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Common carp disrupt ecosystem structure and function through middle-out effects

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Abstract. Middle-out effects or a combination of top-down and bottom-up processes create many theoretical and empirical challenges in the realm of trophic ecology. We propose using specific autecology or species trait (i.e. behavioural) information to help explain and understand trophic dynamics that may involve complicated and non-unidirectional trophic interactions. The common carp (*Cyprinus carpio*) served as our model species for whole-lake observational and experimental studies; four trophic levels were measured to assess common carp-mediated middle-out effects across multiple lakes. We hypothesised that common carp could influence aquatic ecosystems through multiple pathways (i.e. abiotic and biotic foraging, early life feeding, nutrient). Both studies revealed most trophic levels were affected by common carp, highlighting strong middle-out effects likely caused by common carp foraging activities and abiotic influence (i.e. sediment resuspension). The loss of water transparency, submersed vegetation and a shift in zooplankton dynamics were the strongest effects. Trophic levels furthest from direct pathway effects were also affected (fish life history traits). The present study demonstrates that common carp can exert substantial effects on ecosystem structure and function. Species capable of middle-out effects can greatly modify communities through a variety of available pathways and are not confined to traditional top-down or bottom-up processes.

Additional keywords: food webs, ecosystem engineers, shallow lake ecosystems.

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Introduction

The concept of trophic cascades has been a cornerstone and one of the greatest breakthroughs in recent ecological studies for understanding energy flow and community dynamics, especially in aquatic ecosystems (Carpenter *et al.* 1985; Strong 1992; Pace *et al.* 1999). Yet, empirical information and ecological modelling have not always been congruent, despite gaining

widespread interest, to capture this process. Attempts to address this misalignment has resulted in creating a series of feedback loops and the incorporation of food chain length and behavioural components (Schmitz *et al.* 1997). The primary framework of trophic cascades was guided by grouping species according to their respective feeding guilds and subsequent ecological impact (Carpenter and Kitchell 1988). Although simplistic and

intuitive, this approach fails to consider species-specific functional traits or organismal performance metrics that affect cascade direction (e.g. top-down, bottom-up) and magnitude. Grouping species according to trophic position also fails to identify subwebs or weak and indirect links and the degree of effects within a series of reactions (Borer *et al.* 2005). Thus, a more refined understanding of trophic patterns and processes could be achieved by incorporating species-specific traits (DeAngelis 2013; van Veen and Sanders 2013).

Incorporating functional trait information is gaining widespread interest across ecological disciplines to explain ecosystem patterns and processes (de Bello *et al.* 2010; Morales-Castilla *et al.* 2015; Wood *et al.* 2015). Ecosystem function is a product of resource dynamics and ecosystem stability, which are strongly affected by individual species and interspecific relationships (Díaz and Cabido 2001). Therefore, species functional trait information could be a great tool to explain complex community- and ecosystem-level interactions within the realm of trophic cascades (Duffy *et al.* 2007), in addition to species richness and diversity metrics (Noss 1990). Certain species and associated traits can greatly affect resource availability and energy flow for other species (i.e. ecosystem engineers; Jones *et al.* 1994). Species that directly and indirectly modify habitat are particularly important to consider in a functional trait and ecosystem framework.

Species-specific trait information has already given promise and insight into understudied trophic cascade dynamics (Schmitz *et al.* 2004; Greeney *et al.* 2015). Middle-out effects, which do not conform strictly to a bottom-up or a top-down series of reactions (i.e. hybrid of the two), have been described for both freshwater and marine ecosystems (DeVries and Stein 1992; Allen and Fulton 2010). Multiple disturbance pathways exist and can often stem from one species, creating complex and unpredictable bottom-up and top-down effects (DeVries and Stein 1992; Jones *et al.* 1994; Wahl *et al.* 2011). For example, open water omnivores, such as the gizzard shad (*Dorosoma cepedianum*), can affect zooplankton, detritus and phytoplankton densities by direct consumption, subsequently reducing food availability for bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*), which depend on bluegill as prey (DeVries and Stein 1992; Stein *et al.* 1995). Middle-out patterns may manifest themselves through multiple pathways available (opposed to an alternating chain-like pathway for traditional trophic cascades; McQueen *et al.* 1986) and are dependent on habitat, community dynamics and individual species composition. This complexity may require a different approach to understand food webs and illuminate patterns and processes otherwise obscured with traditional trophic cascade thinking. Within a functional grouping, species traits can differ widely and, furthermore, at an interspecies level (DeAngelis 2013). Specific and broad information concerning species traits, such as foraging behaviour (van Veen and Sanders 2013), could strengthen the accuracy, precision and overall utility of food web and trophic ecology conceptual and quantitative models (Schmitz *et al.* 2004).

The aim of the present study was to investigate whether autecological traits could provide a more realistic approach to our understanding of trophic cascade ecology by using traits (such as behaviour) to guide the development of conceptual and

quantitative models (particularly to explain middle-out effects). The benefits could reveal mechanisms relating to lag effects or delays in trophic-level response, how trophic interactions transpire and the proximity and resilience of multiple trophic levels to changes in ecosystem structure and function. We chose to address these trophic cascade questions using freshwater lakes and common carp (*Cyprinus carpio*), considering much of the early conceptual and empirical work was developed on these systems (Carpenter and Kitchell 1988; Pace *et al.* 1999). Common carp served as our focal species to test for middle-out effects and to evaluate how acknowledging species traits (e.g. behaviour) could improve the interpretation of trophic patterns and processes (Fig. 1). For example, common carp foraging behaviour can result in mobilising nutrients (bottom-up) and the reduction of macroinvertebrate densities (top-down). Without incorporating this and other species trait information, it is difficult to understand trophic relationships and effects. Common carp are considered ecosystem engineers (Jones *et al.* 1994; Parkos *et al.* 2003; Matsuzaki *et al.* 2009) because of their inferred ability to affect aquatic systems (i.e. modify habitats) through middle-out effects (Richardson *et al.* 1990; Wahl *et al.* 2011), although limited information has been obtained at the ecosystem level (e.g. lake; Weber and Brown 2009; Vilizzi *et al.* 2015).

The present study used both observational and experimental techniques at a whole-lake ecosystem level to investigate complex middle-out trophic effects. Four identified common carp disturbance pathways were developed from the existing literature and evaluated. These pathways included an adult abiotic, early life feeding, adult biotic and an adult nutrient pathway (see Fig. 1). The study was designed to test the relative support for each pathway, because it is often unclear which mechanism is primarily responsible despite clear patterns or outcomes. Common carp benthic foraging often results in increased water turbidity. However, multiple trophic levels must be examined in concert at the appropriate scale to detect causation and ultimately unravel the mechanisms (or variables) involved. Turbidity may increase, but several indirect or direct pathways exist to reach this outcome. Our goal was to gain more insight to this complex middle-out process by empirically testing each pathway at the ecosystem level rather than at a reduced spatial or temporal scale, as recommended by Vilizzi *et al.* (2015).

Materials and methods

All work described herein was approved by the South Dakota State University Institutional Animal Care and Use Committee (#08-A021).

Study area and metric selection

All lakes sampled were natural and part of the Sandhill ecoregion in north central Nebraska (USA). These lakes depend on groundwater and surface water drainage, with many having flowing springs and seepages. Although the lakes may have 2–3 months of ice cover, winterkills are limited (McCarragher 1977). The observational component included 16 lakes with similar fish assemblages, except that eight lakes contained common carp and eight did not; all lakes had a similar surface area

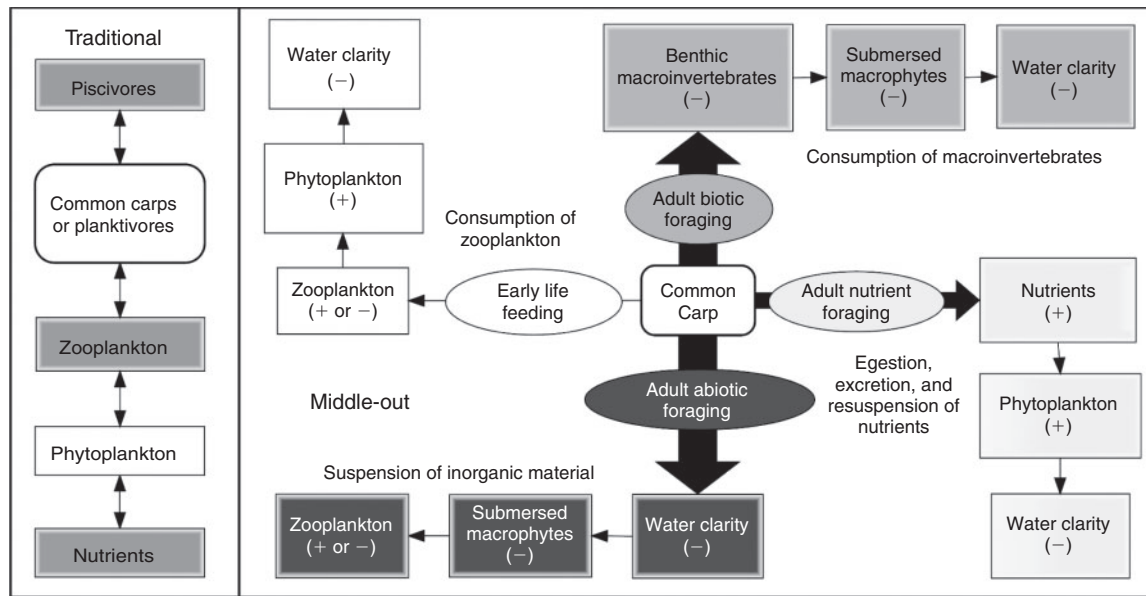


Fig. 1. A schematic demonstrating common carp trophic effects in a traditional (bottom-up, top-down; left) and middle-out (right) framework. A middle-out approach highlights (1) four potential common carp disturbance pathways; (2) direction and trophic position of the pathways; and (3) magnitude (arrow width stemming from common carp, with larger width reflecting a larger disturbance) and potential effect of disturbance (negative sign indicates a decrease; positive sign indicates an increase). Ovals represent the immediate activity and behaviour or process of common carp disturbance. For a summary and review, see [Weber and Brown \(2009\)](#) and [Vilizzi et al. \(2015\)](#).

(carp v. non-carp $F_{1,14} = 1.28$, $P = 0.28$, analysis of variance, ANOVA) and each lake was sampled once during 1998 or 1999 (see Table S1, available as Supplementary material to this paper) using conventional sampling gear (e.g. electrofishing; [Bajer and Sorensen 2012](#)). Common carp size and age structure were not measured across lakes, but rather their presence or absence was assessed. All variables from each lake were sampled concurrently except for vegetation (July 1999).

Two lakes were selected as part of the experimental component. Pony Lake (64 ha) served as the treatment lake and West Long Lake (25 ha) served as the reference lake. Pony Lake was dominated by common carp and existed in a turbid and limited submersed vegetation state ([Kaemingk and Willis 2014](#)). The fish community also included black bullhead (*Ameiurus melas*), fathead minnow (*Pimephales promelas*), golden shiner (*Notemigonus crysoleucas*), green sunfish (*Lepomis cyanellus*), pumpkinseed (*Lepomis gibbosus*), yellow perch (*Perca flavescens*) and grass pickerel (*Esox americanus vermiculatus*), but no top-level piscivores (e.g. largemouth bass or northern pike, *Esox lucius*). West Long Lake existed in a clear water and vegetated state; the fish community was comprised primarily of bluegill, yellow perch, black bullhead and two top-level piscivores, namely largemouth bass and northern pike ([Jolley et al. 2008](#)).

We selected important metrics according to previous studies (for a summary, see [Weber and Brown 2009](#)) across a range of lake trophic levels to identify bottom-up and top-down processes, investigating the relative support of each in a middle-out framework at the ecosystem level ([Fig. 1](#)). Whole-lake middle-out effects were evaluated by comparing metrics across the food web (as in nutrients, phytoplankton,

zooplankton, benthic macroinvertebrates) between lakes using common carp as the treatment (presence or absence) for the observational portion and the removal of common carp for the experimental portion of the study. In addition, representative fish from different trophic feeding guilds (bluegill, insectivore; yellow perch, lower level piscivore; and largemouth bass, higher level piscivore; [Vander Zanden et al. 1997](#)) were also evaluated using dynamic rate function responses (i.e. recruitment, growth and mortality) for the observational component.

Observational approach

Bottom-up effects sampling

Total phosphorous, Secchi disc transparency and chlorophyll-*a* were measured at four random sites within each lake as metrics of primary productivity. Total phosphorus was measured with Hach kits (Hach, Loveland, CO, USA) and chlorophyll-*a* was estimated from duplicate samples of four offshore water samples collected with a 2 m-long vertical tube sampler ([Paukert and Willis 2003](#)). Samples were filtered through glass fibre filters in the field and extracted in the laboratory by methods described by [Lind \(1979\)](#). Submersed vegetation was quantified for all 16 lakes at five to seven transects evenly spaced across each lake. At 50- to 200-m intervals (depending on lake size) along each transect, vegetation within a 1-m² grid beside the boat was classified as either emergent or submersed ([Paukert et al. 2002a](#)). The percentage coverage of submersed vegetation was calculated as the number of sites containing submersed vegetation divided by the total number of sites sampled across all transects in the lake ([Paukert et al. 2002a](#)).

Top-down effects sampling

Zooplankton and benthic macroinvertebrates were sampled at the same four randomly selected sites in each of the 16 lakes examined (for detailed methods, see [Paukert and Willis 2003](#)), representing the available habitat in each lake. Concurrent zooplankton (two replicates) and benthic macroinvertebrates (three samples) were collected at each site. In the laboratory, zooplankton were enumerated and identified to Family for cladocerans (i.e. Bosminidae, Chydoridae and Daphnidae) and as cyclopoid or calanoid copepods and copepod nauplii. The total number of zooplankton of each taxon in a sample was calculated by dividing the number of organisms counted by the proportion of the sample volume processed. Density was then calculated by dividing the number of zooplankters of each taxon by the volume of the water filtered with the tube sampler. A maximum of 120 individuals of each zooplankton taxon was measured. Zooplankton taxon-specific length–dry weight conversions were used to convert length to biomass ($\mu\text{g L}^{-1}$; [Cummins and Wuycheck 1971](#); [Dumont *et al.* 1975](#); [Culver *et al.* 1985](#)). Macroinvertebrates were identified to Order and counted. Density was then calculated by dividing the number of benthic invertebrates of each taxon by the area sampled with the Ekman grab.

Bluegill and yellow perch were sampled at randomly selected locations with 20 overnight sets per lake of double-throated trap nets (i.e. modified fyke nets) with 16-mm bar measure mesh, 1.1 × 1.5-m frames and 22-m leads. Largemouth bass were sampled by pulsed direct current (DC; 200–250 V, 3–6 A) night-time boat electrofishing at 12 randomly selected 10-min stations, in May or June. Scales for age and growth analyses were collected from bluegill, yellow perch and largemouth bass ([Paukert *et al.* 2002b](#)). A total of 10 individuals was aged per 1.0-cm length group of each species per lake. Mean length at age for all species was fitted to a non-linear least-squares regression model (assuming additive errors) with the von Bertalanffy growth function ([Ricker 1975](#)). Models were then used to estimate growth as the time in years for each species to reach preferred lengths (bluegill 200 mm, yellow perch 250 mm, largemouth bass 380 mm; [Gabelhouse 1984](#)). Total instantaneous mortality (Z) was estimated from the descending limb of catch curves for each population ([Ricker 1975](#)). A recruitment variability index (RVI) allowed the estimation of variability in recruitment among lakes with and without common carp for each species ([Guy and Willis 1995](#)). Estimates for the recruitment variability index ranged from –1 to 1, with increasing values indicating less recruitment variability (i.e. consistent).

Statistical analysis

ANOVA (PROC MIXED method in SAS, ver. 9.3; SAS Institute, Cary, NC, USA), was used to determine whether bottom-up effects (i.e. total phosphorus, Secchi disc transparency, submersed vegetation and chlorophyll-*a*), top-down effects (i.e. zooplankton, benthic macroinvertebrates, and fish recruitment, growth and mortality) were evident between lakes with and without common carp. Data were log transformed ($\log_{10}[N + 1]$) when necessary to achieve normality and homogeneity of variance. Differences in treatment means were assessed at $\alpha \leq 0.10$ to guard against a Type II error. We considered a Type II error

more probable because no treatment or variable was applied or manipulated in this portion of the study ([Mapstone 1995](#)).

Four common carp disturbance pathways were compared and evaluated using an information theoretic approach (Akaike's information criterion (AIC); [Burnham and Anderson 2002](#)). Model weights were calculated by taking the relative likelihood of a model and dividing that number by the summation of all model relative likelihoods. The sum of all model weights within a candidate set is equal to 1, with each model given a value between 0 and 1. The highest Akaike weight among the candidate set of models can be interpreted as the percentage chance that it is the best approximating model (among all models considered). Model disturbance pathways included an adult abiotic, early life feeding, adult biotic and an adult nutrient pathway (see [Fig. 1](#)). Logistic regression models (Proc Logistic method in SAS, ver. 9.3; SAS Institute) were developed using the presence or absence of common carp as the response variable and independent variables from each disturbance pathway. Independent variables were selected and grouped according to other common carp studies (for a review, see [Weber and Brown 2009](#)). Some variables are included in multiple models (e.g. submersed macrophytes) but describe different pathways or mechanisms involved. For example, adult biotic foraging for benthic macroinvertebrates may uproot submersed aquatic vegetation, whereas adult abiotic foraging may mobilise sediment and reduce light attenuation for plant growth. Therefore, both the adult biotic foraging pathway and the adult abiotic foraging pathway result in reduced submersed macrophyte density, but the underlying mechanism (or pathway) is different. The greatest level of support is then given to the pathway with the largest global or cumulative effect of each variable in the model (evaluated by differences in AIC corrected for small sample bias, ΔAIC_c , scores and model weights). Including each variable within a series of potential pathways would reveal bottom-up- or top-down-driven common carp effects and place them in a middle-out framework.

Renovation approach

Renovation design

A before–after–control–impact (BACI; [McDonald *et al.* 2000](#)) design was used over a period of 6 years (2005–10) to examine changes in the abiotic components and biotic community before ($n = 3$ years) and after ($n = 3$ years) a fish toxicant (rotenone) was applied to Pony Lake to eradicate the fish community. Four randomly chosen sites were sampled seasonally (i.e. April, spring; July, summer; late September–early October, autumn) within both the treatment and reference (West Long) lake. The BACI design allowed inferences to be made on whether any changes in the treatment lake (Pony Lake) were caused by our treatment or some widespread environmental factor that may affect both lakes (e.g. precipitation, wind, temperature, hydrology).

An attempt was made to eradicate the entire carp-dominated Pony Lake fish community during October 2007 (end of Year 3 and after the autumn 2007 samples were collected) with a rotenone treatment. Rotenone was chosen as the most effective method to eradicate the common carp population ([Weier and Starr 1950](#); [Schrage and Downing 2004](#); [Hicks and Ling 2015](#))

and is an approved fish toxicant for fisheries management in the US by the US Environmental Protection Agency (Finlayson *et al.* 2010). It degrades quickly in the environment through hydrolytic, photolytic and biological processes, and residues are typically undetectable after several days, depending on abiotic and biotic conditions (Finlayson *et al.* 2001). Invertebrate communities have been reported to rebound quickly through recolonisation and regeneration (Beal and Anderson 1993), especially in prairie lakes (Melaas *et al.* 2001).

Liquid rotenone (1855 L) was applied through liquid sprayers mounted just above the lake surface from airboats, and powdered rotenone (222 kg) was delivered to the propeller wash of an outboard motor boat to mix the powder in the lake. An amphibious vehicle equipped with a plant sprayer was also used to apply the liquid in hard-to-access vegetated areas. A target rate of 3 ppm was administered using both powder and liquid formulations. Following the renovation (i.e. restoring the lake back to a desired state), 504 largemouth bass (mean total length 196 mm, range 155–416 mm) and 52 bluegill (mean total length 189 mm, range 112–229 mm) were stocked from a nearby sandhill lake during June of 2009 (1 year after renovation). The fish stocking and addition of a piscivore to Pony Lake (treatment lake) enabled the fish community to more closely resemble that of West Long Lake (reference lake).

Bottom-up and top-down effects sampling

Total phosphorous, Secchi disc transparency and chlorophyll-*a* were measured at four random locations at both the treatment and reference lake. Two samples of unfiltered lake water were collected at each site and frozen for later determination of total phosphorous following the methods of Wetzel and Likens (2000). Chlorophyll-*a* was sampled from duplicate water samples using the same protocol described by Kaemingk *et al.* (2014). Submersed vegetation coverage was quantified during the summer (i.e. July; during peak foliage) using the methods described previously for the observational component (Paukert *et al.* 2002a). Benthic macroinvertebrates and zooplankton samples were collected, processed and converted to biomass ($\mu\text{g L}^{-1}$) from two replicates at each of four offshore sites following methods outlined in Kaemingk *et al.* (2014). Less common taxa were excluded from further analyses because of the number of very small or zero abundances found within each lake.

Fish sampling

Twelve randomly chosen shoreline transects (100 m each) were walked within 3 days of the Pony Lake rotenone renovation in October 2007 and all dead fish were identified, counted and a subsample ($n = 150$) measured (total length (TL); mm). The mean number per transect was extrapolated to the entire shoreline to obtain population estimates. The mean weight of each species was based on length and estimated using species-specific standard weight equations (Murphy *et al.* 1991) and then extrapolated (multiplied by) to the population estimate to obtain the estimated population biomass. Pony Lake was then sampled each year after renovation (i.e. 2008–10) for fish during early June (trap nets and cloverleaf traps for age-0

fish, 2008, 2009, 2010; electrofished entire shoreline, 2009, 2010). Each three-lobed cloverleaf trap was constructed of galvanised 6.4-mm bar mesh, with three 12.7-mm wide openings between lobes to accommodate the entrance of small fish (Kaemingk and Willis 2012). The fish community was also sampled in West Long Lake during 2006, 2008 and 2010 with experimental gill nets (August), night-time electrofishing and trap nets (May) each year (Wanner 2011).

Statistical analysis

We used repeated generalised linear mixed models (PROC MIXED; SAS, ver. 9.3; SAS Institute; McDonald *et al.* 2000) to determine whether bottom-up effects (i.e. total phosphorous, Secchi disc transparency, submersed vegetation and chlorophyll-*a*) or top-down effects (i.e. zooplankton and benthic macroinvertebrates) had occurred in the treatment lake. Data were normalised by performing $\log_{10}(n + 1)$, $(n + 2)^{-1}$ and $\sqrt{(n + 1)}$ transformations to account for the zeros encountered. Macroinvertebrate density and biomass, zooplankton density and biomass, and physiochemical data, which were not normally distributed, were analysed using a quasi-likelihood generalised linear model method (PROC GLIMMIX; SAS ver. 9.3; SAS Institute; McDonald *et al.* 2000). Both linear models allowed for fixed and random effects. The model included fixed treatment (TR), period (B; before or after renovation), seasons nested within periods (S(B)) as an additive factor stabilising variation among the three seasons sampled (i.e. spring, summer and autumn; Louhi *et al.* 2011) and a treatment by period interaction effect (TR \times B). Sampling sites were nested within treatment and included as random effects, and season was nested in each year sampled to control for experimental error on repeated measurements through time (McDonald *et al.* 2000; Pabian and Brittingham 2007). We documented the treatment by time period interaction to evaluate the effects of the renovation in Pony Lake. Following a significant interaction, two contrasts were performed to examine whether least square means differed before and after the treatment in Pony Lake, West Long Lake or both lakes (SAS ver. 9.3; SAS Institute). Vegetation coverage was analysed using a repeated-measures ANOVA (i.e. time as the repeated measure) and the maximum likelihood method (Littell *et al.* 1998).

Least square means were calculated using ANOVA for all significant treatment by time effect variables (except for vegetation coverage) identified in the previous analysis to examine which year after renovation (i.e. Year 1, 2 or 3) the effect occurred (Glasby and Underwood 1996). Seasonal means were treated as the experimental unit where the 3 years before the renovation were compared to Years 1, 2 and 3 after renovation separately for the treatment lake (Pabian and Brittingham 2007). Differences were assessed at $\alpha \leq 0.05$ to guard against a Type I error due to the experimental treatment and nature of this portion of the study (Mapstone 1995).

Results

Observational

Bottom-up effects

Sandhill lakes without common carp had over double mean Secchi depth ($F_{1,14} = 7.31$, $P = 0.02$) and triple the submersed

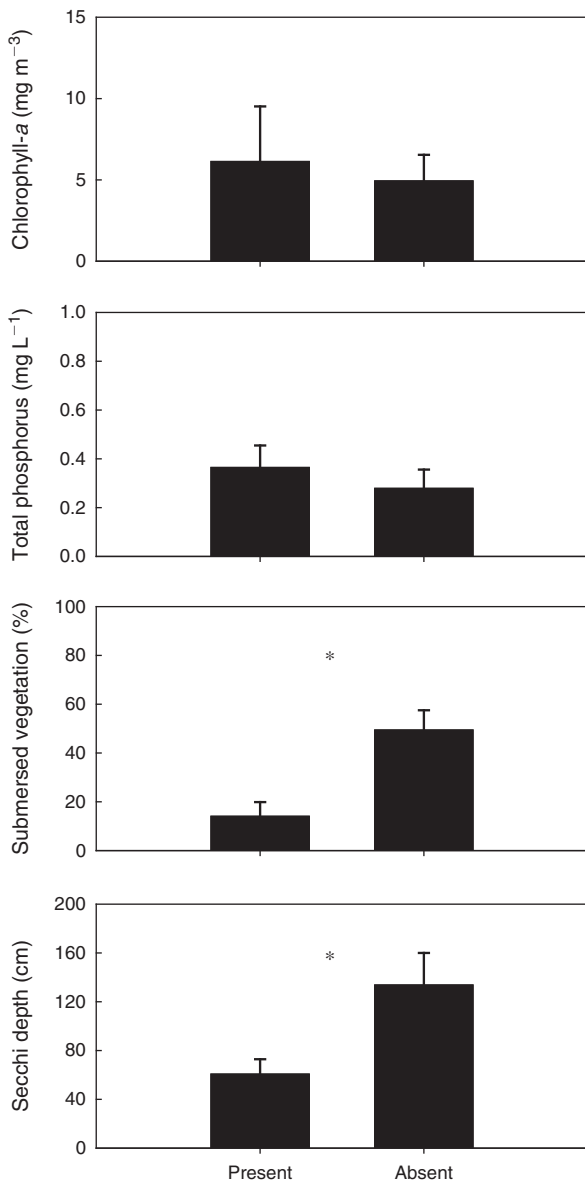


Fig. 2. Mean (\pm s.e.) values of Secchi depth, submersed vegetation lake coverage, total phosphorus and chlorophyll-*a* in eight lakes with common carp present and eight lakes with common carp absent during 1998 and 1999. Asterisks indicate significant differences at $\alpha \leq 0.10$ from a one-way ANOVA.

vegetation coverage compared with lakes with common carp ($F_{1,14} = 14.41$, $P < 0.01$; Fig. 2). However, total phosphorous ($F_{1,14} = 0.63$, $P = 0.44$) and chlorophyll-*a* ($F_{1,14} = 0.63$, $P = 0.44$) levels did not differ between lakes with or without common carp (Fig. 2).

Top-down effects

Lakes with common carp had higher densities ($F_{1,14} = 7.11$, $P = 0.02$) and biomass ($F_{1,14} = 8.46$, $P = 0.01$) of cladoceran zooplankton (Fig. 3). Copepod densities ($F_{1,14} = 1.49$, $P = 0.24$)

and biomass ($F_{1,14} = 1.88$, $P = 0.19$) were similar between lakes with and without common carp (Fig. 3). In addition, no significant differences were detected between lakes with and without common carp relating to total benthic macroinvertebrate densities ($F_{1,14} = 0.41$, $P = 0.53$) because of the wide range of macroinvertebrate densities in lakes without common carp.

Bluegill recruitment, growth and mortality were similar across lakes with and without common carp (recruitment $F_{1,9} = 0.68$, $P = 0.43$; growth $F_{1,8} = 0.01$, $P = 0.94$; mortality $F_{1,6} = 0.32$, $P = 0.59$; Fig. 4). In contrast, yellow perch mortality was greater in lakes with common carp present ($F_{1,9} = 3.84$, $P = 0.08$) and recruitment variability was higher in lakes without common carp ($F_{1,10} = 3.28$, $P = 0.10$; Fig. 4). The top predator, largemouth bass, experienced lower mortality rates ($F_{1,7} = 7.19$, $P = 0.03$) and faster growth rates ($F_{1,7} = 7.09$, $P = 0.03$) in lakes containing common carp (Fig. 4). However, yellow perch growth ($F_{1,10} = 0.27$, $P = 0.61$) and largemouth bass recruitment ($F_{1,8} = 0.78$, $P = 0.40$) did not differ between treatments (Fig. 4).

Middle-out effects

The common carp adult abiotic pathway was the most supported model (i.e. lowest AIC corrected for small sample bias, AIC_c, and highest model weight) compared with the early life feeding, adult biotic and adult nutrient pathway models (Table 1). The adult abiotic pathway included water transparency, submersed macrophytes and zooplankton variables. The next supported model (model weight = 0.23) was the early life feeding pathway, which also included phytoplankton as an additional variable (but minus submersed macrophytes) to that of the abiotic pathway. However, the adult biotic and adult nutrient pathways should not be considered as the most probable middle-out response to common carp effects in these systems (model weights = 0; Table 1; Fig. 1).

Renovation

Fish sampling

The Pony Lake fish community was dominated by adult common carp (76% of the total standing stock) at the time of the October 2007 renovation (Table 2). Post-treatment sampling revealed an incomplete fish community renovation. All species present at the time of the renovation were subsequently detected (in the following spring) but in lower abundances, except for common carp and yellow perch, which were not detected. Alternatively, no changes in the West Long Lake fish community were documented during the study (i.e. same species present).

Bottom-up effects

Secchi depth and submersed vegetation increased in the treatment lake after the renovation ($t = 4.31$, $P < 0.0001$ and $t = 2.47$, $P = 0.04$ respectively; Fig. 5). In contrast, Secchi depth decreased in the reference lake, but no change was observed in submersed vegetation ($t = -4.58$, $P < 0.0001$ and $t = -1.05$, $P = 0.32$ respectively). There was no treatment by time interaction effect for total phosphorous ($F_{1,104} = 0.01$, $P = 0.91$). However, chlorophyll-*a* in the treatment lake decreased after

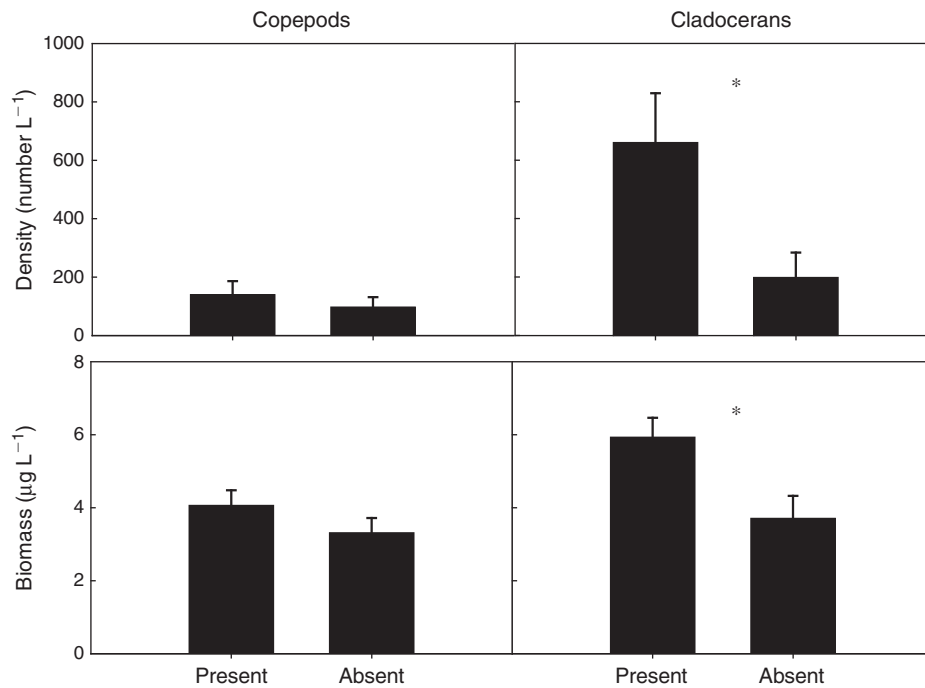


Fig. 3. Mean (\pm s.e.) values of copepod and cladoceran zooplankton density and biomass in eight lakes with common carp present and eight lakes with common carp absent during 1998 and 1999. Asterisks indicate significant differences at $\alpha \leq 0.10$ from a one-way ANOVA.

the renovation ($t = -4.69$, $P < 0.0001$), but there was no difference in the reference lake ($t = 1.80$, $P = 0.07$; Fig. 5).

Top-down effects

Cladoceran and copepod densities decreased in the treatment lake after the renovation ($t = -3.42$, $P < 0.01$ and $t = -6.77$, $P < 0.0001$ respectively), but no change was observed in the reference lake ($t = 0.14$, $P = 0.99$ and $t = 0.59$, $P = 0.94$ respectively). In contrast, cladoceran biomass increased substantially ($t = 2.66$, $P = 0.04$), but copepod biomass decreased ($t = -4.84$, $P < 0.0001$), in the treatment lake after the renovation. No treatment effect was observed in the reference lake for either cladoceran or copepod biomass ($t = 0.10$, $P = 0.99$ and $t = 0.86$, $P = 0.82$ respectively; Fig. 6). Total benthic macroinvertebrate density and biomass were unaffected by the renovation in both the treatment ($t = 2.04$, $P = 0.18$ and $t = 1.69$, $P = 0.09$ respectively) and reference ($t = -0.37$, $P = 0.98$ and $t = 0.11$, $P = 0.91$ respectively) lakes (Fig. 7).

Timing

Almost all variables deviated from pre-renovation levels in the treatment lake by Year 2 after renovation. Secchi depth, a measure of water clarity, was the first metric to respond in the treatment lake following the renovation (Fig. 5). An increase in water clarity was succeeded by a decrease in chlorophyll-*a* and a decrease in both copepod density and biomass in Year 2 (Figs 5, 6). Only cladoceran density experienced a decline by Year 3, whereas no difference was identified for cladoceran biomass within each individual year after renovation, despite an overall significant increase.

Discussion

Common carp reduced water transparency and submersed vegetation density in both studies and caused an increase in phytoplankton (experimental study), altered copepod (experimental study) and cladoceran densities and biomass and affected the fish community. Consequently, middle-out effects were evident in both the observational and experimental studies (summarised in Table 3). It was useful to consider multiple disturbance pathway models (opposed to either top-down or bottom-up) that were generated or hypothesised from the existing literature (Fig. 1). Basic information concerning the life history or behavioural ecology of a species will be imperative to fully understand and identify intricate trophic linkages (Table 1). At least one metric from each trophic level was affected, but the magnitude of each effect differed across levels. A bidirectional effect was evident as both bottom-up and top-down processes were revealed. Placing species in a common functional feeding guild may mask food web effects using a traditional top-down or bottom-up framework (MacNeil *et al.* 1997). Therefore, species traits and autecology may allow for a more robust assessment of trophic linkages (Poff *et al.* 2006; Morales-Castilla *et al.* 2015). Without this specific knowledge of proximity, directionality and causation, it would be difficult to effectively direct and execute successful management or conservation efforts.

The trophic cascade pattern was clear (i.e. middle-out) but the process or pathway was more difficult to interpret. Considering the four major common carp disturbance pathway options (Fig. 1), adult abiotic foraging appeared to be strongest compared with the early life feeding, adult biotic or adult

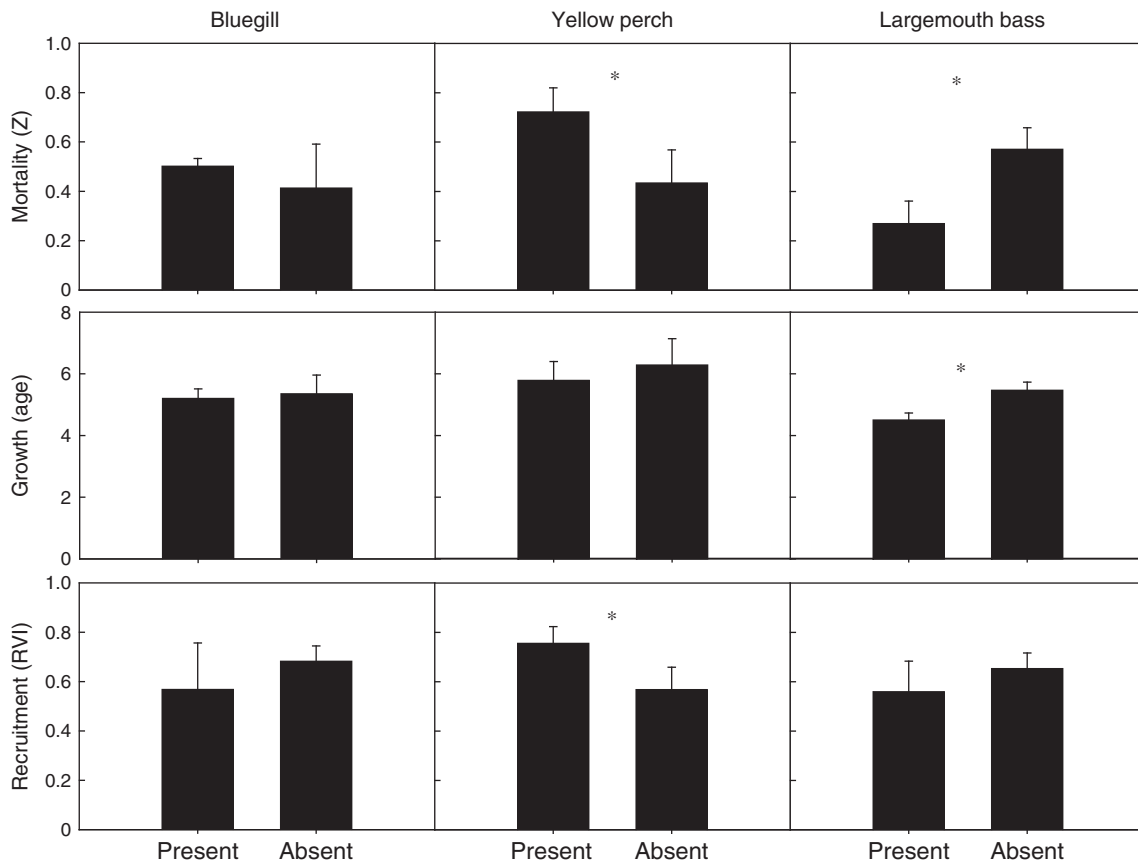


Fig. 4. Mean values (\pm s.e.) of recruitment, growth and mortality for bluegill, yellow perch and largemouth bass in eight lakes with common carp present and eight lakes with common carp absent during 1998 and 1999. Growth describes the time (in years) for each species to reach preferred lengths (bluegill 200 mm, yellow perch 250 mm, largemouth bass 380 mm; Gabelhouse 1984) and Z represents total instantaneous mortality (Ricker 1975). The recruitment variability index (RVI) ranged from -1 to 1 , with increasing values indicating less recruitment variability (i.e. consistent; Guy and Willis 1995). Asterisks indicate significant differences at $\alpha \leq 0.10$ from a one-way ANOVA.

Table 1. Comparison of pathway models (and variables, listed consecutively according to impact proximity) examining middle-out effects of common carp (see Fig. 1)

Results include the number of parameters (K), Akaike information criterion corrected for small sample bias (AIC_c), differences in AIC_c (ΔAIC_c), evidence ratios (ER) and weight of support for each model (W_i)

Pathway model	K	AIC_c	ΔAIC_c	ER	W_i
Adult abiotic (water clarity, submersed macrophytes, zooplankton)	5	14.06	0.00	1.00	0.77
Early life feeding (zooplankton, phytoplankton, water clarity)	5	16.44	2.38	0.30	0.23
Adult biotic (benthic macroinvertebrates, submersed macrophytes, water clarity)	5	24.79	10.72	0.00	0.00
Adult nutrient (nutrients, phytoplankton, water clarity)	5	27.25	13.19	0.00	0.00

nutrient pathways. Water clarity was immediately affected during the first year after renovation and also reduced in the observational lakes with common carp present (see also Schrage and Downing 2004). This reduction in water clarity likely stemmed from the foraging behaviour of adult common carp and physical turbidity, and not by resuspending benthic nutrients (no effect in either study), which would have caused an increase in phytoplankton (Parkos *et al.* 2003). Physical

turbidity can limit light penetration and submersed vegetation growth (Scheffer and Jeppesen 1998). The loss of submersed vegetation coverage observed in both studies may lead to many other deleterious ecosystem effects and even ecological stable state shifts (Scheffer *et al.* 1993), including the shifts in zooplankton community dynamics observed in the present study (van Donk and van de Bund 2002; Weber and Brown 2009).

Table 2. Initial population density and biomass estimates for the fish community in Pony Lake, Nebraska, revealed during the October 2007 rotenone renovation

Species	Mean (\pm s.e.) number per m shoreline	Total abundance	Density (number ha ⁻¹)	Mean weight (g)	Total biomass (kg)	Standing stock (kg ha ⁻¹)
Black bullhead	7.63 \pm 4.01	25 179	393.4	71	1796	28.1
Adult common carp	1.64 \pm 0.44	5412	84.6	2770	14 990	234.2
Age-0 common carp	4.85 \pm 1.01	16 005	250.1	46	737	11.5
Grass pickerel	0.06 \pm 0.03	198	3.1	35	7	0.1
Green sunfish	14.80 \pm 7.00	48 840	763.1	22	1094	17.1
Golden shiner	2.13 \pm 0.32	7029	109.8	17	121	1.9
Pumpkinseed	0.04 \pm 0.03	132	2.1	24	3	0.1
Yellow perch	0.01 \pm 0.01	33	0.5	132	4	0.1
Fathead minnow	805.5 \pm 21.7	2 658 249	41 535.1	1	1914	29.9
Totals	–	2 761 077	43 141.8	–	20 666	322.9

There is far less consistency among studies accounting for common carp effects on zooplankton community composition and dynamics (Vilizzi *et al.* 2015). Typically, common carp cause a reduction in large-bodied zooplankton (Weber and Brown 2009), but we observed the opposite effect. Large-bodied zooplankton densities and biomass (except for biomass in the experimental study) increased as a result of common carp, including small-bodied zooplankton in the experimental study. This pattern could be explained, in part, by the size composition of common carp across lakes examined (Nieoczym and Kloskowski 2014). Smaller carp may preferentially feed on zooplankton compared with larger carp that consume mainly macroinvertebrates; these food habits may also change seasonally (Nieoczym and Kloskowski 2014). The present study did not account for the size or age structure of common carp, but identified that both age-0 (small) and adult (large) common carp were present in the treatment lake. Therefore, future studies should examine the role of common carp size on zooplankton community dynamics across multiple spatial and temporal scales to further resolve these complexities.

We found limited evidence to support the remaining three disturbance pathways, despite their importance or relevance in other studies (Vilizzi *et al.* 2015). Common carp population attributes (e.g. size structure, biomass, recruitment dynamics) and inherent ecosystem properties (e.g. substrate type, trophic state, bathymetry) are likely to cause different common carp ecosystem responses. Our common carp biomass estimate (\sim 245 kg ha⁻¹) was either below or on the low end of the critical biomass threshold typically attributed to widespread ecosystem disturbances (ranging from 200 to 450 kg ha⁻¹; for reviews, see Weber and Brown 2009; Vilizzi *et al.* 2015). However, shallow lakes may be more sensitive to a reduction in submersed macrophytes, compared with deep lakes, causing the observed common carp effects in the present study (Jeppesen *et al.* 1997). Moreover, invertebrate densities are much higher in these lakes compared with other surrounding ecosystems, and these invertebrate abundances do not appear to be strongly affected by fish predation (Paukert and Willis 2003). Therefore, common carp biomass densities may have been below a level necessary to directly reduce invertebrate densities by predation, ultimately limiting support for the early life feeding and adult biotic pathways. In addition, Nebraska sandhill lakes do not

experience much external nutrient loading compared with water bodies with common carp in intensive agriculturally dominated systems (Jackson *et al.* 2010). This may explain why evidence was lacking for the adult nutrient pathway.

It appears trophic levels furthest away from direct impact may still be affected within a middle-out framework, but were weaker or less consistent compared with lower trophic levels. Less than half the fish species trait combinations examined were significant. We hypothesised that bluegill and not piscivores would be most affected, considering bluegill are an insectivore and closer in proximity to common carp-mediated effects (Egertson and Downing 2004; Wolfe *et al.* 2009). However, bluegill growth, recruitment, and mortality did not differ between lakes with and without common carp, but both piscivores (yellow perch and largemouth bass) exhibited differences between lakes. Fewer studies have examined common carp effects on fish species (highlighted in Weber and Brown 2009). Of these studies, most identified a decline in one or more dynamic rate functions (recruitment, growth, mortality; Egertson and Downing 2004; Wolfe *et al.* 2009). Mesocosm studies have documented common carp effects for young centrarchid life stages but not at the adult life stage. Although not directly comparable, largemouth bass recruitment and mortality patterns were similar, whereas growth rate effects in the present study were different compared with these previous mesocosm studies (Wolfe *et al.* 2009; Wahl *et al.* 2011). In contrast, we did not identify bluegill population differences between lakes with or without common carp (Wolfe *et al.* 2009; Wahl *et al.* 2011). Effects on largemouth bass could be more long lasting across life stages (i.e. carry-over effects; Harrison *et al.* 2011) compared with bluegill effects that are evident during the early life history but synergistically decouple as they reach adulthood. To our knowledge, no one has identified common carp effects on yellow perch populations by examining recruitment, growth and mortality. Age-0 yellow perch mortality and recruitment was regulated by zooplankton availability in one of the lakes used for the observational study (Pelican Lake; Kaemingk *et al.* 2014). Thus, because common carp substantially modified zooplankton dynamics and composition, it could explain, in part, the increased mortality and recruitment variability of yellow perch in lakes with common carp. Predator-prey dynamics could also explain the higher mortality of yellow perch

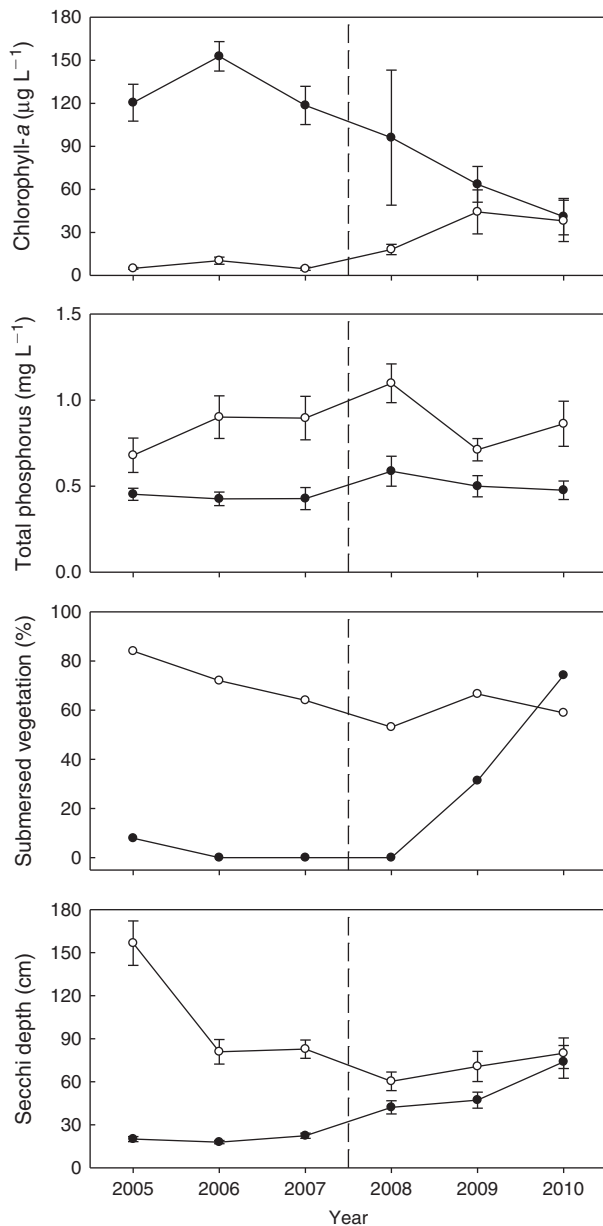


Fig. 5. Mean (\pm s.e.) values of Secchi depth, submersed vegetation lake coverage, total phosphorus and chlorophyll-*a* over the period 2005–10 in the treatment (Pony, closed circles) and reference (West Long, open circles) lakes before and after (denoted by the vertical dashed line) common carp were removed from the treatment lake.

in lakes with common carp. Largemouth bass experienced lower mortality in lakes with common carp, which subsequently may lead to higher largemouth bass predation rates on yellow perch in these systems (Paukert *et al.* 2002b). It is clear that indirect effects channelled through a middle-out process may still affect (but to a lesser degree) trophic levels whose trophic position and distance could have provided a buffer from direct impact (i.e. compartments or subwebs; Krause *et al.* 2003).

The effect on and response time of each trophic level also varied in the experimental study. Most variables quickly

responded (<2 years) after common carp were removed from the treatment lake, despite other studies highlighting a slow regimen shift after a disturbance (Meijer *et al.* 1999; Gulati and van Donk 2002). By Year 3, all significantly modified variables (except cladoceran density) had completely shifted, including submersed macrophytes. Submersed macrophytes appear to be a critical component in shallow lake ecology and are negatively affected by common carp (Miller and Crowl 2006); macrophytes provide sediment stability, nutrient uptake, zooplankton predation refuge and increased grazing opportunities (Kufel and Ozimek 1994; Barko and James 1998). Thus, the removal of common carp allowed the lake to shift from a turbid water and limited submersed macrophyte state to a clear water and high density submersed macrophyte state. The ability to identify potential trophic interactions (e.g. pathways) and incorporating functional traits of specific species (e.g. common carp) in the community could offer the best strategy to address ecosystem-level management problems. Depending on the dominant trophic pathway and inherent ecosystem attributes, these lag effects could be shortened or lengthened but should be considered when assessing trophic ecology dynamics.

Overall, patterns and results were generally similar between observational and experimental studies despite the different approaches and limitations. The experimental portion included only one treatment and one reference lake, therefore preventing large-scale inferences to be made. We also attempted to create a similar fish assemblage between lakes by introducing a top-level piscivore (i.e. largemouth bass) to the treatment lake. It was unclear how effective this strategy was other than the results conformed to a middle-out process (Vilizzi *et al.* 2015), aligning more closely with the hypothesised common carp effects compared with a simple top-down predator effect (McQueen *et al.* 1986). Although the evaluation period in the present study exceeded that of many previous studies, it was likely shorter than what is required to effectively document some ecosystem-level changes (Peterson 1984), such as generation times for fish (see Capon *et al.* 2015). Therefore, caution should be exercised when interpreting and applying these results to other ecosystems (Mac Nally *et al.* 2014; Capon *et al.* 2015). However, our findings reinforce previous work conducted on smaller spatio-temporal scales providing promise of broader utility despite these limitations (Vilizzi *et al.* 2015).

The results of the present study support the middle-out effects trophic cascade concept and further identify the need to include species trait information. Single species studies or understanding the interactions of one keystone species within a community has received criticism (Simberloff 1998). Excluding species trait information (or, in some cases, where information is lacking) could have major implications on the interpretation and understanding of food web ecology and trophic cascades. For example, predicting the direction and strength of food web effects could be greatly enhanced by incorporating habitat use, foraging behaviour and other dynamic predator–prey relationships (Schmitz *et al.* 2004). Moving towards incorporating species traits and organismal performance metrics could address inadequacies and disconnects between empirical studies and ecological food web modelling (van Veen and Sanders 2013). In the present study, known common carp foraging behaviour greatly improved the

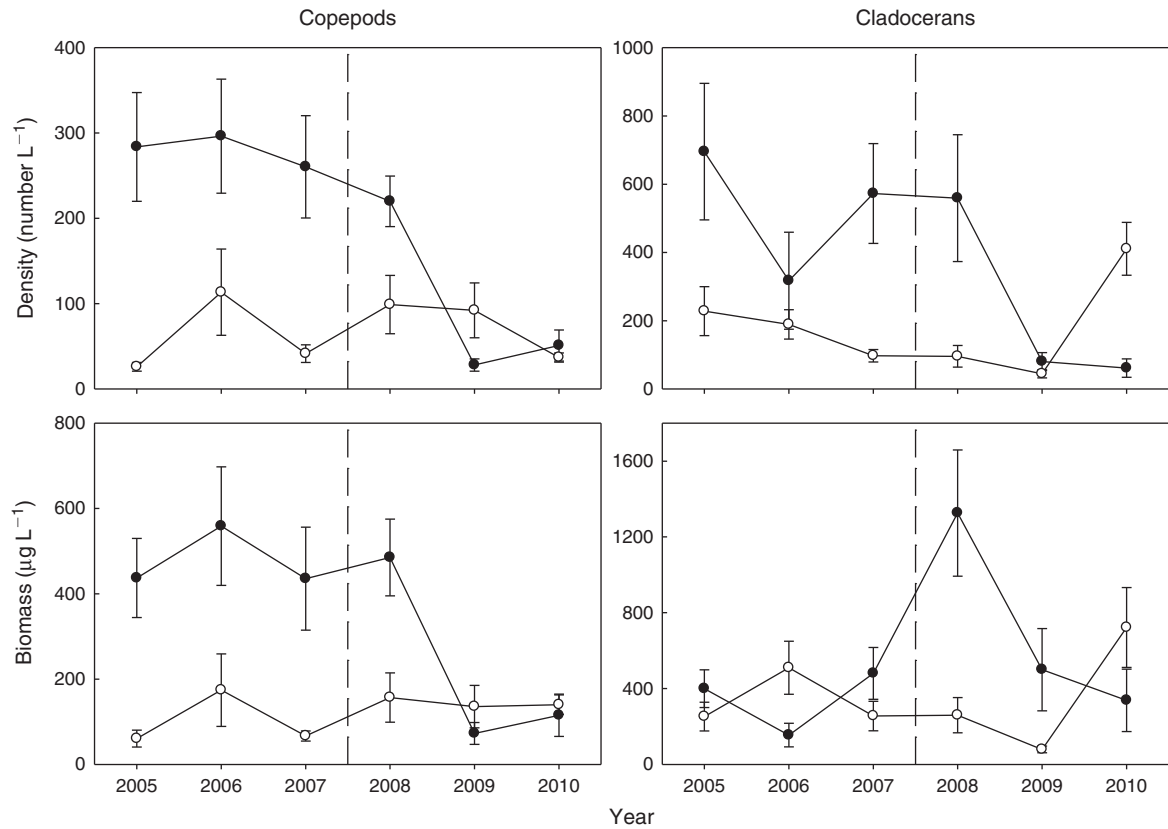


Fig. 6. Mean (\pm s.e.) values of copepod and cladoceran zooplankton density and biomass over the period 2005–10 in the treatment (Pony, closed circles) and reference (West Long, open circles) lakes before and after (denoted by the vertical dashed line) common carp were removed from the treatment lake.

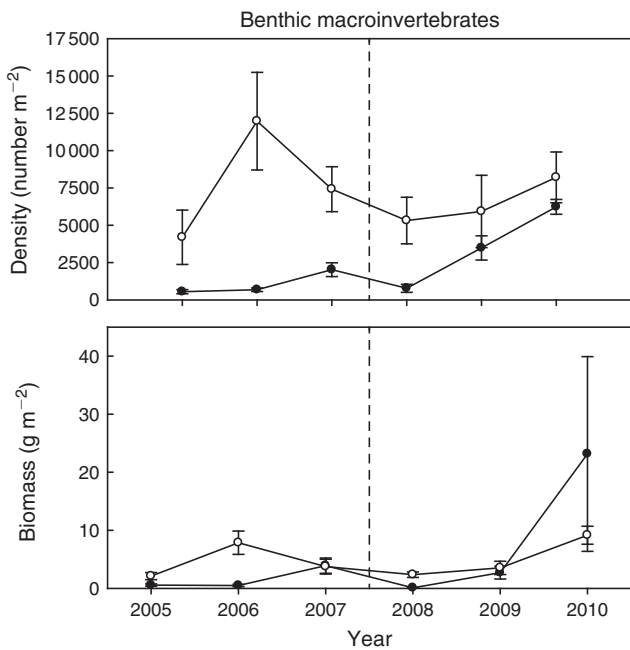


Fig. 7. Mean (\pm s.e.) values of total benthic macroinvertebrate density and biomass over the period 2005–10 in the treatment (Pony, closed circles) and reference (West Long, open circles) lakes before and after (denoted by the vertical dashed line) common carp were removed from the treatment lake.

Table 3. Summary of bottom-up and top-down trophic effects caused by common carp in both observational and experimental studies. Each effect (i.e. ‘yes’) is followed by a sign (positive sign indicates an increase; negative sign indicates a decrease) corresponding to directional effects of common carp within each study. NA, not applicable

Metric	Observational	Experimental
Bottom-up		
Water transparency	Yes (-)	Yes (-)
Submersed vegetation	Yes (-)	Yes (-)
Nutrients	No	No
Phytoplankton	No	Yes (+)
Top-down		
Copepod densities	No	Yes (+)
Copepod biomass	No	Yes (+)
Cladoceran densities	Yes (+)	Yes (-)
Cladoceran biomass	Yes (+)	Yes (+)
Benthic macroinvertebrates	No	No
Fish		
Insectivore	No	NA
Lower-level piscivore	Yes (mortality +, recruitment -)	NA
Upper-level piscivore	Yes (mortality -, growth +)	NA

detection, interpretation and understanding of middle-out effects that would otherwise be difficult to achieve (Morales-Castilla *et al.* 2015).

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