

Hydrogeomorphic features mediate the effects of land use/cover on reservoir productivity and food webs

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Abstract

Although effects of land use/cover on nutrient concentrations in aquatic systems are well known, half or more of the variation in nutrient concentration remains unexplained by land use/cover alone. Hydrogeomorphic (HGM) landscape features can explain much remaining variation and influence food web interactions. To explore complex linkages among land use/cover, HGM features, reservoir productivity, and food webs, we sampled 11 Ohio reservoirs, ranging broadly in agricultural catchment land use/cover, for 3 years. We hypothesized that HGM features mediate the bottom-up effects of land use/cover on reservoir productivity, chlorophyll *a*, zooplankton, and recruitment of gizzard shad, an omnivorous fish species common throughout southeastern U.S. reservoirs and capable of exerting strong effects on food web and nutrient dynamics. We tested specific hypotheses using a model selection approach. Percent variation explained was highest for total nitrogen ($R^2 = 0.92$), moderately high for total phosphorus, chlorophyll *a*, and rotifer biomass ($R^2 = 0.57$ to 0.67), relatively low for crustacean zooplankton biomass and larval gizzard shad hatch abundance ($R^2 = 0.43$ and 0.42), and high for larval gizzard shad survivor abundance ($R^2 = 0.79$). The trophic status models included agricultural land use/cover and an HGM predictor, whereas the zooplankton models had few HGM predictors. The larval gizzard shad models had the highest complexity, including more than one HGM feature and food web components. We demonstrate the importance of integrating land use/cover, HGM features, and food web interactions to investigate critical interactions and feedbacks among physical, chemical, and biological components of linked land–water ecosystems.

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Land use/cover has strong effects on a variety of properties of aquatic ecosystems (Allan 2004; Dodson et al. 2005). The effects of land use/cover on aquatic ecosystems are best understood in the context of hydrogeomorphic (HGM) features such as basin and catchment morphometry and geology and surface and groundwater hydrologic flowpaths. These HGM features, viewed as natural aspects of the landscape, can improve predictive relationships because they can mediate the response of aquatic systems to anthropogenic alterations such as land use change (Knoll et al. 2003; Jones et al. 2004; Schomberg et al. 2005). For example, although land use/cover effects

on streams have received relatively more attention than effects on other aquatic systems (Allan 2004), studies of streams, lakes, reservoirs, and wetlands collectively demonstrate that conversion of land cover from natural cover to agricultural or impervious (urban) uses increases nutrient concentrations in water (Crosbie and Chow-Fraser 1999; Strayer et al. 2003; Jones et al. 2004). However, as much as half or more of the variation in nutrient concentration remains unexplained by land use/cover alone, indicating the importance of incorporating HGM features as well. Indeed, recent lake studies have revealed that the HGM template, from local basin morphometry to regional hydrologic connectivity and climate, can influence lake water chemistry through such mechanisms as groundwater flow and weathering (Soranno et al. 1999; Riera et al. 2000). Furthermore, the HGM template can determine fish species composition through isolation and extinction mechanisms in lakes (Magnuson et al. 1998; Hershey et al. 1999) and through multiple mechanisms determining habitat availability (particularly thermal habitat) in streams (Wang et al. 2003; Brazner et al. 2005). Motivating this line of research has been the growing recognition of complex linkages between food webs (aquatic and terrestrial) and landscapes (Polis et al. 2004; Vanni et al. 2005), development of tools such as geographic information systems, and the pragmatic need of regional and national management agencies to assess aquatic resources at large spatial scales (Hawkins et al. 2000).

Although most studies recognize that both land use/cover and the HGM template clearly affect aquatic ecosystems, in-lake response variables often have been limited to water chemistry and/or zooplankton or fish species composition. A synthetic understanding of the structure and function of aquatic ecosystems in a landscape context requires incorporation of a broader suite of in-lake response parameters and consideration of linkages among land-use features, the HGM template, aquatic food web dynamics, and ecosystem processes.

Food web ecology in lakes has a particularly rich history of studying pelagic interactions, particularly those concerning direct effects of consumption by fish. Over time, indirect effects of fish consumption and nutrient cycling have been increasingly recognized, and more recently, renewed efforts to integrate pelagic and benthic food webs have strengthened our understanding of lakes (Vander Zanden et al. 2005). Similar to research emphasizing the importance of benthivorous fish, our research recognizes the importance of a detritivorous fish species, the gizzard shad, *Dorosoma cepedianum*, to food web and nutrient dynamics in reservoirs.

Reservoirs are particularly good systems for studying a range of land-use and HGM effects because they have large catchment areas relative to their surface-water area and short water residence times relative to natural lakes, which make them likely to be more strongly linked to their surrounding catchments than natural lakes. In addition, gizzard shad is an ideal fish species on which to focus for understanding how land use/cover and HGM variables affect reservoir food webs. As a strong interactor with other food web members, particularly in highly eutrophic

reservoirs (Vanni et al. 2005), gizzard shad appears tightly linked to the surrounding landscape because of its propensity to concentrate and spawn in shallow, inflow areas of reservoirs (Bremigan and Stein 1999), its often detritivorous diet as an adult (Schaus et al. 2002), and the positive relationship between gizzard shad biomass and lake or reservoir nutrient status (Bachmann et al. 1996). Field surveys and manipulative experiments collectively reveal that juvenile (age 0, >30 mm total length [TL]) and adult gizzard shad can (1) negatively affect other zooplanktivorous fishes (Garvey and Stein 1998a), (2) positively or negatively affect the growth of predators (Garvey and Stein 1998b), and (3) increase nutrients available to phytoplankton through consumption of detritus and subsequent excretion (Vanni et al. 2006). Overall, the effects of gizzard shad on reservoir food webs and nutrient cycling are quite variable in magnitude, but appear to increase with reservoir nutrient status (Vanni et al. 2005, 2006). The mechanisms driving variation among reservoirs both in gizzard shad demographics and subsequent effects are not adequately understood and constitute an ideal opportunity to investigate linkages among landscape features and food web dynamics. Therefore, we investigated patterns linking reservoir landscapes to their food webs and their underlying mechanisms by focusing on a gradient of reservoirs spanning a range of agricultural land cover sampled across multiple years.

In this study, we evaluate the predictions of a conceptual framework (Fig. 1) that integrates the effects of land use/cover and HGM features on critical food web interactions in reservoirs that determine gizzard shad recruitment and its subsequent effects (Table 1). Our framework represents the synthesis of small-scale experimental work (Bremigan and Stein 1994, 1997), modeling studies (Vanni et al. 2006), and smaller-scale field sampling (Pollard et al. 1998; Bremigan and Stein 2001; Knoll et al. 2003). We collected data from 11 reservoirs sampled for 3 years for a variety of variables, including land use/cover, HGM variables at multiple spatial scales, reservoir productivity, and food web dynamics focusing on factors underlying larval gizzard shad recruitment (defined as survival to the juvenile stage). We take a bottom-up perspective, ultimately based in land-use practices (that we can measure as land use/cover). We used a model selection procedure to identify the most important predictors of each response variable guided by our conceptual framework (Fig. 1) and corresponding predictions (Table 1). We considered four potential categories of predictors: % agriculture, catchment level HGM features, basin level HGM features, and food web features (Table 1).

We expected that as agricultural land use/cover in the catchment increased, so would nutrient concentrations in the reservoir, primary production rates, and the abundance of small zooplankton taxa, which are critical to larval gizzard shad survival (Bremigan and Stein 1997, 1999, 2001; Fig. 1). Further, we expected that many of these interactions would be mediated by HGM features at catchment and/or reservoir basin scales (Fig. 1). For example, we expected catchment and reservoir basin features to influence reservoir productivity, independent

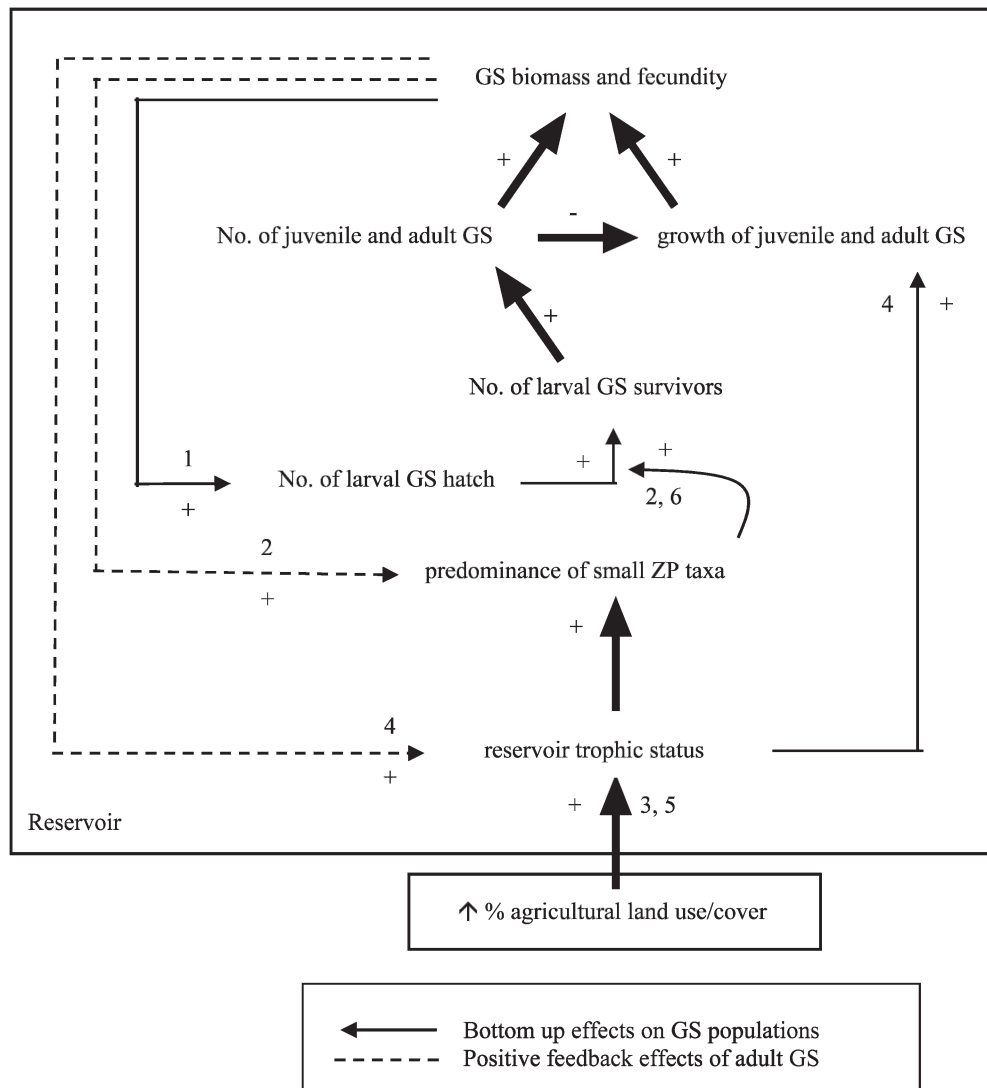


Fig. 1. Conceptual framework illustrating the hypothesized effects of gizzard shad and agricultural land use/cover (mediated by HGM features) on reservoir trophic status, zooplankton assemblages, and larval gizzard shad demographics. Solid arrows represent bottom-up effects linking land use/cover, reservoir trophic status, zooplankton, and larval gizzard shad and are the focus of this work. Dashed arrows represent food web and nutrient effects of juvenile and adult gizzard shad. Positive (+) and negative (-) signs indicate the direction of the hypothesized effect. Numbers correspond to hypothesized mechanisms through which HGM features influence nutrient input and food web interactions. (1) Basin morphometry: increased spawning habitat in shallow reservoirs; (2) basin morphometry: increased overlap with zooplankton prey and lack of DVM refuge in shallow reservoirs; (3) basin morphometry: increased resuspension in shallow reservoirs; (4) Basin morphometry: increased sediment availability to and nutrient transport by gizzard shad in shallow reservoirs; (5) Catchment and hydrology: increased nutrient transport to reservoir in large catchment with many tributaries; (6) Catchment and hydrology: reduced storm influence in small catchments with relatively few tributaries. GS = gizzard shad. ZP = zooplankton.

of the effects of land use/cover, through nutrient transport and resuspension mechanisms. We also expected catchment and basin-scale HGM features to influence larval gizzard shad hatch abundance (through habitat availability and storms), as well as encounter rates of larvae with small zooplankton prey and ultimately larval survival rates.

Methods

Study site—We chose 11 reservoirs that represented a broad range of agricultural land use/cover values (Table 2; Fig. 2) that were sufficiently deep to stratify in summer in the deep area near the dam. Reservoirs were distributed across three Omernik Level III ecoregions, which represent

broad-scale terrestrial differences in geology, soils, vegetation, and land use/cover (Omernik 1987; Fig. 2). Our sampling scheme recognized the longitudinal gradients typical along reservoir flowpaths. Therefore, we sampled each reservoir at a shallow (1–2 m) “inflow” site that was typically well mixed and a stratified “outflow” site at the deepest reservoir area near the dam. In this study, we only report findings from the “inflow” sites because these shallow upstream areas are where most larval gizzard shad production occurs (Bremigan and Stein 1999). See Knoll et al. (2003) for information on how inflow and outflow sites of some of these lakes differ in water-quality variables. The reservoirs are classified as mesotrophic to hypereutrophic with ranges in concentrations of the inflow areas for total phosphorus (TP) (27.8–166 $\mu\text{g L}^{-1}$), total nitrogen (TN) (476–8,467 $\mu\text{g L}^{-1}$), and chlorophyll *a* (Chl *a*) (2.4–45.7 $\mu\text{g L}^{-1}$).

Land use/cover—We used land use/cover GIS data from the Ohio Department of Natural Resources (ODNR) Geographic Information Management Systems database (<http://www.dnr.state.oh.us/gims>) that was originally obtained from thematic mapper imagery taken in 1994 at a pixel resolution of 30 m \times 30 m. We quantified the percent land use/cover of each reservoir’s total catchment (including upstream reservoir and stream catchments). We classified land use/cover into seven categories: agriculture (our focus area, and hereafter referred to as % agriculture), urban, forest, shrub, water, wetland, and barren. However, because agricultural and forest land use/cover across these reservoirs are strongly negatively correlated ($r = -0.99$) and together represent >91% of total catchment land use/cover in all reservoirs except LaDue (82% agriculture and forest, 15% shrub, water, and wetland cover), we only explore agriculture in this analysis as it is the main land use/cover driver of reservoir productivity in these catchments. The majority of the agricultural land is in row-crop agriculture, with soybeans and corn being the dominant row crops.

HGM template: catchment—We chose catchment scale variables to represent the potential for material input to reservoirs and intensity of storm events. For each reservoir, we divided catchment area by reservoir surface area; in addition, to quantify stream flow distance into reservoirs, we used the surface-water data and navigational tools provided in the National Hydrography Dataset (NHD, <http://nhd.usgs.gov/>). We calculated the length of streams flowing into each reservoir two ways by calculating: (1) total upstream distance through all mainstem and tributary streams and (2) upstream distance considering only upstream mainstem streams.

HGM template: basin morphometry—We determined reservoir volume and surface area from bathymetric surveys conducted by ODNR (<http://ohiodnr.com/Home/FishingSubhomePage/LakeMapLandingPage/tabid/19478/Default.aspx>). We obtained retention values (volume: discharge) for 10 of the 11 reservoirs from Bunnell et al. (2006). We divided volume by surface area to estimate

mean depth, we obtained maximum depth from recent ODNR surveys, and we calculated the ratio of maximum to mean depth. Because the shallow and productive inflow areas of reservoirs are critical areas for supporting gizzard shad recruitment, we quantified two new metrics, percent inflow and inflow fetch, that specifically characterize the inflow area. These metrics are meant to reflect the relative amount of inflow area, its general size, and susceptibility to wind resuspension. We used bathymetric maps to calculate these metrics, and we defined the border between the shallow inflow reservoir area and the deeper outflow area by visually assessing where reservoir bathymetry changed from a gradual shoreline slope and shallow (<3 m) depths to a steep-sided shoreline slope and depths >3 m. We chose this depth because larval gizzard shad are concentrated in the top 3 m of water (Arend 2002). Percent inflow is calculated as the percent of the surface area of the reservoir with water depth <3 m (excluding the narrow shoreline bands in outflow reservoir areas). Inflow fetch is the longest open-water distance in the inflow area along the axis of the dominant winds, determined using data from the nearest meteorological station (Ohio Agricultural Research and Development Center; <http://www.oardc.ohio-state.edu/center/weather.htm>).

In-reservoir variables—We sampled the 11 reservoirs weekly during May and June 1998–2000. Because most larval gizzard shad hatch during May and June (Bremigan and Stein 1999), our analysis characterizes the recruitment environment (in terms of nutrient and chlorophyll *a* [Chl *a*] concentrations and zooplankton assemblages) experienced by the majority of larval gizzard shad. Characterizing age-0 gizzard shad dynamics during this early season is particularly important for understanding their subsequent effects on other age-0 fishes (Garvey and Stein 1998a). Because all reservoirs could not be sampled for all parameters in all years, sample sizes ranged 22–27 lake-years across response parameters.

Trophic status—On each sampling event, we identified the depth of the epilimnetic mixed layer from temperature and oxygen profiles. We collected integrated water samples from the mixed layer using an integrated tube sampler for TN, TP, and Chl *a* concentrations. We measured TN with second-derivative spectroscopy after digestion with potassium persulfate (Crumpton et al. 1992), and determined TP by spectroscopic analysis using the acid molybdate method and persulfate digestion. Chl *a* samples were filtered onto Gelman A/E glass-fiber filters, frozen, extracted with acetone, and quantified using a Turner model TD-700 fluorometer calibrated with commercial standards dissolved in acetone.

Zooplankton—We sampled crustacean zooplankton and rotifers during the day on a weekly basis during May–June using a conical 54- μm -mesh net towed from 1 m above the reservoir bottom to its surface. We preserved zooplankton in 70% ethanol. Using the methods of Bremigan and Stein (2001) we counted and identified crustacean zooplankton taxa as follows: cladocerans to genus; copepod adults and

Table 1. Summary of hypothesized predictors of three categories of response variables: reservoir trophic status, zooplankton, and larval gizzard shad. Predictor variables represent five categories: land use/cover (% agriculture), hydrogeomorphic (HGM) features at the catchment scale, HGM features at the local basin scale, trophic status, and food web components. For each response variable, we present the predictor categories hypothesized to have explanatory power, the hypothesized mechanism underlying the relationship, the associated predictor variables, their hypothesized relationships (direction of effect) with the response variable, and the occurrence (yes/no), and documented direction of effect (consistent with predictions [yes/no]) of each predictor variable if included in the best model (lowest *AICc*). % agric = % agricultural land use/cover in the catchment, upstream tribs = total upstream distance through all mainstem and tributary streams of the reservoir, upstream main = total upstream distance considering only upstream mainstem streams, catch : surf = ratio of catchment area to reservoir surface area, max depth = maximum reservoir depth, max : mean = ratio of maximum depth to mean depth. See text for details of statistical methods and description of variables in each predictor category. NA = not applicable; retention rate was not included in the model selection process due to missing data. DVM = diel vertical migration.

Response variable	Predictor category	Hypothesized mechanism	Predictor variable(s) and hypothesized direction of effect	Included in best models? (TP, TN, Chl <i>a</i>)	Direction of effect as predicted? (if in top model) (TP, TN, Chl <i>a</i>)		
Reservoir trophic status: TN, TP, and Chl <i>a</i>	land use/cover	higher nutrient export from catchment	% agric	+	yes, yes, yes	yes, yes, yes	
	HGM: catchment	higher nutrient export from catchment	catchment area	+	no, no, no		
	HGM: basin	higher resuspension within reservoir	catch : surf	+			
			upstream tribs	+			
			upstream main	+			
			mean depth	-	yes, yes, yes	yes, yes, yes	
	HGM: basin	higher reservoir retention rates	max depth	-			
			max : mean	-			
			inflow fetch	+			
			percent inflow	+			
water retention			+	NA			
Zooplankton: Rotifer biomass	trophic status	higher food availability	Chl <i>a</i>	+	yes	yes	
	food web	exploitative competition	crustacean ZP	-	no	no	
	HGM: basin	DVM to avoid planktivory	mean depth	+	no	no	
			max depth	+			
			max : mean	+			
			percent inflow	-			
	trophic status	higher food availability	inflow fetch	-			
			Chl <i>a</i>	+	yes	no	
	Gizzard shad: Larval GS hatch	HGM: catchment	higher storm influence	catchment	-	yes	no
				catch : surf	-		
upstream tribs				-			
upstream main				-			
HGM: basin		more lake area for spawning	mean depth	-	no		
			max depth	-			
			max : mean	-			
			percent inflow	-			
			inflow fetch	+			
			catchment	-	yes	no	
Larval GS survivors	HGM: catchment	higher storm influence		+	yes	no	
				-			

Table 1. Continued.

Response variable	Predictor category	Hypothesized mechanism	Predictor variable(s) and hypothesized direction of effect	Included in best models? (if in top model) (TP, TN, Chl <i>a</i>)	Direction of effect as predicted? (if in top model) (TP, TN, Chl <i>a</i>)
			catch : surf	-	
			upstream tribs	-	
			upstream main	-	
			mean depth	-	yes
			max depth	-	
			max : mean	-	
			percent inflow	+	
			inflow fetch	+	
			larval GS hatch	+	no
			rotifer biomass	+	yes
HGM: basin		higher spatial overlap with prey			
food web		greater larval supply			
food web		higher prey availability			

copepodids as calanoid or cyclopoid; immature copepods as nauplii. We counted and identified rotifers to genus using a compound microscope. We measured crustacean zooplankton total length to the nearest 0.01 mm for the first 22 individuals encountered per taxon. We used taxon-specific, length-dry weight equations for crustacean zooplankton taxa (Dumont et al. 1975; Rosen 1981; Culver et al. 1985) to convert length to biomass. For rotifers, we measured up to 25 individuals from each genus to the nearest 0.1 mm. We calculated rotifer biomass using geometric formulas that approximate the volume of individuals (Ruttner-Kolinsko 1977). We converted rotifer volume to wet weight, assuming a specific gravity of 1. We estimated dry weight as $0.1 \times$ wet weight (Doohan 1973). We aggregated the data into two zooplankton variables for each reservoir—average rotifer biomass at the inflow site and average crustacean biomass at the inflow site—by calculating the mean across sampling dates in May and June.

Larval gizzard shad—We used the methods of Bunnell et al. (2003) to collect and enumerate larval gizzard shad. Briefly, larval gizzard shad were collected weekly during the day in the top meter of water with a neuston net (1 m \times 2 m wide mouth, 0.5-mm mesh) with a flow meter mounted to the mouth to quantify water volume filtered. On each sampling event we conducted two replicate 5-min tows at 1 m s⁻¹, except when high zooplankton densities necessitated shorter tows. Larvae were preserved in 95% ethanol and counted to estimate density. For each date, we calculated mean larval gizzard shad density across the two replicate tows. We measured total length (nearest 0.1 mm) of 50 random larval gizzard shad from one randomly chosen replicate per date using a Sigma Scan digitizing system. We generated indices of larval gizzard shad hatch abundance and large larval gizzard shad survivor abundance by combining density and length data. We used 5–6-mm-TL larvae to generate our larval hatch index because 5 mm is the smallest larval size that is vulnerable to our nets. We used 15-mm-TL fish for our index of large larval survivor abundance because the majority of larval mortality occurs for individuals $< \sim 11$ mm TL (Bremigan and Stein 1999) and because vulnerability to our neuston net declines for larvae > 15 mm TL. Our method accounts for the potential for larval growth rate differences across reservoirs to influence index estimates given that slow-growing larvae will remain in a particular size class longer than will fast-growing larvae (Bremigan and Stein 2001).

Model selection procedure—We conducted transformations when needed to meet statistical assumptions of normality and homogeneity of variance. We used analysis of variance (ANOVA) to determine if response variables varied predictably among the 3 sampling years to determine if sampling year needed to be factored into our model selection procedure. We considered two alternative approaches for evaluating the effects of agricultural land use/cover, catchment- and basin-level HGM features, and food web features on in-lake response variables: (1) classification

Table 2. Location, land use/cover, and hydrogeomorphic features (at the catchment and basin scales) for 11 study reservoirs in Ohio, sampled during 1998–2000. Reservoirs are ordered from left to right in order of increasing % agricultural land use/cover in the catchment, and the number in parentheses is the number from Fig. 2. Land use/cover and hydrogeomorphic variable labels are as for Table 1. Variables with an asterisk (*) were included in the model selection process (see text for details). See text for additional information on landscape variables.

	Burr Oak (1)	Tappan (2)	Ladue (3)	Piedmont (4)	Pleasant Hill (5)	Berlin (6)	Knox (7)	Alum Creek (8)	Delaware (9)	Caesar Creek (10)	Acton (11)
Latitude (°N)	39.551	40.357	41.387	40.188	40.420	40.561	40.458	39.881	40.299	39.493	39.563
Longitude (°W)	82.064	81.208	81.202	81.196	80.658	81.794	82.529	82.907	83.068	84.104	84.737
Land use/cover % agric*	13.5	28.5	35.1	36.6	50.7	53.4	67.1	72.0	82.5	84.2	88.7
HGM: catchment											
Omernik ecoregion	Alleg	Alleg	Erie	Alleg	Erie	Erie	Erie	Corn	Corn	Corn	Corn
Upstream tribs (m)*	87,520	159,426	80,430	214,245	471,545	624,236	25,569	319,157	834,486	484,133	217,350
Upstream main (m)	24,026	15,798	20,688	31,316	53,596	51,089	15,080	50,634	97,221	50,641	37,446
Catchment area (km ²)	86	184	93	220	515	642	80	327	1,011	617	270
Catch : surf*	32.3	19.1	16.4	22.4	165.1	44.7	41.0	35.0	223.2	57.7	112.5
HGM: basin											
Surface area (km ²)	2.66	9.64	5.66	9.81	3.12	14.35	1.95	9.35	4.53	10.70	2.40
Mean depth (m)*	4.1	4.2	3.8	4.1	4.2	4.7	2.2	7.5	3.1	10.6	4.0
Max depth (m)*	10.7	8.5	8.0	9.8	12.1	18	11.9	19.3	10.0	36.3	9.4
Max : mean*	2.6	2.0	2.1	2.4	2.9	3.8	5.4	2.6	3.2	3.4	2.3
Water retention (d)	485	774	473	336	62	153	195	3,056	87	1,196	NA
% inflow*	29.4	21.6	24.8	36.3	54.7	29.5	67.1	8.9	46.6	2.1	34.9
Inflow fetch (km)*	0.51	0.3	0.46	1.09	0.87	1.1	0.81	1.06	0.73	0.35	0.59

Alleg = Western Allegheny Plateau, Erie = Erie Drift Plains, Corn = Eastern Corn Belt Plains.

and regression tree analysis (CART) (Breiman et al. 1993), which generally explains more variation in the response parameter when there are non-linear responses in the data, and (2) multiple linear regression, which performs better if linear relationships dominate the data set. For each response variable, we conducted a CART analysis and linear regression analysis (with the model selection procedure described below) with all the predictor variables hypothesized to be important. We compared the PRE values (proportional reduction in error, analogous to an R^2 value) from the CART analyses to the R^2 values obtained for our best linear models. Linear regression explained substantially more variation (~20% more) for the majority of the response variables and similar amounts of variation for the other response variables. Given the generally better performance of the linear regression, we present the regression-based model selection findings in this article.

We used the same model selection procedure for all response variables. Using a multiple regression approach, we took several steps to avoid problems of multicollinearity among predictor variables (Graham 2003). However, we sought to strike a balance between explanatory power and predictor removal, given that excessive removal of predictors before model building would detract from our ability to determine the overall ability of land use/cover, HGM features, trophic status, and food web factors to explain variation in the response parameters. All statistics were conducted in SAS 9.0 (SAS Institute), using PROC REG for the regression models. For all multiple regression analyses, we compared models using second-order Akaike's Information Criterion (AIC_c) to determine which model

represented the highest parsimony between variation explained and number of predictors included, with a lower AIC_c value representing a better model (Burnham and Anderson 2002). Models that differed by less than two units were deemed to be similarly supported and statistically indistinguishable.

There were three main stages for the analysis. First, we constructed a correlation matrix among % agriculture and all of the HGM predictor variables and eliminated variables that were highly correlated with each other ($r > 0.8$). Second, we conducted multiple regressions for each response variable using only predictors from a single category (catchment HGM, basin HGM, trophic status, or food web) at a time, considering only predictor categories for which there was a hypothesized linkage to the response metric, and building models using all possible combinations of variables within a category (Fig. 1; Table 1). The predictor variables that were in the best category-specific models from this stage were then retained for the next stage that combined categories. We also retained predictors from any models that were statistically indistinguishable from the best category-specific model based on AIC_c . In the third stage, we conducted multiple regressions for each response metric using variables that were retained from stage two. We identified the best model(s) using the AIC_c criteria described above. Finally, we omitted any of the best models if they contained predictors that shared a correlation coefficient >0.3 (Graham 2003). Therefore, our best models are those that have the lowest AIC_c value and no predictors that share a correlation coefficient >0.3 .

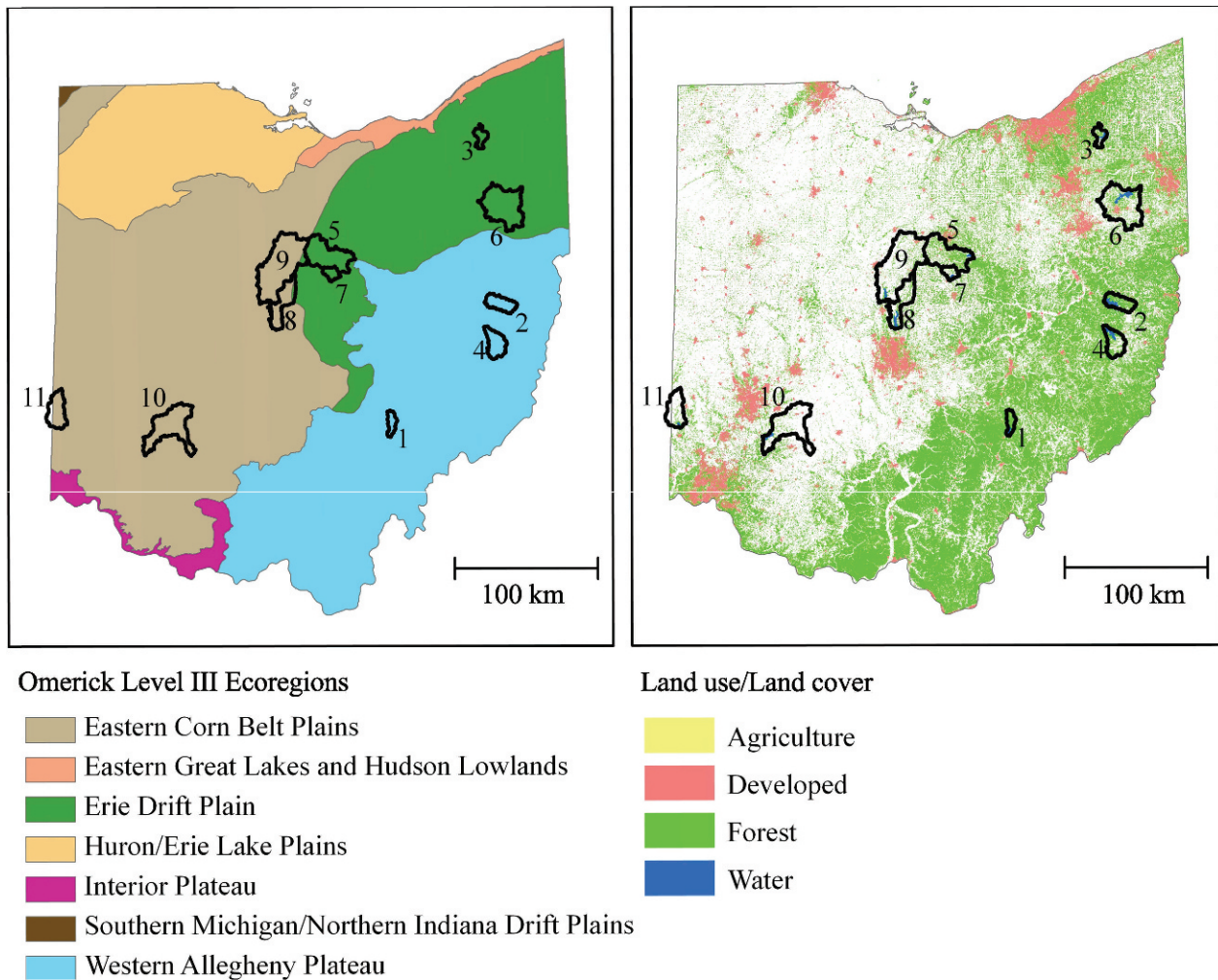


Fig. 2. Maps of the location of the 11 study reservoir catchments and (A) Omernik Level III ecoregions (Omernik 1987) and (B) land use/cover. Reservoirs are numbered from lowest (1) to highest (11) percent agricultural land use/cover in the catchment corresponding to Table 2.

Results

None of the response variables varied with year (p values ranged 0.21–0.95 and R^2 values ranged 0.0–0.12), and thus we did not include year in our model selection procedure.

Correlations among predictor variables—Considering variables in our land use/cover and HGM categories, we observed relatively few occurrences of correlation coefficients >0.80 (Table 3). Generally, correlation coefficients were higher for paired variables within a category than between categories (Table 3). For example, within our catchment scale HGM category, we omitted catchment area and upstream mainstem distance from our model selection procedure because of their high degrees of collinearity with other catchment scale variables and because upstream tributary distance and catchment:surface area generally performed better in univariate regressions with response variables. We also noted high collinearity between some basin level HGM features. We omitted percent inflow from the model selection process because of its high correlation to mean depth ($r = -0.87$),

and because mean depth data are more commonly available than percent inflow. Not surprisingly, maximum depth and average depth also were highly correlated ($r = 0.78$). Because the relative importance of these two variables likely differs among response parameters, we retained both for the model selection procedure, but not together in final models.

Across HGM categories, basin scale features generally had low correlation coefficients with catchment scale features or with % agriculture, with most r values <0.40 . The correlation between catchment scale HGM features and % agriculture was generally higher, with r values with % agriculture ranging 0.39–0.64. Because some food web variables were used as predictors in some models, we also considered correlations between the HGM and food web variables. We saw no correlation coefficients >0.8 , with about half falling between 0.3 and 0.6, and about half being <0.3 .

Reservoir productivity model selection—For TN, the best single-category models from stage two of the model selection process were % agriculture, catchment:surface

Table 3. Correlation matrix and sample size (n = number of lakes) for % agricultural land use/cover and hydrogeomorphic features at the catchment and basin levels. Predictor variable labels are as for Table 1. Correlation coefficients >0.8 are in bold. We did not include both variables in the model building process if their correlation coefficient exceeded 0.8. See text for details on statistical methods.

	% agric	Catchment	Catch: surf	Upstream main	Upstream tribs	Mean depth	Max depth	Max: mean	Inflow fetch	% inflow	Water retention
n	11	11	11	11	11	11	11	11	11	11	9
% agric	1	0.58	0.64	0.56	0.39	0.21	0.44	0.38	0.11	0	0.31
Catchment		1	0.68	0.91	0.96	0.41	0.47	0.14	0.27	-0.16	-0.05
Catch: surf			1	0.74	0.56	-0.08	0.13	0.32	0.13	0.39	-0.26
Upstream main				1	0.9	0.37	0.42	0.12	0.37	-0.12	0.02
Upstream tribs					1	0.51	0.4	-0.1	0.24	-0.31	-0.04
Mean depth						1	0.78	-0.22	-0.11	-0.87	0.68
Max depth							1	0.44	0.1	-0.5	0.46
Max: mean								1	0.32	0.46	-0.15
Inflow fetch									1	0.3	0.1
% inflow										1	-0.72
Water retention											1

area at the catchment scale, and at the basin scale maximum depth, mean depth, maximum:mean depth, and inflow fetch. In stage three, models containing % agriculture consistently explained the highest amount of variation in TN ($R^2 > 0.89$ as opposed to ≤ 0.50 for all other models). Our best model contained a positive effect of % agriculture and a negative effect of inflow fetch (Tables 4A, 5), although the latter was the opposite direction to our predictions. Notably, % agriculture alone explained 89% of the variation in TN, whereas catchment and basin scale features, alone, could at best explain 39% and 10% of the variation in TN, respectively.

The best single category models predicting TP and Chl *a* concentrations included % agriculture alone, catchment: surface area alone, catchment: surface area in combination with upstream tributary distance, and mean depth alone. Results from stage three show that overall, less variation was explained in TP ($R^2 = 0.67$) and Chl *a* ($R^2 = 0.57$) than in TN (Table 4A,B,C). Our best models predicting TP and Chl *a* concentrations included a positive effect of % agriculture as well as a negative effect of reservoir mean depth (as expected), but no catchment scale predictor (Table 5). Unlike the TN models, models containing only catchment and basin scale features still explained close to 50% of the variation in observed TP or Chl *a* concentrations, whereas % agriculture alone explained just 30% and 12% of the variation in TP and Chl *a*, respectively.

Zooplankton model selection—Mean May–June rotifer biomass ranged 0.16–97.64 $\mu\text{g L}^{-1}$ dry weight across reservoirs and years. Of the three rotifer biomass models tested, the model containing only Chl *a* had the lowest *AICc* value and explained the most variation (60%) (Table 4D), with rotifer biomass increasing with Chl *a* as predicted (Table 5). The model containing crustacean zooplankton biomass alone performed quite poorly in comparison (*AICc* value = -16.8) explaining only 26% of the variation in rotifer biomass.

Mean May–June crustacean zooplankton biomass ranged 1.51–231.49 $\mu\text{g L}^{-1}$ dry weight across reservoirs and years. Counter to bottom-up predictions, Chl *a* alone was negatively related to crustacean zooplankton biomass ($R^2 = 0.43$). In addition, for the basin scale HGM models of stage two, nine models with various combinations of mean depth, maximum depth, inflow fetch, and maximum: mean depth performed similarly well. In stage three, the addition of basin level HGM features to the Chl *a* only model resulted in the addition of two variables (inflow fetch and maximum: mean depth), but the three models were not distinguishable according to *AICc* (Table 4E).

Larval gizzard shad model selection—Total May–June hatch abundance of larval gizzard shad ranged 0.04–79.88 larvae m^{-3} across reservoirs and years. For larval gizzard shad hatch abundance, there were three basin-only models (maximum depth, mean depth, and inflow fetch) from the stage two analysis, with *AICc* values ranging -36.4 to -35.8. However, these models explained <7% of the variation in larval gizzard shad hatch abundance. In contrast, a catchment scale model containing only up-

Table 4. Summary of the highest-ranking multiple regression models explaining variation in trophic status, zooplankton, and larval gizzard shad response variables from the 11 Ohio reservoirs sampled during 1998–2000. Predictor variable labels are as for Table 1. In each case, the best model is defined as the model with the lowest *AICc* score (and any model(s) with an *AICc* score that differed from the lowest score by < 2) and for which no two predictors had a correlation coefficient of *r* > 0.3 (as per Graham 2003). Inclusion of predictor variables was based on hypothesized relationships, as summarized in Fig. 1 and Table 1. Column headings include *n* (number of observations), σ^2 (residual sum of squares divided by *n*), *AICc*, and *R*² (proportion of variance explained by the model). GS = gizzard shad. ZP = zooplankton.

Land use/cover	HGM: catchment scale	HGM: basin scale	Food web or trophic status	<i>n</i>	σ^2	<i>AICc</i>	<i>R</i> ²
A) Model predicting TN	% agric	inflow fetch		22	0.012	−89.7	0.92
B) Model predicting TP	% agric	mean depth		27	0.012	−111.4	0.67
C) Model predicting Chl <i>a</i>	% agric	mean depth		27	0.050	−73.7	0.57
D) Model predicting rotifer biomass			Chl <i>a</i>	23	0.196	−32.9	0.60
E) Models predicting crustacean ZP biomass			Chl <i>a</i>	26	0.131	−48.4	0.43
		inflow fetch	Chl <i>a</i>	26	0.119	−48.4	0.48
		max : mean	Chl <i>a</i>	26	0.125	−47.0	0.45
F) Models predicting larval GS hatch abundance	upstream tribs			21	0.087	−46.5	0.42
	upstream tribs	max : mean		21	0.080	−45.5	0.47
	upstream tribs	inflow fetch		21	0.084	−44.7	0.44
G) Models predicting larval GS survivor abundance	upstream tribs	inflow fetch	rotifer biomass	21	0.046	−54.0	0.79
	upstream tribs		rotifer biomass	21	0.054	−53.9	0.75

stream tributary distance explained 42% of the variation in hatch abundance (*AICc* = −46.5). and including all relevant categories in stage three resulted in two additional models that were indistinguishable from the upstream tributary distance model (Table 4F). In contrast to our expectation that catchment scale HGM features would have a negative effect on larval gizzard shad hatch abundance because of greater storm influence (e.g., potentially flushing larvae completely out of the system), we documented a positive relationship between upstream tributary distance and larval hatch abundance (Table 5).

Total May–June abundance of larval gizzard shad survivors ranged 0.63–49.90 larvae m^{−3} across reservoirs and years. Abundance of larval gizzard shad survivors was the most complex response variable to model, because so many factors were hypothesized to affect larval survival (see Table 1). Considering the single category models from stage two, three basin level models, all containing inflow fetch, performed best, with *AICc* values ranging −34.4 to −32.5 and explaining 28–32% of the variation in survivor abundance. At the catchment scale, upstream tributary distance (*AICc* = −35.8, *R*² = 0.33) outperformed catchment : surface area alone (*AICc* = −33.0, *R*² = 0.24)

Table 5. Summary of the slope coefficient estimates and standard errors associated with each predictor from the best models for trophic status, zooplankton, and larval gizzard shad (Table 4) response variables. Predictor variable labels are as for Table 1.

Response variable	Predictor variable	Estimate	SE	<i>p</i> value
TN	% agric	1.29	0.10	<0.0001
	inflow fetch	−0.23	0.10	0.0315
TP	% agric	0.52	0.09	<0.0001
	mean	−0.73	0.14	<0.0001
Chl <i>a</i>	% agric	0.67	0.18	0.0008
	mean depth	−1.40	0.28	<0.0001
Rotifer biomass	Chl <i>a</i>	1.58	0.28	<0.0001
Crustacean ZP biomass	Chl <i>a</i>	−0.91	0.21	0.0003
Larval GS hatch	upstream tribs	1.01 × 10 ^{−6}	2.71 × 10 ^{−7}	0.0014
Larval GS survivors	upstream tribs	8.41 × 10 ^{−7}	2.39 × 10 ^{−7}	0.0027
	inflow fetch	0.41	0.25	0.1187
	rotifer biomass	0.40	0.07	<0.0001

and was comparable to the model with both catchment level predictors ($AICc$ value = -33.6 , $R^2 = 0.35$). The rotifer biomass alone model performed best of the single category models, with an $AICc$ value of -39.8 and explaining 45% of the variation in larval survivor abundance. Larval gizzard shad hatch abundance also performed relatively well ($AICc = -37.6$, $R^2 = 0.39$). Due to the potential importance of controlling for hatch abundance when considering survivor abundance, we considered hatch abundance in stage three. Results from stage three show that a combined model with one predictor from each category (upstream tributary distance, inflow fetch, and rotifer biomass) performed best overall ($AICc = -54.0$), with a substantially higher R^2 (0.79) than any single category model (Table 4G). However a model without inflow fetch was not distinguishable from this three variable model. As expected, inflow fetch and rotifer biomass were positively related to larval gizzard shad survivor abundance. Counter to our expectation, but similar to our findings for larval hatch abundance, survivor abundance was positively related to upstream tributary distance (Table 5).

Discussion

Existing uncertainty regarding the relative importance and quantitative nature of HGM and land use/cover effects on aquatic systems requires the implementation of studies that include a broad range of HGM features, reflecting multiple spatial scales (catchment and local basin scales) and multiple trophic levels. Although the number of land use/cover studies in streams far exceeds that for lakes and reservoirs, even in streams only limited understanding exists regarding the mediating influence of HGM features on the effects of land use/cover. Additionally, knowledge of the relative importance of land use/cover and the HGM template across multiple spatial scales, and their subsequent effects on stream biota, is incomplete (Johnson et al. 1997; Wiley et al. 1997; Allan 2004). Our study demonstrates a robust approach that could be applied to a variety of aquatic systems. We have built upon previous studies by exploring the effects of land use/cover and HGM features on critical food web interactions, guided by a conceptual framework that integrates experimental, modeling, and field approaches. Our findings demonstrate strong support for our hypothesis that HGM features mediate bottom-up effects of land use/cover. Specifically, the relative importance of HGM features was particularly high for TP and Chl *a*, as well as larval gizzard shad hatch and survivor abundance, indicating that HGM features do mediate some food web interactions, particularly those determining larval gizzard shad demographics.

What is the relative importance of land use/cover and HGM features to reservoir trophic status?—Our findings demonstrate that agricultural land use/cover is more tightly linked to TN than to TP or Chl *a*. Across 22 reservoir-years, the total percent variation explained was highest for TN, intermediate for TP, and lowest for Chl *a*, corresponding to the relative importance of % agriculture in

explaining variation. The tighter linkage between % agriculture and TN likely reflects higher export coefficients associated with TN transport from agricultural watersheds relative to P-related export coefficients (Vanni et al. 2001), as well as a tighter correlation between % agriculture with nitrogen (nitrate) inputs than with phosphorus inputs (M.J. Vanni, unpubl.). Although TP and Chl *a* levels were positively associated with % agriculture, it alone could explain much less variation in TP (30%) or Chl *a* (12%) than TN (89%), consistent with the findings of Knoll et al. (2003). In contrast, HGM features appeared to play a strong role in determining TP and Chl *a* levels in these reservoirs through either material input (as represented by catchment : surface area) or resuspension within reservoirs (as represented by mean depth). Correlations within HGM categories prevent us from attributing these effects solely or specifically to catchment : surface area or mean depth (see Table 3). Rather, our analysis identifies the relative importance of the two spatial scales, while providing insights into the particular variables that can explain the most variability in TP and Chl *a*.

With growing recognition of the importance of non-point sources to nutrient dynamics, numerous studies have quantified general relationships between agricultural land use/cover and nutrient concentrations in streams (reviewed by Allan 2004), wetlands (Crosbie and Chow-Fraser 1999), lakes (Dodson et al. 2005), and reservoirs (Knoll et al. 2003; Jones et al. 2004). Because of differences in methodologies and approaches among studies, direct comparisons are difficult to generate. For example, studies sometimes aggregate TN and TP or Chl *a* values into a composite trophic score, thus preventing a comparison among relationships between agricultural land use/cover and specific nutrient or trophic components. Qualitatively similar findings to ours were obtained in a study of Missouri reservoirs, which found a tighter relationship between percent of catchment in cropland land use/cover and TN ($R^2 = 0.71$) than TP ($R^2 = 0.62$) (Jones et al. 2004). Also, Jones et al. (2004) found that indices of retention time and depth improved the TP relationship ($R^2 = 0.77$ compared to 0.62) more so than the TN relationship (maximum $R^2 = 0.76$ compared to 0.71). This pattern is not surprising given the transport mechanisms of nitrogen vs. phosphorus across the landscape to aquatic ecosystems. Peterjohn and Correll (1984) found the major pathway of nitrogen loss from terrestrial landscapes to be subsurface flow, whereas phosphorus loss was split fairly evenly between surface runoff and groundwater flow.

To what extent do HGM features mediate food web interactions?—We expected land use/cover and HGM features to indirectly influence zooplankton assemblages and gizzard shad demographics through their effects on reservoir productivity. In addition, we hypothesized that HGM features also would influence crustacean zooplankton and gizzard shad attributes through additional pathways. As expected, rotifer biomass was positively correlated with Chl *a*; but, crustacean zooplankton biomass was negatively related to Chl *a*. Rotifer biomass and crustacean biomass were weakly negatively correlated

across our data set (correlation coefficient = -0.50). Pollard et al. (1998) noted that exploitative competition with crustacean zooplankton likely structures rotifer assemblages in an interannual analysis of our most productive reservoir (Acton). However, negative correlation between these two zooplankton groups could also result from predation of rotifers by copepods, contrasting vulnerability of rotifers and crustaceans to predation by adult gizzard shad and other zooplanktivores, or differential vulnerability of rotifers and crustaceans to poor water quality (e.g., pesticides or sediments) associated with agricultural land use/cover (Hanazato 1998).

Our findings support the general pattern that zooplankton assemblages become increasingly dominated by small taxa under conditions of increasing productivity and/or turbidity (Sprules 1980). Interestingly, the strength of this pattern likely varies with both temporal and spatial scales, reflecting a complex mix of drivers operating at different scales. For example, in their study of the highly productive Acton reservoir, Pollard et al. (1998) detected no consistent differences in the relative predominance of rotifers vs. crustacean zooplankton between the relatively productive, turbid inflow area and the deeper outflow area near the dam (considering April–November). Thus, within a system and in a given year, the predicted relationship between zooplankton size structure and productivity or turbidity was not apparent. However, Pollard et al. (1998) noted that the relative predominance of rotifers varied substantially among years, likely due to interannual differences in predation pressure by gizzard shad on crustacean zooplankton and subsequent competitive interactions between crustacean zooplankton and rotifers, illustrating the importance of these top-down interactions as well. Our study demonstrates that across reservoirs, a consistent pattern of increasing rotifer dominance with increasing reservoir productivity or turbidity exists when viewing seasonal (May–June) average zooplankton values. The relative inability of HGM features to contribute to predictions of crustacean zooplankton biomass suggests that zooplankton may be particularly dependent on food web interactions, with a relatively minor connection to the HGM context of the reservoir, compared to higher and lower trophic levels.

Our ability to predict larval hatch abundance was surprisingly reliant on the catchment scale HGM feature upstream tributary distance. Reservoirs with more contributing tributaries supported higher total larval gizzard shad hatch abundances on a per square meter basis. We were surprised that local basin features did not explain more variation in hatch abundance, given that previous research has documented much higher hatch concentrations in inflow areas compared to deeper outflow areas (Bremigan and Stein 1999). The morphometry of a basin likely plays a stronger role in determining total larval production, i.e., reservoirs with more inflow area will support more larvae, but not necessarily a higher concentration of larvae m^{-2} in the inflow area. Upstream tributary distance may reflect higher adult abundance in these reservoirs, although juvenile and adult gizzard shad catch per effort were not correlated to upstream tributary distance ($R^2 = 0.12$) in a subset of seven of our reservoirs (M.T. Bremigan, unpubl.).

More contributing tributaries might maintain higher sediment inflow and hence higher detrital quality, potentially positively affecting adult gizzard shad condition and reproductive success, but we lack data to test this hypothesis. Tributaries also might represent increased spawning habitat with subsequent congregation of larvae in the inflow areas that we sampled. These hypotheses merit future research.

Findings regarding factors that promote high abundance of large larval gizzard shad survivors, or recruits, matched several, but not all, of our predictions. The two best models explained 75% and 79% of the variation in survivor abundance and documented positive relationships with biomass of rotifer prey and inflow fetch (as expected) and upstream tributary distance (contrary to expectations). Previous experiments have demonstrated that larval gizzard shad prefer small zooplankton prey (<0.40 mm; Bremigan and Stein 1994) and enjoy higher survival when it is available (Bremigan and Stein 1997). Field analyses in a subset of these reservoirs have shown positive correlations between survival of weekly larval hatch cohorts and small zooplankton availability at the time of hatching, but not between the seasonal averages of survivor abundance and zooplankton (Bremigan and Stein 1999) as found in this study. Our findings also indicate that the HGM setting of a reservoir influences gizzard shad demographics. We detected higher production of large survivors in reservoirs with a relatively large shallow inflow area (as denoted by inflow fetch), supporting our prediction that shallow reservoirs may increase encounter rates between larval gizzard shad and their rotifer prey. These findings support the idea that reservoirs with relatively large hatch and “nursery” areas for larval gizzard shad support strong year classes. We find it surprising that larval hatch abundance was not in the top model. This finding points to the importance of the recruitment environment, prey availability, and post-hatch larval survival to understand and predict recruitment.

Application and generality—Our findings point toward the ecological mechanisms that underlie the disproportionate increase in benthivorous and detritivorous fishes that commonly occurs as lake or reservoir trophic status increases (Olin et al. 2002). In the case of southeastern U.S. reservoirs, increasing nutrient input (resulting from land use/cover and HGM effects) sets the stage for food web change not only through increased primary production, but also HGM effects on population demographics (e.g., the relationship between larval gizzard shad survivors and catchment scale features) and by positive food web feedbacks that become established. Most notably, gizzard shad increase nutrient levels through consumption of sediment-bound detritus; this effect appears to increase disproportionately with productivity levels (Vanni et al. 2005, 2006). In addition, juvenile and adult gizzard shad can reduce crustacean zooplankton abundance, to the possible advantage of rotifers (and ultimately their larval gizzard shad consumers). These underlying effects of the HGM template on productivity and food web interactions are also consistent with a recent study of German lakes in which Mehner et al. (2005) recognized that well-established

patterns of changes in fish species composition along a productivity gradient are likely driven more by HGM features (particularly lake depth) than productivity per se (Mehner et al. 2005). Similarly, Jeppesen et al. (1997) have proposed that depth is a key factor determining the strength of top-down control in lakes, with shallow, low macrophyte lakes (similar to the inflow areas of Ohio reservoirs) most likely dominated by food web interactions supporting a turbid lake state.

Our approach represents a framework that can wisely be applied to evaluate the effects of other landscape-oriented human activities on lakes within the HGM context (Soranno et al. in press). According to this framework, the HGM template constrains material input into lakes and mediates the effects both of human activities and food web interactions. Our approach recognizes that food web interactions not only are influenced by the physical environment, but may themselves influence the environment through ecosystem engineers (Jones et al. 1994). Specifically, as ecosystem engineers, gizzard shad function to integrate environmental conditions with productivity by generating feedbacks within the food web. Our understanding is built through integration of multiple approaches and multiple spatial scales. Our holistic, process-based framework reflects the necessity of integrating HGM and human drivers, at several spatial scales, to understand complex interactions structuring linked aquatic-terrestrial ecosystems.

References

- ALLAN, J. D. 2004. Landscapes and riverscapes: The influence of land use on stream ecosystems. *Annu. Rev. Ecol. Syst.* **35**: 257–284.
- AREND, K. A. 2002. How turbidity, light intensity, and zooplankton size structure influence larval gizzard shad, crappie, and bluegill foraging, growth, and depth distribution across a productivity gradient. M. S. thesis. The Ohio State University.
- BACHMANN, R. W., B. L. JONES, D. D. FOX, M. HOYER, L. A. BULL, AND D. E. CANFIELD. 1996. Relations between trophic state indicators and fish in Florida (USA) lakes. *Can. J. Fish. Aquat. Sci.* **53**: 842–855.
- BRAZNER, J. C., D. K. TANNER, N. E. DETENBECK, S. L. BATTERMAN, S. L. STARK, L. A. JAGGER, AND V. M. SNARSKI. 2005. Regional, watershed, and site-specific environmental influences on fish assemblage structure and function in western Lake Superior tributaries. *Can. J. Fish. Aquat. Sci.* **62**: 1254–1270.
- BREIMAN, L., J. FRIEDMAN, R. A. OLSHEN, AND C. J. STONE. 1993. Classification and regression trees. Chapman and Hall/CRC.
- BREMIGAN, M. T., AND R. A. STEIN. 1994. Gape-dependent larval foraging and zooplankton size: implications for fish recruitment across systems. *Can. J. Fish. Aquat. Sci.* **51**: 913–922.
- , AND ———. 1997. Experimental assessment of the influence of zooplankton size and density on gizzard shad recruitment. *Trans. Am. Fish. Soc.* **126**: 622–637.
- , AND ———. 1999. Larval gizzard shad success, juvenile effects, and reservoir productivity. *Trans. Am. Fish. Soc.* **128**: 1106–1124.
- , AND ———. 2001. Variability in larval gizzard shad recruitment across Ohio reservoirs: exploring causal mechanisms and implications for fisheries management. *Ecol. Appl.* **11**: 1425–1437.
- BUNNELL, D. B., M. J. GONZALEZ, AND R. A. STEIN. 2003. Zooplankton biomass enhances growth, but not survival, of first-feeding *Pomoxis* spp. larvae. *Can. J. Fish. Aquat. Sci.* **60**: 1314–1323.
- , R. S. HALE, M. J. VANNI, AND R. A. STEIN. 2006. Predicting crappie recruitment in Ohio reservoirs with spawning stock size, larval density, and chlorophyll concentrations. *North Am. J. Fish. Manage.* **26**: 1–12.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer-Verlag.
- CROSBIE, B., AND P. CHOW-FRASER. 1999. Percentage land use in the watershed determines the water and sediment quality of 22 marshes in the Great Lakes basin. *Can. J. Fish. Aquat. Sci.* **56**: 1781–1791.
- CRUMPTON, W. G., T. M. ISENHART, AND P. D. MITCHELL. 1992. Nitrate and organic N analyses with second derivative spectroscopy. *Limnol. Oceanogr.* **37**: 907–913.
- CULVER, D. A., M. M. BOUCHERLE, D. J. BEAN, AND J. W. FLETCHER. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. *Can. J. Fish. Aquat. Sci.* **42**: 1380–1390.
- DODSON, S. I., R. A. LILLIE, AND S. WILL-WOLF. 2005. Land use, water chemistry, aquatic vegetation, and zooplankton community structure of shallow lakes. *Ecol. Appl.* **15**: 1191–1198.
- DOOHAN, M. 1973. An energy budget for adult *Brachionus plicatilis* Muller (Rotatoria). *Oecologia* **13**: 351–362.
- DUMONT, H. J., I. VANDELDELDE, AND S. DUMONT. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* **19**: 75–97.
- GARVEY, J. E., AND R. A. STEIN. 1998a. Competition between larval fishes in reservoirs: The role of relative timing of appearance. *Trans. Am. Fish. Soc.* **127**: 1021–1039.
- , AND ———. 1998b. Linking bluegill and gizzard shad prey assemblages to growth of age-0 largemouth bass in reservoirs. *Trans. Am. Fish. Soc.* **127**: 70–83.
- GRAHAM, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* **84**: 2809–2015.
- HANAZATO, T. 1998. Response of a zooplankton community to insecticide application in experimental ponds: A review and the implications of the effects of chemicals on the structure and functioning of freshwater communities. *Environ. Pollut.* **101**: 361–373.
- HAWKINS, C. P., R. H. NORRIS, J. N. HOGUE, AND J. W. FEMINELLA. 2000. Development and evaluation of predictive models for measuring the biological integrity of streams. *Ecol. Appl.* **10**: 1456–1477.
- HERSHEY, A. E., AND OTHERS. 1999. A geomorphic-trophic model for landscape control of arctic lake food webs. *Biosci.* **49**: 887–897.
- JEPPESSEN, E., J. P. JENSEN, M. SONDERGAARD, T. LAURIDSEN, L. J. PEDERSEN, AND L. JENSEN. 1997. Top-down control in freshwater lakes: The role of nutrient state, submerged macrophytes and water depth. *Hydrobiologia* **342/343**: 151–164.
- JOHNSON, L. B., C. RICHARDS, G. E. HOST, AND J. W. ARTHUR. 1997. Landscape influences on water chemistry in Midwestern stream ecosystems. *Freshwater Biol.* **37**: 193–208.
- JONES, C. G., J. H. LAWTON, AND M. SHACHAK. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–386.
- JONES, J. R., M. F. KNOWLTON, D. V. OBRECHT, AND E. A. COOK. 2004. Importance of landscape variables and morphology on nutrients in Missouri reservoirs. *Can. J. Fish. Aquat. Sci.* **61**: 1503–1512.

- KNOLL, L. B., M. J. VANNI, AND W. H. RENWICK. 2003. Phytoplankton primary production and photosynthetic parameters in reservoirs along a gradient of watershed land use. *Limnol. Oceanogr.* **48**: 608–617.
- MAGNUSON, J. J., W. M. TONN, A. BANERJEE, J. TOIVONEN, O. SANCHEZ, AND M. RASK. 1998. Isolation vs. extinction in the assembly of fishes in small northern lakes. *Ecology* **79**: 2941–2956.
- MEHNER, T., M. DIEKMANN, U. BRAMICK, AND R. LEMCKE. 2005. Composition of fish communities in German lakes as related to lake morphology, trophic state, shore structure and human-use intensity. *Freshwater Biol.* **50**: 70–85.
- OLIN, M., M. RASK, J. RUUHUARVI, M. KURKILAHTI, P. ALA-OPAS, AND O. YLONEN. 2002. Fish community structure in mesotrophic and eutrophic lakes of southern Finland: The relative abundances of percids and cyprinids along a trophic gradient. *J. Fish Biol.* **60**: 593–612.
- OMERNIK, J. M. 1987. Ecoregions of the conterminous United States. *Annals of the Association of American Geographers* **77**: 118–125.
- PETERJOHN, W. T., AND D. L. CORRELL. 1984. Nutrient dynamics in an agricultural watershed: Observations on the role of a riparian forest. *Ecology* **5**: 1466–1475.
- POLIS, G. A., M. E. POWER, AND G. R. HUXEL. 2004. Food webs at the landscape level. The Univ. of Chicago Press.
- POLLARD, A. I., M. J. GONZALEZ, M. J. VANNI, AND J. L. HEADWORTH. 1998. Effects of turbidity and biotic factors on the rotifer community in an Ohio reservoir. *Hydrobiology* **387/388**: 215–223.
- RIERA, J. L., J. J. MAGNUSON, T. K. KRATZ, AND K. E. WEBSTER. 2000. A geomorphic template for the analysis of lake districts applied to the Northern Highland Lake District, Wisconsin, U. S. A. *Freshwater Biol.* **43**: 301–318.
- ROSEN, R. A. 1981. Length – dry weight relationships of some freshwater zooplankton. *J. Freshw. Ecol.* **1**: 225–229.
- RUTTNER-KOLINSKO, A. 1977. Suggestions for biomass calculations of plankton rotifers. *Commun. Int. Assoc. Theor. Appl. Limnol.* **8**: 71–76.
- SCHAUS, M. H., M. J. VANNI, AND T. E. WISSING. 2002. Biomass-dependent diet shifts in omnivorous gizzard shad: Implications for growth, food web, and ecosystem effects. *Trans. Am. Fish. Soc.* **131**: 40–54.
- SCHOMBERG, J. D., H. HOST, K. B. JOHNSON, AND C. RICHARDS. 2005. Evaluating the influence of landform, surficial geology, and land use on streams using hydrologic simulation modeling. *Aquat. Sci.* **67**: 528–540.
- SORANNO, P. A., K. E. WEBSTER, K. S. CHERUVELIL, AND M. T. BREMIGAN. In press. The lake landscape-context framework: Linking aquatic connections, terrestrial features and human effects at multiple spatial scales. *Verh. Internat. Verein. Limnol.*
- , ———, J. L. RIERA, T. K. KRATZ, J. S. BARON, P. A. BUKAVECKAS, G. W. KLING, D. S. WHITE, N. CAINE, R. C. LATHROP, AND P. R. LEAVITT. 1999. Spatial variation among lakes within landscapes: Ecological organization along lake chains. *Ecosystems* **2**: 395–410.
- SPRULES, W. G. 1980. Zoogeographic patterns in size structure of zooplankton communities, with possible applications to lake ecosystem modeling and management, p. 642–656. *In* W. C. Kerfoot [ed.], *Evolution and Ecology of zooplankton communities*. Univ. Press of New England.
- STRAYER, D. L., R. E. BEIGHLEY, L. C. THOMPSON, S. BROOKS, C. NILSSON, G. PINAY, AND R. J. NAIMAN. 2003. Effects of land cover on stream ecosystems: Roles of empirical models and scaling issues. *Ecosystems* **6**: 407–423.
- VANDER ZANDEN, M. J., T. E. ESSINGTON, AND Y. VADEBONCOEUR. 2005. Is pelagic top-down control in lakes augmented by benthic energy pathways? *Can. J. Fish. Aquat. Sci.* **62**: 1422–1431.
- VANNI, M. J., W. H. RENWICK, J. L. HEADWORTH, J. D. AUCH, AND M. H. SCHAUS. 2001. Dissolved and particulate nutrient flux from three adjacent agricultural watersheds: A five-year study. *Biogeochemistry* **54**: 85–114.
- , AND OTHERS. 2005. Linking landscapes and food webs: effects of omnivorous fish and watersheds on reservoir ecosystems. *Biosci.* **55**: 155–167.
- , AND ———. 2006. Nutrient cycling by fish supports relatively more primary production as lake productivity increases. *Ecology* **87**: 1696–1709.
- WANG, L., AND OTHERS. 2003. Watershed, reach, and riparian influences on stream fish assemblages in the Northern Lakes and Forest Ecoregion, U. S. A. *Can. J. Fish. Aquat. Sci.* **60**: 491–505.
- WILEY, M. J., S. L. KOHLER, AND P. W. SEELBACH. 1997. Reconciling landscape and local views of aquatic communities: Lessons from Michigan trout streams. *Freshw. Biol.* **37**: 133–148.

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