

Top-down effects of an invasive omnivore: detection in long-term monitoring of large-river reservoir chlorophyll-*a*

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Abstract Invasive species are capable of altering ecosystems through the consumption of basal resources. However, quantifying the effects of invasive species in large ecosystems is challenging. Measuring changes in basal resources (i.e., phytoplankton) at an ecosystem scale is an important and potentially translatable response vital to the understanding of how introduced species influence ecosystems. In this study, we analyzed patterns of early summer chlorophyll-*a* in a large-river reservoir in response to invasion of silver carp (*Hypophthalmichthys molitrix*). We used 25 years of ecological data from a 30-km reach of Kentucky Lake collected before and after silver carp establishment. We found significant decreases in chlorophyll-*a* within certain reservoir habitats since establishment of silver carp. Additionally, environmental and biological drivers of phytoplankton production showed no significant differences before and after invasion. These results suggest seasonal, and habitat-specific

consumptive effects of invasive silver carp on an important basal food web resource. Further, our results convey the utility of long-term quantitative biological and physiochemical data in understanding ecosystem responses to elements of global change (i.e., species invasions). Importantly, the observed changes in the basal food web resource of Kentucky Lake may apply to other ecosystems facing invasion by silver carp (e.g., Laurentian Great Lakes). Our study offers insight into the mechanisms by which silver carp may influence ecosystems and furthers our understanding of invasive omnivores.

Keywords Phytoplankton · Trophic ecology · Invasive species · Asian carp · Omnivory

Introduction

Invasive species are considered a leading threat to ecosystem function and biodiversity on a global scale (Ehrenfeld 2010; Bellard et al. 2016). Consumptive effects of invasive species are capable of altering ecosystem functions by changing recipient community energy flow (Ellis et al. 2011; Walsh et al. 2016). More specifically, invasive species can disrupt food webs through direct herbivory (Capps et al. 2014) and predation on native species (Vander Zanden et al. 1999). Consumptive effects of invasive species can also lead to competition with native assemblages for food resources (Strayer et al. 1999), while suppressing certain trophic linkages, subsequently transforming (Townsend 2003; Baxter et al. 2004) and/or simplifying ecosystem structure (Strayer et al. 1999; Sagouis et al. 2015). Ecosystems with more simplified trophic structure may be less resilient to disturbances (Tilman et al. 2006; Cross et al. 2013) and more susceptible to trophic cascades (Strong 1992; Finke and Denno 2004).

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Invasive omnivores are particularly threatening to ecosystem function because of their ability to directly and indirectly influence multiple trophic levels through resource consumption (Lodge et al. 1994; Thompson et al. 2007). Many aquatic ecosystems are characterized by having strong trophic links (Carpenter et al. 1985; Strong 1992); thus, the effects of invasive omnivores can significantly alter food web dynamics of recipient aquatic communities (Gallardo et al. 2016). The omnivorous rusty crayfish (*Orconectes rusticus*) is arguably one of the most prolific aquatic invaders of the US. Through the consumption and suppression of detritus, mollusks, insects and fish eggs, the rusty crayfish has been shown to have strong direct and indirect effects on numerous aquatic ecosystem functions (Strayer 2010 and references therein). Although invertebrates have served as a model system for studying the effects of omnivorous invaders on recipient aquatic food webs (Strayer 2010), far less is known about the effects of highly mobile omnivorous vertebrates such as fish.

The silver carp (*Hypophthalmichthys molitrix*) is an omnivorous fish that has invaded much of the central US and is a leading concern for many freshwater ecosystems (Chick and Pegg 2001). Within the US, silver carp populations have reached some of the highest reported global densities and are predicted to invade and disrupt food webs within the Laurentian Great Lakes (Sass et al. 2010; Zhang et al. 2016). Silver carp are filter feeding fish that voraciously and indiscriminately consume planktonic algae (i.e., phytoplankton), zooplankton, and detritus in the water column (Wang et al. 1989; Williamson and Garvey 2005; Sampson et al. 2009). Several studies have documented the suppression of basal resources by silver carp (Fukushima et al. 1999; Xie and Yang 2000; Lu et al. 2002; Xiao et al. 2010; Sass et al. 2014), while others have shown strong linkages affecting native fish condition (Irons et al. 2007; Sampson et al. 2009) and community structure (Solomon et al. 2016). Previous studies provide important information on the consequences of silver carp consumption for zooplankton and native fish: however, there remains uncertainty surrounding the combination of effects through the consumption of both phytoplankton and zooplankton. Examining long-term phytoplankton dynamics in ecosystems invaded by silver carp may further our understanding of the mechanisms underlying complex effects and ultimately enhance our knowledge of invasive omnivores and the threats they pose.

Kentucky Lake, located in western Kentucky, US, is a large-river reservoir where populations of silver carp were recently established (Kentucky Department of Fish and Wildlife Resources, KDFWR unpublished data). Commercial harvest data from KDFWR suggest that significant populations of silver carp had become established in Kentucky Lake by 2005, and recent (July 2015) sampling efforts have shown all life stages were present in the system (N.

Jackson, KDFWR personal communication). Based on commercial harvest data, we have defined 2005 as the start of the post-establishment and 2005–2013 collectively as the post-establishment period.

A 30-km reach of Kentucky Lake has been part of the Kentucky Lake Long-Term Monitoring Program (KLMP) since July 1988. The KLMP has continuously sampled (i.e., every 16 days, 32 days in winter) information on physical, chemical, and biological parameters, including chlorophyll-*a* (chl-*a*). The KLMP dataset provides a unique opportunity to investigate the influence of silver carp invasion on a large-river reservoir ecosystem that may improve our inference of potential effects in other invaded ecosystems (e.g., the Mississippi River Basin) and in predicting future effects in systems facing invasions (e.g., the Laurentian Great Lakes). Furthermore, the KLMP contains over 25 years of long-term quantitative physical and biological data and thus provides the opportunity to account for factors that influence chl-*a* at the ecosystem level (Carpenter et al. 1995; Schindler 1998; Dodds et al. 2012) that may prove useful in untangling the multiple trophic influences of invasive omnivores.

In this study, we tested the following two hypotheses (1) phytoplankton biomass has declined since the establishment of silver carp in Kentucky Lake, suggesting that this invasive omnivore has ecosystem level consumptive effects. (2) Ecological variables important to phytoplankton production: zooplankton density (cladocera and copepods), water temperature, and nutrients (soluble reactive phosphorous) have remained unchanged since the establishment of silver carp, suggesting that changes observed in phytoplankton biomass were not caused by unrelated ecosystem changes.

Methods

Study site

We used long-term ecological data collected by Hancock Biological Station (HBS) from a 30-km study reach of Kentucky Lake (Fig. 1). Kentucky Lake is a large, shallow main-stem reservoir approximately 296 km long with a surface area of 64,874 hectares and the last impoundment along the Tennessee River (Bukaveckas et al. 2002). Kentucky Lake is characterized as mesotrophic, seasonally nutrient limited, and is the largest reservoir of the eastern US (Bukaveckas et al. 2002; Yurista et al. 2004). Hydrologically, the Kentucky Lake ecosystem has a lotic main channel (average retention time = 31 days, estimated by dam discharge and lake volume from 1988 to 2013 Hancock Biological Station unpublished data), lentic side arm embayments (average retention time \approx 100 days, estimated by embayment volume, tributary and dam discharge from 1990 to 1991, Johnson 1992) with embayment mouths characterized as an

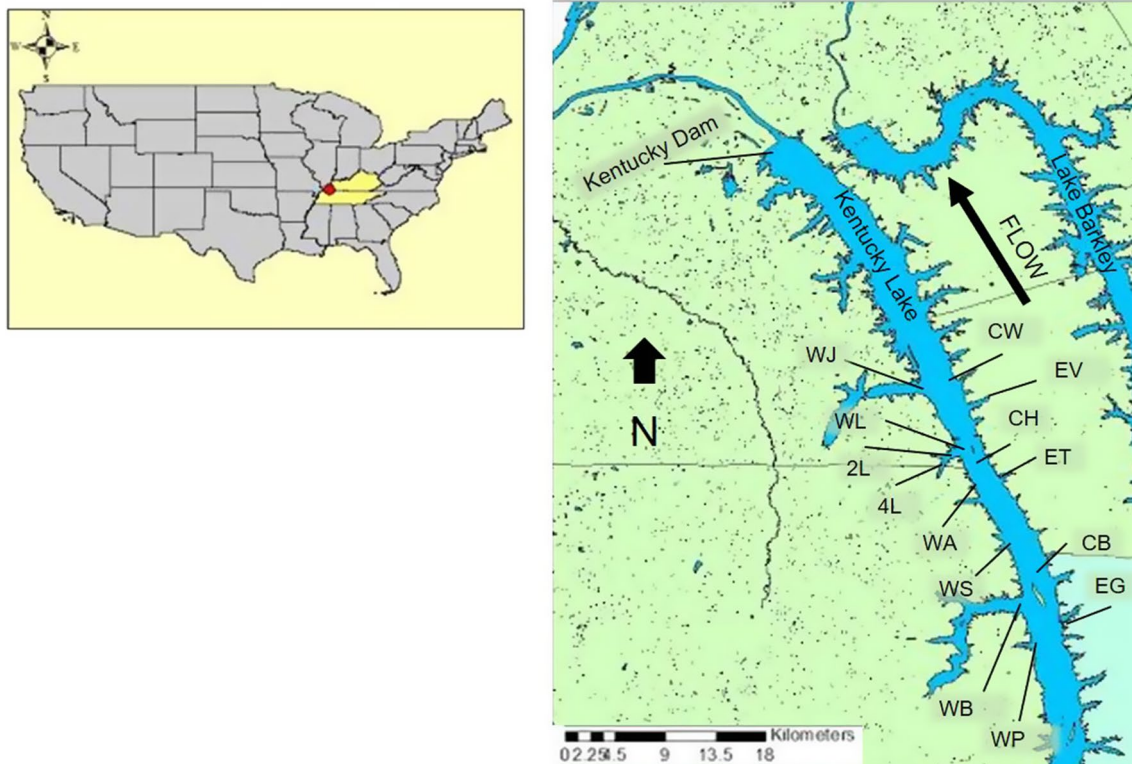


Fig. 1 The location of Kentucky Lake showing Hancock Biological Station's (HBS) Kentucky Lake Long-Term Monitoring Program (KLMP) sampling sites used in this study. Embayment sites included

2 and 4L. Mouth sites included EG, ET, EV, WA, WB, WJ, WL, WP, WS. Channel sites included CB, CH and CW. This section of the Tennessee River flows in a northern direction depicted by the arrow

intermediate habitat (Bukaveckas et al. 2002; Yurista et al. 2004).

Long-term data, experimental framework

On a sampling event, the KLMP collects data on a suite of ecological variables (Table S1) at 16 sites from a range of habitats (Fig. 1); for a more detailed description of the KLMP, see White et al. (2007). To test our predictions, we analyzed chl-*a* concentrations along with physical and chemical covariates during early summer (April–June) from 1989 to 2013. Our analysis focused on data collected from early summer sampling events ($n = 6$) from each site ($n = 14$) for each year ($n = 25$). We focused on early summer to reduce the influence of seasonal variability from natural processes and water-level management. April sampling events were chosen as the starting point of our analysis as this month consistently reached water temperatures of 15 °C. Additionally, in Kentucky Lake, early summer is the principal time of year for phytoplankton production (particularly diatoms and green algae) relevant for higher trophic levels (i.e., nutritionally, Demott and Müller-Navarra 1997) as water temperatures rise and nutrient availability remains high prior to seasonal limitations of July and August when

unpalatable cyanobacteria dominate (Figure S1; Bukaveckas et al. 2002; Yurista et al. 2004). Additionally, the temporal analysis focused on the proposed establishment timing and population increase of silver carp in Kentucky Lake; pre- (1989–2004) and post (2005–2013)-establishment time periods. Despite not having population estimates for silver carp in Kentucky Lake, commercial harvest of this fish has increased by over 450X from 127 kg in 2006 to 57,290 kg in 2014 (KDFWR unpublished data), consistent with exponential population growth quantified in neighboring watersheds (Sass et al. 2010). As part of the temporal analysis, we accounted for potential habitat differences by categorizing the fourteen study sites (Fig. 1) into three major reservoir habitats: embayments, embayment mouths, and sites within the main channel, hereafter referred to as site type. Our analysis included 2 embayment sites (2 and 4 L), located within a larger embayment with an average depth of 2.64 m and an average retention time of 100 days (Fig. 1). Additionally, a total of 9 embayment mouth sites were included with sites on the eastern shore: EG, ET and EV, and the western shore: WA, WB, WJ, WL, WP, and WS with an average depth of 6.87 m and characterized as intermediate between embayments and the main channel (Fig. 1). Finally, a total of three main channel sites were included CB, CH, CW, and

were distributed longitudinally along the main stem of the study reach with an average depth of 16.89 m and an average retention time of 32 days (Fig. 1).

Biological variables

The KLMP measures chl-*a* at each site by collecting a 1L water sample from a depth of 1 m. Chl-*a* water samples were placed in a dark iced cooler, transported to the laboratory and processed using a standard pigment extraction procedure (Clesceri et al. 1989) yielding $\mu\text{g chl-}a \text{ L}^{-1}$ that was used in this study as a surrogate of phytoplankton biomass. Zooplankton were sampled at each site in triplicate with a 15 L Schindler trap (243 μm mesh sieve) at a depth of 5 m, or half the water column depth at shallower sites (Levine et al. 2014). Zooplankton samples were placed on ice and transferred to the laboratory, preserved with buffered 4% formalin and Copepoda and Cladocera were identified to lowest practical taxon with a stereo dissecting microscope (Levine et al. 2014). All zooplankton taxa counts were converted to individuals L^{-1} . For our analysis, we included densities of copepod and cladoceran (including invasive *D. lumholzi* and excluding predatory *Leptodora kindtii*) as indices for herbivorous and omnivorous zooplankton densities, respectively.

Physical and chemical variables

Water temperature was measured with a Yellow Springs Instruments® 6600 multi-meter probe at the surface and 1 m intervals to the bottom; however, because we focused on near surface algae, our analysis considered only measurements from surface to the 2 m depth (i.e., approximately the depth of the photic zone) and it should be noted that Kentucky Lake is polymictic and remains well mixed all year. Soluble Reactive Phosphorous (SRP) was measured from water samples collected at 1 m and analyzed in the laboratory (Clesceri et al. 1989) yielding mg P L^{-1} . For more detailed descriptions of sample collections and processing, see: White et al. (2007), or protocols can be accessed through an online data request.

Analysis

Chlorophyll-*a*, zooplankton density (cladoceran and copepod), SRP and temperature were analyzed using separate linear mixed effects models. Chl-*a*, zooplankton density, SRP and temperature were a function of the fixed effects of establishment period and site type and the random effects of sampling month, year, and sampling date nested within year and site nested within year. Nested random effects account for the non-independence of samples taken at the same site in the same year. Further, to control for the non-independence of samples taken across all sites within the same year

we included cruise number nested within year as a random effect through explicit nesting.

Chlorophyll-*a*, cladoceran density, and copepod density were natural log-transformed to meet assumptions of normality. Statistical analyses were conducted using R version 3.3.1 (R Development Core Team 2014). All mixed effects models were fit with the lme4 package (Bates et al. 2014) and significance was tested using a Kenward–Roger denominator degrees of freedom approximation (Kenward and Roger 1997; Bolker et al. 2009). Post hoc comparisons of least squares means and confidence intervals for response variables within site type, before and after establishment, were calculated using lsmeans function (Lenth and Hervé 2014).

Results

We analyzed data from 25 years of the KLMP across 14 sites sampled 6 times each year (2 in each of April, May and June) totaling approximately 2100 samples. We had missing data, yet each variable was represented across all years and missing data represented less than 15% of the data over the study period and less than 0.6% on average within a given year with the exception of SRP. Over the entire study period, chl-*a* was missing 10%, temperature was missing 12%, cladoceran and copepod density were missing 14%, and SRP was missing 29% or an average of 1.2% on a given year.

Long-term patterns of chl-*a* and ecological factors showed considerably high inter- and intra-site variability across Kentucky Lake before and after silver carp establishment. Firstly, long-term patterns of chl-*a* were variable across all site types; however, chl-*a* showed a significant interaction effect between site type and silver carp establishment period ($P = 0.002$, Table 1) with a 22% decrease of chl-*a* in embayment and embayment mouth sites (Tables 2, 3) while no differences were detected in channel sites (Tables 2, 3) before and after establishment (Fig. 2). Patterns in chl-*a* suggest habitat-specific reductions in chl-*a* coinciding with silver carp establishment that are not apparent in a time series plot across all site types (Fig. 3), highlighting the importance and interpretation of habitat-specific effects. There was a significant interaction effect of cladoceran density between site type and silver carp establishment period ($P = 0.003$, Table 1), but there were no significant differences in cladoceran density among site types before and after establishment ($P > 0.3$, Tables 2, 3), suggesting herbivorous zooplankton density remained unchanged across Kentucky Lake before and after silver carp establishment (Fig. 3). There were no differences detected in copepod density before and after establishment of silver carp ($P = 0.983$, Table 1); furthermore, we found no interactions in copepod density between site types and establishment period:

Table 1 Kenward-Roger analysis of variance table with Kenward-Roger approximations for degrees of freedom testing for differences in natural log-transformed Chlorophyll-*a* ($\mu\text{g Chl-}a\text{ L}^{-1}$), Cladoceran Density (Individuals L^{-1}), Copepod Density (Individuals L^{-1}) Soluble Reactive Phosphorous (mg P L^{-1}) and un-transformed Temperature ($^{\circ}\text{C}$) among site types in pre- (1989–2004) and post (2005–2013)-establishment periods in Kentucky Lake

Source of variation	Num. <i>df</i>	Den. <i>df</i>	<i>F</i>	<i>P</i>
Chlorophyll-<i>a</i>				
Establishment period	1	24.87	6.07	0.021
Site type	2	11.18	14.34	0.001
Establishment period \times site type	2	307.46	6.56	0.002
Cladoceran density				
Establishment period	1	24.14	0.02	0.905
Site type	2	11.53	8.85	0.005
Establishment period \times site type	2	324.64	5.76	0.003
Copepod density				
Establishment period	1	25.47	0.00	0.983
Site type	2	11.74	15.0	0.001
Establishment period \times site type	2	323.81	1.22	0.296
Soluble reactive phosphorous				
Establishment period	1	28.67	0.00	0.958
Site type	2	11.67	12.5	0.001
Establishment period \times site type	2	343.03	0.53	0.587
Temperature				
Establishment period	1	23.41	0.92	0.346
Site type	2	11.36	0.21	0.815
Establishment period \times site type	2	302.48	2.26	0.107

($P = 0.296$, Tables 2, 3), suggesting that omnivorous copepod density remained unchanged across Kentucky Lake since silver carp establishment (Fig. 3). Physiochemical parameters, temperature and SRP showed high variability and no significant differences after the establishment of silver carp ($P > 0.3$, Table 1). Further, both temperature and SRP showed no significant interaction effects between site type and period ($P > 0.1$, Tables 2, 3) indicating that these physiochemical parameters were consistent before and after establishment (Fig. 3).

Discussion

Consumptive effects of invasive species can have fundamental consequences for ecosystem functions (Strayer et al. 1999). However, few experiments or data are designed to capture the broad temporal and spatial scales over which invaded ecosystems are affected (Carpenter et al. 1995; Schindler 1998; Dodds et al. 2012). Our analyses show that within certain reservoir habitats chl-*a* concentrations have declined considerably since establishment of invasive silver carp (Fig. 2). Phytoplankton is the dominant primary

producer within main-stem reservoirs (Kimmel et al. 1990). Additionally, phytoplankton has been shown to be an important trophic base within riverine food webs (Thorp and Delong 2002) and can contribute a significant carbon source to surrounding terrestrial ecosystems through food web linkages (Kautza and Sullivan 2016). The reductions in chl-*a* since the establishment of silver carp were greatest within embayment and embayment mouth habitats compared to the main channel, suggesting context dependency of invasive species effects (Fig. 2). Our analyses also tested competing hypotheses as potential drivers of trends in chl-*a*, including herbivorous cladoceran, omnivorous copepods, SRP and temperature. These ecological variables showed no differences since the establishment of silver carp; thus, our findings remain strongly consistent with our original hypothesis. If chl-*a* is a reasonable predictor of phytoplankton biomass within Kentucky Lake, then our analysis presents evidence of top-down effects of invasive silver carp within the Kentucky Lake ecosystem.

Alternative hypotheses

Ecosystem level changes in basal resources can be caused by any number of exogenous and internal forces, making it challenging to disentangle the effects of a specific perturbation or process (Dodds et al. 2012). For example, large-scale regime shifts brought about by ecosystem succession, especially in the case of reservoir aging, can lead to changes in water clarity and subsequent phytoplankton dynamics (Holz et al. 1997). Similarly, changes in land use leading to increased or decreased nutrient loading have been shown to have interactive effects on long-term water quality and ecosystem function in the Laurentian Great Lakes (Scavia et al. 2014). Additionally, changes in consumer community structure and abundance can have strong top-down or bottom-up forces on phytoplankton (Schaus and Vanni 2000). Furthermore, reservoir ecosystems are unique in that water levels are managed for human needs (Lehner et al. 2011), and hydrology can vary widely in concert with any combination of internal and external drivers of ecosystem change. Indeed, it is important to carefully consider the intricacy of multiple ecological factors and how these components may interact with perturbations when drawing conclusions from large-scale ecological data.

We present data suggesting that changes in a basal resource coinciding with silver carp establishment are not explained by patterns of ecological covariates. Patterns in higher trophic levels (i.e., zooplankton), nutrients (i.e., soluble reactive phosphorous) and temperature remained unchanged since the establishment of silver carp, suggesting that our inference is not confounded with aspects of primary consumer density, pollution, or climate change. Additionally, supplementary analyses show that reservoir

Table 2 Estimates of Least Squares means contrasts of natural log-transformed Chlorophyll-*a* ($\mu\text{g Chl-}a\text{ L}^{-1}$), Cladoceran Density (Individuals L^{-1}), Copepod Density (Individuals L^{-1}), Soluble Reactive Phosphorous (SRP, mg P L^{-1}) and Temperature ($^{\circ}\text{C}$) comparing pre- (1989–2004) and post (2005–2013)-establishment periods in Kentucky Lake

	Chlorophyll- <i>a</i>				Cladoceran density			
	Contrast	<i>df</i>	<i>t</i> ratio	<i>P</i>	Contrast	<i>df</i>	<i>t</i> ratio	<i>P</i>
Site type								
Channel	−0.08	205.8	−0.93	0.352	−0.13	27.49	−0.46	0.650
Embayment	−0.24	260.3	−2.72	0.007	+0.13	31.65	0.65	0.653
Mouth	−0.25	145.8	−3.22	0.002	−0.02	22.64	0.94	0.941
	Copepod density				SRP			
	Contrast	<i>df</i>	<i>t</i> ratio	<i>P</i>	Contrast	<i>df</i>	<i>t</i> ratio	<i>P</i>
Site type								
Channel	−0.07	23.78	−0.20	0.847	−0.001	34.76	−0.35	0.731
Embayment	0.37	26.06	0.94	0.354	−0.001	42.54	0.37	0.716
Mouth	−0.16	21.04	−0.43	0.670	+0.000	24.99	0.12	0.907
	Temperature							
	Contrast	<i>df</i>	<i>t</i> ratio	<i>P</i>	Contrast	<i>df</i>	<i>t</i> ratio	<i>P</i>
Site type								
Channel		0.87		137.15			1.040	0.300
Embayment		0.85		138.60			1.009	0.315
Mouth		0.69		135.31			0.827	0.410

Table 3 Means \pm SE of Chlorophyll-*a* ($\mu\text{g Chl-}a\text{ L}^{-1}$), cladoceran density (Individuals L^{-1}), copepod density (Individuals L^{-1}) Soluble Reactive Phosphorous (mg P L^{-1}) and temperature ($^{\circ}\text{C}$) comparing pre- (1989–2004) and post (2005–2013)-establishment periods across site types (Channel, Embayment, Mouth) in Kentucky Lake

	Chlorophyll- <i>a</i>				Cladoceran density			
	Pre	\pm SE	Post	\pm SE	Pre	\pm SE	Post	\pm SE
Site type								
Channel	11.95	1.12	11.05	1.13	1.35	1.94	1.18	1.51
Embayment	23.62	1.13	18.50	1.14	0.46	1.95	0.52	1.99
Mouth	18.39	1.10	14.34	1.11	0.89	1.93	0.87	1.96
	Copepod density				SRP			
	Pre	\pm SE	Post	\pm SE	Pre	\pm SE	Post	\pm SE
Site type								
Channel	2.26	1.42	2.10	1.51	0.007	0.002	0.008	0.002
Embayment	0.71	1.45	1.02	1.53	0.012	0.001	0.012	0.002
Mouth	1.53	1.40	1.31	1.48	0.018	0.002	0.017	0.002
	Temperature							
	Pre	\pm SE	Post	\pm SE	Pre	\pm SE	Post	\pm SE
Site type								
Channel		20.88		0.51		21.75		0.67
Embayment		20.91		0.52		21.75		0.68
Mouth		21.04		0.51		21.73		0.67

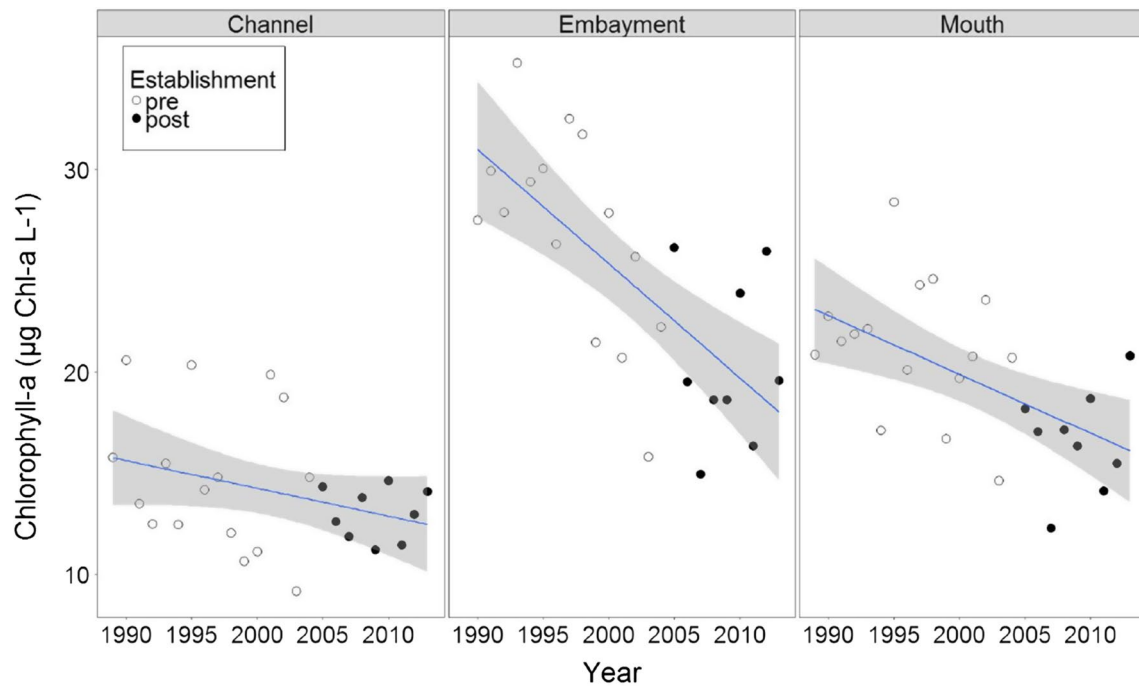


Fig. 2 Yearly mean values with line of best fit with gray shading of 95% confidence interval of chlorophyll-*a* ($\mu\text{g chl-}a\text{ L}^{-1}$) from the early summer (April–June) comparing between pre- (white circles, 1989–2004, $n = 1223$) vs. post (black circles, 2005–2013, $n = 674$) silver carp (*Hypophthalmichthys molitrix*) establishment periods, while accounting for habitat differences (site type). There was a significant interaction effect of chlorophyll-*a* between

site type and silver carp establishment period ($F_{2,307.5} = 6.56$, $P = 0.002$) showing a decrease in chlorophyll-*a* in embayment sites (pre $n = 165$, post $n = 97$) of 22% (23.62 ± 1.13 vs. $18.50 \pm 1.14\ \mu\text{g chl-}a\text{ L}^{-1}$) ($t_{260.3} = -2.72$, $P = 0.007$) and mouth sites (pre $n = 794$, post $n = 432$) of 22% (18.39 ± 1.10 vs. $14.34 \pm 1.11\ \mu\text{g chl-}a\text{ L}^{-1}$) ($t_{148.8} = -3.22$, $P = 0.002$), and no differences in channel sites before and after establishment in Kentucky Lake (pre $n = 264$, post $n = 145$)

discharge measured at Kentucky Dam did not differ significantly since establishment of silver carp ($P = 0.716$, Figure S2; Tables S2, S3, S4). Moreover, long-term patterns in Secchi depth, a measure of water column clarity, significantly increased post-invasion ($P = 0.001$, Figure S3; Tables S2, S3, S4) consistent with our findings of decreasing chlorophyll-*a* and inconsistent with patterns of reservoir aging (Tilzer 1988; Holz et al. 1997). Likewise, patterns in invasive herbivorous (*Daphnia lumholtzi*) do not explain observed patterns in chl-*a* as no differences in overall cladoceran zooplankton density were detected ($P = 0.905$, Fig. 3). Unfortunately, information on fish community structure or abundance for Kentucky Lake is unavailable and we were unable to explore how this factor may have interacted with system dynamics before and after invasion. Above all, our use of these data was not experimental, and we are unable to describe causal mechanisms of ecosystem change. However, 25 years of data and the patterns and trends within this dataset offer a robust foundation from which we can unravel components of ecological stochasticity and ultimately provide inference to large-scale patterns of basal resources coinciding with invasion.

Potential effects of silver carp

The ability of silver carp to suppress phytoplankton is disputed in the literature. Several studies suggest a negative relationship between silver carp density and phytoplankton biomass, through the consumption and pelletization of phytoplankton cells (Starling 1993; Xie 1999; Fukushima et al. 1999; Lu et al. 2002; Xiao et al. 2010). However, others (Lin et al. 2014 and citations therein) have concluded that silver carp are inefficient at ingesting/digesting smaller sized algae ($<10\ \mu\text{m}$) causing shifts in phytoplankton assemblages to those dominated by nanoplankton which are then fertilized by silver carp excretion. Our results contrasted with previous work showing no effects because those studies primarily occurred in eutrophic, tropical-subtropical experimental enclosures of smaller sized ecosystems with phytoplankton assemblages dominated by cyanobacteria (exceptions see, Radke and Kahl 2002; Lin et al. 2014). In contrast, the phytoplankton community of Kentucky Lake during the early summer (April–June) is typically dominated by diatoms and green algae (Bukaveckas et al. 2002, Figure S1); paralleling communities of many temperate mesotrophic systems and those of higher latitudes (Wetzel 2001).

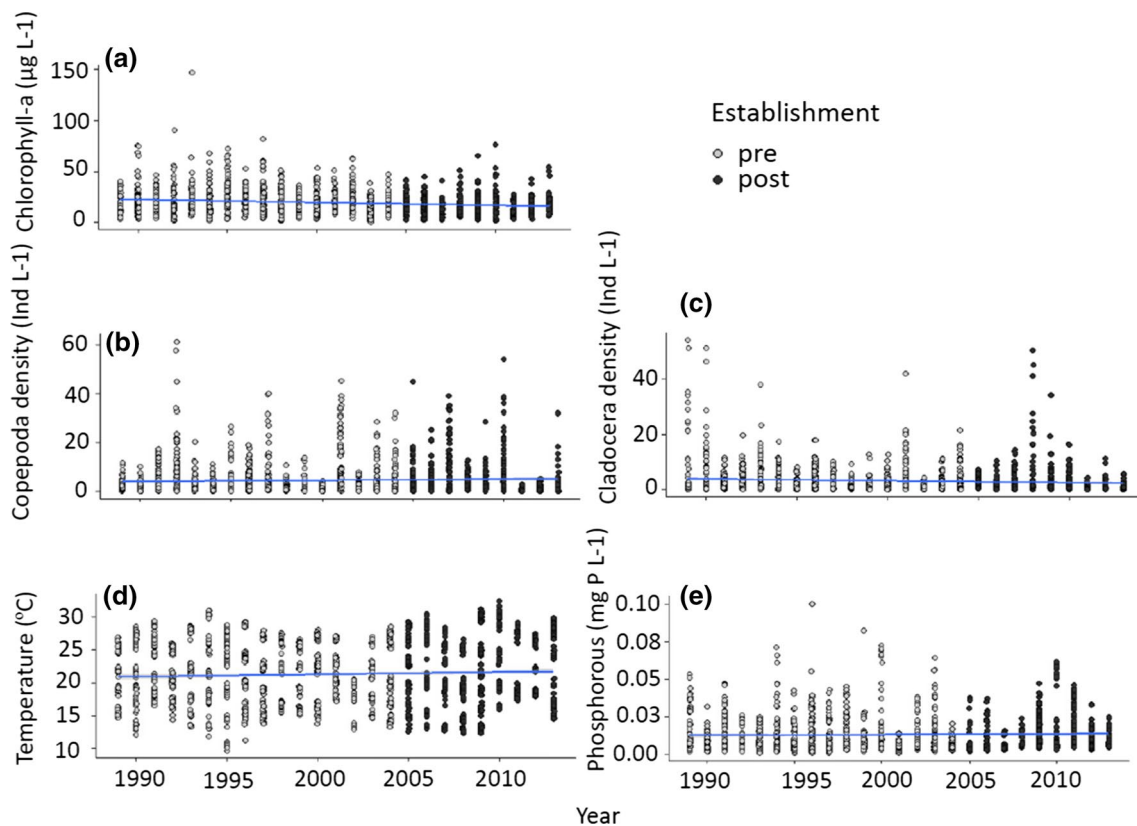


Fig. 3 Time series plots with line of best fit of early summer (April–June) **a** chlorophyll-*a* ($\mu\text{g chl-}a\text{ L}^{-1}$), ($n = 1897$), **b** copepod density (Ind L^{-1}) ($n = 1801$), **c** cladoceran density, including invasive *D. lumholzi* (Ind L^{-1}) ($n = 1802$), **d** water temperature ($^{\circ}\text{C}$) ($n = 1839$)

e soluble reactive phosphorous (mg p L^{-1}) ($n = 1491$) from 1989 to 2013 comparing between pre- (gray circles, 1989–2004) vs. post (black circles, 2005–2013)-silver carp (*Hypophthalmichthys molitrix*) establishment periods, across all sites in Kentucky Lake

To better understand how varying phytoplankton communities may respond differentially to silver carp invasion we provide supplementary analysis of Kentucky Lake chl-*a* in late summer (July–August) when cyanobacteria dominate (Bukaveckas et al. 2002, Figure S1). Late summer concentrations of chl-*a* show no silver carp effect on phytoplankton biomass (Tables S2, S3, S4; Figure S5) suggesting that cyanobacteria are less susceptible to suppression by silver carp than green and diatom algal communities. Collectively, our analyses suggest that the seasonality of phytoplankton communities may be important in explaining invader effects and help to further explain discrepancies between our results and other studies. Within mesotrophic systems, late spring-early summer is the principal time of year for zooplankton to acquire high quality resources such as diatoms and green algae (Brett and Muller-Navarra 1997; Demott and Müller-Navarra 1997). Therefore, we argue that the reductions of early summer phytoplankton biomass would be more limiting and have higher cascading potential compared to changes in late summer. Perhaps silver carp effects are exceptional in temperate systems with substantial diatom production,

such as Kentucky Lake and the greater Mississippi River Basin, which may explain changes noticed in this and other studies in similar systems (Irons et al. 2007; Sass et al. 2014; Solomon et al. 2016).

Habitat-specific patterns showing reductions in chl-*a* indicate that silver carp had greater consumptive effects in slower flow habitats compared to a faster flow main channel habitat. Previous studies have shown that silver carp prefer slower flow habitats (Calkins et al. 2012) and perhaps silver carp within Kentucky Lake concentrate and feed in these more favorable off channel embayments and transitional embayment mouths. Within Kentucky Lake, retention time is at least $\approx 65\%$ longer within the Ledbetter embayment than in the main channel; subsequently, lower levels of autochthonous (e.g., phytoplankton) resources may be cycling through and replenishing food webs of these relatively enclosed habitats (Bukaveckas et al. 2002) increasing embayment susceptibility to top-down pressures. If silver carp have greater top-down effects in lentic vs. lotic habitats it may be a generalizable pattern helpful in predicting silver carp effects throughout the Mississippi Basin and Laurentian Great Lakes.

Though speculative, it may be instructive to consider the habitat context of invader effects. Kreps et al. (2012) found that native snails experience higher predation from invasive rusty crayfish on hard compared to soft substrates suggesting that the habitat preference of the invader is important in explaining consumptive effects. Furthermore, Vander Zanden et al. (1999) found that habitat-specific effects of an invasive predator led to a decoupling of pelagic and littoral lake food webs once mediated by a native predator, indicating that invader habitat specificity can restructure entire food webs. Understanding where and why invasive species effects are most significant within an invaded system can provide insight into the complex relationships occurring between invaders and recipient food webs (Vander Zanden et al. 1999; Kreps et al. 2012).

Conclusion

Our analysis suggests ecosystem changes, namely reductions in phytoplankton biomass within lentic habitats since the establishment of silver carp. If silver carp are capable of reducing phytoplankton biomass within lentic-like sections of large reservoirs and rivers, then mechanisms by which this invasive omnivore affects recipient communities can be further explained. Reduction of phytoplankton may cause declines in herbivorous zooplankton, possibly cascading upwards to native planktivores such as the threatened paddlefish (*Polyodon spathula*) and forage fish (*Dorosoma* spp.), which are important for top predators (e.g., birds and fish). Empirical work has shown that invasive omnivores have direct and indirect negative effects on multiple trophic levels (Lodge et al. 1994; Gallardo et al. 2016). The results of our study suggest that an invasive omnivore has directly affected a dominant basal resource; however, the direct and indirect effects on higher trophic levels and neighboring terrestrial ecosystems remain unknown. Species introductions are occurring at unprecedented rates, and understanding their influences on ecosystem functions remains a challenge for ecologists (Vander Zanden et al. 1999; Ricciardi et al. 2013). Our analyses suggest an important ecosystem level change resulting from species invasion and highlight the value of long-term data in exploring ecosystem and invasion ecology.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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