benthic macroinvertebrates in the respective treatments. Although Oligochaeta inhabit deep in the sediments and can therefore avoid crayfish predation (Parkyn et al. 1997), carp can nevertheless prey on these macroinvertebrates. In addition, the benthivorous fish Gizzard shad (*Dorosoma cepedianum* Lesueur) has been reported to reduce chironomid biomass through bioturbation rather than predation (Gido 2003). Thus, bioturbation by carp may have also contributed to the reduction of benthic macroinvertebrates.

Invasive ecosystem engineers as potential drivers for stable-state changes

Invasive ecosystem engineers not only modify or destroy the habitats of other species, but they also alter the flow of nutrients, physical resources or energy, and thereby change the character of the invaded systems (Crooks 2002; Carlsson et al. 2004; Byers et al. 2006). For example, Carlsson et al. (2004) reported that the introduced golden apple snail (*Pomacea canaliculata* Lamarck) released nutrients through grazing activities and increased phytoplankton biomass, consequently inducing a shift from a clear water phase to a turbid water phase in natural wetlands in Laos. These researchers also showed that such regime shifts can occur at a relatively low snail density. Likewise, in our experiments, carp and crayfish reduced the biomass of submerged macrophyte and increased

phytoplankton biomass at relatively low animal biomasses, although the mechanisms were probably different. Both the experiment and meta-analysis indicated that crayfish could be much stronger drivers for stable-state changes than carp because of their strong direct impacts on submerged macrophytes. Thus, when an order of prioritization is necessary, crayfish control should be prioritized to prevent their strong direct impacts on submerged macrophytes, as documented in this and previous studies. However, extrapolation of these results to the field situation requires caution because stable-state changes are usually discussed in the context of large spatio-temporal scales (Scheffer 1998). Nevertheless, the approach used in our study—the combination of a field enclosure experiment and a meta-analysis—may have sound potential for exploring ecological interactions and inferring mechanistic backgrounds.

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