

Influence of local-scale abiotic and biotic factors on stress and nutrition in invasive silver carp

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Received: 26 January 2014 / Revised: 30 March 2014 / Accepted: 4 April 2014 / Published online: 16 April 2014
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Abstract Community structure and dynamics in aquatic ecosystems are influenced by a variety of abiotic and biotic factors including productivity, species composition, and temperature. These factors may also affect local-scale community resilience to nonnative species invasions. We used habitat characteristics, zooplankton concentrations, fish abundances, and species composition and richness data collected by two fish population monitoring programs to define relationships that influence stress and nutrition in invasive silver carp (*Hypophthalmichthys molitrix*). We collected blood samples and quantified nutritional (alkaline phosphatase, cholesterol, protein, and triglycerides) and stress metrics (cortisol and glucose) from individuals across three distinct time periods. Nutritional patterns in silver carp were explained by temperature and food resources, indicating elevated

feeding in warmer months. Patterns in blood-based stress parameters were most strongly driven by environmental characteristics, elevating with high water temperatures and increased turbidity. Nutrient levels and community richness parameters did not influence the stress or condition of silver carp, likely due to the absence of limiting resources or competition for this species. Together, our results provide insights into the factors that may influence the spread and distribution of silver carp, as well as the characteristics of habitats that could be vulnerable to future silver carp invasion.

Keywords Competition · Conservation · Environmental characteristics · Invasion · Nonnative species

Handling editor: M. Power

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Introduction

Several theories contribute to our understanding of community structure and dynamics, with numerous hypotheses describing the range of complex interactions and interrelationships among species and their habitats (Tonn, 1990; Tilman, 2004). Community interactions may be driven by local-scale factors including biotic processes (e.g., competition for limiting resources, species richness/composition) and/or abiotic processes (e.g., habitat complexity) (Tonn & Magnuson, 1982; Tonn, 1990). Greater species richness may improve ecosystem resiliency

(Duffy, 2009), but is inadequate for explaining what maintains baseline ecosystem processes (Tonn & Magnuson, 1982). Species composition (e.g., functional groups, classified by physiological and morphological differences) is also important because compositional differences have the potential to exert strong influences on ecosystem processes (Tonn & Magnuson, 1982; Tilman et al., 1997). The ability of assemblages to resist nonnative invasions may also be influenced by species richness and composition, competition, predation, and environmental variability (i.e., abiotic factors) (Gido & Brown, 1999; Ricciardi & MacIsaac, 2011). A local-scale study can provide a snapshot of community and species interactions at a specific point in time, but those interactions may be complex and fluid, especially in a large river ecosystem.

Large river ecosystems are intriguing and understudied when addressing questions of community structure (but see Vannote et al., 1980). Large rivers experience substantial seasonal and habitat variation that may play a role in influencing community dynamics at a local scale (Junk et al., 1989). Habitat alterations may also occur through processes such as levying or impounding for commercial navigation, flood control, and/or agriculture purposes, which can affect channel morphology, flow regimes, and physical–chemical attributes (Schlosser, 1990). These disturbances can lead to large inter-annual variation in habitat conditions (e.g., more frequent water-level fluctuations, flooding, sedimentation, and nutrient loading) (Koel & Sparks, 2002). Together, these alterations may impact local species diversity by increasing colonization and establishment potential for invasive species (Gido & Brown, 1999). For example, water temperature may inhibit or promote the individual growth of an invader as it varies across time and space (Shea & Chesson, 2002). As a result, it is important to examine multiple time points annually when studying large rivers due to their unpredictable abiotic characteristics. An organism's stress and nutritional condition may also vary seasonally with changes in habitat conditions, and fish may exhibit behavioral and physiological responses to temperature (Lowe et al., 2006). Quantifying the nutritional and stress physiology of an invasive species may help identify abiotic and biotic factors influencing their success and to allow for predictions of suitable habitat conditions in other un-invaded systems.

Physiology is a discipline that aims to link an organism and its population to the environment (Ricklefs & Wikelski, 2002). Individual nutrition and stress have previously been shown to vary with biotic and abiotic conditions of the environment, and can provide insights into population and community structure and dynamics. Assessing fish health using blood chemistry is valuable, as nutritional condition represents a relationship between fitness and energy stores (Congleton & Wagner, 2006). Nutritionally deficient organisms may experience reduced foraging ability, poor growth, reduced swimming performance, and/or decreased survival relative to individuals that are more satiated (Gingerich et al., 2010; Wagner et al., 2010). The metabolism of poikilotherms is directly influenced by environmental factors (temperature, oxygen, and salinity) (Tonn, 1990; Wootton, 1998), which can alter the energy requirements for fishes seasonally. During periods of low nutritional inputs, fish may not have sufficient energy to allocate to reproduction, potentially reducing fitness (Wootton, 1998). Reductions in energy due to limited food intake may also result in the induction of a stress response in an individual, making the quantification of stress a tool that can help define the health of an organism. Stress is also metabolically expensive, can potentially cause a loss of performance at an organismal level, and can negatively impact fitness through reducing the energy available for activity and reproduction, which may subsequently limit population growth (Kassahn et al., 2009; Schreck, 2010). Quantifying the interactions of abiotic and biotic factors and their relationship with organismal stress and nutrition is critical for understanding how those various factors are perceived and dealt with by individuals (Wingfield, 2013). Further, such studies can promote a supplementary comprehension of what underlies the link between physiology, invasive species, and community structure and dynamics.

Silver carp (*Hypophthalmichthys molitrix*) (SVCP) are invasive, planktivorous, filter-feeding fishes that have successfully established in the Mississippi River Basin (MRB) and have the potential to disperse and invade neighboring watersheds depending upon the suitability of habitats (Herborg et al., 2007; Kolar et al., 2007). More importantly, SVCP have the potential to negatively affect freshwater ecosystems (Kolar et al., 2007; Sass et al., 2010). For example, the presence of SVCP has negatively affected the body

condition of native gizzard shad (*Dorosoma cepedianum*) (GZSD) and bigmouth buffalo (*Ictiobus cyprinellus*) potentially due to dietary overlap (Irons et al., 2007; Sampson et al., 2009). Nevertheless, there is a critical need to better define how abiotic and biotic factors influence the nutritional condition and stress in SVCP at a local scale, as this information can provide valuable insights into mechanisms controlling future abundance, spread, and distribution of these invaders. The objective of our study was to quantify the effects of local-scale abiotic, biotic, and community-related parameters on the stress and nutritional condition of wild-caught SVCP in the La Grange Reach, Illinois River, Illinois, USA (LGR). We hypothesized that SVCP nutritional condition would decrease and stress levels would increase with greater community-related parameters associated with potential competition (e.g., species abundance and richness). We also hypothesized reciprocal effects on nutrition and stress with higher quality abiotic habitat features (e.g., productive, eutrophic ecosystems based on water quality characteristics), due to greater food availability.

Materials and methods

Field analysis

We collected SVCP in association with two long-term fish population monitoring programs coordinated by the Illinois River Biological Station (IRBS); the Long-Term Resource Monitoring Program (LTRMP) and the Long-Term Illinois, Mississippi, Ohio, and Wabash River Fish Population Monitoring Program (LTEF) (Gutreuter et al., 1995; Tyszko et al., 2012). The LTRMP and LTEF are designed to sample and enumerate the entire fish community of large rivers using a standardized series of protocols that date back to 1989 and 1957, respectively (Irons et al., 2007; McClelland et al., 2012). As part of these sampling protocols, we collected SVCP from the LGR, located near Havana, Illinois (LTRMP Field Station 6, latitude: 40°18'N, longitude: -90°3'W) during June–October, 2011. The LGR is a 129-km stretch of the Illinois River extending from the La Grange Lock & Dam at river km 126 upstream to the Peoria Lock & Dam at river km 255. The LGR is highly disturbed with extensive anthropogenic modifications (e.g., impoundments, agriculture, and altered flood regimes)

and a high abundance and biomass of established, invasive SVCP (Koel & Sparks, 2002; Sass et al., 2010). Sampling was divided into three time periods: mid-summer = June 15–July 31, late-summer = August 1–September 15, and early fall = September 16–October 31. We sampled blood from up to 12 (range 10–12) SVCP in the LGR during each of the three time periods in 2011. Although we acknowledge limitations to performing our study at one location (i.e., spatial and temporal correlation, replication), an ecosystem response is of theoretical and practical interest because it allows for the inclusion of abiotic and biotic processes that are typically difficult to incorporate in an artificial system (Carpenter et al., 1995; Schindler, 1998). The LGR experiences high seasonal variability in climate, fish community structure, and primary production (Koel & Sparks, 2002; McClelland et al., 2012). Thus, we were able to sample fish experiencing a range of abiotic and biotic characteristics over the three distinct time periods.

We collected SVCP primarily using pulsed-direct current (DC) electrofishing according to methods outlined in Gutreuter et al. (1995) and Tyszko et al. (2012). However, about half of the SVCP analyzed in the current study leapt on board the boat prior to being immobilized by electricity. Silver carp exhibit a jumping behavior when startled (Green & Smitherman, 1984), which can make their capture by electroshocking difficult. Fish that voluntarily leapt on board were sampled for blood in a manner identical to those that were stunned by electricity. Immediately after capturing a fish, we collected blood according to methods outlined in Liss et al. (2013). One mL of whole blood was collected, placed into a microcentrifuge tube, and spun at 6,600 RPM for 3 min to separate plasma from red cells. Plasma was removed and placed into two additional 1.5 ml microcentrifuge tubes. Plasma and red cells were flash frozen in a dry shipper charged with liquid nitrogen, and transported to the University of Illinois at Urbana-Champaign and stored in a <-75°C freezer until processing. We drew blood from all individuals, irrespective of collection method, in less than 3 min to obtain a baseline value of stress and nutrition that would not be influenced by sampling procedures (Romero & Reed, 2005; Congleton & Wagner, 2006). We also recorded total length (mm) and weight (g) of each fish.

Water quality parameters within the LGR were collected from fixed sites every 2 weeks during fish

sampling periods and from a set of randomly selected locations at quarterly intervals according to established protocols in 2011 (APHA, 1992; Soballe & Fischer, 2004). Water quality parameters included water temperature, Secchi disk transparency, dissolved oxygen (DO), pH, turbidity, conductivity, velocity, total phosphorus (TP), total nitrogen (TN), suspended solids, and chlorophyll *a*, which we used as a representation of habitat quality. In 2011, zooplankton collections were conducted monthly during May–November in the LGR. For each sample, 30 l of water was pumped through a 55 μm filter, and this procedure was replicated three times at each site per month. We examined the integrated zooplankton community and concentration throughout the entire water column by attaching a weight to a hose and lifting that hose from the bottom to the surface of the water while pumping. Zooplankton samples were preserved in a sugar-buffered formalin solution and transported to the IRBS for analysis. We enumerated and identified the macrozooplankton samples with a zooplankton counting wheel. Zooplankters were identified as rotifers to Genus, cladocerans to Genus, and copepods to Family. An estimate of the number of zooplankton in each sample was determined by dividing the sample concentrate volume by the volume of subsamples required to reach 100 zooplankton, and multiplied by the number of zooplankton counted in the subsample(s). This number was then divided by the volume filtered to get an estimate of the number of zooplankton in 1 l of river water for each sample. Each predictor variable was averaged across all sampling episodes within a time period, resulting in a single mean parameter value per time period.

Species richness, community composition richness, and catch per unit effort (CPUE, number of fish h^{-1}) for all fish captured by electrofishing during each time period were quantified in accordance with LTRMP protocols (<http://www.umesc.usgs.gov/ltrmp.html>) (Ickes & Burkhardt, 2002). Community composition, quantified as the number of functional groups present, was defined according to functional groups identified in Poff & Allan (1995). To develop these functional groups, diet information was taken from Becker (1983), Pflieger (1975), and the Ohio Department of Natural Resources (http://www.dnr.state.oh.us/Home/species_a_to_z/AZFish/tabid/17913/Default.aspx) and used to assign fish to the following functional feeding groups: benthic invertivores, general invertivores, herbivore-

detritivores, omnivores, piscivores, planktivores, and surface/water column invertivores (Poff & Allan, 1995). A list of all fish species collected during this time period is available at http://www.umesc.usgs.gov/data_library/fisheries/fish_page.html. Again, each predictor variable was averaged across all sampling episodes within a time period, resulting in a single mean parameter value per time period.

Laboratory analysis

We analyzed plasma alkaline phosphatase (ALP) (U l^{-1}), cholesterol (mg dl^{-1}), cortisol (ng ml^{-1}), glucose (mg dl^{-1}), protein (g dl^{-1}), and triglycerides (mg dl^{-1}) in a manner identical to Liss et al. (2013). The cortisol EIA kit used (ADI-900-071, Enzo Life Sciences, Pennsylvania, USA) has been identified as accurate and precise when used for fishes (Sink et al., 2008), and has a lower detection limit of $0.0567 \text{ ng ml}^{-1}$. Individual cortisol values that were below the sensitivity limit of the kit were treated as being equal to the lowest detection limit value for the kit ($0.0567 \text{ ng ml}^{-1}$) (Haddy & Pankhurst, 1999; Ramsay et al., 2006). Triglycerides and ALP have been shown to represent a short-term, recent feeding nutritional component, while cholesterol has been shown to represent a long-term body energy reserve nutritional component. Protein can be representative of a short-term feeding or long-term body energy reserves (Congleton & Wagner, 2006; Guerreiro et al., 2012). Cortisol and glucose are associated with the stress response of teleost fishes (Barton, 2002; Wagner & Congleton, 2004).

Statistical analyses

At the outset of analyses, we developed a correlation matrix with the different water quality predictor variables to identify correlated terms and avoid colinearity within the data. Following colinearity analyses, we identified three abiotic (environmental) variables that were representative of the different water quality parameters measured: water temperature, TP, and suspended solids. More specifically, water temperature was inversely correlated with conductivity, DO, and Secchi disk transparency ($P < 0.05$) and positively correlated with turbidity, chlorophyll *a*, and suspended solids ($P < 0.05$). TP

Table 1 Correlation matrices showing relationships between water quality predictor variables used in regression analyses

Water quality parameter	Negative correlation	Positive correlation	No correlation
Temperature	Conductivity	Turbidity	TN
	Dissolved oxygen	Chlorophyll <i>a</i>	Velocity
	Secchi disc	Suspended solids	pH
Total Phosphorous	Secchi disc	TN	Total phosphorous
	Chlorophyll <i>a</i>	Velocity	Turbidity
	Dissolved oxygen	Suspended solids	Temperature
	pH	Conductivity	
Suspended Solids	Secchi disc	Total phosphorous	Velocity
	Dissolved oxygen	Chlorophyll <i>a</i>	Conductivity
	pH	Turbidity	TN
		Temperature	

All correlations are significant at $\alpha = 0.05$

was negatively correlated with Secchi disk transparency, chlorophyll *a*, DO, and pH ($P < 0.05$) and positively correlated with TN, velocity, conductivity, and suspended solids ($P < 0.05$). Suspended solids correlated negatively with pH, DO, and Secchi disk transparency ($P < 0.05$) and correlated positively with TP, chlorophyll *a*, turbidity, and temperature ($P < 0.05$) (Table 1). Together, water temperature, TP, and suspended solids represented the 11 water quality parameters analyzed.

After completing colinearity analyses, we used a two-step statistical approach to define how environmental variables influenced blood-based metrics. First, to quantify the variation in environmental parameters across time periods, we used a one-way analysis of variance (ANOVA), which allowed us to visualize trends in environmental parameters. Each predictor variable was treated as a nested parameter within time period because measurements from all sampling episodes were averaged in each of the three time periods. Second, we used simple linear regression, followed by Akaike's Information Criterion corrected for small sample sizes (AICc), to define the relationship between nutritional and stress parameters (response variables) and total length, water quality variables, zooplankton concentrations, fish relative abundances (CPUE), species richness, and species composition (predictor variables) over the three time periods sampled. Comparisons using AICc allowed us to quantify and rank the best approximating model for each blood variable (Hegyi & Garamszegi,

2011; Symonds & Moussalli, 2011). Based on the ΔAICc , a value $0 \leq \Delta\text{AICc} \leq 2$ shows substantial support that a model is the best fit to the data, while an $\Delta\text{AICc} > 10$ shows little support (Symonds & Moussalli, 2011). Following best-fit model determination for each nutritional and stress parameter (defined here as $\Delta\text{AICc} < 4$), post hoc analyses were performed to visualize trends in the data. We performed all statistical analyses using JMP version 10.0 (SAS Institute, North Carolina, USA). Rejection of the null hypothesis (α) for all tests was 0.05. All values were reported as mean \pm standard error of the mean (SEM) where appropriate. We used the null hypothesis of no variation in stress or nutrition (i.e., physiological parameters) for SVCP across abiotic or biotic habitat characteristics nested within time periods.

Results

Silver carp total length, weight, and the six measured physiological parameters were highly variable across the three time periods in the LGR (Table 2). Total length and weight were strongly correlated ($P < 0.0001$, $r = 0.94$); therefore, only total length was included. Out of 32 cortisol readings for SVCP, nine fish had cortisol concentrations below the detection limit of the kit and were treated as being equal to the lowest detection limit value (Haddy & Pankhurst, 1999; Ramsay et al., 2006). Abiotic and biotic environmental parameters also varied across the three time periods

Table 2 Sample size, minimum, maximum, mean, median, and standard error mean values for nutritional and stress characteristics of silver carp *H. molitrix* sampled in the La Grange Reach, Illinois River during 2011

Parameter	N	Min	Max	Mean	Median	Standard error mean
Triglycerides (mg dl ⁻¹)	30	14.8	233.4	93.4	86.6	7.9
Cortisol (ng ml ⁻¹)	32	0.06	102.5	19.3	7.8	5.2
Cholesterol (mg dl ⁻¹)	32	159.0	592.0	228.5	213.4	13.2
Glucose (mg dl ⁻¹)	32	21.5	63.3	39.6	38.6	1.9
Protein (g dl ⁻¹)	32	3.0	4.8	3.8	3.7	0.08
ALP (U l ⁻¹)	32	6.7	71.3	35.0	35.7	3.7
Total weight (g)	32	800.0	2540.0	1195.6	1130.0	61.0
Total length (mm)	32	450.0	617.0	493.8	486.5	6.0

Table 3 Mean values for water quality parameters, zooplankton concentrations, and fish species richness and abundance for the La Grange Reach, Illinois River during 2011

Parameter	Mid-summer	Late-summer	Early fall
Secchi disk transparency (cm)	20.7 ± 0.6 ^a	20.9 ± 0.7 ^a	21.9 ± 0.6 ^a
Temperature (°C)	30.9 ± 0.1 ^a	31.6 ± 0.2 ^a	15.1 ± 0.4 ^b
DO (mg l ⁻¹)	5.0 ± 0.2 ^c	7.97 ± 0.4 ^b	9.3 ± 0.1 ^a
pH	7.9 ± 0.02 ^c	8.2 ± 0.04 ^a	8.1 ± 0.02 ^b
Turbidity (NTU)	63.7 ± 2.6 ^a	66.4 ± 3.2 ^a	58.5 ± 2.9 ^a
Conductivity (µS cm ⁻¹)	774.8 ± 7.1 ^a	626.5 ± 8.9 ^b	753.6 ± 12.6 ^a
Velocity (m s ⁻¹)	0.2 ± 0.03 ^a	0.04 ± 0.01 ^b	0.12 ± 0.02 ^a
TP (mg l ⁻¹)	0.4 ± 0.02 ^a	0.4 ± 0.02 ^a	0.4 ± 0.03 ^a
TN (mg l ⁻¹)	2.9 ± 0.1 ^a	1.9 ± 0.08 ^b	2.3 ± 0.1 ^b
Suspended solids (mg l ⁻¹)	65.0 ± 3.5 ^a	63.8 ± 3.5 ^a	57.2 ± 3.4 ^a
Chlorophyll <i>a</i> (µg l ⁻¹)	44.3 ± 2.6 ^b	85.9 ± 4.2 ^a	34.6 ± 1.8 ^b
Rotifers (rotifers l ⁻¹)	118.5 ± 10.1 ^a	90.8 ± 7.9 ^a	105.7 ± 17.0 ^a
Copepods (copepods l ⁻¹)	3.1 ± 0.3 ^a	0.9 ± 0.1 ^c	1.9 ± 0.3 ^b
Cladocerans (cladocerans l ⁻¹)	2.7 ± 0.3 ^a	2.8 ± 0.3 ^a	0.3 ± 0.1 ^b
Total zooplankton (total zoop. l ⁻¹)	124.4 ± 10.1 ^a	94.5 ± 7.8 ^a	107.9 ± 17.1 ^a
Species richness	38	49	45
Planktivore and omnivore richness	13	16	16
Plantivore richness	3	2	3
CPUE_excluding SVCP (fish h ⁻¹)	179.2	319.7	328.5
CPUE_GZSD (fish h ⁻¹)	99.2	120.3	34.5
CPUE_SVCP (fish h ⁻¹)	8.3	46.8	26.0

CPUE refers to fish caught per electroshocking hour, GZSD refers to gizzard shad (*Dorosoma cepedianum*), SVCP refers to silver carp (*H. molitrix*), and excluding SVCP refers to the abundance of all other fishes caught during sampling. All values are reported as the mean ± SEM where appropriate. Results of statistical analyses are reported as superscript letters, with dissimilar letters indicating significant differences of an individual parameter across time periods (ANOVA, $P < 0.05$)

(ANOVAs, $P < 0.05$; Table 3). Mean water temperatures were twice as warm in the mid- and late-summer relative to the early fall sampling period (ANOVA, $P < 0.05$; Table 3). Mean cladoceran concentrations were nearly 10-fold greater in the mid- and late-summer

relative to the early fall (ANOVA, $P < 0.05$; Table 3). Average relative abundances of GZSD were lowest in the early fall compared to the other sampling periods.

Variability in ALP activities (the amount of enzyme causing the hydrolysis of ALP per minute at room

Table 4 Model selection results relating predictor variables to variation in ALP activities and plasma glucose concentrations for wild-caught silver carp (*H. molitrix*) collected in the La Grange Reach, Illinois River across three time periods in 2011

Parameter	Model	AICc	Δ AICc	Model likelihood	AICc weight
ALP	CPUE_GZSD (fish h ⁻¹)	251.44	0.00	1.00	0.68
	Temperature (°C)	254.06	2.61	0.27	0.18
	Cladocerans (cladocerans l ⁻¹)	254.73	3.29	0.19	0.13
	Suspended solids (mg l ⁻¹)	260.34	8.89	0.01	0.01
	Planktivore richness	279.92	28.48	0.00	0.00
	CPUE_excluding SVCP (fish h ⁻¹)	287.91	36.47	0.00	0.00
	Planktivore and omnivore richness	288.70	37.25	0.00	0.00
	CPUE_SVCP (fish h ⁻¹)	289.95	38.51	0.00	0.00
	Rotifers (rotifers l ⁻¹)	289.99	38.54	0.00	0.00
	Copepods (copepods l ⁻¹)	290.64	39.19	0.00	0.00
	Total zooplankton (total zoop. l ⁻¹)	290.74	39.29	0.00	0.00
	Total length (mm)	291.01	39.57	0.00	0.00
	Species richness	291.05	39.61	0.00	0.00
	TP (mg l ⁻¹)	291.06	39.62	0.00	0.00
	Glucose	Suspended solids (mg l ⁻¹)	233.28	0.00	1.00
Cladocerans (cladocerans l ⁻¹)		234.21	0.92	0.63	0.26
Temperature (°C)		234.42	1.14	0.57	0.24
CPUE_GZSD (fish h ⁻¹)		236.95	3.67	0.16	0.07
CPUE_excluding SVCP (fish h ⁻¹)		241.42	8.13	0.02	0.01
Planktivore and omnivore richness		242.17	8.89	0.01	0.00
TP (mg l ⁻¹)		246.19	12.91	0.00	0.00
Species richness		246.62	13.33	0.00	0.00
Total zooplankton (total zoop. l ⁻¹)		247.44	14.16	0.00	0.00
Copepods (copepods l ⁻¹)		247.57	14.28	0.00	0.00
Planktivore richness		247.91	14.63	0.00	0.00
Rotifers (rotifers l ⁻¹)		248.09	14.80	0.00	0.00
CPUE_SVCP (fish h ⁻¹)		248.10	14.82	0.00	0.00
Total length (mm)		248.65	15.37	0.00	0.00

Models are ranked by differences in AIC values (Δ AICc), and the model with the lowest Δ AICc value is the best fit to the data, with AICc weight determining the best approximating model. CPUE refers to fish caught per electroshocking hour, GZSD refers to gizzard shad (*Dorosoma cepedianum*), SVCP refers to silver carp, and excluding SVCP refers to the abundance of all other fishes caught during sampling

temperature) in the plasma of wild-caught SVCP was best explained by the CPUE of GZSD; models that included water temperature and cladoceran concentration also provided substantial support (Δ AICc = 2.61 and 3.29, respectively) (Table 4). The r^2 values between ALP activity (dependent variable) and CPUE of GZSD, water temperature, and cladoceran concentration (independent variables) were 0.71, 0.69, and 0.68, respectively, providing the variability in ALP activity of SVCP attributed to each of these parameters. Analysis of variance results

indicated that ALP values were significantly greater in the mid- and late-summer months compared to the early fall [$N = 32$, $F_{(2, 31)} = 35.57$, $P < 0.0001$].

Variability in the plasma glucose concentration of SVCP was best explained by suspended solid concentrations, with cladoceran concentration, water temperature, and the CPUE of GZSD also providing substantial support (Δ AICc = 0.92, 1.14, and 3.67, respectively) (Table 4). Plasma glucose concentrations were positively correlated with each of the predictor variables from the regression analyses

Table 5 Model selection results relating predictor variables to variation in cortisol, cholesterol, triglycerides, and protein concentrations for wild-caught silver carp (*H. molitrix*) collected in the La Grange Reach, Illinois River across three time periods in 2011

Parameter	Model	AICc	Δ AICc	Model likelihood	AICc weight	
Cortisol	Planktivore richness	309.71	0	1	0.17	
	CPUE_GZSD (fish h ⁻¹)	310.64	0.93	0.63	0.11	
	CPUE_SVCP (fish h ⁻¹)	311.27	1.55	0.46	0.08	
	Rotifers (rotifers l ⁻¹)	311.28	1.56	0.46	0.08	
	Temperature (°C)	311.44	1.72	0.42	0.07	
	Cladocerans (cladocerans l ⁻¹)	311.53	1.82	0.4	0.07	
	Copepods (copepods l ⁻¹)	311.59	1.88	0.39	0.07	
	Total zooplankton (total zoop. l ⁻¹)	311.65	1.94	0.38	0.06	
	Species richness	312	2.29	0.32	0.05	
	Suspended solids (mg l ⁻¹)	312.12	2.4	0.3	0.05	
	TP (mg l ⁻¹)	312.15	2.44	0.3	0.05	
	Planktivore and omnivore richness	313.01	3.29	0.19	0.03	
	CPUE_excluding SVCP (fish h ⁻¹)	313.1	3.38	0.18	0.03	
	Total length (mm)	313.21	3.5	0.17	0.03	
	Cholesterol	Total length (mm)	371.91	0	1	0.08
		CPUE_SVCP (fish h ⁻¹)	372.28	0.38	0.83	0.07
Rotifers (rotifers l ⁻¹)		372.28	0.38	0.83	0.07	
Copepods (copepods l ⁻¹)		372.29	0.38	0.83	0.07	
Total zooplankton (total zoop. l ⁻¹)		372.29	0.38	0.83	0.07	
Species richness		372.3	0.39	0.82	0.07	
TP (mg l ⁻¹)		372.3	0.39	0.82	0.07	
Planktivore richness		372.31	0.41	0.82	0.07	
Planktivore and omnivore richness		372.34	0.44	0.8	0.07	
CPUE_excluding SVCP (fish h ⁻¹)		372.35	0.45	0.8	0.07	
CPUE_GZSD (fish h ⁻¹)		372.45	0.54	0.76	0.06	
Temperature (°C)		372.46	0.56	0.76	0.06	
Suspended solids (mg l ⁻¹)		372.47	0.56	0.76	0.06	
Cladocerans (cladocerans l ⁻¹)		372.47	0.56	0.76	0.06	
Triglycerides		CPUE_GZSD (fish h ⁻¹)	314.43	0	1	0.17
		Temperature (°C)	315.86	1.43	0.49	0.08
	Cladocerans (cladocerans l ⁻¹)	315.88	1.45	0.48	0.08	
	Suspended solids (mg l ⁻¹)	316.03	1.59	0.45	0.08	
	Planktivore richness	316.18	1.75	0.42	0.07	
	Total length (mm)	316.35	1.92	0.38	0.06	
	CPUE_SVCP (fish h ⁻¹)	316.71	2.28	0.32	0.05	
	Rotifers (rotifers l ⁻¹)	316.71	2.28	0.32	0.05	
	Copepods (copepods l ⁻¹)	316.78	2.35	0.31	0.05	
	Total zooplankton (total zoop. l ⁻¹)	316.79	2.36	0.31	0.05	
	Species richness	316.85	2.42	0.3	0.05	
	CPUE_excluding SVCP (fish h ⁻¹)	316.87	2.44	0.3	0.05	
	TP (mg l ⁻¹)	316.87	2.44	0.3	0.05	
	Planktivore and omnivore richness	316.89	2.46	0.29	0.05	

Table 5 continued

Parameter	Model	AICc	Δ AICc	Model likelihood	AICc weight
Protein	Total length (mm)	37.58	0	1	0.11
	Total zooplankton (total zoop. l ⁻¹)	37.78	0.2	0.91	0.1
	Copepods (copepods l ⁻¹)	37.78	0.2	0.91	0.1
	Species richness	37.81	0.23	0.89	0.1
	Rotifers (rotifers l ⁻¹)	37.83	0.25	0.88	0.1
	CPUE_SVCP (fish h ⁻¹)	37.83	0.25	0.88	0.1
	TP (mg l ⁻¹)	37.86	0.27	0.87	0.09
	Planktivore and omnivore richness	38.6	1.02	0.6	0.07
	CPUE_excluding SVCP (fish h ⁻¹)	38.78	1.2	0.55	0.06
	Planktivore richness	39.19	1.61	0.45	0.05
	Suspended solids (mg l ⁻¹)	41.89	4.31	0.12	0.01
	CPUE_GZSD (fish h ⁻¹)	42.09	4.51	0.1	0.01
	Cladocerans (cladocerans l ⁻¹)	42.12	4.54	0.1	0.01
	Temperature (°C)	42.14	4.56	0.1	0.01

Models are ranked by differences in AIC values (Δ AICc), and the model with the lowest Δ AICc value is the best fit to the data, with AICc weight determining the best approximating model. CPUE refers to fish caught per electroshocking hour, GZSD refers to gizzard shad (*Dorosoma cepedianum*), SVCP refers to silver carp, and excluding SVCP refers to the abundance of all other fishes caught

($P < 0.05$), and the r^2 value for the relationship between plasma glucose concentration and suspended solids was 0.38, between glucose and cladoceran concentration was 0.36, for glucose and water temperature was 0.36, and between glucose and the CPUE of GZSD was 0.31. Results from the ANOVA indicated that plasma glucose concentrations were significantly greater in the mid- and late-summer periods compared to the early fall [$N = 32$, $F_{(2, 31)} = 9.06$, $P < 0.001$].

All competing AICc models had Δ AICc < 4.0 for cortisol, cholesterol, and triglycerides (Table 5). The r^2 value for the best-fit model (planktivore richness) and cortisol was 0.11. Cholesterol had an r^2 value of 0.02 with the best-fit model of total length. Triglycerides and the CPUE of GZSD had an r^2 of 0.04. The best-fit model (total length) for protein had an r^2 value of 0.13 (Table 5). These models do not appear to provide a meaningful interpretation of these physiological variables.

Discussion

For wild-caught, invasive SVCP collected in the LGR, ALP activities in plasma were positively correlated with water temperature, cladoceran concentrations,

and the CPUE of GZSD, particularly during the mid- and late-summer sampling periods. Alkaline phosphatase is a nutritional parameter, and previous research has shown that elevated quantities of ALP can be related to the processing of energy substrates by the liver. Decreased ALP activities have been observed in starving fish (Sandnes et al., 1988; Congleton & Wagner, 2006). Previous research with Atlantic salmon (*Salmo salar*) also documented a positive correlation between plasma ALP activities and water temperature (Sandnes et al., 1988). There is substantial diet overlap between GZSD and SVCP as both are filter-feeding fishes that consume zooplankton, including cladocerans (Shuang-lin & De-shang, 1994; Sampson et al., 2009). Wahl et al. (2008) documented an increase in cladoceran concentrations in warmer water temperatures throughout the summer in the Illinois River (i.e., mid- and late-summer), thereby elevating potential food resources for filter-feeding fishes. This finding is similar to our results, which showed that cladoceran concentrations were more than 10-fold greater in the mid- and late-summer relative to the early fall. Interestingly, Sampson et al. (2009) reported that SVCP found in Illinois and Mississippi river backwaters primarily consumed rotifers (98%), with cladocerans only comprising 0.04% of their diet. Similarly, GZSD consumed

rotifers as a main prey item (Sampson et al., 2009). The mesh size used to collect zooplankton in our study (55 μm) may have underestimated the rotifer community in the LGR (Chick et al., 2010). As such, cladoceran concentrations may also act as a proxy for other food quality parameters that were not captured by our study. Regardless, ALP in the plasma of SVCP likely correlates positively with GZSD CPUE because feeding conditions were optimal for both species during those time periods. Both species were likely consuming cladocerans at high rates relative to other times of the year. The GZSD relative abundances may have increased in collections as a result of their movement into the area because of the ample food supply. Water temperature also plays a major role in the feeding rates of fishes. Metabolism typically increases with warmer water temperatures, elevating the rate at which fishes must acquire food to balance metabolic costs and optimize growth (Kitchell et al., 1977; Burel et al., 1996). Specifically for SVCP, feeding is reduced in temperatures $<15^{\circ}\text{C}$ (Kolar et al., 2007). In our study, the mean temperature was about 15°C in the early fall, which may be why SVCP ALP activities were significantly lower during this time period. Water temperatures were $\geq 30^{\circ}\text{C}$ in mid- and late-summer, likely resulting in the need for increased feeding rates. Together, our results demonstrate that variation in SVCP feeding rates, quantified by ALP activities in plasma, was likely driven by cladoceran concentrations and elevated water temperatures in the mid- and late-summer.

Plasma glucose for SVCP was positively correlated with suspended solids, cladoceran concentrations, water temperature, and the CPUE of GZSD. Plasma glucose is a reliable indicator of stress and correlates with a wide range of environmental stressors, including water temperature, suspended solids, and salinity (Menge & Sutherland, 1987; Wells & Pankhurst, 1999). Our results indicate that, while SVCP feeding was likely not impaired during the mid- or late-summer (i.e., our proxy of SVCP feeding, ALP, did not decrease with increased GZSD CPUE), they may still be experiencing external stressors due to the density of GZSD as potential competitors, which may explain the positive relationship between CPUE of GZSD and plasma glucose. Alternatively, season and water temperature can exert a strong influence on the hormonal rates of reaction to stress, with greater temperatures causing biological reaction rates to

increase (McLeese et al., 1994; Pottinger & Carrick, 2000). In our study, mean water temperatures recorded during the mid- and late-summer sampling periods were $\geq 30^{\circ}\text{C}$, a temperature shown to induce negative physiological disturbances in SVCP (Kolar et al., 2007). Warmer water temperatures can also increase the maintenance energy cost of an individual (von Oertzen, 1985), which can elicit a stress response (Akar, 2011). Elevated concentrations of suspended solids in the water may reduce visibility or cause abrasions, potentially resulting in an increase in stress for fish (Redding et al., 1987). Silver carp also have specialized, sponge-like gill rakers that allow them to consume very small suspended particles (3–4 μm) (Omarov, 1970; De-Shang & Shuang-Lin, 1996). Elevated concentrations of suspended solids may, therefore, increase the potential for SVCP gill rakers to become clogged, which may trigger a stress response. Interestingly, temperature and suspended solids showed negative and positive correlations (respectively) with dissolved oxygen. This could indicate that dissolved oxygen may have influenced stress in SVCP. Finally, concentrations of plasma glucose have been shown to decline in fasted fishes (Congleton & Wagner, 2006). Our study used baseline physiological metrics (i.e., blood was drawn in under 3 min), indicating that it should be possible to use glucose as a reliable indicator of nutrition (Romero & Reed, 2005; Gingerich et al., 2010). As such, high concentrations of plasma glucose may indicate increased SVCP feeding (by proxy of increased glucose concentrations in our data) in the mid- and late-summer compared to the early fall. This is also in accordance with our results of SVCP ALP values (similarly acting as a representation for feeding), which indicated increased feeding in the mid- and late-summer relative to the early fall. Irrespective of the mechanism, concentrations of glucose in the plasma of SVCP were positively correlated with suspended solids, water temperature, the CPUE of GZSD, and cladoceran concentrations.

A surprising number of blood-based physiological metrics did not have a single, clear best-fit model to explain trends in the data, indicating that variation in the response variables was not explained by the predictors we quantified. For example, none of the models had $\Delta\text{AICc} > 4$ for cortisol, cholesterol, and triglycerides. All protein models had $\Delta\text{AICc} < 5$. There are a number of plausible explanations for these

findings. One potential explanation is due to a lack of scope or variability in the observed physiological parameters because of limited sample size. For example, plasma cortisol concentrations had a mean of 19.3 ng ml^{-1} and a SEM of 5.2, showing little population-level variation. Similarly, plasma protein concentration was 3.8 g dl^{-1} and a SEM of 0.08. Regardless of collection method (i.e., electroshock or leapt into boat), blood was drawn in less than 3 min from all fish, and is therefore reflective of background stress levels in a population that is considered resting or stress free (Barton et al., 2002; Romero & Reed, 2005). Similarly, protein is a nutritional parameter and can respond to changes in body condition (Farbridge & Leatherland, 1992), which clearly was not fluctuating in SVCP in our system based on the lack of variability in the data. Alternatively, the timing of our sampling may not have been ideal to observe variation in some of the parameters measured. Triglyceride concentrations, for example, increase after feeding (Congleton & Wagner, 2006). Silver carp are constantly filter feeding (Dong & Li, 1994; Shuang-lin & De-shang, 1994), suggesting that there may not be a time when their triglyceride concentrations would decrease unless food was limited. Similarly, cholesterol concentrations are representative of body energy reserves and decrease in fasted fish (Congleton & Wagner, 2006; Hasler et al., 2011). At a local scale, the duration of our study may not have been sufficient to document the shift of energy from feeding to body reserves. Future studies should corroborate these hypotheses by sampling across a greater duration of time (e.g., inter- and intra-annually). Although we did not use the gonadosomatic index (GSI) as a predictor variable in our study, it is possible that GSI values varied in the SVCP we collected because our study occurred across three time periods. This may have influenced the nutritional and stress status of the individuals in our results. Reproduction correlates negatively with feeding (e.g., decreases feeding rate, is metabolically expensive, can deplete energy stores) (Encina & Granado-Lorencio, 1997; Mommsen et al., 1999; Liss et al., 2013). Reproduction has also been documented to increase stress in fishes (Akar, 2011; Liss et al., 2013). Irrespective, results from our study show that, for a large number of nutritional and stress metrics quantified, there were no distinct best-fit models to describe variation in the nutrition or stress of SVCP.

Several abiotic and biotic environmental factors quantified during sampling also failed to predict patterns for stress and nutrition in SVCP. These predictor variables have previously been shown to influence the structure and dynamics of a community through resource availability and competition, community-level performance, and/or habitat complexity. For example, TP, overall species abundance, species composition, and species richness were not drivers of any of the stress or nutrition metrics of wild SVCP in the LGR. Previous research has shown that concentrations of TP drive productivity in freshwater systems, and can be used as a predictor of planktonic community structure and abundances (Schindler, 1974; Jeppesen et al., 2000). Higher concentrations of TP should result in greater planktonic concentrations [which are a major food source for SVCP (Buck et al., 1978; Cooke et al., 2009)]; thus, elevated concentrations of TP should also translate to more food for SVCP. In our study, the concentration of TP was comparable with other rivers in the MRB (Donner, 2003) and would classify the LGR as eutrophic (Cooke et al., 2009). However, TP was negatively correlated with chlorophyll *a* (i.e., phosphorus was not limiting), which may support our findings of why TP was unrelated to our proxies for nutritional performance. TP in aquatic systems has also been correlated with an increase in species richness and diversity (Jeppesen et al., 2000; Pegg & McClelland, 2004). Community composition is another important driver of ecosystem processes for aquatic and grassland plant communities that can influence productivity, biomass accumulation, and resource availability (Tilman et al., 1997; Tonn & Magnuson, 1982). More specifically, species-rich environments have greater resource use across trophic levels, potentially making them less prone to invasion (Gido & Brown, 1999; Duffy, 2009). Based on the community richness, composition, and overall abundance data, the LGR can be considered species rich. The lower (downstream) reaches in the Illinois River (including the LGR) have a greater fish species richness, and abundance relative to the upstream reaches in the Illinois River (north of the Peoria Lock & Dam) (Pegg & McClelland, 2004; McClelland et al., 2012). This is common as large floodplain rivers exhibit a more diverse environmental landscape downstream, allowing for greater productivity (Schlosser, 1991). In spite of this distinction, SVCP have

been able to colonize, establish, and their populations have grown exponentially (Sass et al., 2010). This is in accordance with our study for SVCP in the LGR, as concentrations of cholesterol, cortisol, protein, and triglycerides were not driven by species richness, composition, or overall abundance. Although the Illinois River is considered species rich, it has also been highly impacted by humans, reducing the natural variability of the river (Koel & Sparks, 2002), and causing degradation (Karr et al., 1985). This may have also influenced the establishment of SVCP and facilitated their increase in population. Regardless, our study provides evidence, that for several stress and nutritional metrics quantified, SVCP are not limited by the abiotic or biotic habitat characteristics we tested, which may provide a further explanation for the successfulness of SVCP as invaders.

Our results provide insights and information on the factors that may be influencing the distribution and spread of SVCP, as well as the characteristics of habitats that could be vulnerable to future SVCP invasion. More specifically, the stress and nutrition of SVCP do not appear to be strongly influenced by many biotic or abiotic factors. Four of the six physiological parameters quantified in SVCP were not related to a suite of habitat characteristics tested. This may suggest that SVCP stress and nutrition were not generally correlated with abiotic and biotic factors of the LGR, and the suite of environmental variables we examined had little influence on SVCP stress or nutrition. In contrast, variation in stress and nutrition appears to be related to factors that operated at larger scales, including water temperature, food availability, and suspended solids. Because SVCP are able to consume food down to 3–4 μm , which is lower than the vast majority of native fishes (Omarov, 1970; De-Shang & Shuang-Lin, 1996), they are likely not competing for food resources with native fishes and may not experience negative physiological consequences across a range of habitat variables. Thus, efforts to predict future environments that may be susceptible to SVCP invasions should focus on quantifying factors that include food availability and thermal regime, as opposed to smaller-scale variables such as phosphorous concentration or community composition. Despite these caveats, and while our results may suggest few definitive drivers of variation for important physiological metrics, our study further emphasizes the successfulness of invasive SVCP in the wild.

Acknowledgements This research was supported by the Illinois Department of Natural Resources and the United States Fish and Wildlife Service Federal Aid in Sportfish Restoration Project [F-101-R]. This research was also supported by the University of Illinois Graduate College: College of Agricultural, Consumer and Environmental Sciences; and Department of Natural Resources and Environmental Sciences. The authors thank the staff of the Illinois Natural History Survey's Illinois River Biological Station, The Long-Term Illinois, Mississippi, Ohio, and Wabash Rivers Fish Population Monitoring Program, and the Upper Midwest Environmental Sciences Center.

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