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Experimental Evidence for the Effects of Common Carp (*Cyprinus carpio* L., 1758) on Freshwater Ecosystems: A Narrative Review with Management Directions for Turkish Inland Waters

Lorenzo VILIZZI[*], **Ali Serhan TARKAN**

Muğla Sıtkı Koçman University, Faculty of Fisheries, 48000 Kötekli Campus /Muğla, Turkey

ABSTRACT

The management of common carp *Cyprinus carpio* has become a priority issue in most of its native range and where it has been introduced. This is because of the effects (both documented and anecdotal) on freshwater ecosystems that the species is able to exert. To provide a general framework for future management of introductions of this species, this study presents a near-comprehensive, “narrative” review (complementing a “systematic” review: Vilizzi, Tarkan, Copp 2015) of experimental studies of the impacts of common carp spanning almost nine decades. Based on 139 experiments presenting results for a total of 400 “assessments” aimed at evaluating the effects of *C. carpio* on selected ecological components, a conceptual model linking both abiotic (i.e. turbidity/suspended solids, nitrogen, phosphorus) and biotic components (i.e. phytoplankton/ chlorophyll *a*, aquatic macrophytes, zooplankton, benthic invertebrates, amphibians, waterfowl, fish) was refined. Given the status of *C. carpio* as a species of low concern in Turkish inland waters and its overall unsuccessful recruitment in stocked reservoirs, in the light of the present findings it is suggested that environmental managers should consider targeting shallow (natural) lakes for successful fisheries yields, but conditional upon careful assessment of the economic benefits vs. ecological risks involved.

Keywords: Laboratory, field, natural, reservoirs, shallow lakes

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*** CORRESPONDING AUTHOR**

lorenzo.vilizzi@gmail.com
Tel : +90 252 211 1888
Fax: +90 252 211 1887

Sazanın (*Cyprinus carpio* L., 1758) Tatlısu Ekosistemlerine Etkileri İçin Deneysel Kanıt: Türkiye İç Suları İçin Yönetim Yönlendirmeleri Derlemesi

Öz: Sazan *Cyprinus carpio* balığının yönetimi türün doğal olarak bulunduğu alanların çoğunda ve aşılandığı alanlarda öncelikli bir konu haline gelmiştir. Bu durum türün tatlısu ekosistemlerine yaptığı hem belgelenmiş hem de anlatılan etkileri nedeniyle ortaya çıkmaktadır. Bu türün aşılamalarının gelecekteki yönetimi için genel bir çerçeve oluşturmayı amaçlayan bu çalışma, sazanın etkileri üzerine gerçekleştirilen deneysel çalışmaların neredeyse 90 yıllık bir taramasını içeren ve yakın zamanda bu konuda yayımlanan “sistematik” bir derlemenin (Vilizzi, Tarkan, Copp 2015) tamamlayıcısı olacak şekilde dizayn edilen kapsamlı bir derlemesidir. Seçilmiş ekolojik bileşenler üzerine *C. carpio*’nun etkilerini değerlendirmeyi hedefleyen 139 deneysel çalışmaya dayalı toplam 400 “değerlendirme” için, abiotik (bulanıklık/askıda katı madde, nitrojen, fosfor) ve biotik (fitoplankton/klorofil a, sucul makrofitler, zooplankton, bentik omurgasızlar, amfibiler, su kuşları ve balıklar) faktörleri ilişkilendiren kavramsal bir model önceki çalışmalardan ayıklanmıştır. *C. carpio*’nun Türkiye içsularındaki ekosistem etkileri anlamında az endişe veren durumu ve stoklandığı rezervuarlardaki başarısız stok oluşturma durumundan dolayı, elde edilen bulgular ışığında çevresel yöneticilerin bu balıktan başarılı balıkçılık ürünleri elde edebilmek için stoklamalarda sığ doğal gölleri hedeflemesi gerektiği ancak bunun türün ekonomik yararlarına karşı içerdiği ekolojik riskleri de hesaba katarak yapması gerektiği önerilir.

Anahtar kelimeler: Laboratuvar, arazi, doğal, rezervuar, sığ göller

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Introduction

The management of common carp (*Cyprinus carpio* L., 1758) has become an issue of increasing priority in both its natural and introduced ranges. In North America (McCrimmon 1968; Moyle 1984) and Australia (Koehn 2004), *C. carpio* is highly invasive because it is a generalist species and efforts are being made to mitigate the species” detrimental effects on freshwater ecosystems (Balon 1974, 2004). In contrast, *C. carpio* has been accepted as "naturalised" (sensu Copp et al. 2005) having established self-sustaining populations centuries ago (e.g. central Europe) and is thought to pose little or no threat to the environment (e.g. Arlinghaus and Mehner 2003; Szücs et al. 2007). However, in some areas where it has naturalised (e.g. Western Europe and Thrace/Anatolia in Turkey), the species status is being re-assessed due to increasing awareness of the potential risks posed to the native biota (Almeida et al., 2013; Tarkan et al., 2014; Copp et al., 2015), despite the species being highly prized for sports fish (e.g. Arlinghaus and Mehner 2003; Hickley and Chare 2004; Rapp et al. 2008), representing a valuable and productive fishery (e.g. Shumka et al. 2008; Mrdak 2009; Harlioğlu 2011), traditional ethnic food fish (Balon 1974). Finally, in several areas of its native distribution there is concern over the progressive disappearance of wild populations of *C. carpio* (e.g. Balon 1995; Mabuchi et al. 2006; Li et al. 2007; Yousefian 2011; Yousefian and Laloei 2011), which has led the species to be listed as "vulnerable" in these areas (IUCN Red List of Threatened Species: http://www.iucnredlist.org/details/6181/0).

Given the kaleidoscope of public perception about this ubiquitous freshwater fish (Vilizzi 2012), it is not surprising that a large number of experimental studies aimed at evaluating its effects on the environment has been carried out over the past nine decades. Recently, these experiments were extensively reviewed by Vilizzi et al. (2015a) in an up-to-date meta-analysis of the topic. In that review, a quantitative approach was employed based on causal criteria analysis (Webb et al. 2013), which has allowed an extensive evaluation of *C. carpio* effects on freshwater ecosystems. These have included: (i) an historical and biogeographical evaluation of supporting experimentation; (ii) identification and gauging of risk areas; (iii) assessment of the extent of impacts and strength of evidence in support; (iv) refinement of a global conceptual model of effects; (v) determination of potential critical biomass threshold(s); and (iv) provision of guidelines for future experiment-based investigations.

Yet, in Vilizzi et al.'s (2015a) study no account was made for a more "layman-oriented" approach that would allow environmental managers and stakeholders (generally, with more limited technical background but higher authority in the decision-making process) to appreciate the highlighted research priorities in view of the successful management of *C. carpio* in both natural and invaded freshwater ecosystems. The aim of this paper is therefore to complement Vilizzi et al.'s (2015a) technically-oriented "systematic" review (sensu Webb et al. 2013) with a narrative review similar to other studies in the environmental sciences (e.g. Niemi et al. 1990 and Yount and Niemi 1990; Vilizzi et al. 2013a and Gawne et al. 2012). As a prototypical study area, the outcomes of the findings are then discussed relative to the current status of *C. carpio* in Turkish inland waters, where an evaluation of the species biology and ecology has been under way with the ultimate objective to provide an overarching framework for future management actions (Vilizzi et al. 2013b, 2014a,b, 2015b,c).

Materials and Methods

To evaluate the effects of *C. carpio* on freshwater ecosystems, ten abiotic and biotic ecological components were investigated. Abiotic components included: turbidity/suspended solids, nitrogen and phosphorus; biotic components included: phytoplankton/chlorophyll *a*, aquatic macrophytes, zooplankton, benthic invertebrates, amphibians, waterfowl and fish.

A "near-comprehensive" collection (see Balon 1989 for caveats) of experimental studies of *C. carpio* effects on freshwater ecosystems was compiled from published literature sources, including peer-reviewed papers, thesis dissertations and, in some cases, gray literature (i.e. reports). Following Copp et al. (2009), investigations were included if one or more of the study's components had immediate/eventual application to natural freshwater ecosystems, thus entirely excluding aquacultural studies (e.g. Knösche et al. 2000; Frei et al. 2007; Kloskowski 2011a; Adámek and Maršálek 2013). Also, following Weber and Brown (2009), control/management-oriented restoration studies, including those providing mitigation of an impact prior to intervention (e.g. Pinto et al. 2005; Bio et al. 2008; Thomasen and Chow-Fraser 2012), were excluded.

As per Diamond (1983), experiments were first categorised, based on location, into laboratory, field or "natural". Laboratory experiments were defined as those conducted in a specially-designed environment (i.e. aquaria/ponds located in laboratory/outdoor facilities), in which variables can be easily controlled. Field experiments were those carried out in the species own environment (i.e. semi-natural ponds or natural ponds/water bodies), in which more limited control on the variables of interest is generally possible. Whereas, natural experiments were those in which one or more of the (independent) variables of interest (e.g. *C. carpio* biomass) vary naturally so that their effects on the response variable(s) (e.g. turbidity, macrophyte cover) can be quantified.

The second level of categorisation was applied to laboratory and field experiments according to type of “arena” used, ranging from aquaria to natural water bodies. By definition, natural experiments were carried out in a natural water body, and artificial ponds were defined as man-made (e.g. concrete) ponds, generally located at outdoor facilities. Whereas, semi-natural ponds encompassed those fed by a natural river/lake water and/or long-established for human usage. Finally, the plot type used (i.e. enclosures or exclosures: sensu Aerts et al. 2009) was also recorded, so that enclosure experiments were those in which *C. carpio* were stocked within a confined space; this contrasted exclosure experiments, which prevented *C. carpio* from accessing a confined area of water, thereby evaluating the species effects as a “free-ranging” organism.

Notably, studies that dealt with two or more experimental set-ups were reviewed separately; whereas, where the outcomes of an experiment were published in more than one paper, the corresponding references were evaluated together. As explained in Vilizzi et al. (2015a), this categorisation has allowed to arrange the experiments along a “reductionism–holism” continuum, ranging from a higher level of manipulation/control (e.g. laboratory experiments) to a higher level of generality (e.g. field and, especially, natural experiments).

Narrative review

Laboratory experiments

Aquaria

In an un-replicated experiment using two glass tanks (one treatment and one control), 0+ *C. carpio* increased nitrogen and phosphorus concentrations over the course of three weeks (Nuttall and Richardson 1991). However, based on extrapolated data the contribution of excretion to the net nutrient budget of a typical small lake was thought to be negligible at a *C. carpio* biomass comparable to that estimated to be detrimental for natural Australian water courses.

In a series of experiments using equal-sized aquaria, 0+ *C. carpio* at different densities increased turbidity and chlorophyll *a* and depressed growth of sago pondweed *Potamogeton pectinatus*, either directly through herbivory or indirectly by shade stress from increased turbidity and periphyton growth (Sidorkewicj et al. 1996, 1999a,b). These laboratory-based findings, which overall supported those from a related field (Sidorkewicj et al. 1998: Field experiments – Stocked water body) and a natural experiment (Fernández et al. 1998: Natural experiments), were aimed to provide insights into the management of *C. carpio* for weed control in irrigation channels of Argentina, but also to quantify the species negative effects on plant growth whenever preservation of aquatic macrophyte cover is sought.

As part of a study evaluating the potential of *C. carpio* to act as a biological control agent against invasive golden apple snail *Pomacea canaliculata* in Asia, the species was found to be a successful predator on adult individuals >20 mm (Yusa et al. 2006). And in another series of aquarium-based assays, 0+ *C. carpio* were found to consume more plant tissue of rough stonewort *Chara aspera* and less of four other species of aquatic macrophytes containing structural or chemical deterrents (Miller and Provenza 2007). These laboratory-based findings helped recommend which plants should be used in restoring larval/juvenile habitat refugia for endangered June sucker *Chamistes liorus* in Utah Lake (USA). Further, a related field experiment (Miller and Crowl 2006: Field experiments– Exclosures within a water body) showed how experiments conducted at different scales can help link theory with application.

Age 0+ *C. carpio* held in aquaria consumed meiobenthos (i.e. small benthic invertebrates 0.2–0.5 mm body length) thereby reducing the abundance of oligochaetes, crustaceans and especially nematodes (Spieth et al. 2011). Combined with a cage-based laboratory experiment (op. cit.: Enclosures within tanks), the results indicated that meiobenthos may represent a significant, yet often overlooked, food resource for 0+ *C. carpio*. These findings were supported by another series of experiments involving different size classes of 0+ *C. carpio* of the fully-scaled and mirror phenotypes, which indicated both size- and strain-related differences in the rate of consumption of the nematode *Caenorhabditis elegans* (Weber and Traunspurger 2014a). As a result of a related aquarium-based experiment, in which however no effects on nitrogen, phosphorus and chlorophyll *a* were detected, a conclusion was made that 0+ *C. carpio* may be able to exert top-down control of meiobenthic communities (Weber and Traunspurger 2014b).

Finally, in the only aquarium-based experiment evaluating the effects on fish, 0+ *C. carpio* was found to reduce growth of native crucian carp *Carassius carassius*, even though caution was suggested in extrapolating the results to natural situations due to the spatial constraints intrinsic to the study (Busst and Britton 2015).

Enclosures within tanks

Age 0+ *C. carpio* confined in cages within tanks were found to consume significant amounts of meiobenthos (mainly nematodes) by direct feeding from the sediment (Spieth et al. 2011). Combined with an aquarium-based laboratory experiment (op. cit.: Aquaria), these findings showed that meiobenthos can act as an important food source for *C. carpio*.

Tanks

A series of tank-based experiments investigated how 0+ *C. carpio* may alter zooplankton structure and benthic compartments in lake and pond communities. Results indicated that: (i) 0+ *C. carpio* increased nitrogen (but not phosphorus) and phytoplankton whilst partly suppressing large zooplankton (Cladocera) and enhancing small zooplankton (nauplii) through nutrient release by trophic cascade effects (Qin and Threlkeld 1990); (ii) at stocking densities similar to biomass levels found in reservoirs of central United States, 0+ *C. carpio* increased phosphorus and phytoplankton, reduced densities of benthic invertebrates and altered zooplankton community structure (Richardson et al. 1990); and (iii) 0+ *C. carpio* increased sediment re-suspension from benthivorous feeding leading in turn to increased levels of turbidity and nitrogen (but not phosphorus) and reducing zooplankton and benthic invertebrate abundance (Cline et al. 1994). Overall, findings from these experiments suggested that at high biomass 0+ *C. carpio* can significantly alter the abiotic and biotic components of shallow water columns.

A synergistic effect between phosphorus loading and 0+ *C. carpio* in increasing turbidity, nutrients (including nitrogen and phosphorus) and chlorophyll *a* was detected at high fish densities (Drenner et al. 1998), with findings supported by a larger-scale, pond-based laboratory experiment (op. cit.: Artificial ponds). Pending validation under real-world settings, it was concluded that populations of *C. carpio* can play an important role in the eutrophication process of lakes. Further, in a related experiment similar results were obtained for nitrogen and chlorophyll *a* and an increase in zooplankton also was observed at 0+ *C. carpio* biomass mirroring that reported in the wild for North America and Australia (Chumchal and Drenner 2004).

In (un-replicated) experimental tanks with and without plants, *C. carpio* at different densities displaced native benthic crayfish acocil *Cambarellus montezumae*, suggesting behavioural alteration effects (Hinojosa-Garro and Zambrano 2004). However, despite similar findings from a related pond-based laboratory experiment (Zambrano and Hinojosa 1999: Exclosures within artificial ponds), it was concluded that the potential for impacts on entire crayfish populations in shallow ponds of Mexico remained overall unknown.

An increase in chlorophyll *a* (but without variation in phosphorus contents) accompanied by a change in zooplankton grazer community composition, a decrease in benthic invertebrates and a reduction in native fish growth were documented after introducing 0+ *C. carpio* into mesocosms at different replacement densities for those of the native fish fauna (Carey and Wahl 2010). However, these negative effects were minimised with increasing native richness, supporting the theory of biotic resistance of more diverse native communities to invasive species. However, limitations in extrapolating these laboratory-based findings to population-level impacts of non-native fish were emphasised. Caution with extrapolations was also suggested in a study on 0+ *C. carpio* predation (held together with non-native eastern mosquitofish *Gambusia holbrooki* and European perch *Perca fluviatilis*) upon tadpoles of the endangered Booroolong frog *Litoria booroolongensis*, a species occurring predominantly along streams flowing west of the Great Dividing Range in south-eastern Australia (Hunter et al. 2011).

In mesocosms stocked at high densities, *C. carpio* were found to increase turbidity and nutrient levels (including nitrogen and phosphorus), decrease macrophyte biomass and benthic invertebrate abundance, and alter zooplankton structure (i.e. by increasing the relative abundance and density of rotifers and copepods), but without causing changes in chlorophyll *a* (Fischer et al. 2013). Notably, these effects occurred regardless of the presence of black bullhead *Ameiurus melas*, indicating that this native species, albeit tolerant of degraded ecosystems, is not a source of physical changes to the environment as is *C. carpio*. However, caution was suggested before making inferences to natural systems, due to the small size of the mesocosms and the high fish densities used in the experimental study. And in another experiment using mesocosms stocked with different density combinations of *C. carpio* and bighead carp *Hypophthalmichthys nobilis* (another invasive species of the Mississippi River Basin, USA), a decline in phosphorus concentrations occurred over the study period and this was accompanied by a reduction in macrozooplankton densities and macroinvertebrate richness (Nelson 2014).

Differences in continuous (*C. carpio* foraging and excretion), pulsed (carcass decomposition) and disrupted (*C. carpio* introduced and subsequently removed) nutrient subsidies were analysed in a mesocosm experiment (Weber and Brown 2013). The results indicated higher turbidity and lower macrophyte cover in continuous and, to some extent, pulsed systems, higher nitrogen, phosphorus and chlorophyll *a* content in pulsed systems, increased zooplankton densities in continuous systems, and higher chironomid density in control and disrupted relative to continuous and pulsed systems. Based on the same experimental set-up, the detrimental effects of 0+ *C. carpio* stocked at different densities due to increased turbidity, nitrogen and phosphorus concentrations as well as phytoplankton availability, reduced macrophyte cover and Cladocera body size (but with no effects on benthic invertebrates) were regarded as comparable to those commonly recognised for adult *C. carpio* (Weber and Brown 2015). Based on those findings, it was suggested that 0+ *C. carpio* can cause dramatic and wide-ranging impacts on freshwater ecosystems, even at biomass values below 175 kg ha^{-1}.

Enclosures within artificial ponds

Using within-pond enclosure plots stocked with *C. carpio* as an example of benthophagous fish, an increase in phosphorus and chlorophyll *a* was recorded, and this was attributed to the species digesting activities rather than by its direct stirring of sediments (Lamarra 1975). Supported by lake-based natural experiments on individual fish excretion, these findings suggested that removal of bottom-feeding *C. carpio* from lakes would significantly reduce phosphorus loadings. Under similar experimental conditions, 1+ *C. carpio* depressed density, biomass and production of tubificids (oligochaetes), suggesting that these may represent an important component of the species diet (Riera et al. 1991).

In a more comprehensive, longitudinal (i.e. over time) experiment, *C. carpio* held in ponds at two (low and high) stocking densities reflecting those occurring in the wild was found to increase turbidity, phosphorus, chlorophyll *a* and zooplankton biomass whilst reducing aquatic macrophyte cover and benthic invertebrate biomass (Parkos et al. 2003). This was unlike a native benthivorous species, channel catfish *Ictalurus punctatus*, which only affected phosphorus concentrations and altered zooplankton community structure. These findings suggested that *C. carpio* is able to exert a stronger influence on water quality and aquatic community structure compared to some native fish, even at the biomass of 174 kg ha^{-1}.

A deeper insight into the conflicting results around the mechanisms behind nutrient mobilisation by *C. carpio* was provided through a pond experiment, which indicated that fish size (hence, not only biomass) should also be accounted for (Driver et al. 2005). Thus, at a range of densities similar to those recorded in the wild (i.e. invaded freshwater systems of south-eastern Australia), large *C. carpio* (≈2 kg mean body weight) mobilised phosphorus through sediment re-suspension, whereas small *C. carpio* (0.6–0.7 kg mean body weight) did so mainly *via* excretion. Also, *C. carpio* was found to increase turbidity, nitrogen, phosphorus and chlorophyll *a*, and to reduce emergent and floating vegetation cover.

As part of an experiment evaluating the effectiveness of plastic mesh cover to reduce the negative effects of *C. carpio* on aquatic ecosystems, the following responses (at a biomass comparable to that reported from North American water bodies) were recorded: (i) increased turbidity and nutrient levels (including nitrogen and phosphorus); (ii) altered zooplankton community structure (i.e. increased density, though not biomass, and decreasing abundance over time); (iii) decreased aquatic macrophyte cover and benthic invertebrate abundance; but (iv) no change in chlorophyll *a* contents (Parkos et al. 2006). A conclusion was reached that lack of effective reduction of *C. carpio*-induced effects may limit the usefulness of mesh substrate cover as a tool for habitat restoration.

In one of the few experimental studies on the effects on native fish species, *C. carpio* increased turbidity and reduced macrophyte cover but was found to not affect spawning and larval growth of the native fishes largemouth bass *Micropterus salmoides* and bluegill *Lepomis macrochirus* (Wolfe et al. 2009). These results were attributed to the nest-guarding reproductive strategies of the two native species, which involve fanning the nest to oxygenate the eggs and prevent silt accumulation on the eggs. However, in the presence of *C. carpio*, growth of the same species slowed down during the juvenile period.

In another study on the role of *C. carpio* as biological control agent for golden apple snail, complete removal of the juvenile stages of this gastropod in the presence of *C. carpio* was recorded, but together with a significant reduction in aquatic macrophyte cover (Wong et al. 2009). These findings, which were later supported by a field-based study (Ip et al. 2014: Field experiments – Enclosures within a water body), suggested that caution should be exercised when introducing *C. carpio* as a control agent in wetlands with a high diversity of aquatic macrophytes and (possibly) benthic invertebrates.

At a biomass range similar to that generally used under experimental conditions and observed in the wild, *C. carpio* was found to disrupt trophic cascades in eutrophic ponds through strong bottom-up effects at multiple levels, but with some notable exceptions compared to findings from other studies (Wahl et al. 2011). Thus, whilst turbidity and nutrient levels (including nitrogen and phosphorus) increased, aquatic macrophyte cover, benthic invertebrate biomass and growth of juvenile largemouth bass and bluegill decreased, but with zooplankton biomass remaining unaffected and chlorophyll *a* biomass unexpectedly decreasing. The latter response was attributed to the continued presence of some aquatic macrophyte cover that, along with increased turbidity, may have contributed to reduce light penetration sufficiently to depress chlorophyll *a* concentrations. A conclusion was reached that *C. carpio* can have strong direct and indirect negative effects on several aquatic ecosystem components throughout their native and introduced ranges.

Finally, evidence was provided that the presence of a benthivorous freshwater fish species such as *C. carpio* depressed the overall abundance, biomass and secondary production of meiofaunal assemblages (with the exception of rotifers), altered the size structure of a natural meiofaunal community and affected both species richness and composition (though not diversity) of nematodes (Weber and Traunspurger 2015a,b).

Exclosures within artificial ponds

In small exclosures within experimental ponds, 0+ *C. carpio* exerted differential, direct effects on some soft-rooted aquatic macrophyte species and on benthic invertebrate communities (Zambrano and Hinojosa 1999). Further support to these findings was provided by a related natural (Zambrano et al. 1999: Natural experiments) and field experiment (Tapia and Zambrano 2003: Field experiments – Semi-natural ponds).

Artificial ponds

In possibly the first controlled (albeit un-replicated) experiment on *C. carpio* impacts, the destruction of aquatic vegetation was evident 51 days following introduction of the species into one half of a hatchery pond (Black 1946). In another experiment (Mraz and Cooper 1957), increased turbidity was recorded in two ponds stocked with *C. carpio* along with largemouth bass, bluegill and black crappie *Pomoxis nigromaculatus*. In that study, production of largemouth bass was found to be depressed, suggesting that proper management of fish-rearing ponds and small lakes should involve control of non-native fish surplus. Conversely, in another (un-replicated) experiment in artificial ponds and paddocks (of unspecified area) no effects of *C. carpio* on either turbidity or zooplankton were detected at two different stocking densities. This study concluded that introduction of this species for aquaculture into Nigerian waters would unlikely result in deleterious effects on the aquatic ecosystems of the region (Olaniyan 1961).

In a study on the effects of fish on plankton communities in ponds, 0+ *C. carpio* stocked at various densities increased zooplankton abundance, whereas no differences in phytoplankton were recorded between stocked and un-stocked ponds, or in those stocked with different numbers of fish (Grygierek et al. 1966). In another study, despite enhanced growth rates of 0+ and 1+ *C. carpio* in high- compared to low-fertility ponds (stocked at densities within the mean values reported for lakes and reservoirs of midwestern states in the USA), no significant interactions were found with either zooplankton, benthos or smallmouth bass *Micropterus dolomieu* (Haines 1973). Conversely, in another experiment *C. carpio* significantly reduced largemouth bass and bluegill standing crop (Forester and Lawrence 1978). This was likely a result of increased turbidity and decreased abundance of benthic invertebrates (i.e. oligochaetes and nematodes), but also of nest damage and invasion of fish spawning grounds by *C. carpio* within the ponds.

By contrast, inconclusive results (likely attributable to experimental design limitations) were achieved as regards interaction/competition between *C. carpio* and two Australian native fish species (namely, golden perch *Macquaria ambigua* and silver perch *Bidyanus bidyanus*) in experimental ponds (Hume et al. 1983). Also, no clear-cut effects on turbidity, macrophytes and zooplankton were detected in that study, nor in a related natural experiment conducted at the waterbody level (Hume et al. 1983; Fletcher et al. 1985: Natural experiments).

Stocking of 0+ *C. carpio* in drainable ponds in the Netherlands together with two other planktivorous species (namely, common bream *Abramis brama* and roach *Rutilus rutilus*) resulted in increased levels of turbidity and phytoplankton/chlorophyll *a*, lower densities of large zooplankton and higher densities of small zooplankton, but no change in nutrient levels (including nitrogen and phosphorus) (Meijer et al. 1990b). That study concluded that removal of planktivorous and benthivorous fish from shallow mesotrophic lakes in the Netherlands may result in pronounced benefits from reduced turbidity levels. Similarly, benthivorous feeding by *C. carpio* caused sediment re-suspension, which increased linearly with stocked fish biomass (Breukelaar et al. 1994a,b). And in another experiment, *C. carpio* reduced the biomass of benthic invertebrates through both direct (i.e. foraging) and indirect (i.e. shifts in microhabitat) effects, resulting in increased turbidity and phytoplankton, reduced aquatic vegetation cover and altered zooplankton community structure (Tátrai et al. 1994, 1997). The aim of those two experiments was to evaluate the effects of benthivorous *C. carpio* on the littoral zone of shallow lakes.

Increased turbidity and loss of aquatic macrophytes by uprooting (rather than herbivory) of soft-leaved aquatic species were observed in ponds stocked with *C. carpio* at two different density ranges, with more severe effects under (simulated) high- compared to low-impact conditions (Roberts et al. 1995). However, nutrient levels did not increase, possibly a result of the low phosphorus content of the sediments. The aim of the study was to re-examine the potential of *C. carpio* to affect negatively ecosystem structure and processes under Australian conditions, even though caution was suggested in extrapolating the findings to field situations because of limited supporting data at the natural waterbody level.

Angler catch rates for largemouth bass were found to be significantly lower in ponds containing *C. carpio* due to increased turbidity from its feeding behaviour (but with no effects on macrophytes), forcing the native centrarchid to locate alternative lures (Drenner et al. 1997). The stocking of artificial ponds with 0+ *C. carpio* as well as largemouth bass and bluegill, to simulate more realistic assessments of *C. carpio* effects, led to increased turbidity and chlorophyll *a* (but without any changes in nitrogen and phosphorus), decreased number of aquatic macrophyte species, increased zooplankton densities, and had no effect on fish (Drenner et al. 1998). These results, which were supported by a tank-based laboratory experiment (op. cit.: Tanks), were regarded as amenable to further testing and validation in larger and more environmentally-complex natural systems.

The impact of *C. carpio* on a rhizomatous macrophyte was investigated in replicated ponds divided into two halves (treatment and control) over two consecutive years (Swirepik 1999). The results suggested that well-anchored aquatic macrophyte species show tolerance to the physical disturbance associated with *C. carpio* benthic feeding (also found to increase turbidity); however, these same macrophyte species may become vulnerable to *C. carpio* disturbance during their regenerating and recruitment stages. In that study, the implications for aquatic macrophyte and riverine management, including the importance of excluding *C. carpio* from Australian wetlands, were also addressed.

In another pond-based experiment (carried out alongside a laboratory experiment, op. cit.: Exclosures within artificial ponds), *C. carpio* were found to increase turbidity and negatively impact on soft-leaved Canadian pondweed *Elodea canadensis,* but with no effects on benthic abundance (Zambrano and Hinojosa 1999). Specifically, high densities of 0+ *C. carpio* resulted in increased intra-specific competition and in a non-linear relationship with turbidity, suggesting a switch effect mechanism from clear- to turbid-water system conditions in shallow lakes. This shift was brought about by a combination of "dredging activities" (i.e. pumping sediments to the surface) and benthic foraging by *C. carpio*, and was enhanced by wind-induced sediment resuspension. The experiment also indicated that *C. carpio* at a biomass of ≈31 kg ha^{-1} would start suffering from intra-specific competition, and that at 50–75 kg ha^{-1} (L. Zambrano, pers. comm.) a significant increase in turbidity would already occur. Further support for the effects of *C. carpio* on turbidity was provided by a related natural experiment (Zambrano et al. 1999: Natural experiments).

The postulated top-down (trophic cascade) effects of a reduction in the biomass of planktivorous fish resulting in increased zooplankton and decreased phytoplankton biomass were tested by adding *C. carpio* to experimental ponds. This experiment resulted in "reversed effects" by *C. carpio* involving increased phytoplankton and decreased zooplankton abundances, accompanied by increased turbidity. Conversely, weak statistical evidence was provided for effects on nutrient levels (including nitrogen and phosphorus). Outcomes of the experiment were eventually extrapolated to turbid Australian lakes, though with a caveat for the higher turbidity levels typical of the latter compared to the experimental ponds employed in the study (Khan et al. 2003).

In artificial ponds stocked at various 0+ *C. carpio* densities, higher abundances of native crayfish acocil were recorded in the few areas with aquatic macrophytes left in ponds stocked at higher densities (Hinojosa-Garro and Zambrano 2004). Even though these interaction effects between *C. carpio* and crayfish acocil were supported by two related laboratory- (op. cit.: Tanks) and field-based experiments (op. cit.: Field experiments – Semi-natural ponds), caution was suggested when extrapolating the results up to entire populations of crayfish acocil under sub-tropical conditions. Further, *C. carpio* biomass did not affect turbidity, but was significantly correlated positively to nutrients, chlorophyll *a* and to the abundance of rotifers (but not with that of other zooplankton taxa), and negatively to guppy grass *Najas guadalupensis* (but not with overall aquatic macrophyte biomass) (Chumchal et al. 2005). These results emphasised the importance of biomass-dependent fish effects on aquatic ecosystems.

Field experiments

Enclosures within semi-natural ponds

In a study of *C. carpio* effects on nutrient dynamics and littoral community composition, bioturbation by "small" fish (at a biomass range similar to that found in natural ponds and lakes of North America) resulted in higher turbidity levels (Matsuzaki et al. 2007). At the same time, excretion activities increased nitrogen and phytoplankton biomass but decreased phosphorus contents. These changes led in turn to a reduction in aquatic macrophytes and benthic invertebrates (respectively due to limited light availability and lack of suitable microhabitat) and to an increase in the abundance of small-sized zooplankton. A conclusion was reached that *C. carpio*, through a combination of excretion and bioturbation mechanisms, can initiate in water bodies a regime shift from a (macrophyte-dominated) clear state to a (phytoplankton-dominated) turbid state. Further, based on a related experiment it was shown that even at low biomass can *C. carpio* as an "ecosystem engineer" exert large impacts on suspended solids, nutrients (including nitrogen and phosphorus), phytoplankton and benthic invertebrates (Matsuzaki et al. 2009a). Non-linear relationships between these response variables and *C. carpio* also indicated that such engineering effects saturate at biomass levels of ≈200–300 kg ha^{-1}. Although these findings were supported by a meta-analysis of previous studies, caution was suggested when extrapolating results to field situations, as stable-state changes in lakes typically occur at larger spatio-temporal scales that those achievable under controlled experimental conditions.

Stocking of 1+ *C. carpio* within cages caused complete disappearance of the larval anurans common spadefoot *Pelobates fuscus* and European tree frog *Hyla arborea*, and this was accompanied by a significant reduction in aquatic macrophyte biomass and benthic invertebrate (Anisoptera) abundance (Kloskowski 2011b). Combined with a pond-based field experiment (op. cit.: Semi-natural ponds), although with a caveat for possible greater mortalities of amphibians and invertebrates within cages, the results suggested that *C. carpio* predation and related effects may be primarily responsible for animal diversity loss in invaded communities, and that such effects may act prior to/or independent of an ecosystem's switch to a turbid phase. These findings were further supported by a related study using pond fisheries as a model system for research on fish–bird interactions, where 1+ *C. carpio* totally eliminated the young larvae of palatable amphibians by consuming them along with other digestible items of similar size (Kloskowski 2011c).

Semi-natural ponds

In an unreplicated experiment carried out in conjunction with biomanipulation studies at the waterbody level, *C. carpio* stocked with other benthivorous cyprinids (i.e. common bream and roach) increased turbidity (Meijer et al. 1990a). This suggested that *C. carpio* removal through biomanipulation can lead to higher water transparency in natural lakes. In another unreplicated study, age 0+ and older *C. carpio* caused a significant increase in suspended solids and phytoplankton, with resuspended sediment amounts being up to five to six times greater than the biomass of stocked fish (Lewkowicz and Żurek 1991). However, these effects were found to be more pronounced in shallower (80 cm) compared to deeper (160 cm) ponds. Further, within the constraints of pond-based experiments, survival of small tadpoles of the natterjack toad *Bufo calamita* was found to increase in the presence of small *C. carpio* (<10 cm, unspecified length), which selectively consumed predatory benthic invertebrates (Denton and Beebee 1997).

As part of a study on the ecological effects of *C. carpio* introduction for aquaculture in rural central Mexico, the significant positive correlations between *C. carpio* abundance and turbidity and negative correlations with aquatic macrophyte cover and benthic organisms previously reported from the laboratory (Zambrano and Hinojosa 1999: Laboratory experiments – Enclosures within artificial ponds and Artificial ponds) and under natural conditions (Zambrano et al. 1999: Natural experiments) were further tested and largely confirmed by stocking 0+ *C. carpio* in (unreplicated) semi-natural ponds (Tapia and Zambrano 2003). In the same study, the mole salamander *Ambystoma* sp. was found to be present only in shallow ponds without *C. carpio*. And in yet another related study, populations of the native crayfish acocil were reduced in semi-natural ponds due to habitat depletion by *C. carpio* at higher stocking densities (Hinojosa-Garro and Zambrano 2004). These results were supported by laboratory experiments in tanks and artificial ponds (Hinojosa-Garro and Zambrano 2004: Laboratory experiments – Exclosures within artificial ponds and Artificial ponds).

Increased turbidity, nutrients (including nitrogen and phosphorus) and chlorophyll *a* coupled with decreased aquatic macrophyte cover in the presence of *C. carpio* were reported in a series of large experimental wetland cells located in a degraded coastal wetland of Canada (Badiou 2005; Badiou and Goldsborough 2010). Notably, these findings were supported by a related field experiment (Badiou 2005: Enclosures within a water body). Also, in a large-scale, multi-year experimental study conducted in a bird sanctuary consisting of several man-made ponds, *C. carpio* negatively affected waterfowl through both direct and indirect pathways by reducing: (i) macroalgae and macrophytes both directly (i.e. through consumption and uprooting) and indirectly (i.e. through increased turbidity, mainly by sediment resuspension and suppression of large-bodied grazers of phytoplankton); (ii) benthic invertebrate biomass, directly through consumption and indirectly by habitat destruction; and consequently (iii) availability of plant and animal food resources to waterbirds, which increasingly preferred *C. carpio*-free ponds as the breeding season progressed (Haas et al. 2007).

The effects of *C. carpio* on aquatic communities, with emphasis on amphibians and waterfowl, were investigated through a series of experiments in managed *C. carpio* ponds at fish farms in Poland. Size-structured interactions between amphibian populations and *C. carpio* indicated that “large” fish (i.e. older than 0+) negatively impacted amphibian breeding performance, possibly due to reduced habitat suitability as a result of *C. carpio* foraging behaviour (Kloskowski 2009). These findings were confirmed in a follow-up experiment, which recorded lower amphibian species richness in ponds stocked with 1+ and 2+ (hence, larger) *C. carpio* compared to ponds containing 0+ individuals (Kloskowski 2010). Size-structured stocking of *C. carpio* ponds further showed that the abundance of benthic invertebrates, larval amphibians and some waterfowl (i.e. ducks and grebes) decreased with increasing fish size, unlike that of the piscivorous great crested grebe *Podiceps cristatus*, which preferred ponds with medium-sized *C. carpio* and was positively associated with total *C. carpio* biomass (Kloskowski et al. 2010). The overall adverse effects of *C. carpio* on aquatic biodiversity were further confirmed by pond-based experiments showing higher turbidity and phytoplankton abundance and lower aquatic vegetation cover in high- relative to low-*C. carpio* density ponds (Kloskowski 2011b). Also, bottom-up feeding by 1+ *C. carpio* reduced amphibian prey availability to the red-necked grebe *Podiceps grisegena* (Kloskowski 2011c).

The efficacy of *C. carpio* as a biocontrol agent of rice pest insects in the Philippines was assessed in rice field plot trials and indicated that densities of stemboring moths and chironomid midges was significantly reduced, whereas abundance levels of other arthropods were not significantly affected (Halwart et al. 2012). And in yet another evaluation of the role of *C. carpio* as a biological control agent for golden apple snail in the Philippines, *C. carpio* was found to be a more effective predator than Nile tilapia *Oreochromis niloticus* in rice fields (Halwart et al. 2014).

In ponds of the lower Waikato River flood plain (New Zealand), higher densities of ornamental “nishikigoi” or “koi” (redundantly, “koi carp”) were found to be associated with increased turbidity and relatively low macroinvertebrate abundance (Garrett-Walker 2014). The importance of body size in the structuring of aquatic communities was emphasised in yet another study in which *C. carpio* over time increased turbidity, phosphorus and phytoplankton, altered zooplankton and benthic invertebrate community structure, but did not affect macrophyte biomass/composition (Nieoczym and Kloskowski 2014, 2015). Notably, limitations with most of these field experiments were highlighted when drawing conclusions at larger scales, even though in two of the above studies results from semi-natural pond systems were cross-supported by findings from artificial ponds.

Enclosures within a water body

Using enclosures within a marsh, a negative correlation was found between *C. carpio* stocked at three different densities and amount of aquatic vegetation, but without effects on turbidity (Robel 1961). A conclusion was reached that, despite evidence for aquatic macrophyte damage by *C. carpio*, more research would be needed to understand the full complex of marsh-level relationships with this invasive fish. In this respect, after stocking *C. carpio* at low and high densities within enclosures in an Ontario lake (USA), consistent and severe losses in vegetation biomass accompanied by dramatic decreases in benthic invertebrate numbers were recorded, in spite of no effects on turbidity, nutrients and chlorophyll *a* (Macrae 1979). These results again suggested that *C. carpio* can exert negative impacts on some aquatic ecosystem components of shallow lakes.

Based on enclosures in a shallow temporary marsh in the Camargue (southern France), a negative relationship was found between *C. carpio* biomass and amount of aquatic vegetation left at the end of the experiment, but without effects on turbidity (Crivelli 1983). Also in that study, aquatic macrophyte loss was attributed to mechanical damage, similar to previous findings from North

America. The *C. carpio*'s negative effects on sago pondweed were later confirmed by another field experiment in South Dakota (USA), even though native black bullhead also produced similar impacts (Berry et al. 1990; Kolterman 1990). And in yet another field enclosure experiment conducted in a North American lake, *C. carpio* negatively affected benthic community structure and dynamics mostly by habitat modification and, to a lesser extent, by direct predation (Wilcox and Hornbach 1991). Finally, as part of a study aimed at quantifying the impacts of resource limitation and *C. carpio* predation on benthic midge populations in a western New York marsh (USA), 0+ fish held in small cages were found to reduce benthic midge larval densities (Batzer 1998). Notably, as a key component of that study, tests of cage artefacts were conducted to overcome potential confounding effects.

To address limitations with laboratory experiments conducted in plantless (outdoor) tanks, enclosures were installed in a degraded marsh (Cootes Paradise, Lake Ontario, Canada) to study the impact of a range of *C. carpio* biomasses on water quality and zooplankton in the absence of aquatic macrophytes (Lougheed et al. 1998). Results indicated that *C. carpio* increased turbidity and nitrogen, caused variation in phosphorus concentrations, but did not alter chlorophyll *a* contents and zooplankton biomass. Also, a 20 NTU turbidity threshold was identified above which aquatic plant diversity would significantly decrease. However, caution was suggested when extrapolating experimental outcomes from closed (i.e. enclosure) systems to the entire ecosystem due to likely differences in flow, turbulence and settling of particles. Findings from that study, which were backed up under natural conditions (op. cit.: Natural experiments Tanks), were ultimately aimed at informing remedial actions for marsh restoration/ biomanipulation programmes. Also, in a follow-up experiment using the same set-up, feeding activities of *C. carpio* caused sediment resuspension, with turbidity increasing with number of *C. carpio* per enclosure (Chow-Fraser 1999). These results were further supported by a related monitoring programme (op. cit.: Natural experiments).

In a degraded semi-arid floodplain wetland (Las Tablas de Daimiel National Park, Spain), *C. carpio* held in enclosures increased suspended solids, nutrients and chlorophyll *a*, decreased zooplankton biomass (Angeler et al. 2002a), but augmented bacterial zooplankton (Angeler et al. 2002b). Also, density of picoplankton did not change significantly in response to *C. carpio*-mediated changes in trophic state (i.e. increased turbidity, nutrient levels and chlorophyll *a*), but only relative to water levels following draw-down (Angeler and Rodrigo 2004). Similar findings were also obtained for seston size structure (Angeler et al. 2007). Notably, the very high stocking biomass range used in the above studies was chosen to reflect the natural *C. carpio* population biomass often encountered in the wetland under drought conditions. However, caution was recommended when extrapolating results based on field enclosure experiments to entire ecosystems.

In a comparative, multi-species enclosure experiment aimed at investigating top-down and bottom-up processes in shallow lakes, *C. carpio* increased suspended solids, phosphorus (but not nitrogen) and chlorophyll *a*, reduced aquatic macrophyte growth and benthic invertebrate numbers, and altered zooplankton structure due to smaller (<1.0 mm) individuals replacing larger (>1.0 mm) ones (Williams et al. 2002; Williams and Moss 2003). In that study, the observed decrease in aquatic macrophytes was attributed to increased epiphyton growth rather than to direct impacts from uprooting, and this started to occur at a *C. carpio* biomass >200 kg ha^{-1}. A conclusion was reached that interactions between top-down and bottom-up processes may be complex and likely to be entwined in a reciprocal feedback mechanism, which should be taken into account whenever attempting restoration programmes.

Using mesocosms in a Canadian marsh, *C. carpio* stocked at densities similar to those in the surrounding waters increased turbidity, nutrient levels, chlorophyll *a* and zooplankton abundance, whilst decreasing aquatic macrophyte cover and benthic invertebrate biomass (Badiou 2005). These results were confirmed by a related field experiment (Badiou 2005; Badiou and Goldsborough 2010: Semi-natural ponds). Further, in a shallow lake in north-central Utah (USA), *C. carpio* held in enclosures significantly affected species composition, abundance and diversity of macrophytes, which in turn decreased total benthic invertebrate diversity (Miller and Crowl 2006). Results of the latter experiment were supported by a related field experiment (op. cit.: Exclosures within a water body).

Within enclosures in a lake located on the south bank of the River Waal (Netherlands), *C. carpio* resuspended settled algae from the sediment, caused increased nutrients and chlorophyll *a*, but did not affect zooplankton (Roozen et al. 2007). Resuspension was considered to be an important mechanism affecting both phytoplankton biomass and community composition in shallow lakes. However, despite recognised limitations with the above enclosure experiment and a related survey of

93 floodplain lakes investigating relationships between suspended solids and phytoplankton biomass (op. cit.: Natural experiments), the combined observations were nonetheless deemed to provide strong support for the hypotheses being tested.

In a shallow Turkish "soda lake", *C. carpio* significantly increased turbidity and chlorophyll *a* and decreased aquatic macrophyte density, even though effects on nutrients and zooplankton remained unclear (Özbay 2008). These findings indicated that *C. carpio* can exert impacts also in such specialised habitats, which are characterised by a combination of high pH and salinity due to high concentrations of alkaline salts.

In a subtropical freshwater reservoir, *C. carpio* stocked within enclosures (at densities consistent with previous experimental fish manipulations) increased total suspended solids, nutrients (including Fe and Mn) and chlorophyll *a*, decreased aquatic macrophyte, epiphyte and periphyton biomass, but did not affect zooplankton abundance (Akhurst et al. 2012). Effects of benthivorous *C. carpio* on water quality deterioration were overall more pronounced than those of piscivorous native Australian bass *Macquaria novemaculeata* and non-native eastern mosquitofish. The results suggested that non-native fish removal may prove an effective management tool in sub-tropical systems for maintaining high water quality, justifying the need for biomanipulation regardless of the mechanisms (i.e. top-down or bottom-up) responsible for degraded water quality. Notably, in that study enclosure artefacts were also investigated to rule out their possible influence on the experimental outcomes.

Stocking small replicated enclosures at very high *C. carpio* densities, an immediate increase was recorded in suspended solids (Wells 2013). In a field experiment set up to support previous findings under laboratory conditions (Wong et al. 2009: Laboratory experiments – Enclosures within artificial ponds), *C. carpio* proved a very effective predator, hence biological control agent, on golden apple snail, even though it was also found to reduce significantly aquatic macrophyte abundance by grazing (Ip et al. 2014). Recommendations were made for the introduction of this species in wetlands, with preference given to black carp *Mylopharyngodon piceus*, which was found not to affect macrophytes. Finally, using mesocosms stocked with low and high *C. carpio* densities and different combinations of nutrient enrichment, turbidity, nitrogen and phytoplankton biomass increased as expected (but not phosphorus concentrations) and there was also a reduction in macrophyte cover (Badiou and Goldsborough 2015). From that study, it was concluded that the presence of *C. carpio* would mimic the effects of eutrophication, which would occur at a biomass of less than 600 kg ha^{-1}.

Stocked water body

After stocking Lake Klawój (Poland) with 0+ *C. carpio* over two consecutive years, a considerable decrease in the abundance and biomass of the invertebrate fauna was recorded, and this was attributed to direct feeding effects (Guziur and Wielgosz 1975). In Australia, stocking of two billabongs (= oxbow lakes) on the flood plain of the Murrumbidgee River using replicated high and low *C. carpio* biomass treatments demonstrated a significant impact on turbidity and intensity of algal blooms, but dependent on *C. carpio* biomass and sediment type (King et al. 1997). Also, rates of particle settlement throughout the experiment were greater in the high *C. carpio* treatment of each billabong, even though manipulations of *C. carpio* biomass did not affect algal biomass at the sediment surface (Robertson et al. 1997).

In Argentine irrigation channels, *C. carpio* stocked at two different densities with and without prior removal of aquatic vegetation reduced growing plant biomass (low densities) or eliminated existing vegetation (high densities), with increases in turbidity directly proportional to the size of the feeding individuals (Sidorkewicj et al. 1998). These findings were supported both in the laboratory (Sidorkewicj et al. 1996, 1999a,b: Laboratory experiments – Aquaria) and under natural conditions (Fernández et al. 1998: Natural experiments). Finally, accidental stocking of *C. carpio* into Lake Heiliger See (Germany) resulted in a pronounced reduction in benthos biomass, but apparently without negative effects on the native fish fauna (Barthelmes and Brämick 2003).

Exclosures within a water body

After placing sets of two or three circular exclosure plots in three lakes of Wisconsin (USA), an improvement in aquatic vegetation growth was observed in one of the treatments, where floating long-leaf pondweed *Potamogeton nodosus* thrived (Threinen and Helm 1954). Results of this experiment were supported by a series of interventions involving exclusion of *C. carpio* from a shallow bay near the study area. In a lake in Pennsylvania (USA), two replicated fenced and un-fenced "quadrats" (= plots) were set up at two locations and monitored over three consecutive years, with fencing/un-fencing treatments of each quadrat reversed in each year to avoid compounding effects resulting from the presence of a fence

(Tryon 1954). Even though turbidity remained similar, plant material biomass was considerably lower in the un-fenced relative to the fenced quadrats. These results were attributed to the mechanical effects of *C. carpio* uprooting and "splashing" habits, and were further supported by gut content examination indicating only algal consumption. However, caution was suggested in interpreting these experimental results, as the effects of fencing on plant growth remained unknown.

Based on small exclosure plots deployed in a marsh adjacent to Lake Erie (Michigan, USA), *C. carpio* were found to have a negative effect on aquatic macrophytes both by direct consumption (mainly of *Chara* spp.) and by uprooting them whilst foraging (King and Hunt 1967). In the same study, destruction of aquatic vegetation was further confirmed by a related *C. carpio* removal experiment. Also, growth of aquatic macrophytes was observed within small cages placed on the bottom of a lake in the Netherlands; whereas, the absence or low densities of aquatic macrophytes elsewhere in the lake were attributed to the digging behaviour of cyprinid fish including *C. carpio* (ten Winkel and Meulemans 1984). Aquatic vegetation surveys in other lakes of the area further supported the findings.

Macrophyte production was significantly greater inside small exclosures located in a tailwater reservoir than outside, where sediment disturbance also was higher (Harris and Gutzmer 1996). And in a coastal marsh, total suspended solids, chlorophyll *a* together with shoot density and above-ground biomass of aquatic macrophytes were significantly higher within small *C. carpio* exclosure wooden "boxes" relative to controls—although even higher values of the above components were recorded in turbidity exclosures (Sager et al. 1998). Further, following exclusion of *C. carpio* from cages placed in a marsh, there was variation in the abundance of epiphytic midges, which was attributed to increased populations of invertebrate competitors and predators in the absence of fish directly suppressing midge populations (Batzer et al. 2000).

Cyprinus carpio was amongst the fish species responsible for predation upon invasive zebra mussel *Dreissena polymorpha* Dreissenidae in a large floodplain river, as indicated upon comparison with cage exclosures (Bartsch et al. 2005). Also using small exclosures, molluscivorous fish including *C. carpio* played a pivotal role in limiting numbers of invasive bivalves (including dreissenids) in coastal wetlands of the Laurentian Great Lakes (Canada), where the abundance of native unionid mussels was found to have declined (Bowers et al. 2005). However, the possibility of reduced water currents within the enclosures as an experimental artefact was also taken into account. Overall, the above results were confirmed by another cage-based, exclosure experiment indicating that large-bodied molluscivorous fish including *C. carpio* can limit zebra mussel numbers in coastal wetlands (Bowers and de Szalay 2007). Importantly, in that study the possibility that exclosures may have affected fish predation was also considered.

In a shallow Turkish lake, exclusion of *C. carpio* along with other fish species and waterfowl did not significantly affect growth of sago pondweed, nor did it influence benthic invertebrate abundance (Sandsten et al. 2005). This lack of significant effects was attributed to the lake's nutrient levels being lower than the threshold level at which herbivory may tip the balance towards the turbid state in cold temperate lakes. The study concluded that the trophic state of a lake should be accounted for when evaluating the effects of *C. carpio* herbivory. Further, even though exclusion of *C. carpio* from small plots increased the biomass of aquatic macrophytes, it was speculated that other yet-unidentified mechanisms associated with the presence of planktivorous fish may be even more important in inducing a shift in aquatic macrophyte species composition on top of the direct action of *C. carpio* uprooting (Evelsizer and Turner 2006).

After installing large, fully-fenced and partly-fenced (i.e. open control) exclosures in two different sides of Utah Lake (USA) around existing sago pondweed beds, *C. carpio* significantly decreased total stem length of aquatic macrophytes in the open controls; whereas, no substantial differences in chlorophyll *a*, zooplankton abundance, and benthic invertebrate diversity, abundance and taxon richness were observed between open controls and exclosures. The study concluded that, although *C. carpio* can negatively affect aquatic macrophyte species, the underlying mechanisms (i.e. direct and indirect effects) remain uncertain (Miller and Crowl 2006). Results of that study were compared to those of a related field experiment (op. cit.: Enclosures within a water body).

Using exclosures with area an order of magnitude larger than the largest employed in any previous experiments, and ensuring an appropriate level of replication and control based on *a priori* power analysis, free-ranging *C. carpio* were found to increase turbidity, decrease macrophyte biomass and cover as well as benthic invertebrate richness and diversity, and alter zooplankton structure within one year since artificial inundation of a semi-arid floodplain wetland in South Australia (Vilizzi et al. 2014c). Also, an estimation of *C. carpio* biomass within the wetland indicated that at 68 kg ha^{-1}

C. carpio would already be able to induce a shift from clear- to turbid-water state.

Natural ponds

Through a series of intervention measures involving blasting/screening previously isolated/connected natural ponds to allow/prevent *C. carpio* access, respectively, the effects of *C. carpio* on several abiotic and biotic aquatic ecosystem components were studied in a degraded marsh of south-central Manitoba (Canada) (Hnatiuk 2006; Parks 2006; Hertam 2010). Results from combined surveys over four years indicated that *C. carpio* contributed to habitat degradation by increasing turbidity, nutrient levels and phytoplankton abundance, and by reducing aquatic macrophyte cover. Also, ponds with direct connection (hence, *C. carpio* access) to the marsh had fewer invertebrates and amphibians as well as mixed-species fish assemblages, contrary to screened ponds, where fish communities of tolerant small-sized species were present.

Natural experiments

An extensive survey across lentic and lotic habitats of the lower Goulburn River catchment (south-eastern Australia) found no correlation between turbidity and *C. carpio* biomass, and provided only circumstantial evidence for reduction of aquatic macrophyte cover attributable to *C. carpio* (Hume et al. 1983; Fletcher et al. 1985). High temporal and spatial variability inherent in the large-scale systems under investigation were thought to have hindered the outcomes of those surveys, even though a related laboratory experiment led to similar inconclusive results (Hume et al. 1983: Laboratory experiments – Exclosures within artificial ponds). Further, whilst increased concentrations of suspended solids, nitrogen and phosphorus due to the roiling activity of *C. carpio* were identified in bare stretches of irrigation channels of the Murray-Darling Basin, south-eastern Australia (Bowmer et al. 1994), only spatially mismatched distributions were detected between high *C. carpio* densities and high sedimentary phosphorus loadings in irrigation drains of the Murrumbidgee River, New South Wales (Meredith et al. 1995).

In Lake Begnas (Nepal), *C. carpio* stocked with other major carp species was found to exert adverse effects on native fishes due to its benthivorous feeding habits (Swar and Gurung 1988). Similarly, in the Columbia River (Washington, USA), *C. carpio* and three native fish species were responsible for predation upon the eggs of white sturgeon, whose populations were found to have declined following river habitat modifications (Miller and Beckman 1996). Finally, enhanced stocking of native *C. carpio* in Lake Balaton (Hungary) was deemed responsible for increased competition for food resources with silver bream *Blicca bjoerkna* along vegetated shoreline habitats, whose potential loss due to human-induced changes may represent an additional cause for inter-specific competition (Specziár et al. 1998).

Two extensive surveys of the irrigation system of the lower valley of the Rio Colorado (southern Argentina) identified strong environmental gradients between *C. carpio* biomass, turbidity and aquatic macrophyte abundance (Fernández et al. 1998). Evidence was provided for a significant and predictable impact on channel turbidity, which was in turn associated with reduced submersed plant growth. However, caution was suggested in interpreting these findings due to the limited power of correlative analyses in establishing causal relationships. Results of that study were backed up both in the laboratory (Sidorkewicj et al. 1996, 1999a,b: Laboratory experiments – Aquaria) and field (Sidorkewicj et al. 1998: Field experiments – Stocked water body), and led to conclude that *C. carpio*, if properly managed, may play a potentially beneficial role for weed control in Argentine irrigation systems.

Sampling of 19 wetlands of the Great Lakes Basin (Ontario, Canada), which were selected to range from pristine to severely degraded to ensure a large gradient of disturbance, indicated a strong negative correlation between turbidity and number of submersed macrophyte species (Lougheed et al. 1998). Even though *C. carpio* biomass reduction schemes were advocated as a remedy towards improved water clarity (hence, increased aquatic macrophyte abundance), the likely contribution of other stressors at the individual marsh level was also acknowledged. Notably, the above relationships were tested and supported by a field study (op. cit.: Field experiments – Enclosures within a water body). Also, results from a four-year monitoring programme in Cootes Paradise Marsh (Lake Ontario) indicated that *C. carpio* along with wind contributed to increased turbidity levels (Chow-Fraser 1999). Finally, during base-flow conditions, significantly higher concentrations of suspended solids were observed in the outflows compared to the inflows of three impoundments along an urban stream in southern Ontario (Barton et al. 2000). This suggested that, at least in one of the impoundments, *C. carpio* was responsible for elevated sediment export from bioturbation.

A survey of 12 sub-tropical, semi-natural shallow ponds in the Acambay region (central Mexico) indicated that stocking of *C. carpio* above a threshold value may cause detrimental impacts at several trophic levels, resulting in increased turbidity and decreased abundance of macrophytes, molluscs (gastropods) and other benthic invertebrates (Zambrano et al. 1999). However, no significant relationships were found between *C. carpio* biomass and nutrients (including nitrogen and phosphorus), phytoplankton and zooplankton, nor was there a quantifiable effect on an endemic fish species, the dark-edged splitfin *Girardinichthys multiradiatus*. Part of the outcomes of this correlational study was supported by a suite of experiments (Zambrano and Hinojosa 1999: Laboratory experiments – Exclosures within artificial ponds and Artificial ponds; Tapia and Zambrano 2003: Field experiments – Semi-natural ponds), with suspected impacts on endemic mole salamander being confirmed in the latter experiment, and those on endemic crayfish acocil in a follow-up study carried out under both laboratory (Hinojosa-Garro and Zambrano 2004: Laboratory experiments – Tanks and Artificial ponds) and field conditions (Hinojosa-Garro and Zambrano 2004: Field experiments – Semi-natural ponds). Further, a high food web overlap between *C. carpio* together with invasive Nile tilapia and crayfish acocil was detected in the Xochimilco aquatic system (Mexico City) (Zambrano et al. 2010).

Water quality sampling of inflows and outflows of Lake Eymir (Turkey) suggested that benthivorous feeding by dominant *C. carpio* together with tench *Tinca tinca* were responsible for elevated turbidity, nutrient levels (including nitrogen and phosphorus) and chlorophyll *a* as well as for reduced abundance of large zooplankton grazers (Beklioğlu et al. 2000). And in Lakes Marmara and Uluabat (Turkey), a strong inverse correlation was detected between *C. carpio* biomass and aquatic macrophyte cover (Beklioglu et al. 2006).

Sampling of 32 eutrophic to hyper-eutrophic lakes of Iowa (USA), nutrient enriched due to agriculture, pointed to positive correlations between *C. carpio* and white crappie *Pomoxis annularis* CPUE (catch-per-unit-effort) and negative with bluegill and black crappie (Egerston and Downing 2004). These findings (with a caveat for chance correlations owing to contrasting habitat requirements) suggested adaptation by the former native fish species to turbid, shallow waters, and an impact of *C. carpio* on the latter two species through interference with reproduction and growth. Also, in the mesotrophic, alkaline Chenango Lake (New York, USA), the sharp decline in submersed macrophyte vegetation cover measured over a ten-year period was attributed to both direct and indirect effects of *C. carpio* (Titus et al. 2004). On the contrary, introduction, establishment and spread of *C. carpio* in Lake Naivasha (Kenya) resulted in a substantial increase in aquatic macrophyte areal cover (Britton et al. 2007). This unexpected response was putatively attributed to avoidance by non-native red swamp crayfish *Procambarus clarkii* of vegetated areas occupied by *C. carpio*.

A negative association between non-native fish including *C. carpio* and water clarity was quantified from a survey of 49 small lakes in North Island, New Zealand (Rowe 2007). Interaction between *C. carpio* and fish were also investigated in three estuarine areas of the Western Mediterranean (Spain), with findings of lower catch per unit effort of native thicklip grey mullet *Chelon labrosus* supporting the "juvenile competitive bottleneck hypothesis" (Cardona et al. 2008). Whereas, results from of a macroinvertebrate community survey in a man-made wetland complex (South Skunk and Mississippi drainage basins, USA) suggested that *C. carpio* increased turbidity and reduced macroinvertebrate abundance in two of the study wetlands (Stewart and Downing 2008).

Based on a five-year study of the relationships between *C. carpio*, aquatic macrophytes and waterfowl, a threshold for *C. carpio* biomass of ≈100 kg ha^{-1} was identified above which a dramatic decline in vegetation cover and waterfowl abundance would occur (Bajer et al. 2009). The strength of these findings was based on several lines of evidence from the study area (a restored shallow lake in the midwestern USA), including strongly-related temporal series of predictor (i.e. *C. carpio* biomass) and response variables (i.e. vegetative cover and waterfowl abundance), absence of abiotic disturbance during the study period, a relatively stable fish community throughout, and support from laboratory and field experiments as reported from elsewhere in the literature.

A six-year survey of 129 lakes in Iowa (USA) found those with high catch rates of *C. carpio* to be characterised by high levels of turbidity, nitrogen and phosphorus concentration and phytoplankton biomass combined with low catch rates of sight-feeding, predatory sport fishes including largemouth bass, bluegill and black crappie (Jackson et al. 2010). Whereas, the opposite was true of water bodies with low *C. carpio* catch rates. A threshold biomass (2 kg per night of netting) was also identified above which lakes of the region would more likely to be in a turbid-water state. Another survey of 81 lakes across eastern South Dakota (USA) identified inverse threshold (0.6 fish per net night) relationships among relative abundances of *C. carpio* and those of several native fishes including black bullhead, black crappie, bluegill, white bass *Morone chrysops*, northern pike

Esox lucius, largemouth bass and smallmouth bass (Weber and Brown 2011). Also, lakes with higher abundances of *C. carpio* had higher levels of turbidity, nitrogen, phosphorus and chlorophyll *a*. Those findings were found to be consistent with the "biotic-abiotic constraining hypothesis", which argues that biotic factors can regulate fish populations regardless of abiotic conditions. Finally, in two lakes in Wisconsin (USA), a significantly lower number of several waterfowl species estimated in one of the lakes was attributed to the detrimental effects of *C. carpio* on wild rice *Zizania palustris* (Caithamer 2012).

Based on stable isotope and gut content analysis of native carp gudgeon group *Hypseleotris* spp. and 0+ *C. carpio* in three shallow water bodies within an Australian riparian system, an overlap in dietary resources and trophic positions was found to occur between the two species during hydrological recession (i.e. low-water conditions) (Mazumder et al. 2012). This suggested that *C. carpio* surviving prior to re-flooding of wetlands would take advantage of subsequent breeding and dispersal opportunities. Whereas, biomass of *C. carpio* (together with redbelly tilapia *Coptodon* cf. *zillii*) was found to affect residual somatic condition of the endangered Baja California killifish *Fundulus lima* in two drainage systems of Baja California Sur (Mexico) (Andreu-Soler and Ruiz-Campos 2013).

Invasion by *C. carpio* of Delta Marsh wetland (Manitoba) combined with that of a cattail hybrid *Typha* × *glauca* was implicated in the destruction of nesting environment for the western grebe *Aechmophorus occidentalis* (La Porte et al. 2014). Notably, the impact of *C. carpio* was related to its spawning activities in vegetated areas of the marsh, with violent "thrashing" being implicated in the destruction of grebe nests. Finally, contrary to expectations the presence of *C. carpio* in Lake Patzcuaro (Mexico) was not found to be negatively related to native species density and biomass, even when *C. carpio* density and biomass were positively correlated to water turbidity levels. With a caveat for the need of longer time-series data, it was argued that degraded environmental conditions in Lake Patzcuaro cannot be solely attributed to *C. carpio*, which after 40+ years of presence in the ecosystem can be considered to be integrated into its trophic processes (Ramírez-Herrejón et al. 2015).

Results and Discussion

In total, 139 experiments from 130 studies were reviewed, resulting in 400 "assessments" (i.e. an experiment that evaluates the effects of *C. carpio* on a certain ecological component) (Table 1). Since publication of Vilizzi et al. (2015a), ten additional experiments involving 27 assessments from eleven studies were added to the database (i.e. Yusa et al. 2006; Halwart et al. 2012, 2014; Garrett-Walker 2014; Weber and Traunspurger 2014a,b, 2015a,b; Badiou and Goldsborough 2015; Nelson 2014; Ramírez-Herrejón et al. 2015). Based on the outcomes of the current review, the previously-documented simultaneous alteration by *C. carpio* of bottom-up and top-down processes through a "middle-out" framework (Weber and Brown 2009) was confirmed and three additional pathways were identified (Figure 1) (see also Vilizzi et al. 2015a). Accordingly, resuspension of bottom sediments by *C. carpio* as a result of its benthic foraging leads to: (i) increases in turbidity, nutrient levels (also through excretion mainly by 0+ individuals) and phytoplankton production; (ii) reductions in benthic invertebrate abundance, diversity and richness (also by direct feeding); and (iii) the uproot of aquatic macrophytes (sometimes also consumed directly). Increased levels of turbidity, nutrient and phytoplankton negatively affect: (i) aquatic macrophyte growth through shading and smothering; (ii) benthic invertebrates by clogging of attachment sites; and (iii) zooplankton by altering community structure. In addition, previously unreported direct impacts on amphibians, waterfowl and fish as a result of foraging activities and/or spawning behaviour were identified. These direct and indirect effects ultimately cause most shallow-lake ecosystems to switch from a macrophyte-dominated, clear-water (oligotrophic) state to a phytoplankton-dominated, turbid-water (eutrophic) state (see alternative equilibrium theory: Scheffer et al. 1993). The resulting degraded habitat conditions negatively affect the abundance and richness of amphibians, waterfowl and native fishes (mainly piscivores and sight predators), and severely compromise amenity values (e.g. sport fishing, tourism industry).

Only four out of the experiments reviewed were carried out in Turkey, namely those by Beklioğlu et al. (2000, 2006), Sandsten et al. (2005) and Özbay (2008). Based on Vilizzi et al.'s (2015a) review, this country and, especially, the corresponding risk areas of Thrace and Anatolia (Tarkan et al. 2014) were categorised as "low risk" due to *C. carpio* being semi-naturalised, having low invasiveness, and being the object of overall positive public perception and low scientific concern (Vilizzi 2012; Tarkan et al. 2014). However, despite the limited sample size, outcomes of the assessments from the above experiments still supported the conceptual model for *C. carpio* effects on freshwater ecosystems (Figure 1), even though the strongest relationships pointing to water quality deterioration and reduction in macrophyte cover and biomass and in invertebrate abundance were, not surprisingly, detected based on the natural (hence, more holistic and less reductionist: Vilizzi et al. 2015a) experiments carried out by Beklioğlu et al. (2000, 2006) in shallow water bodies of north-west Anatolia.

Aside from the above (quantitative) experiments, qualitative observations have also been made on the putative effects of *C. carpio* in Turkish freshwater ecosystems. Wildekamp et al. (1999) pointed to serious degradation of the habitat for *Aphanius anatoliae splendens*, a threatened endemic cyprinodontid of Lake Salda, where *C. carpio* and rainbow trout *Onchorynchus mykiss* have been introduced. Innal and Erk'akan (2006) indicated that, whilst the introduction of *C. carpio* into Kara Lake in the early 1990s has threatened the endemic toros amphibian *Rana holtzi*, competition between *T. tinca* and *C. carpio* in Kayaboğazi Dam Lake and in Çamkoru Pond has prevented the latter species from maintaining viable populations; whereas, competition for food and space between *C. carpio* and crucian carp was reported in Mumcular Dam Lake. Finally, Zengin and Buhan (2007) discussed the negative effects that stocking of *C. carpio* in the Almus-Atatürk Dam lakes may have exerted on the native fish fauna.

In a recent, country-level evaluation of non-native and translocated freshwater fish species, Tarkan et al. (2015) considered *C. carpio* to be one of five "problematic" species (i.e. together with eastern mosquitofish, big-scale sand smelt *Atherina boyeri*, Gibel carp *Carassius gibelio* and topmouth gudgeon *Pseudorasbora parva*) that have established extensive populations and are considered invasive. However, unlike those other species the major impacts that have been attributed to *C. carpio* have been related to the accidental introductions of Gibel carp and topmouth gudgeon as contaminants of regular stockings of *C. carpio* itself. The latter is common practice in water bodies and, especially, man-made reservoirs of Anatolia and is being promoted by government agencies to enhance the species fisheries in response to demands from local communities. Specifically, the government agencies responsible for *C. carpio* stockings country-wide aim to compensate the economic losses faced by local communities as a result of private land encroachment from reservoir construction by providing an alternative, fisheries-related source of revenue. Yet, there is mounting evidence that the economic objectives of these regular stocking practices have fallen behind expectation. This is due to the overall poor recruitment of *C. carpio* in this type of water bodies (i.e. V-shaped profile reservoirs with limited spawning grounds for *C. carpio*), which, as indicated above, has represented a pathway of introduction of non-native (pest) species that have instead flourished.

Ecologically, and in the light of the above considerations, further stocking of *C. carpio* into man-made reservoirs of Anatolia, other than those where the species is already present (Çetinkaya 2010), may still be regarded as feasible.

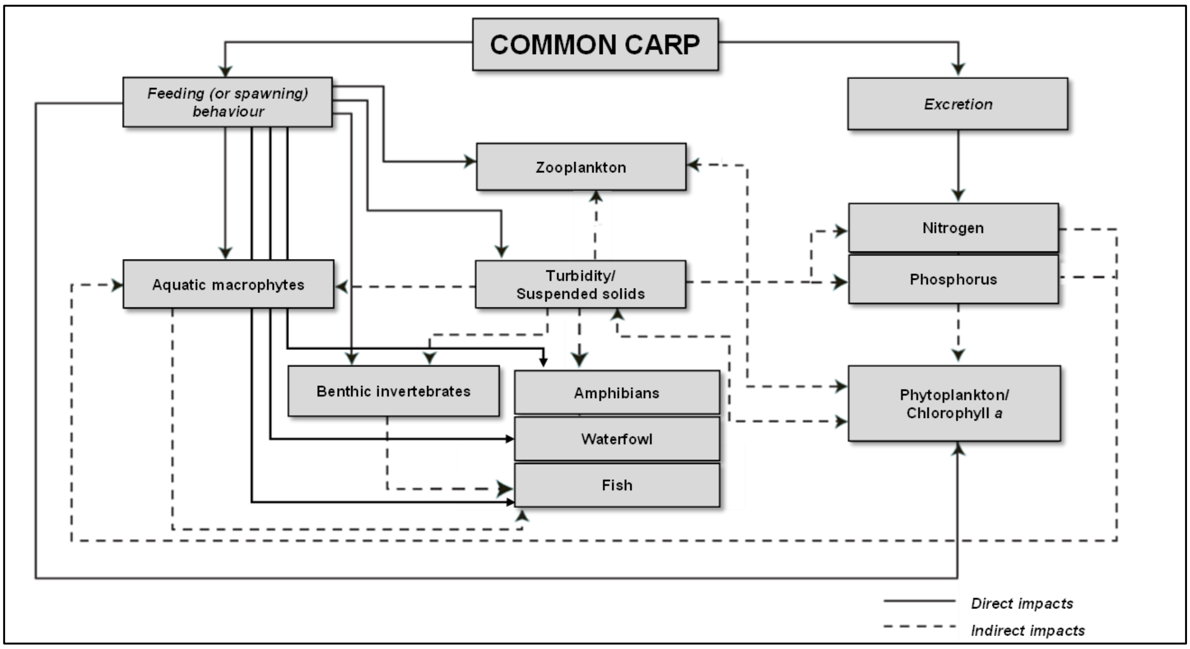

Figure 1. Conceptual model of the effects of *C. carpio* on freshwater ecosystems (after Vilizzi et al. 2015a).

Table 1. Reviewed experiments evaluating the effects of *C. carpio* on freshwater ecosystems.

Experiment	Country	Abiotic			Biotic						
		Water quality			Vegetation		Invertebrates		Vertebrates		
		TU	*N*	*P*	*PH*	*MA*	*ZP*	*BI*	*AM*	*WF*	*FI*
Laboratory											
Aquaria											
Nuttall and Richardson (1991)	Australia		+	+							
Sidorkewicj et al. (1996)	Argentina	+				−					
Sidorkewicj et al. (1999a)	Argentina	+			+						
Sidorkewicj et al. (1999b)	Argentina	+			+	−					
Yusa et al. (2006)	Japan							−			
Miller and Provenza (2007)	USA					Δ					
Spieth et al. (2011)	Germany							−			
Weber and Traunspurger (2014a)	Germany					−					
Weber and Traunspurger (2014b)	Germany		0	0		−	0				
Busst and Britton 2015	UK										−
Enclosures within tanks											
Spieth et al. (2011)	Germany							−			
Tanks											
Qin and Threlkeld (1990)	US		+	0	+		Δ				
Richardson et al. (1990)	USA			+	+		Δ	−			
Cline et al. (1994)	USA	+	+	0			−	−			
Drenner et al. (1998)	USA	+	+	+	+						
Chumchal and Drenner (2004)	USA		+		+		+				
Hinojosa-Garro and Zambrano (2004)	Mexico							−			
Carey and Wahl (2010)	USA			0	+		Δ	−			−
Hunter et al. (2011)	Australia								−		
Enclosures within artificial ponds											
Lamarra (1975)	USA			+	+						
Riera et al. (1991)	France							−			
Parkos et al. (2003)	USA	+		+	+	−	+	−			
Driver et al. (2005)	Australia	+	+	+	+	−					
Parkos et al. (2006)	USA	+	+	+	0	−	Δ	−			
Wolfe et al. (2009)	USA	+				−					Δ
Wong et al. (2009)	China					−		−			
Wahl et al. (2011)	USA	+	+	+	−	−	0	−			−
Weber and Traunspurger (2015a,b)	Germany							−			
Exclosures within artificial ponds											
Zambrano and Hinojosa (1999)	Mexico					−		−			
Artificial ponds											
Black (1946)	USA					−					
Mraz and Cooper (1957)	USA	+									−
Olaniyan (1961)	Nigeria	0					0				
Grygierek et al. (1966)	Poland				0		+				
Haines (1973)	USA						0	0			0
Forester and Lawrence (1978)	USA	+						−			−
Hume et al. (1983)	Australia	0				0	0				0
Meijer et al. (1990b)	Netherlands	+	0	0	+		Δ				
Breukelaar et al. (1994a,b)	Netherlands	+									
Tátrai et al. (1994, 1997)	Netherlands	+			+	−	Δ	−			
Roberts et al. (1995)	Australia	+	0			−					
Drenner et al. (1997)	USA	+				0					−
Drenner et al. (1998)	USA	+	0	0	+	−	+				0
Swirepik (1999)	Australia	+				−					
Zambrano and Hinojosa (1999)	Mexico	+				−		0			
Khan et al. (2003)	Australia	+	0	0	+		−				
Hinojosa-Garro and Zambrano (2004)	Mexico							−			
Chumchal et al. (2005)	USA	0	+	+	+	−	Δ				
Field											
Enclosures within semi-natural ponds											
Matsuzaki et al. (2007)	Japan	+	+	−	+	−	+	−			
Matsuzaki et al. (2009a)	Japan	+	+	−	+	−	+	−			
Kloskowski (2011b)	Poland					−		−	−		
Kloskowski (2011c)	Poland								−		
Semi-natural ponds											
Meijer et al. (1990a)	Netherlands	+									
Lewkowicz and Žurek (1991)	Poland	+			+						
Denton and Beebee (1997)	UK							−	+		
Tapia and Zambrano (2003)	Mexico	+				−		−	−		
Hinojosa-Garro and Zambrano (2004)	Mexico							−			
Badiou (2005); Badiou and Goldsborough (2010)	USA	+	+	+	+	−					
Haas et al. (2007)	Germany	+			+	−	−	−		−	
Kloskowski (2009)	Poland								−		
Kloskowski (2010)	Poland								−		

Table 1. Continued.

Experiment	Country	Abiotic			Biotic						
		Water quality			Vegetation		Invertebrates		Vertebrates		
		TU	*N*	*P*	*PH*	*MA*	*ZP*	*BI*	*AM*	*WF*	*FI*
Kloskowski et al. (2010)	Poland							−	−	Δ	
Kloskowski (2011b)	Poland	+			+	−					
Kloskowski (2011c)	Poland									−	
Halwart et al. (2012)	Philippines							−			
Garrett-Walker (2014)	New Zealand	+						−			
Halwart et al. (2014)	Philippines							−			
Nieoczym and Kloskowski (2014, 2015)	Poland	+		+	+	0	Δ	−			
Enclosures within a water body											
Robel (1961)	USA	0				−					
Macrae (1979)	Canada	0	0	0	0	−		−			
Crivelli (1983)	France	0				−					
Berry et al. (1990); Kolterman (1990)	USA	0				−					
Wilcox and Hornbach (1991)	USA							−			
Batzer (1998)	USA							−			
Lougheed et al. (1998)	Canada	+	+	Δ	0		0				
Chow-Fraser (1999)	Canada	+									
Angeler et al. (2002a)	Spain	+	+	+	+		−				
Angeler et al. (2002b)	Spain	+	+	+	+		+				
Williams et al. (2002); Williams and Moss (2003)	UK	+	0	+	+	−	Δ	−			
Angeler and Rodrigo (2004)	Spain	+	+		+		0				
Badiou (2005)	USA	+	+	+	+	−	+	−			
Miller and Crowl (2006)	USA					−		−			
Angeler et al. (2007)	Spain	+	+				−				
Roozen et al. (2007)	Netherlands		+	+	+		0				
Özbay (2008)	Turkey	+	0	0	+	−	0				
Akhurst et al. (2012)	Australia	+	+	+	+	−	0				
Wells (2013)	USA	+									
Ip et al. (2014)	China					−		−			
Badiou and Goldsborough (2015)	USA	+	+	0	+	−					
Stocked water body											
Guziur and Wielgosz (1975)	Poland							−			
King et al. (1997); Robertson et al. (1997)	Australia	+			+						
Sidorkewicj et al. (1998)	Argentina	+				−					
Barthelmes and Brämick (2003)	Germany							−			0
Exclosures within a water body											
Threinen and Helm (1954)	USA					−					
Tryon (1954)	USA	0				−					
King and Hunt (1967)	USA					−					
ten Winkel and Meulemans (1984)	Netherlands					−					
Harris and Gutzmer (1996)	USA	+				−					
Sager et al. (1998)	Canada	+			+	−					
Batzer et al. (2000)	USA							Δ			
Bartsch et al. (2005)	USA							−			
Bowers et al. (2005)	USA							−			
Sandsten et al. (2005)	Turkey					0		0			
Evelsizer and Turner (2006)	USA					−					
Miller and Crowl (2006)	USA				0	−	0	0			
Bowers and de Szalay (2007)	USA							−			
Vilizzi et al. (2014c)	Australia	+				−	Δ	−			
Natural ponds											
Hnatiuk (2006); Parks (2006); Hertam (2010)	Canada	+	+	+	+	−		−	−		−
Natural											
Hume et al. (1983); Fletcher et al. (1985)	Australia	0				Δ					
Swar and Gurung (1988)	Nepal										−
Bowmer et al. (1994)	Australia	+	+	+							
Meredith et al. (1995)	Australia			0							
Miller and Beckman (1996)	USA										−
Fernández et al. (1998)	Argentina	+				−					
Lougheed et al. (1998)	Canada	+				−					
Specziár et al. (1998)	Hungary										−
Chow-Fraser (1999)	Canada	+									
Zambrano et al. (1999)	Mexico	+	0	0	0	−	0	−			0
Barton et al. (2000)	Canada	+									
Beklioğlu et al. (2000)	Turkey	+	+	+	+		−				
Egertson and Downing (2004)	USA										Δ
Titus et al. (2004)	USA					−					

Table 1. Continued.

Experiment	Country	Abiotic			Biotic						
		Water quality			Vegetation		Invertebrates		Vertebrates		
		TU	*N*	*P*	*PH*	*MA*	*ZP*	*BI*	*AM*	*WF*	*FI*
Beklioglu et al. (2006)	Turkey					−					
Britton et al. (2007)	Kenya					+					
Rowe (2007)	New Zealand	+									
Cardona et al. (2008)	Spain										−
Stewart and Downing (2008)	USA	+						−			
Bajer et al. (2009)	USA					−				−	
Jackson et al. (2010)	USA	+	+	+							−
Zambrano et al. (2010)	Mexico								−		
Weber and Brown (2011)	USA	+	+	+	+						−
Caithamer (2012)	USA									−	
Mazumder et al. (2012)	Australia										−
Andreu-Soler and Ruiz-Campos (2013)	Mexico										−
La Porte et al. (2014)	USA									−	
Ramírez-Herrejón et al. (2015)	Mexico										0

Freshwater ecosystem components: *TU* = Turbidity/Suspended solids; *N* = Nitrogen; *P* = Phosphorus; *PH* = Phytoplankton/ Chlorophyll *a*; *MA* = Aquatic macrophytes; *ZP* = Zooplankton; *BI* = Benthic invertebrates; *AM* = Amphibians; *WF* = Waterfowl; *FI* = Fish. For each assessment (i.e. experiment evaluating the effects of *C. carpio* on a certain component) notation for outcomes is as follows: + (Increase); − (decrease); Δ (non-directional change, i.e. increase/decrease or one direction, i.e. increase or decrease, for a sub-set of the component and no change for the other); 0 (no change).

This is because little or no ecologically detectable "direct" impacts by *C. carpio* on the native fauna are expected, even though preventative measures should be adopted to avoid the accidental and concomitant introduction of noxious non-native species (Tarkan et al. 2014), with possibility of increased threats to the conservation of the native (fish) faunas. Alternatively, and considering the potential of *C. carpio* to represent a highly productive fishery for Turkish inland waters (Turkish Statistical Institute 2014), it is argued that, if successful stocking of this species is to be achieved (i.e. in terms of later recruitment of 0+ individuals into exploitable stocks), then shallow (natural) lakes in lieu of man-made reservoirs could be targeted. This is because of the species capacity to colonise successfully such habitats, as indicated by experimental evidence (Beklioğlu et al. 2000, 2006) and ecological models (Tan and Beklioglu 2006; Beklioglu and Tan 2008). However, before the implementation of stocking programmes into shallow water bodies can be considered, a proper assessment of the economic benefits vs. ecological risks involved is required (Vilizzi 2012), lest perceived socio-economic benefits ultimately prevail over ecological concerns.

In conclusion, and within a broader worldwide perspective, the pairing of technical and more layman-oriented contributions as achieved with the present review (i.e. as a complement to Vilizzi et al. 2015a) is expected to improve the dialogue between scientists and environmental managers/stakeholders. As in the case for Turkey, this will facilitate the gauging of outcomes from the general framework of *C. carpio* effects on the environment relative to risk level of the study area, as could be the case of the potential stocking of shallow water bodies of amenity value.

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