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# Effects of Common Carp on Aquatic Ecosystems 80 Years after "Carp as a Dominant": Ecological Insights for Fisheries Management

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*The introduction of fishes into habitats outside their native range may result in dramatic ecosystem alterations. Circumpolar introductions of common carp Cyprinus carpio commonly induce perturbations to shallow lakes, inducing a phase shift from clear to turbid water. Cahn (1929) first reported a phase shift following common carp introduction. Since then, ecologists have sought to understand ecosystem responses to common carp perturbation. We present a synthesis on how common carp can affect aquatic ecosystems through a middle-out framework due to their capability to alter bottom-up and top-down processes. Common carp affect bottom-up processes by modifying nutrient and turbidity concentrations and phytoplankton abundance and diversity through benthic foraging, whereas zooplankton and benthic invertebrates can be affected by top-down processes through predation and reduced foraging efficiency. Common carp also reduce aquatic macrophytes that may switch lakes from the clear to turbid water equilibrium. Restoration efforts seeking to return ecosystems to the clear water state have attempted to remove common carp populations through numerous methods with varying success. Restoration efforts should focus on entire ecosystems (humans, habitats, and biota) in conjunction with common carp reductions to achieve the greatest success at minimizing the effects of common carp and to return lakes to the clear water state.*

**Keywords** alternative equilibrium, ecosystem effects, ecosystem engineer, invasive species, middle-out, bottom-up

## INTRODUCTION

I remember ... fine catches of large-mouth bass, great northern pike, and delightful pan fish of various species.. . . Carp appeared in Pike lake and reproduced well. . . . The waters of the pond became muddy, turbid; the vegetation began to disappear. Fishing fell off, slowly at first, and finally died completely. . . . When the first sein came in I had visions of seeing some beautiful fish, but the first draw disillusioned me: there was nothing but carp. The second draw was the same; also the third. (Cahn, 1929)

Common carp *Cyprinus carpio* is a native of Europe and Asia but has been introduced worldwide to every continent, except for Antarctica, for angling and commercial purposes (Edwards and Twomey, 1982; Panek, 1987) with global harvest rates for human consumption exceeding 181,000 metric

tons (Banarescu and Coad, 1991). In Europe and Asia, common carp are highly prized and managed intensively as a sport fish for recreational and food purposes (O'Grady and Spillett, 1985; Wedeking et al., 2001; Arlinghaus and Mehner, 2003) with highly specialized recreational angling techniques (Arlinghaus and Mehner, 2003; Arlinghaus and Niesar, 2005). In North America and Australia, common carp often dominate fish communities, are broadly regarded as a nuisance species, incur vast economic costs, and management efforts are directed toward control and removal (Shields, 1958; Wydoski and Wiley, 1999; Pimentel et al., 2000; Tapia and Zambrano, 2003; Koehn, 2004; Lougheed et al., 2004). As a result of stocking and dispersal, common carp now occur in 95% of water bodies in Mexico (Hinojosa-Garro and Zambrano, 2004) and represent 90% of fish biomass in southeastern Australia (Harris and Gehrke, 1997). Although common carp are abundant in aquatic ecosystems worldwide, predictive models suggest habitat is suitable for common carp to spread further throughout North and South America and Asia (Zambrano et al., 2006).

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Common carp thrive in large, shallow, highly conductive lakes (Egertson and Downing, 2004); yet, common carp are generalists, allowing them to live in a wide range of abiotic (i.e., temperature, dissolved oxygen, pH, turbidity) (Crivelli, 1981; Edwards and Twomey, 1982) and biotic conditions (i.e., food resources (detritus, macroinvertebrates, zooplankton, plant material, etc.)) (Michel and Oberdorff, 1995; Zambrano and Hinojosa, 1999; Garcia-Berthou, 2001; Britton et al., 2007). Common carp mature early, between 2 and 3 years of age (Panek, 1987; Brumley, 1996), are highly fecund (up to 2,000,000 eggs per female) (Swee and McCrimmon, 1966), and are fractional spawners (i.e., multiple protracted spawning events) (Swee and McCrimmon, 1966; Banarescu and Coad, 1991; Smith and Walker, 2004). Common carp also experience rapid growth (Maitland and Campbell, 1992; Vilizzi and Walker, 1999; Phelps et al., 2008b), on average reaching 163 mm by age 1, 279 mm by age 2, and 366 mm by age 3 in North America (Jackson et al., 2008). The combination of early maturation, rapid growth, and ecological plasticity allow common carp populations to expand rapidly and attain extremely high biomass (113-3,144 kg · ha$^{-1}$) (Panek, 1987; Harris and Gehrke, 1997; Barton et al., 2000; Britton et al., 2007).

Since Cahn's (1929) observations, an extensive body of literature has been devoted to elucidating common carp effects in aquatic ecosystems. We conducted a literature survey for ecosystem effects of common carp using the keywords common carp, ecosystem, nutrients, turbidity, macrophytes, phytoplankton, invertebrates, and zooplankton. We also searched for literature that reported attempts to manage common carp populations or their affects on aquatic ecosystems using the keywords removal, restoration, prevention, reclamation, biomanipulation, control, trap, and management. Both searches were conducted using two online databases, Web of Science and Fish and Fisheries Worldwide. Additional references were obtained searching though Transactions of the American Fisheries Society, North American Journal of Fisheries Management, and common carp bibliographies found during open online searches (e.g., FishBase). Based on these searches, we identified 37 controlled studies that evaluated the effects of common carp on at least one of our key words (Table 1). Using this database, we calculated the percentage of studies that found an increase, decrease, or no effect of common carp on nutrients, turbidity, chlorophylla, phytoplankton, small-bodied and large-bodied zooplankton, macrophytes, benthic invertebrates, and fishes. Occasionally, both increases and decreases were observed as effects on one of the variables within the same study; hence, the effects of common carp on some variables total more than 100%. We also identified 23 studies that attempted to control or reduce common carp populations or effects (Table 2). Using this literature base, we summarize what is understood about this long-established invasive species and how they may alter aquatic ecosystems through middle-out processes.

As a preface, we describe alternative equilibrium theory of shallow lakes and depict how common carp may function as ecosystem engineers (Jones et al., 1994), driving the shift in equilibrium from clear to turbid water. Other omnivorous fish have been previously described to regulate ecosystems through middle-out processes due to their ability to avoid predation, achieve high biomass, reduce invertebrate abundance, and increase nutrient availability (e.g., Stein et al., 1995). We proceed by illustrating how common carp fit into a middle-out framework based on their ability to dominate fish assemblages in shallow lakes and regulate food webs from the bottom-up by mobilizing nutrients and top-down by reducing invertebrate abundance. We conclude by discussing how ecosystem variability may influence the effect of common carp on aquatic ecosystems, how intersystem variability should be considered and incorporated into management efforts to improve shallow lake ecosystems, review past management efforts to control common carp, common carp population ecology, and how shallow lake ecosystems respond to common carp removal.

## ALTERNATIVE EQUILIBRIUM THEORY

Shallow lake ecosystems commonly exist in either one of two alternative equilibria, clear or turbid water (Scheffer, 1990, 1998; Scheffer et al., 1993). The clear water state is characterized by low water column nutrients and phytoplankton biomass, abundant aquatic macrophyte growth, and a diverse aquatic biota, whereas the turbid water state is characterized by the opposing conditions (Scheffer et al., 1993; Ibelings et al., 2007). Many environmental characteristics and ecological processes (i.e., external and internal nutrient loading, food web structure, and wind exposure) are responsible for the persistence or transformation between states in shallow lake ecosystems, but the relationship between aquatic macrophytes and turbidity is of primary importance (Scheffer et al., 1993). Aquatic macrophytes are vital because they stabilize sediment, reduce wind-driven sediment resuspension, and compete with phytoplankton for nutrients. Both clear and turbid water stable states are resistant to change, and, at either equilibrium, a large perturbation is needed to shift the system to the alternative state (Scheffer et al., 1993). Fishes can serve important roles in dictating the stable state of shallow lake ecosystems. Lakes dominated by planktivorous fishes tend to be in the turbid water state due to predation on zooplankton, primarily *Daphnia* spp. which release phytoplankton from top-down control (Carpenter et al., 1985; Scheffer et al., 1993). Lakes dominated by piscivorous fishes tend to be in the clear water state due to their ability to regulate planktivorous fishes, releasing zooplankton from predation, which in turn control phytoplankton (Carpenter et al., 1985; Scheffer et al., 1993).

### Bottom-Up Effects

Bottom-up processes affect aquatic ecosystems by regulating nutrient availability to higher trophic levels (McQueen et al., 1986). Fishes can directly and indirectly affect nutrient cycling through multiple pathways (Carpenter et al., 1992; Vanni 1996). Common carp link benthic and pelagic food webs through

**Table 1** Citation, location, experimental conditions, and common carp population characteristics from literature evaluating the effects of common carp on aquatic ecosystems

| Citation | Location | Surface area (m$^2$) | Depth (m) | Substrate | Duration (days) | Carp length (cm) | Carp biomass (kg · ha$^1$) |
|---|---|---|---|---|---|---|---|
| Angeler et al., 2002 | Spain | 2 | 2 | NA | 42 | 27 | 5,500–6,500 |
| Chumchal and Drenner, 2004 | Texas, USA | 5 | 2 | Sand | 30 | NA | 670 |
| Chumchal et al., 2005 | Texas, USA | 3,600 | 1 | Clay, loam | 28 | NA | 0–465 |
| Chumchal et al., 2005 | Literature survey | Variable | Variable | Variable | Variable | Variable | Variable |
| Cline et al., 1994 | Mississippi, USA | 3 | <1 | Sand, clay | 12 | 31 | 2,270 |
| Crivelli, 1983 | France | 64 | <1 | Mud, clay | 71 | NA | 0–725 |
| Drenner et al., 1997 | Texas, USA | 3,800 | NA | NA | 1460 | Fingerling | 566 |
| Drenner et al., 1998 | Texas, USA | 1,500–6,400 | <1 | NA | 520 | Fingerling | 7 |
| Egertson and Downing, 2004 | Iowa, USA | Variable | Variable | Variable | NA | Variable | Variable |
| Evelsizer and Turner, 2006 | Canada | 9 | <1 | NA | 80 | NA | NA |
| Forester and Lawrence, 1978 | Alabama, USA | 1,000 | NA | NA | 570 | NA | 230 |
| Haines, 1973 | Michigan, USA | 25 | 1 | Gravel | 450 | NA | 70 |
| Hinojosa-Garro and Zambrano, 2004 | Mexico | 500 | 1 | NA | NA | 5 | 5–6 |
| Khan et al. 2003 | Australia | 8 | 3 | NA | 30 | 14 | 520 |
| King and Hunt, 1967 | Michigan, USA | 49 | <1 | Organic, marl, loam | 60 | NA | 448–560 |
| King et al., 1997 | Australia | 2,800–8,000 | 4 | Silt, clay, loam | 180 | 31-70 | 100–1,180 |
| Lougheed et al., 1998 | Canada | 50 | <1 | Sand, silt | 15 | 13-60 | 23–2,100 |
| Matsuzaki et al., 2009 | Japan | 4 | <1 | NA | 35 | 14 | 160–480 |
| Matsuzaki et al., 2009 | Meta-analysis | Variable | 1 | Variable | Variable | Variable | Variable |
| Meijer et al., 1990a | Netherlands | 50 | 1 | NA | 150 | 2 | 60 |
| Meijer et al., 1990b | Netherlands | 1,000 | 2 | NA | 180 | 3 | 320 |
| Miller and Crowl, 2006 | Utah, USA | 6–70 | <1 | Mud, clay | 30–42 | 15–19 | 17 |
| Parkos et al., 2003 | Illinois, USA | 600 | 2 | Clay | 70 | NA | 0–476 |
| Parkos et al., 2006 | Illinois, USA | 600 | 2 | Clay | 90 | 43–69 | 300 |
| Richardson et al., 1990 | Oklahoma, USA | 4 | 2 | NA | 55 | 7 | 5 |
| Roberts et al., 1995 | Australia | 12 | <1 | Plastic | 8, 20 | 15–25 | 170–526 |
| Robertson et al., 1997 | Australia | 2,800-8,500 | 4 | Silt, clay, loam | 120 | NA | 100–1,180 |
| Roozen et al., 2007 | Netherlands | 2 | <1 | Silt, clay | 10 | 23 | 128 |
| Sidorkewicj et al., 1998 | Argentina | 200 | <1 | Sandy clay loam | 128 | 11-39 | 18–535 |
| Sidorkewicj et al., 1999 | Argentina | 2 | <1 | Sand, clay, loam | 30 | 1 | 50–90 |
| Stewart and Downing, 2008 | Iowa, USA | 1,500-20,000 | 2 | NA | NA | NA | NA |
| Tapia and Zambrano, 2003 | Mexico | 10,000-15,000 | 1 | NA | 210 | Fingerling | 17–25 |
| Threinen and Helm, 1954 | Wisconsin, USA | 37 | <1 | Sand, muck | NA | NA | NA |
| Wilcox and Hornbach, 1991 | Minnesota, USA | 15 | <1 | Sand, silt, clay | 42 | 50 | 2,300–16,900 |
| Williams and Moss, 2003 | United Kingdom | 4 | 1 | NA | 42 | 15 | 0–700 |
| Williams et al., 2002 | United Kingdom | 4 | 2 | NA | 35–42 | NA | 200–800 |
| Wolfe, 2006 | Illinois, USA | 600 | 2 | Clay | 45–60 | NA | 371 |
| Zambrano and Hinojosa, 1999 | Mexico | 500 | 1 | NA | 330 | 5 | 140–560 |
| Zambrano et al., 1999 | Mexico | 8,000-80,000 | <1 | Mud | 330 | 13–44 | 0–4 |

NA = Not available.

benthic foraging activities and subsequent excretion (Lamarra, 1975). Common carp increased water column nutrients in 75% of the surveyed literature, whereas 4% found a decrease in nutrients (Figure 1). Common carp may directly and indirectly increase water column phosphorus, nitrogen, and ammonia as a result of benthic foraging activities (Cline et al., 1994; Lougheed et al., 1998; Parkos et al., 2003), excretion (Lamarra, 1975; Qin and Threlkeld, 1990), or destruction and subsequent decomposition of aquatic macrophytes (Carpenter and Lodge, 1986; Figure 2). Common carp may also interact synergistically with external nutrient loading to further enhance the eutrophication process (Drenner et al., 1998). Increases in common carp biomass may induce a commensurately greater effect in water column nutrients and fascilitate eutrophication processes (Lougheed et al., 1998; Parkos et al., 2003; Chumchal et al., 2005).

Excretion by benthivorous fishes may also increase water column nutrients, phytoplankton production (Lamarra, 1975; Qin and Threlkeld, 1990; Schaus and Vanni, 2000; Chumchal and Drenner, 2004), and nutrient flux (Carpenter et al., 1992). Although nutrient mobilization may be beneficial in moderate- to low-productivity lakes by increasing primary productivity, common carp are often implicated for increasing eutrophication of shallow lakes (Cahn, 1929; Egertson and Downing, 2004; Schrage and Downing, 2004; Chumchal et al., 2005). At least 50% of the phosphorus excreted by common carp may be readily available for phytoplankton production (Lamarra, 1975), indicating a potential direct pathway. However, the effect of common carp on water column nutrients is likely to vary as a result of common carp diet and habitat variability. Small common carp (<100 cm) that consume primarily zooplankton instead

**Table 2** Citation, location, ecosystem properties, management action, and common carp and ecosystem responses to different common carp control and management studies

| Citation | Location | Surface area (ha) | Depth (m) | Management action | Effect on carp | NU | TU | Chl a | PHY | ZP | MAC | BI | Fish |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Anderson, 1950 | Ohio, USA | 102 | 2 | Rotenone | 13,600 kg removed | NA | - | NA | NA | NA | + | NA | NA |
| Barton et al., 2000 | Canada | 0.6 | 1 | Drawdown, electrofishing, seine | 490 kg·ha$^{-1}$ COC removed (all) | NA | — | NA | NA | NA | NA | + | NA |
| Beklioglu et al., 2003 | Turkey | 125 | 3 | Gill netting | 57% reduction in COC and tench | + | — | — | — | + | + | NA | + |
| Bonneau, 1999 | North Dakota, USA | 712 | 3 | Trap net, rotenone | 676,000 kg removed | None | — | NA | — | + | + | + | NA |
| Bulow et al., 1988 | Tennessee, USA | 78,500 | NA | Fish barrier | Stopped movement | NA | NA | NA | NA | NA | NA | NA | NA |
| Cahn, 1929 | Wisconsin, USA | NA | NA | Drawdown, seining | 17, 123 kg removed | NA | NA | NA | NA | NA | NA | NA | NA |
| Cahoon, 1953 | North Carolina, USA | 12,140 | 1 | Barracade, commercial seine | 769, 108 kg removed | NA | — | NA | NA | NA | + | NA | + |
| King and Hunt, 1967 | Michigan, USA | 18 | <1 | Poison | 2,100-2,700 kg·ha$^{-1}$ | NA | NA | NA | NA | NA | + | NA | NA |
| Lougheed and Chow-Fraser, 2001 | Canada | 250 | <2 | Fishway installation | >90% reduction | None | — | NA | — | + | + | NA | NA |
| Lougheed et al., 2004 | Canada | 250 | <3 | Fishway installation | 50 kg·ha$^{-1}$; 95% reduction | NA | — | NA | — | + | + | NA | + |
| Meijer et al., 1990a | Netherlands | 3.5 | 2 | Seine and electrofishing | reduced to 120-145 kg·ha$^{-1}$ | + | — | — | NA | None | + | NA | NA |
| Moss et al., 2002 | United Kingdom | 6.75 | 1 | Draining, netting | 1,850 kg removed | — | NA | — | NA | + | + | NA | NA |
| Parkos et al., 2006 | Illinois, USA | 0.06 | 2 | Substrate barrier | NA | None | None | None | NA | None | None | None | NA |
| Pinto et al., 2005 | Australia | 58 | NA | Electrofishing, gill nets, biomanipulation | >4,000 kg removed | NA | — | NA | — | NA | NA | NA | NA |
| Ricker and Gottschalk, 1940 | Indiana, USA | 3,900 | 3 | Seine | 41,000 kg removed | NA | — | NA | NA | NA | + | NA | + |
| Roozen et al., 2007 | Netherlands | 0.0002 | 1 | Substrate barrier | NA | NA | — | — | — | None | NA | NA | NA |
| Rose and Moen, 1953 | Iowa, USA | 3,459 | 2 | Seining | 2,834 kg·ha$^{-1}$ removed | NA | NA | NA | NA | NA | + | NA | + |
| Schrage and Downing, 2004 | Iowa, USA | 76 | <1 | Rotenone | 75% removed | — | — | NA | — | + | + | + | NA |
| Schwartz, 1986 | Pennsylvania, USA | NA | 13 | Big-M trap, baited | 68-1 70 /net night | NA | NA | NA | NA | NA | NA | NA | NA |
| Shields, 1958 | South Dakota, USA | 32,380 | 30 | Drawdowns during spawning | Reduced age-0 carp abundance | NA | NA | NA | NA | NA | NA | NA | NA |
| Stuart et al., 2006 | Australia | NA | NA | Williams cage | <23 captured in 24 h | NA | NA | NA | NA | NA | NA | NA | NA |
| Verrill and Berry, 1995 | Minnesota, USA | 3,342 | 1 | Drawdown, electric barrier | Stopped movement | NA | NA | NA | NA | NA | NA | NA | NA |
| Weier and Starr, 1950 | Ohio, USA | 100 | 2 | Rotenone | 13,600 removed | NA | — | NA | NA | NA | NA | NA | NA |

+ Denotes an increase and − denotes a decrease following the application of common carp management strategy.

NA = not applicable or not available. NU = nutrients (P and N), TU = turbidity, Chl a = chlorophyll *a*, PHY = phytoplankton, ZP = zooplankton, MAC = macrophytes, BI = benthic invertebrates, fish = effect on recruitment, growth, or survival.
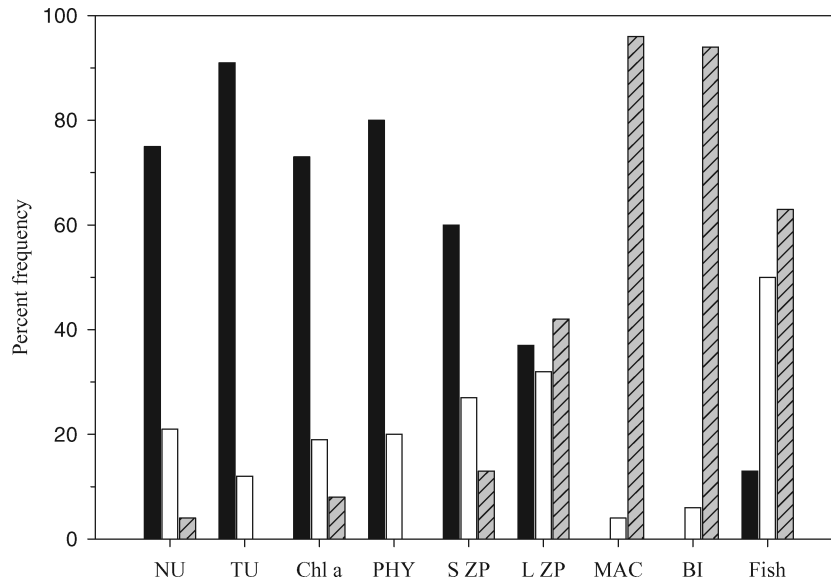
**Figure 1** Percentage of surveyed common carp literature that found an increase (black), no effect (open), or decrease (grey hatch) on nutrient availability (NU; P and N), turbidity (TU), chlorophyll *a* (Chl a), phytoplankton (PHY), small-bodied zooplankton (S ZP), large-bodied zooplankton (L ZP), macrophytes (MAC), benthic invertebrates (BI), and fishes (Fish) as a result of common carp.

of benthic invertebrates may not have an effect on nutrients (Meijer et al., 1990a, 1990b). Additionally, common carp may not mobilize nutrients in ecosystems with hard substrate types that do not facilitate benthic foraging behaviors (Robel, 1961; Crivelli, 1983; Havens, 1993; Roberts et al., 1995); sediments composed of large, dense particles (i.e., sand, gravel, cobble) are not resuspended by common carp foraging behaviors. Because common carp do not increase water column nutrients in systems with hard substrates, bioturbation, not excretion, is likely the major driver behind elevated water column nutrients.

Benthivorous fish abundance may explain a large proportion of organic and inorganic turbidity in small shallow lakes (Meijer et al., 1990a; Barton et al., 2000). Increased turbidity has numerous deleterious effects on aquatic ecosys-

tems, including reduced light penetration, primary productivity, aquatic macrophyte growth (Skubinna et al., 1995; Hootsmans et al., 1996; Sidorkewicj et al., 1996), zooplankton filtering efficiency (Kirk and Gilbert, 1990; Kirk, 1991), and foraging abilities of visual planktivorous (Vinyard and O'Brien, 1976; Miner and Stein, 1996) and piscivorous fishes (Reid et al., 1999; Vogel and Beauchamp, 1999; De Robertis et al., 2003). Common carp resuspend solids (Lammens, 1991) and increase turbidity (Cline et al., 1994; Parkos et al., 2003; Chumchal et al., 2005) as they search for food and expel non-food items. Turbidity increased in 91% of the surveyed literature, and no literature identified a decrease in turbidity as a result of common carp feeding behavior (Figure 1). Large common carp can effectively penetrate up to 12 cm
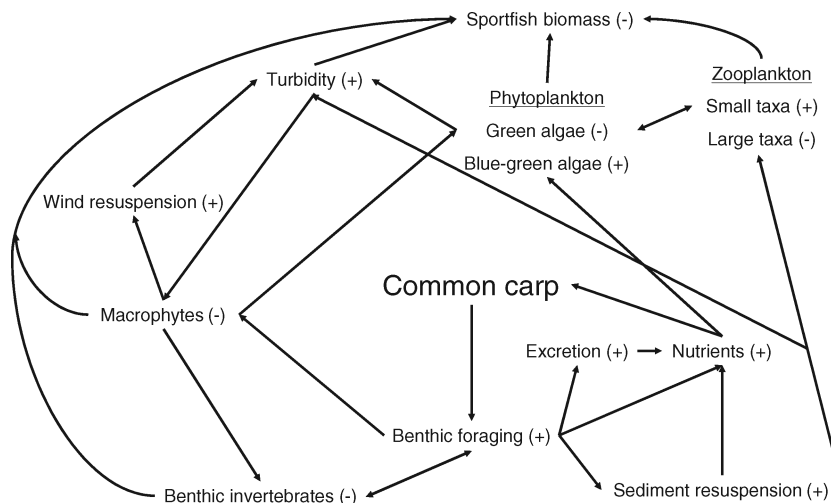


**Figure 2** Common carp populations can have a middle-out effect on aquatic ecosystems by restructuring communities through both top-down and bottom-up processes. Directional arrows indicate pathways that common carp affect ecosystem processes and biomass of multiple trophic levels. Positive sign (+) indicates an increase, whereas a negative sign (−) indicates a decrease as an effect of common carp.

into the substrate while searching for food (Panek, 1987), disturbing more than the sediment surface layer and resuspending fine particles. Similar to nutrient cycling, studies where turbidity did not increase with common carp presence may have been conducted with small common carp (<100 mm) that had not switched to benthic foraging or had been conducted on hard or large-particle substrates (i.e., Haines, 1973). Common carp may increase turbidity more than some native benthivores (Parkos et al., 2003) in a short amount of time (i.e., <18 hr; Roberts et al., 1995) and at low abundances (i.e., 5–7 kg · ha$^{-1}$; Richardson et al., 1990; Drenner et al., 1998; Zambrano et al., 1999). Turbidity may increase with common carp biomass (King et al., 1997; Parkos et al., 2003; Britton et al., 2007) or ecosystems may quickly switch to a turbid water equilibrium once common carp biomass surpasses a critical threshold (i.e., 320 kg · ha$^{-1}$; Zambrano and Hinojosa, 1999). Lower densities of common carp may also result in an equilibrium shift but over a prolonged duration (Zambrano and Hinojosa, 1999).

Phytoplankton provides an important energy source in aquatic food webs (Bunn and Boon, 1993; Hecky and Hesslein, 1995). Increases in nutrient loading, turbidity, and common carp biomass may induce an indirect shift in phytoplankton communities from one dominated by chlorophyta (green algae), an important energy source for higher trophic levels, to noxious and often toxic cyanobacteria (blue-green algae) (Williams and Moss, 2003) that more commonly compete with macrophytes for nutrients and light. Phytoplankton production increased in 80% and chlorophyll *a*, a metric of phytoplankton biomass, increased in 73% of the surveyed literature in the presence of common carp. Decreases in phytoplankton production (0%) and chlorophyll *a* (8%) were rarely observed (Figure 1).

### *Top-Down Effects*

Planktivorous fishes can structure aquatic ecosystems through top-down processes by reducing invertebrate communities through predation that in turn releases algal communities from predatory control by zooplankton (Carpenter et al., 1985). Although common carp effects on many aquatic trophic levels are well defined, effects on zooplankton communities are less predictable. Common carp have been associated with increases and decreases in zooplankton diversity, size structure, and abundance. Reductions (Meijer et al., 1990b; Lougheed et al., 1998) and increases in zooplankton biomass (Richardson et al., 1990; Drenner et al., 1998; Parkos et al., 2003) have been observed as an effect of common carp populations. Additionally, size structure of zooplankton communities generally shifts from large-bodied to small-bodied taxa in the presence of common carp. Biomass or numerical abundance of large-bodied zooplankton taxa increased in 37% and decreased in 42% of the surveyed literature (Figure 1). In contrast, small-bodied zooplankton taxa increased in 60% and declined in 13% of the surveyed literature (Figure 1). In some instances, common carp had little or no

effect on zooplankton communities (27–32%) (Qin and Threlkeld, 1990; Cline et al., 1994; Chumchal et al., 2005).

Variable effects of common carp on zooplankton communities are likely due to differences in common carp population size structure and intrinsic ecosystem differences, suggesting ecosystems can be affected through alternative pathways that are life stage and habitat dependent. Adult common carp populations may indirectly affect zooplankton abundance and size structure through nutrient mobilization or a reduction in zooplankton grazing capabilities through increased turbidity (Meijer et al., 1990b; Richardson et al., 1990; Lougheed et al., 1998; Parkos et al., 2003). Increases in zooplankton biomass may be a result of increased phytoplankton biomass (i.e., prey resources) (King et al., 1997; Drenner et al., 1998; Khan et al., 2003) or by a reduction in the abundance of benthic invertebrates (Cline et al., 1994; Parkos et al., 2003; Miller and Crowl, 2006) that may prey on zooplankton (Johnson and Crowley, 1980). Increases in zooplankton biomass with common carp abundance may also be an indirect effect of shifts in zooplankton size structure away from populations dominated by large-bodied species toward smaller-bodied species (Meijer et al., 1990b; Richardson et al., 1990). Increased inorganic turbidity, commonly associated with adult common carp, can inhibit ingestion of phytoplankton by large-bodied zooplankton (Kirk and Gilbert, 1990; Kirk, 1991), thereby reducing the abundance of these large-bodied grazers. Shifts in zooplankton size structure from large- to small-bodied species may have a larger influence on phytoplankton than zooplankton density (McQueen et al., 1986). Large-bodied zooplankton can regulate phytoplankton biomass (Meijer et al., 1990a), whereas small-bodied zooplankton taxa are ineffective grazers. A switch in zooplankton size structure is another mechanism driving the switch in shallow lakes from a clear to turbid water state (Scheffer, 1990; Scheffer et al., 1993).

In contrast to indirect effects of adult common carp on zooplankton, early life stages (<100 mm) of common carp directly consume zooplankton (Sibbing, 1988; Meijer et al., 1990b; Garcia-Berthou, 2001; Britton et al., 2007). Similar to bluegill *Lepomis macrochirus* in north temperate lakes (Carpenter et al., 1985) or gizzard shad *Dorosoma cepedianum* in hypereutrophic midwestern reservoirs (Stein et al., 1995), high abundances of zooplanktivorous common carp may directly reduce zooplankton population abundance and size structure (Meijer et al., 1990b; Richardson et al., 1990; Schrage and Downing, 2004) through predation on *Daphnia* spp., increasing phytoplankton biomass and decreasing water quality (Khan et al., 2003). This trophic cascade may occur rapidly, with increases in chlorophyll *a* observed within 5 days of common carp introduction (Khan et al., 2003). However, common carp juveniles (>100 mm total length (TL)) shift to benthic prey (Britton et al., 2007). This flexibility in prey resources releases common carp from bottom-up control by allowing them to exploit multiple prey resources but allows for only a small window of opportunity to reduce zooplankton abundance.

Common carp switch to foraging on detritus, annelids, chironomids, amphipods, and odonates around 100 mm TL (Panek,

1987; Sibbing, 1988; Garcia-Berthou, 2001; Britton et al., 2007) and may reduce benthic invertebrate abundance, diversity, evenness, and richness (Lellak, 1978; Wilcox and Hornbach, 1991; Parkos et al., 2003; Stewart and Downing, 2008). Benthic invertebrates decreased in response to common carp in 94% of the surveyed literature (Figure 1). Benthic invertebrate populations may shift toward large-bodied species due to selective predation by common carp on small-bodied prey (Covich and Knezevic, 1978). Annelids, chironomids, and odonates experience large reductions even at low common carp densities (Wojcik-Migala, 1966; Cline et al., 1994; Zambrano et al., 1999). When common carp populations are greatly reduced, benthic invertebrate communities may shift to less tolerant species that were previously present only at extremely low abundances (Barton et al., 2000). Common carp may also reduce abundance of *Decapoda*, although this is likely an indirect response to a decrease in macrophytes and the periphytic community rather than direct predation (Hinojosa-Garro and Zambrano, 2004). Common carp may be more efficient at consuming benthic invertebrates than native fish species (Zambrano et al., 1999; Parkos et al., 2003), potentially competing with native benthivores. As benthic invertebrate populations decline in response to common carp predation, common carp increase foraging time and expel additional sediment into the water column (Werner and Anholt, 1993), enhancing the turbid water state.

Aquatic macrophytes are vital to the clear water stable state due to their ability to stabilize sediment, compete with phytoplankton for light and nutrients, provide invertebrates a food resource and refugia, and habitat for fishes (Carpenter and Lodge, 1986; Grimm and Backx, 1990; Meijer et al., 1990b; Scheffer et al., 1993; Hanson and Butler, 1994). Aquatic macrophytes generally disappear once turbidity approaches 20 nephelometric turbidity units (Scheffer, 1990; Lougheed et al., 1998). Macrophyte loss increases organic turbidity through loss of competition with phytoplankton and inorganic turbidity by increasing wind-driven sediment resuspension (Scheffer, 1990, 1998; Scheffer et al., 1993). Aquatic macrophytes are generally reduced in the presence of common carp (96% of the surveyed literature; Figure 1). Aquatic macrophyte diversity and abundance may be reduced or eliminated (Threinen and Helm, 1954; Crivelli, 1983; Parkos et al., 2003; Miller and Crowl, 2006) when common carp biomass approaches $200 \, kg \cdot ha^{-1}$ (Williams et al., 2002; Matsuzaki et al., 2009). Rarely do adult common carp directly consume macrophytes (Crivelli, 1983; Roberts et al., 1995). Instead, common carp destroy aquatic macrophytes on hard substrates through collisions and increased algal growth that compete with aquatic macrophytes for light and nutrients (Sidorkewicj et al., 1999; Miller and Provenza, 2007). On soft substrates, common carp directly dislodge aquatic macrophyte roots from the sediment (King and Hunt, 1967; Crivelli, 1983; Parkos et al., 2003) and increase sediment turbidity, nutrient release, and algal biomass, attenuating light needed for aquatic macrophyte growth (Crowder and Painter, 1991; Bronmark and Weisner, 1992; Lauridsen et al., 1994; Skubinna et al., 1995; Sidorkewicj et al., 1999).

Some systems remain dominated by macrophytes in the presence of common carp and remain in the clear water state (Lougheed et al., 1998). Shallow ecosystems that permit substrate light penetration even under turbid conditions allow macrophytes to persist in the presence of common carp (Zambrano and Hinojosa, 1999; Evelsizer and Turner, 2006). Additionally, aquatic macrophyte taxa vary in their vulnerability to common carp perturbation (King and Hunt, 1967; McCrimmon, 1968; Evelsizer and Turner, 2006). Factors, including root system, soil type preference, shade tolerance, tissue strength, and timing of seed dispersal, all likely influence macrophyte susceptibility. Aquatic macrophytes with a shallow or weak root system are easily uprooted by foraging behavior, especially in fine, loose substrates (Crivelli, 1983; Roberts et al., 1995; Parkos et al., 2003), whereas macrophytes with soft tissues may be more easily damaged in collisions (Zambrano and Hinojosa, 1999). Submergent species may be more susceptible than emergent species because they generally have weaker root systems and are more influenced by turbidity (Roberts et al., 1995). However, even aquatic macrophytes with deeper or stronger root systems that are resistant to common carp foraging may also be eliminated as a result of increased turbidity from foraging-induced sediment resuspension.

Information on interactions among common carp and other fish species is limited. Only 21% of the surveyed literature evaluated the effects of common carp on recruitment, growth, or survival of fishes, of which 75% found some sort of rate function decline (Figure 1). Common carp are adapted to highly eutrophic ecosystems and experience population increases with increasing lake productivity, whereas native fish populations may decline under similar conditions (Maceina et al., 1996; Egertson and Downing, 2004). Common carp may degrade spawning habitat or disrupt spawning behavior (Forester and Lawrence, 1978; Panek, 1987) and have been shown to consume eggs of some fishes (Miller and Beckman, 1996). Fishes growth rates are sometimes reduced in the presence of common carp. Common carp have reduced growth rates but increased survival of juvenile centrarchids (Wolfe, 2006); reduced growth was believed to be a result of reduced prey availability and poor foraging efficiency, whereas increased survival was attributed to reduced predation under more turbid conditions. Bluegill and black crappie *Pomoxis nigromaculatus* populations have declined with an increase in common carp population size (Egertson and Downing, 2004). Largemouth bass *Micropterous salmoides* and smallmouth bass *Micropterus dolomieui* may not be affected by common carp abundance (Haines, 1973; Forester and Lawrence, 1978), although angler catch rates of largemouth bass may be reduced when common carp are present (Drenner et al., 1997). White crappie *Pomoxis annularis* populations may increase with common carp abundance (Egertson and Downing, 2004), possibly due to their adaptations for turbid conditions (Carlander, 1977), suggesting that the effects of common carp on fish communities may be species specific. Fish species that can adapt to conditions associated with the presence of common carp may not be affected, whereas those with specific niches for biotic
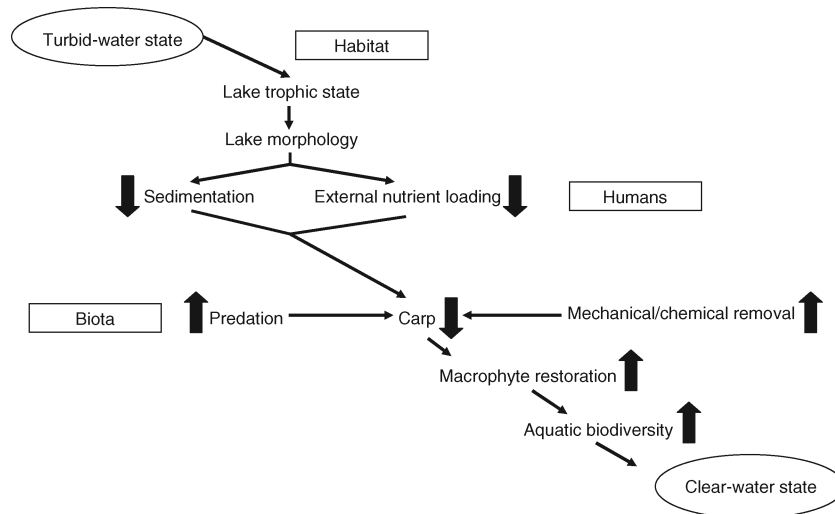
**Figure 3** Successful shallow lake restoration efforts must consider the entire ecosystem (humans, habitat, and biota), not just common carp, to improve water quality. Thin arrows indicate progression of restoration efforts to return turbid water lakes to the clear water state, whereas bold arrows represent desired response of ecosystem resulting from restoration efforts.

and abiotic conditions may experience reductions in growth or survival, especially during vulnerable early life stages.

### Remedial Measures

Frequently, fish and wildlife managers are interested in common carp removal as a lake reclamation tool (Weier and Starr, 1950; Cahoon, 1953; Marking, 1992; Schrage and Downing, 2004; Figure 3). Common carp removal may be one counteractive reclamation strategy necessary to decrease internal nutrient cycling, increase water transparency, reestablish aquatic macrophytes, and return shallow lakes to the clear water state. However, removal of common carp is difficult, costly, and time-consuming (i.e., Lougheed et al., 2004; Schrage and Downing, 2004). Numerous studies have noted a common carp biomass threshold of $250–450 \, kg \cdot ha^{-1}$ where common carp populations can influence biotic and abiotic ecosystem properties (Fletcher et al., 1985; Parkos et al., 2003; Schrage and Downing, 2004). Other research has indicated both lower ($5 \, kg \cdot ha^{-1}$; Richardson et al., 1990) and higher ($750 \, kg \cdot ha^{-1}$; Lougheed et al., 1998) thresholds of common carp biomass affect ecosystems, suggesting ecosystem variability has a strong effect on the ability of common carp to transform shallow lake ecosystems. Depending upon the ecosystem, more than 70% of common carp biomass may have to be removed to realize improvements in biotic and abiotic variables (Meijer et al., 1999; Barton et al., 2000; Zambrano et al., 2001; Schrage and Downing, 2004). Removing less common carp biomass may (Beklioglu et al., 2003) or may not (Schrage and Downing, 2004) produce desired results.

In addition to biomass, individual common carp size and ecosystem size, substrate, and trophic state influence common carp effects on ecosystems (Sidorkewicj et al., 1998; Williams

et al., 2002; Chumchal and Drenner, 2004) and must be considered when formulating management plans. Specialized common carp angling techniques (i.e., ground baiting) may also contribute toward eutrophication and should be addressed where common carp angling is popular (Arlinghaus and Niesar, 2005). Common carp populations may be partially regulated by lake morphometry and experience population declines with increasing water depth and population increases with lake surface area and trophic state (Gerking, 1950; Egertson and Downing, 2004). Therefore, lakes should be prioritized and decisions must be made to determine where restoration efforts are best directed. For example, low abundance common carp populations may be easy to further reduce, but such efforts might have little ecological effect on aquatic ecosystems. Highly abundant common carp populations are difficult to remove and may not be easily managed, but reductions can have tremendous ecological effects. Shallow, productive ecosystems with fine, loose sediment, and low abundance and diversity of aquatic macrophytes are most vulnerable to common carp perturbation and would experience the greatest improvements in water quality following common carp removal (Drenner et al., 1998; Chumchal and Drenner, 2004). Many undesirable effects of common carp are reduced in lakes that are less productive or have hard substrate, indicating a need for improved land management practices that reduce sedimentation, nutrient loading, and lake eutrophication (Figure 3). For example, common carp have had little effect on suspended solids or turbidity in lakes with sand, gravel, or cobble substrate, even at high densities (Robel, 1961; Meijer et al., 1990a; Drenner et al., 1998; Sidorkewicj et al., 1999). Although common carp are a major contributor to aquatic system degradation, other factors leading to increased nutrients and turbidity (i.e., wind, bioturbation, algal abundance, substrate, external and internal nutrient loading, fish community, land management practices) may act synergistically with common carp

and must be considered when planning large-scale ecosystem renovation (Figure 3).

Numerous control techniques have been attempted to manage common carp populations, including chemical and physical removal, destruction of common carp spawning habitat, water level manipulation, fish barriers, and predator introduction (Ricker and Gottschalk, 1940; McCrimmon, 1968; Panek, 1987; Marking, 1992; Pinto et al., 2005; Parkos et al., 2006; Table 2). Numerous lake restoration projects have been undertaken and advancement toward improving shallow lake ecosystems has been made. However, success is far from certain, and unexpected results are common. In our review, nearly all surveyed literature documented some sort of desirable effect as a result of management actions; however, we caution that success is far from certain because projects that are unsuccessful are rarely published. A previous review of nuisance fish control projects found that removals were successful about 50% of the time (Meronek et al., 1996). Common carp appear to densely congregate in deep areas of lakes during fall and winter and in spring in shallow vegetated bays (Penne and Pierce, 2008). Targeting common carp aggregations may make removal efforts more successful. When possible, lake drawdowns congregate fish and increase success of removal efforts (Barton et al., 2000) or may make overwintering at northern latitudes difficult. When lake drawdowns are not possible, baiting sites with grain may increase catches (Cahoon, 1953) or the effectiveness of chemical applications. Chemical removal is a popular removal technique (Anderson, 1950; Marking, 1992; Meronek et al., 1996; Bonneau, 1999); however, non-target species are also vulnerable (Panek, 1987; Marking, 1992). Chemical spot treatments in areas of common carp aggregations may be an option to minimize undesirable effects on the surrounding lake community and increase removal success on large water bodies (Marking, 1992; Bonneau, 1999). Physical removal techniques have included seining, electrofishing, gill netting, and a variety of trap types, and their effectiveness and implementation is often dictated by habitat type (Schwartz, 1986; Meijer et al., 1990a; Barton et al., 2000; Stuart et al., 2001; Beklioglu et al., 2003; Pinto et al., 2005). Chemical applications may be most effective in small lakes but have decreased success on larger water bodies, whereas physical removal has the opposite trend (i.e., more successful in large systems) (Meronek et al., 1996). Poison baits have also been suggested to target common carp populations and minimize effects on other species (Rach et al., 1994), but field trials have been unsuccessful (Bonneau, 1999). Even when removal efforts are successful, only short-term benefits may accrue because common carp recolonize quickly (Barton et al., 2000). Preventative measures (i.e., electrical barriers, fish weirs, traps, etc.) established prior to removal efforts are suggested to reduce the likelihood of common carp recolonization (Bulow et al., 1988; Verrill and Berry, 1995; Lougheed and Chow-Fraser, 2001).

Management plans may benefit by considering common carp population dynamics. Common carp specific models have been developed to evaluate how populations may respond to varying management practices (Brown and Walker, 2004). Fast-growing, short-lived populations may be best controlled though management actions directed at reducing recruitment (Brown and Walker, 2004). Daughterless carp technology may skew sex ratios heavily toward males over multiple generations, eventually causing population collapse (Grewe, 1996) and could also be used to control short-lived populations (Brown and Walker, 2004). Long-lived, slow-growing populations may be better controlled and reduced through reducing adult population (Brown and Walker, 2004). However, removal of adult common carp may release survivors from density-dependant mechanisms, leading to increased recruitment (Thresher, 1997) or individual growth. Thus, not only must adult common carp populations be reduced, but recruitment must be addressed. Taking advantage of biological weaknesses may provide managers an opportunity to reduce common carp populations. Common carp recruitment appears to be erratic (Mraz and Cooper, 1957; Wichers, 1976; Lubinski et al., 1984; Mueller and Downen, 2000) but may be synchronized over large geographic areas, influenced by summer temperatures, precipitation, and strong wind events (Phelps et al., 2008a) instead of a simple stock-recruitment relationship (Mraz and Cooper, 1957). Common carp spawn over aquatic macrophytes in waters generally less than 0.5 m (Edwards and Twomey, 1982). Wet years with flooding of littoral vegetation provide spawning habitat, while warm years with few strong wind events may increase egg and larval survival (Phelps et al., 2008a). Drawdowns during spawning may reduce spawning habitat and recruitment (Shields, 1958) and have been successfully implemented in Australia (Koehn et al., 2000). Barriers preventing adult common carp access to spawning areas may also reduce recruitment (Stuart et al., 2001). Additionally, physical agitation of water in shallow spawning bays may damage eggs. However, effects of all these techniques on native fishes should be considered when formulating a set of management strategies.

Common carp may have fewer undesirable effects in their native range compared to invaded habitats. Comparing common carp populations and effects across native and introduced ranges may also provide insight into their biology and ecology that can be incorporated into management strategies. Common carp grow slower, are smaller on average, and achieve lower density populations in Europe compared to North America (Crivelli, 1981, 1983). Common carp populations in Europe may be partially regulated by apex predators (i.e., northern pike *Esox lucius*), whereas predators seem to have little impact on common carp populations in their introduced range (Crivelli, 1983). Managing apex predators may be one method to control common carp recruitment in North America (Hansson et al., 1998). It remains unknown why common carp are less preyed on in North America, but predator size, abundance, habitat use, and alternative prey are potential factors. Northern pike, native to both Europe and North America, may at times include a large proportion of common carp in their diet, possibly affecting common carp year-class strength (Sammons et al., 1994; Paukert et al., 2003). However, few common carp management strategies have

incorporated predator management (but, see Ricker and Gottschalk, 1940; Pinto et al., 2005). Identifying other differences in common carp populations and their effects among Asia, Europe, North American, and Australian waters may result in more effective control and successful lake rehabilitation efforts.

Across ecosystems, common carp removal may be more successful in less productive systems, resulting in improved water quality and native fish abundance (Cahoon, 1953; Meijer et al., 1990a; Barton et al., 2000); however even highly productive lakes have returned to the clear water state following common carp removal (Schrage and Downing, 2004). Lake response to successful fish removal can be rapid. Removal of common carp can reduce nutrient availability to primary producers (Schrage and Downing, 2004; Moss et al., 2002), and zooplankton abundance and size structure may increase (Bonneau, 1999; Moss et al., 2002; Lougheed et al., 2004; Schrage and Downing, 2004). These changes may induce a decrease in phytoplankton biomass (Bonneau, 1999; Lougheed et al., 2004; Schrage and Downing, 2004) because phytoplankton is regulated by zooplankton growing instead of nutrients, returning lakes to the clear water state (Beklioglu et al., 2003; Schrage and Downing, 2004). Inorganic turbidity can also be reduced by reducing bioturbation (Meijer et al., 1990a; Bonneau, 1999; Lougheed and Chow-Fraser, 2001; Schrage and Downing, 2004). Reduced turbidity allows reestablishment of aquatic macrophytes from existing seed banks. One of the keys to lake restoration may lie in unlocking the ability of aquatic ecosystems to remain dominated by macrophytes under common carp perturbation. Certain macrophyte species appear more susceptible to destruction by common carp than others (Crivelli, 1983; Roberts et al., 1995; Zambrano and Hinojosa, 1999), and identification of "carp-tolerant" species may provide an avenue to rehabilitate shallow aquatic systems. For example, eurasian water milfoil *Myriophyllum spicatum* can persist under highly turbid conditions and in the presence of abundant common carp populations (Drenner et al., 1997, 1998; Chumchal et al., 2005), can improve water quality (Drenner et al., 1998), and may be a management option in its native range. Common carp directly damage macrophytes during spawning activities in shallow embayments. Management actions that prevent the movement of adult common carp into these habitats may not only reduce their effects on aquatic macrophytes (Lougheed and Chow-Fraser, 2001), but also increase native fishes spawning success and reduce common carp reproduction. The abundance of many fish species (i.e., black crappie, bluegill, pumpkinseed (*Lepomis gibbosus*), yellow perch) may be linked to vegetation density (Lougheed et al., 2004). In lakes where aquatic macrophytes are restored, successful recruitment of other fish populations may occur (Rose and Moen, 1953; Scheffer et al., 1993).

Long-term success of management actions in the surveyed literature was difficult to assess because only immediate changes in ecosystem properties were generally reported. Success will rarely be achieved during one-time management manipulations (i.e., Lougheed et al., 2004; Schrage and Downing, 2004), and no single restoration technique, aside from complete drawdown and renewal, provides a "silver bullet" to eliminate common carp populations and restore aquatic systems. Instead, long-term management practices that include the appropriate biological monitoring methodology to evaluate progress, determine obstacles, and adapt management actions accordingly may prove most beneficial. Management strategies that consider the entire ecosystem and apply multiple techniques, targeting all life stages of common carp, are likely to provide desirable, longest-lasting results (Figure 3).

## *SUMMARY*

Cahn (1929) first documented common carp-induced shifts in equilibrium of shallow lakes. Since then, our understanding of the mechanisms underlying those shifts have substantially advanced. The influence of common carp on aquatic systems is complex. We have reviewed the literature on pathways that common carp engineer ecosystems and transform shallow lakes to the turbid water state. Common carp in shallow lakes increase turbidity, phytoplankton, and blue-green algae; mobilize nutrients; and decrease macrophytes, macroinvertebrates, and fishes (Lamarra, 1975; Parkos et al., 2003; Egertson and Downing, 2004). Common carp populations function as ecosystem engineers by regulating bottom-up and top-down processes. Introduced common carp are not regulated by top-down processes (i.e., experience minimal predation) and are not limited by bottom-up processes (i.e., prey resources); thus, common carp can regulate ecosystems through a middle-out framework. Ecosystem effects imposed by common carp may be greater than those caused by other native benthivores and occur even at relatively low common carp densities, with increases in undesirable ecosystem effects with increases in common carp biomass (Parkos et al., 2003; Chumchal et al., 2005). Ecosystem engineering by common carp can transform lakes from clear to turbid water, with ecosystem-wide consequences (Scheffer, 1998; Haas et al., 2007). Opportunities exist to further evaluate common carp effects in terms of lake morphometry and across aquatic ecosystem types (lakes, rivers, and reservoirs). Additional research is needed to better understand the population and behavioral ecology of this widely introduced species. We encourage research focusing on basic biological and ecological aspects of common carp that will inevitably lead to improved management recommendations and control techniques. Eradication of common carp is difficult and unlikely; however, we advocate innovative ideas to reduce the effects of common carp on aquatic ecosystems. Although we focused on common carp, numerous other invasive species (e.g., round goby *Neogobius melanostomus*, silver carp *Hypophthalmichthys molitrix*, bighead carp *Hypophthalmichthys nobilis*, Eurasian ruffe *Gymnocephalus cernuus*, and rusty crayfish *Orconectes rusticus*) also have tremendously influenced aquatic systems. We believe the theoretical framework of this article (species ecology/ecosystem-based approach) can be applied to other invasive species to better understand and predict their effects on ecosystems and formulate successful management strategies.

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