A simplified approach for estimating age-0 gizzard shad prey supply and predator demand

N. T. EVANS & D. E. SHOUP

Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK, USA

D. C. GLOVER

Center for Fisheries, Aquaculture and Aquatic Sciences, Southern Illinois University, Carbondale, IL, USA

Abstract Gizzard shad, *Dorosoma cepedianum* (Lesueur), often compose a majority of the prey biomass in southern US reservoirs. Previous studies suggest prey limitation frequently occurs in these systems, suggesting that fisheries managers need tools to evaluate the production potential of the populations they manage. Bioenergetics modelling was used to quantify the abundance of age-0 gizzard shad necessary to sustain multiple piscivore species with diverse growth rates, population sizes, mortality rates and diets. Gizzard shad biomass at the 50th percentile of published values was insufficient to support seven piscivore species in 69% of the simulations, suggesting that above-average prey biomass is required to support multiple piscivore populations at high abundance and growth rates. To help guide management, estimates of the gizzard shad biomass needed to sustain piscivore communities are provided for management situations in which coarse-scale (low, medium or high) growth, population size and percent of shad in diet data are available.

KEYWORDS: bioenergetics, Clupeidae, *Dorosoma cepedianum*, predator–prey balance, prey availability, reservoir.

Introduction

Gizzard shad, *Dorosoma cepedianum* (Lesueur), are often the most abundant species in the fish communities in which they occur (Miranda 1983; Stein *et al.* 1995; Bachmann *et al.* 1996) and the predominant prey for piscivores in lakes and reservoirs throughout the southern and midwestern United States (Noble 1981; Storck 1986; Johnson *et al.* 1988). Additionally, most abundant piscivores typically consume only gizzard shad < 100 mm TL, and even the less abundant larger piscivores typically only consume gizzard shad < 200 mm TL (Moore 1988; Dennerline & Van Den Avyle 2000; Vatland & Budy 2007), even when larger prey within the piscivores' gape limits are abundant (Bonds 2000). However, gizzard shad possess the ability to grow rapidly to sizes exceeding 100 mm TL (Tisa 1988; Dicenzo *et al.* 1996; Michaletz 1998a) or even > 200 mm TL in some systems (Bodola 1955; Berry 1957; Schramm & Pugh 1996) during their first year of life. As such, most piscivores only consume age-0 gizzard shad, as older individuals typically exceed the predators'

preferred sizes (Johnson *et al.* 1988; Bonds 2000). Older gizzard shad (especially those > 200 mm TL), therefore, contribute to total forage biomass but are too large to contribute to the 'available prey' biomass (Ney 1990; Cyterski & Ney 2005). Furthermore, lakes that contain a high biomass of large gizzard shad often have poor gizzard shad recruitment (Smith 1959; Sammons *et al.* 1998; Ostrand *et al.* 2001) further constraining the potential prey available to the piscivore community as fewer age-0 fish are produced each year. Therefore, it is possible for a system containing high gizzard shad biomass to be prey limited if the gizzard shad size distribution is skewed towards large individuals.

Most previous studies that have investigated predator–prey balance concluded that prey biomass was equal to, or only slightly greater than, predator demand (e.g. Cyterski *et al.* 2003; Irwin *et al.* 2003; Raborn *et al.* 2007; Vatland *et al.* 2008), demonstrating that prey limitation is likely a frequent occurence. Prey limitation may be even more common than these studies suggest if a more comprehensive or management-centric view of predator

doi: 10.1111/fme.12062

demand and prey availability is used (Ney 1990). Previous studies typically quantified predator demand by estimating *in situ* piscivore consumption, which was then compared to available prey biomass or other estimates of prey production in the system. From a fisheries management perspective, predator demand is more correctly defined as the amount of prey needed for predators to survive and grow at optimal rates or at least rates necessary to achieve management objectives (Ploskey & Jenkins 1982; Ney 1990). Using this management-centric definition, predator demand is, by definition, predicted to always be greater than actual consumption in prey-limited systems (i.e. systems where insufficient food limits predator survival or growth; Ney 1990). Therefore, when assessing prey sufficiency, it is necessary to have an objective measure of predator demand (i.e. one based on the prey abundance needed to achieve a management goal) rather than simply assessing whether current consumption is within the current prey production capacity of a system. Further, even if predator demand can be adequately defined and quantified relative to management goals, it is difficult to quantify how much prey biomass is needed to meet this demand. Some prey will die from causes other than predation, prey abundance must be high enough for predators to have reasonable encounter rates to find and consume prey, and some prey must survive to provide reproduction in future years (Ney 1990). The 'available prey' will be assessed at a much higher level than what is sustainably realistic if one or more of these factors are not considered. Lastly, all piscivores in a system must be considered simultaneously to accurately assess whether prey abundance is adequate to meet any species-specific management goal. Many lakes in the USA contain six to nine piscivores. Piscivore populations in multipiscivore fisheries are more likely to have decreased growth and population size than in fisheries with fewer predator species (Ploskey & Jenkins 1982). Although it can be quite time consuming to collect data from all predator populations, it would clearly provide an incomplete picture of total predator demand if data from some piscivores were missing. A tool that allows estimates of prey biomass required to meet consumption for all piscivores in a system (with population characteristics consistent with management goals) without requiring arduous sampling would be beneficial.

Prey limitation has important implications for the management of sport fishes. For example, competition for limited age-0 gizzard shad prey will result in decreased predator population sizes, reduced growth or both. A management objective of achieving increased population size or growth rate of a single piscivore species in a multiple piscivore system will likely come at the expense of reduced growth or abundance of other piscivores sharing the prey resource within the system (Ploskey & Jenkins 1982). These types of interspecific interactions are even more likely to occur when managers introduce additional piscivores into the system (Raborn *et al.* 2004; Schulze *et al.* 2006). Therefore, it is critical that managers are able to quantify the predator demand required by all piscivores, at the desired population sizes and growth rates for each species, to assess the sufficiency of the available prey relative to the management goals.

The purpose of this study was to provide fisheries managers with a tool to rapidly estimate the gizzard shad abundance required to maintain multispecies fisheries in southern US reservoirs. Data were compiled from previous studies that encompassed the range of predator population attributes (growth and mortality rates, population size and percent of gizzard shad in their diet) and prey supply typical of southern US reservoirs. These data were then used to parameterise species-specific population-level bioenergetics models and quantify the prey supply necessary to meet predator demand (i.e. at the community level by combining consumption of all predators) across a range of observed population parameters for each piscivore in the community. Model outputs tabulated via a simple coarse categorisation scheme are provided as a tool to help guide management decisions for multispecies sport fisheries in southern US reservoirs.

Methods

Modelling approach

Predator demand of age-0 gizzard shad was determined for seven piscivore species commonly found within southeastern US reservoirs when the populations had different levels of predator growth rates, mortality rates, population sizes and proportion of gizzard shad occurrence in piscivore diets (levels of population characteristics came from the published literature). Specifically, bioenergetics models were used to estimate age-specific consumption required to grow at scenario-specific rates for largemouth bass, *Micropterus salmoides* (Lacepède), white bass, *Morone chrysops* (Rafinesque), flathead catfish, *Pylodictis olivaris* (Rafinesque), blue catfish, *Ictalurus furcatus* (Lesueur), white crappie, *Pomoxis annularis* Rafinesque, large moronids [striped bass, *M. saxatilis* (Walbaum) or hybrid striped bass *M. saxatilis* × *M. chrysops*; hereafter referred to as striped bass] and percids [walleye, *Sander vitreus* (Mitchill) or saugeye *S. vitreus* × *S. canadensis* (Griffith & Smith); hereafter referred to as saugeye]. Individual consumption estimates were then scaled to population-level consumption

estimates for each piscivore species via extrapolation to a stable age distribution based on scenario-specific population size and annual mortality schedule. Total consumption of age-0 gizzard shad by multispecies piscivore communities was then determined via summation across ages and predator species. As such, it was assumed that the addition of a piscivore species to a reservoir would result in additive consumptive demand, which is likely conservative with respect to the prey biomass required to sustain predator populations as interference competition could occur resulting in reduced growth or population size of piscivores rather than gizzard shad consumption to the full extent predicted by the model. Total age-0 gizzard shad demand was determined for all possible combinations of three levels (i.e. low, medium, high) of growth rates, mortality rates, population sizes and proportion of gizzard shad in the diet for each piscivore species. Thus, the generated model output provided estimates of prey demand under a wide range of population attributes that have been observed in the literature for each species.

Modelling was accomplished via Visual Basic for Applications (VBA) in Microsoft Excel using the available bioenergetics models for largemouth bass (Rice et al. 1983; energy density 4186 J g^{-1}), saugeye [Zweifel et al. 2010; energy density 4186 J g^{-1} (Kitchell et al. 1977)], flathead catfish (Roell & Orth 1993; energy density 4184 J g^{-1}), striped bass (Hartman & Brandt 1995; energy density 6488 J g^{-1}) and white crappie (Zweifel 2000; energy density 4184 J g^{-1}). Bioenergetics models were not available for blue catfish or white bass; parameters from Blanc and Margraf (2002) developed for channel catfish were used to model blue catfish (energy density = 5437 J g^{-1}; Eggleton & Schramm 2002), and the striped bass model was used as a surrogate for white bass.

Modelling scenarios

Literature values (Tables S1–S8) were used to determine low, medium and high parameter values for each of the four input parameters for the piscivores: growth (in g mass, derived from mean length-at-age and reported weight–length relationships), mortality, initial population size and proportion of gizzard shad by weight in their diet. Piscivore annual mortality rates were assumed constant across ages given that estimates were typically derived from catch-curve analyses of age-1+ fish. Age-specific estimates were used for all other parameters. With the exception of diet proportions (see below), low, medium and high parameter values were represented by the 10th, 50th (median) and 90th percentile of all literature values, respectively. The 10th and 90th percentile estimates were chosen to ensure that the simulations

would be applicable to the majority of systems throughout the southeastern United States without being influenced by extreme outliers. Only published data from lentic populations were used to derive estimates.

Diet data were not as common in the literature as other parameters (Supplementary Data Table S1), such that it was inappropriate to use the 10th and 90th percentiles for this parameter. Rather, the mean from the two lowest and two highest published values of the proportion of gizzard shad consumed for each age class was used to represent low and high proportions, respectively; the medium proportion was calculated as described above (the median published values). Length-specific piscivore diets were assigned to age classes based on age-length relationships when diets were not reported according to age classes in the literature. The percentages for alternative prey types (i.e. diet items other than gizzard shad) were calculated by age class using the same procedure. Because averaging diet percentages across studies led to cases where the total diet did not sum exactly to 100%, the unadjusted mean proportion of gizzard shad was used and the relative differences among the mean diet proportions for alternative prey types were used to proportionally divide the remaining non-gizzard shad portion of the diet. Diet categories and the associated energy densities used in the bioenergetics models included gizzard shad = 5105 J g^{-1}, other fish = 4602 J g^{-1}, insects = 3138 J g^{-1}, crayfish = 4393 J g^{-1}, zooplankton = 1987 J g^{-1} (Pope et al. 2001) and freshwater mussels = 264 J g^{-1} (Eggleton & Schramm 2004).

All possible combinations of the low, medium and high levels for each of the four input parameters were modelled for each age class of each species ($3^4 = 81$ simulations per cohort). Models were run using a start date of 15 June for all species, which is the approximate time of year when age-0 gizzard shad are large enough that they begin to appear in piscivore diets (Houser & Netsch 1971; Buynak et al. 1992; Michaletz 1997).

All modelling scenarios were modelled at three temperature regimes representative of the northern latitude (coolest temperatures), central latitude (warmer temperatures) and southern latitude (warmest temperatures) reservoirs in the southeastern United States (Fig. 1). The northern latitude temperature regime was based on temperature data recorded from Kentucky Lake, KY (1 January 2008–30 December 2008; E. Ganus, Tennessee Wildlife Resource Agency, unpublished data). The central latitude temperature regime was based on temperature data collected from Possum Kingdom Reservoir, TX (1 January 2007–30 December 2007; J. Sullivan, Texas Commission on Environmental Quality, unpublished data). The southern latitude temperature regime was based on temperature data collected from Lake
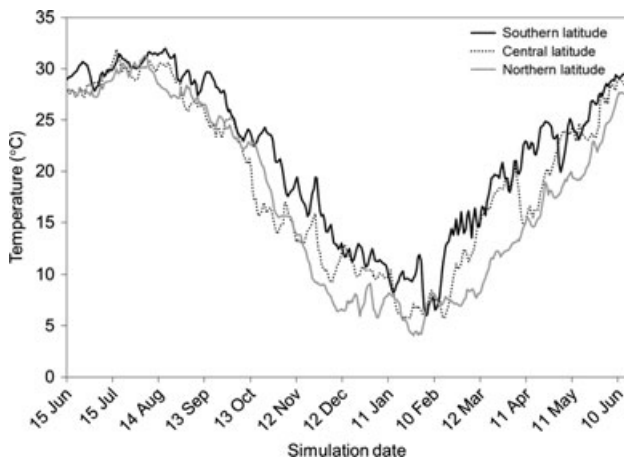
Figure 1. Temperature regimes used for bioenergetic modelling of southern US reservoir temperature conditions. Southern latitude temperature regime is based on temperatures logged from Lake Buchanan, TX; central latitude temperature regime is based on temperatures logged from Possum Kingdom Reservoir, TX; and northern latitude temperature regime is based on temperatures logged from Kentucky Lake, KY.

Buchanan, TX (15 June 2010–14 June 2011; K. Bodine, Texas Parks and Wildlife Department, unpublished data). Given that gizzard shad and other lentic fishes are known to congregate between 0 and 4 m in depth (Byrd 1952; Overholtz *et al.* 1977; Kubecka & Wittingerova 1998), water temperatures recorded via temperature loggers suspended at a mean depth of 1.79 ± 0.26 m were used for the bioenergetics modelling.

Conversion of biomass to numbers of gizzard shad required to sustain piscivore demand

To compare predator consumption with gizzard shad abundances, the number of shad required to sustainably meet predator demand on simulation day 60 (Ney 1981) was calculated by accounting for non-predation sources of mortality (from published values) and the number of surviving gizzard shad required to sustain age-0 production through recruitment (calculation details given below). Simulation day 60 corresponds to 15 August, which is typically when gizzard shad are sampled (Michaletz 1998b; Cyterski *et al.* 2003; Hale *et al.* 2008) and is, therefore, germane to the time period in which realistic management objectives could be assessed.

To produce this day-60 benchmark, daily consumption of gizzard shad from the predator bioenergetics models (in grams) was first converted to numbers of individuals using the mean daily mass of gizzard shad estimated for each day by a bioenergetics model (Sebring 2002). Low, medium and high gizzard shad growth rates (10th percentile, median and 90th percentile of published val-

ues) were modelled. A start mass of 0.166 g [20 mm standard length, approximate size when predators begin using gizzard shad as prey (Hale 1996; Michaletz 1997; Dennerline & Van Den Avyle 2000)] was used in all cases, and end masses of 33.4 g (low), 60.5 g (medium) and 96.0 g (high) were used to model low, medium and high gizzard shad growth rates (Bodola 1955; Pierce 1977; Schramm & Pugh 1996; Cyterski *et al.* 2003). Next, the number of gizzard shad was adjusted to account for annual non-predation mortality. Published annual mortality rates (A) for age-1+ individuals (which experience very limited predation mortality; Hale 1996; Michaletz 1997) were used as low (0.55), medium (0.70) and high (0.85) non-predation mortality values (Tisa 1988; Michaletz 1998a; Clayton & Maceina 2002). Finally, the number of additional age-0 gizzard shad required to sustain the population through reproduction was accounted for using established population equations. Specifically, the net reproductive rate (R_0) was calculated as follows:

$$R_0 = \sum_{x=0}^{k} (l_x {}^* m_x),$$

where l_x is the probability of surviving from time 0 to time x [calculated as S^t, where S = annualised survival ($S = 1-A$) using the above mortality rates], m_x is the per-capita birth rate (mean number of offspring produced per individual during year x, three values were used as explained below), and k is the maximum lifespan (which was set at 6 years; Schramm & Pugh 1996; Clayton & Maceina 2002; Cyterski *et al.* 2003). This was modelled using low (175.1), medium (233.5) and high (350.3) gizzard shad per-capita birth rates [medium value from Cyterski *et al.* (2003), low and high values represent 50% reduction or increase of this value]. The resulting R_0 values were used to calculate the number of gizzard shad that must survive to sustain the population through future reproduction (N_{rs}) given the number of individuals that will be consumed by predators (N_c) and the annualised survival rate (S) as follows:

$$N_{rs} = N_c {}^* \left[\left(1 - \frac{1}{R_0 {}^* S^2} \right)^{-1} - 1 \right],$$

which is a finite solution to the convergent infinite series of the sum of reproductive output from all future cohorts (additional explanation and derivation details provided in Evans 2009). Therefore, the population must have $N_c + N_{rs} = N_0$ age-0 gizzard shad produced on May 15th to sustainably meet the predator demand (N_c). These adjustments could not be performed for total prey consumption because the other prey types consumed do

not have adequate published growth, mortality and fecundity data that are required for the analysis. Other prey types could be adjusted for specific systems with knowledge of the required parameters.

Modelling piscivore community consumption

Model output from the 81 simulation scenarios (i.e. combinations of piscivore population characteristics) for each of the seven species was converted to units of number of gizzard shad required for sustainability on simulation day 60. This was carried out under 27 different combinations of gizzard shad population parameters [three levels of gizzard shad growth, three levels of non-predation mortality and reproductive needs (at three per-capita birth rates), resulting in 2187 total simulations per species (81 piscivore population scenarios × 27 prey population scenarios)]. It was not feasible to calculate all possible combinations of total gizzard shad consumed by all seven species in the piscivore community because the combinations were too numerous ($2187^7 = 2.39 \times 10^{23}$ combinations). Therefore, 100 000 randomly selected Monte Carlo simulations were used. Each Monte Carlo simulation was conducted by randomly selecting one of the 81 simulations for each of the seven piscivore species and summing the estimated biomass consumed by these seven piscivores over the year. One set of gizzard shad population characteristics was then randomly selected and used to convert the total predator consumption estimates to units of number of gizzard shad required for sustainability on simulation day 60. These values were converted to kg ha^{-1} using the estimated mean daily masses for gizzard shad from day 60 and were compared with published age-0 gizzard shad biomasses estimated in late summer (July-August; Olmstead 1974; Johnson *et al.* 1988; Aumen *et al.* 1992; Michaletz 1998b; Cyterski *et al.* 2003; Hale *et al.* 2008). The impact of the three levels of gizzard shad growth rates, mortality rates and per-capita birth rates on the amount of gizzard shad required to sustain piscivores was compared via Kolmogorov–Smirnov sensitivity analysis ($\alpha = 0.05$).

Accuracy of coarse-scale models

The accuracy of the low, medium and high parameterisation system at estimating predator demand for age-0 gizzard shad was evaluated by comparing estimates obtained from this study's model (Table 1) with published predator demand estimates from studies that used detailed parameterisation techniques. Piscivore population data from Norris Reservoir, TN [largemouth bass, striped bass and walleye (Raborn *et al.* 2002, 2007)] and

Smith Mountain Lake, VA [largemouth bass and striped bass (Cyterski *et al.* 2002)] were first assigned to low, medium or high categories (growth – mortality – initial population size – percent by weight of gizzard shad in the diet) based on whether the actual measured parameter was closest to the 10th percentile, median or 90th percentile of published values (see Supplementary Data). The corresponding model output presented in Table 1 was then used to estimate total annual consumption of age-0 gizzard shad for these real populations. Lastly, these coarse-parameter estimates (from Table 1) were compared with the more detailed estimates reported in the respective studies to determine how much error is introduced when low, medium or high parameterisation was used instead of more precisely measured parameters.

Results

Single-species bioenergetics models estimated different amounts of gizzard shad consumption when using the same input parameters for all species (Fig. 2). Temperature effects on consumption were minor for all piscivore species relative to the differences observed among species. The relative ranking (lowest to highest total consumed gizzard shad biomass) of the 81 combinations of input parameters varied among species, but the differences in ranked order were generally small between species (i.e. certain combinations were always ranked near the top or bottom of the list even if the exact order varied among species). Although the model results suggest flathead catfish were the most energetically efficient species (the modelled fish grew more per gram of gizzard shad consumed) and striped bass were the least efficient (Fig. 2), the differences in population parameters among species (i.e. based on the range of values reported in the literature) frequently were large enough to overcome differences in species-specific energetic efficiency, such that the species that had the highest or lowest consumption of gizzard shad for a given simulation was highly variable (Table 1). Due to the similarity of results between the three temperature regimes, only the central latitude temperature regimes estimates are reported hereafter.

The estimated biomass of gizzard shad on simulation day 60 required to meet predator demand for the remainder of the simulated year (accounting for non-predation mortality and required reproductive sustainability) varied from < 1 to > 100 kg ha^{-1} depending on species and the chosen population characteristics (Table 1). Sensitivity analysis indicated that of the three gizzard shad population parameters (mortality, growth rate and fecundity), only non-predation mortality significantly ($P \le 0.5$) affected the day 60 gizzard shad biomass estimates (Fig. 3). Lower age-0 gizzard shad biomass was

Table 1. Mean age-0 gizzard shad biomass (kg ha⁻¹) required on simulation day 60 (15 August) from bioenergetics models to sustainably meet predator consumption for the rest of the year at three gizzard shad productivity potentials based on non-predation mortality (low, medium and high; corresponding to age 1+ gizzard shad annual mortality rates of A = 0.55, 0.70 and 0.85, respectively). Piscivore population parameters are numerically coded in order as growth – mortality – initial population size – percent by weight gizzard shad; low (1), medium (2) and high (3) parameters correspond to the 10th percentile, 50th and 90th percentile of published values for each piscivore species

Population parameters	Flathead catfish			White bass			Striped bass			Saugeye			Largemouth bass			Blue catfish			White crappie		
	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High
1-1-1-1	0.07	0.09	0.19	7.34	10.23	22.87	3.30	4.53	9.90	3.65	5.01	9.93	0.02	0.03	0.06	0.75	1.01	2.21	4.36	5.88	12.51
1-1-1-2	0.09	0.12	0.24	8.35	11.63	26.02	4.11	5.64	12.30	5.38	7.38	14.62	0.26	0.35	0.77	2.89	3.87	8.52	7.36	9.94	21.23
1-1-1-3	0.14	0.18	0.37	9.19	12.80	28.65	4.75	6.52	14.23	6.22	8.53	16.91	0.65	0.87	1.96	3.25	4.34	9.55	8.76	11.85	25.35
1-1-2-1	0.39	0.48	1.01	13.11	18.27	40.84	12.63	17.33	37.87	17.77	24.37	48.34	0.58	0.78	1.75	1.00	1.34	2.95	18.63	25.11	53.43
1-1-2-2	0.50	0.62	1.28	14.91	20.77	46.46	15.71	21.57	47.07	26.16	35.90	71.14	7.34	9.91	22.17	3.86	5.16	11.37	31.44	42.44	90.64
1-1-2-3	0.76	0.94	1.95	16.41	22.86	51.16	18.17	24.96	54.45	30.26	41.52	82.28	18.55	25.08	56.16	4.33	5.78	12.74	37.40	50.60	108.23
1-1-3-1	0.72	0.89	1.86	18.87	26.30	58.82	21.96	30.14	65.85	40.30	55.28	109.64	1.41	1.90	4.28	1.25	1.67	3.69	49.85	67.19	142.95
1-1-3-2	0.92	1.14	2.37	21.47	29.92	66.91	27.31	37.51	81.84	59.34	81.42	161.36	17.90	24.18	54.08	4.82	6.45	14.21	84.12	113.55	242.50
1-1-3-3	1.40	1.74	3.61	23.63	32.92	73.67	31.60	43.39	94.67	68.62	94.16	186.62	45.26	61.18	137.00	5.41	7.23	15.92	100.05	135.37	289.56
1-2-1-1	0.03	0.04	0.08	1.76	2.49	5.78	1.34	1.85	4.11	1.62	2.22	4.47	0.01	0.01	0.03	0.29	0.39	0.87	0.44	0.63	1.54
1-2-1-2	0.04	0.05	0.11	1.99	2.80	6.51	1.75	2.41	5.34	2.59	3.55	7.15	0.10	0.13	0.31	1.20	1.61	3.56	0.74	1.06	2.66
1-2-1-3	0.07	0.08	0.17	2.11	2.97	6.92	2.02	2.79	6.19	2.98	4.09	8.23	0.28	0.38	0.88	1.42	1.90	4.20	1.17	1.66	4.09
1-2-2-1	0.17	0.21	0.44	3.15	4.44	10.32	5.13	7.07	15.71	7.87	10.81	21.76	0.12	0.17	0.39	0.39	0.52	1.16	1.88	2.67	6.57
1-2-2-2	0.23	0.28	0.59	3.55	5.00	11.63	6.68	9.22	20.43	12.59	17.29	34.79	1.42	1.93	4.44	1.60	2.15	4.75	3.15	4.51	11.34
1-2-2-3	0.35	0.44	0.91	3.76	5.31	12.35	7.75	10.68	23.68	14.50	19.91	40.05	4.06	5.52	12.80	1.90	2.54	5.61	4.98	7.09	17.47
1-2-3-1	0.31	0.38	0.81	4.53	6.40	14.87	8.91	12.29	27.32	17.86	24.51	49.36	0.49	0.68	1.58	0.49	0.66	1.45	5.03	7.14	17.59
1-2-3-2	0.42	0.52	1.09	5.10	7.20	16.75	11.62	16.02	35.52	28.56	39.23	78.91	5.73	7.80	17.98	2.01	2.68	5.93	8.42	12.08	30.34
1-2-3-3	0.65	0.81	1.68	5.42	7.65	17.79	13.47	18.58	41.18	32.88	45.15	90.83	16.43	22.38	51.85	2.37	3.17	7.01	13.33	18.98	46.75
1-3-1-1	0.01	0.01	0.02	0.70	1.00	2.41	1.22	1.68	3.73	0.51	0.70	1.45	0.00	0.00	0.01	0.06	0.08	0.17	0.13	0.19	0.51
1-3-1-2	0.01	0.01	0.02	0.78	1.11	2.69	1.59	2.20	4.89	0.94	1.29	2.68	0.01	0.02	0.05	0.27	0.36	0.81	0.22	0.32	0.90
1-3-1-3	0.02	0.02	0.04	0.82	1.18	2.84	1.85	2.55	5.67	1.07	1.48	3.07	0.05	0.07	0.18	0.36	0.49	1.09	0.39	0.57	1.52
1-3-2-1	0.03	0.04	0.08	1.24	1.78	4.30	4.65	6.41	14.29	2.46	3.39	7.05	0.05	0.07	0.18	0.08	0.10	0.23	0.56	0.82	2.19
1-3-2-2	0.05	0.06	0.13	1.39	1.99	4.81	6.10	8.42	18.70	4.56	6.27	13.03	0.41	0.57	1.45	0.36	0.48	1.08	0.92	1.38	3.83
1-3-2-3	0.08	0.10	0.21	1.47	2.10	5.08	7.07	9.76	21.68	5.21	7.18	14.91	1.41	1.97	5.02	0.48	0.65	1.45	1.65	2.42	6.49
1-3-3-1	0.05	0.07	0.15	1.79	2.56	6.19	8.09	11.15	24.85	5.59	7.69	16.00	0.12	0.17	0.43	0.10	0.13	0.29	1.49	2.18	5.87
1-3-3-2	0.09	0.11	0.24	2.00	2.86	6.93	10.61	14.64	32.51	10.33	14.23	29.55	1.00	1.40	3.53	0.45	0.60	1.35	2.47	3.69	10.25
1-3-3-3	0.15	0.18	0.39	2.12	3.02	7.31	12.30	16.97	37.69	11.83	16.28	33.83	3.44	4.81	12.25	0.61	0.81	1.81	4.40	6.47	17.35
2-1-1-1	0.11	0.14	0.29	13.08	18.11	40.15	5.55	7.59	16.53	6.58	9.00	17.75	0.04	0.05	0.11	1.91	2.55	5.57	6.88	8.92	17.51
2-1-1-2	0.15	0.19	0.39	14.84	20.55	45.58	7.11	9.72	21.13	9.78	13.39	26.34	0.48	0.65	1.44	7.29	9.74	21.29	11.70	15.18	29.84
2-1-1-3	0.23	0.29	0.60	16.22	22.46	49.83	8.21	11.23	24.42	11.30	15.47	30.44	1.23	1.66	3.67	8.12	10.85	23.70	13.07	17.02	33.74
2-1-2-1	0.59	0.74	1.55	23.35	32.34	71.69	21.24	29.04	63.25	31.99	43.80	86.35	1.06	1.43	3.17	2.54	3.40	7.43	29.36	38.07	74.75
2-1-2-2	0.79	0.98	2.05	26.51	36.70	81.39	27.20	37.20	80.85	47.57	65.14	128.17	13.83	18.63	41.34	9.72	12.99	28.40	49.96	64.82	127.45
2-1-2-3	1.21	1.51	3.15	28.96	40.10	88.98	31.43	42.98	93.44	54.98	75.27	148.13	35.33	47.57	105.39	10.83	14.47	31.60	55.81	72.68	144.10
2-1-3-1	1.10	1.37	2.87	33.63	46.56	103.24	36.93	50.49	109.97	72.57	99.34	195.87	2.58	3.48	7.72	3.18	4.24	9.28	78.56	101.86	200.00
2-1-3-2	1.45	1.81	3.78	38.17	52.85	117.21	47.29	64.68	140.57	107.91	147.74	290.72	33.74	45.45	100.85	12.15	16.24	35.49	133.67	173.42	340.97
2-1-3-3	2.24	2.79	5.82	41.70	57.75	128.13	54.64	74.74	162.45	124.70	170.73	335.99	86.17	116.05	257.07	13.54	18.08	39.50	149.31	194.44	385.53

(continued)

Table 1. (continued)

Population parameters	Flathead catfish			White bass			Striped bass			Saugeye			Largemouth bass			Blue catfish			White crappie		
	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High
2-2-1-1	0.05	0.06	0.14	3.67	5.13	11.77	2.38	3.27	7.28	3.08	4.22	8.42	0.02	0.02	0.05	0.69	0.92	2.04	0.61	0.83	1.92
2-2-1-2	0.07	0.09	0.19	4.12	5.76	13.23	3.26	4.48	9.91	4.98	6.81	13.56	0.20	0.28	0.62	2.79	3.74	8.24	1.06	1.46	3.39
2-2-1-3	0.12	0.15	0.31	4.37	6.11	14.02	3.77	5.17	11.46	5.73	7.84	15.60	0.58	0.78	1.76	3.27	4.37	9.62	1.41	1.96	4.62
2-2-2-1	0.27	0.34	0.71	6.56	9.16	21.03	9.12	12.53	27.86	15.00	20.53	40.97	0.24	0.33	0.74	0.92	1.23	2.72	2.59	3.54	8.20
2-2-2-2	0.39	0.49	1.03	7.36	10.29	23.63	12.47	17.13	37.92	24.22	33.15	65.96	2.95	3.98	8.99	3.73	4.98	10.99	4.54	6.23	14.47
2-2-2-3	0.62	0.77	1.62	7.80	10.91	25.04	14.41	19.80	43.85	27.86	38.14	75.88	8.38	11.31	25.48	4.36	5.83	12.83	6.04	8.36	19.74
2-2-3-1	0.50	0.62	1.32	9.44	13.20	30.28	15.86	21.79	48.43	34.02	46.56	92.93	0.98	1.33	2.99	1.15	1.54	3.39	6.92	9.48	21.94
2-2-3-2	0.72	0.90	1.90	10.61	14.82	34.02	21.67	29.78	65.93	54.93	75.20	149.61	11.96	16.14	36.41	4.66	6.23	13.73	12.14	16.67	38.70
2-2-3-3	1.14	1.42	2.98	11.24	15.71	36.06	25.05	34.42	76.24	63.19	86.50	172.12	33.95	45.81	103.21	5.45	7.29	16.03	16.16	22.36	52.80
2-3-1-1	0.01	0.01	0.03	1.56	2.21	5.24	2.18	3.00	6.68	1.00	1.37	2.82	0.00	0.00	0.01	0.12	0.16	0.36	0.16	0.23	0.58
2-3-1-2	0.02	0.02	0.05	1.74	2.46	5.85	3.00	4.13	9.16	1.86	2.55	5.21	0.03	0.04	0.10	0.56	0.75	1.67	0.28	0.41	1.04
2-3-1-3	0.03	0.04	0.08	1.84	2.60	6.17	3.47	4.77	10.59	2.13	2.92	5.96	0.10	0.14	0.33	0.74	0.99	2.21	0.42	0.60	1.58
2-3-2-1	0.05	0.06	0.14	2.79	3.94	9.35	8.34	11.46	25.54	4.88	6.69	13.70	0.10	0.14	0.32	0.16	0.22	0.48	0.68	0.96	2.46
2-3-2-2	0.10	0.12	0.26	3.11	4.40	10.44	11.49	15.80	35.05	9.07	12.43	25.36	0.88	1.20	2.87	0.74	1.00	2.22	1.21	1.73	4.45
2-3-2-3	0.16	0.21	0.44	3.28	4.64	11.01	13.28	18.25	40.52	10.38	14.22	29.02	2.94	4.02	9.58	0.99	1.32	2.95	1.80	2.58	6.75
2-3-3-1	0.09	0.12	0.26	4.02	5.67	13.47	14.50	19.93	44.41	11.07	15.17	31.08	0.24	0.33	0.78	0.20	0.27	0.60	1.81	2.57	6.59
2-3-3-2	0.18	0.23	0.49	4.48	6.33	15.03	19.98	27.46	60.94	20.58	28.19	57.51	2.15	2.93	7.00	0.93	1.24	2.78	3.25	4.63	11.90
2-3-3-3	0.30	0.38	0.80	4.73	6.68	15.86	23.09	31.74	70.45	23.55	32.26	65.81	7.18	9.80	23.36	1.24	1.66	3.68	4.81	6.91	18.07
3-1-1-1	0.16	0.20	0.43	20.81	28.69	63.40	8.55	11.64	25.16	10.37	14.18	27.92	0.06	0.08	0.18	5.74	7.68	16.92	17.30	21.60	39.07
3-1-1-2	0.22	0.27	0.57	23.59	32.52	71.86	10.91	14.86	32.10	15.69	21.46	42.16	0.77	1.04	2.30	21.67	29.00	63.80	29.79	37.19	67.29
3-1-1-3	0.33	0.42	0.87	25.67	35.39	78.23	12.60	17.16	37.07	18.12	24.78	48.69	2.01	2.70	5.94	23.88	31.95	70.25	32.78	41.03	74.72
3-1-2-1	0.87	1.08	2.26	37.16	51.23	113.21	32.70	44.53	96.26	50.46	69.01	135.86	1.70	2.28	5.03	7.66	10.25	22.56	73.89	92.25	166.86
3-1-2-2	1.15	1.43	2.99	42.12	58.06	128.32	41.74	56.87	122.82	76.36	104.42	205.13	22.22	29.89	66.04	28.90	38.67	85.08	127.22	158.83	287.37
3-1-2-3	1.77	2.20	4.60	45.84	63.20	139.70	48.21	65.68	141.85	88.17	120.58	236.90	57.60	77.41	170.43	31.85	42.61	93.68	139.96	175.22	319.09
3-1-3-1	1.60	2.00	4.18	53.51	73.78	163.02	56.85	77.42	167.36	114.46	156.53	308.16	4.15	5.57	12.26	9.57	12.81	28.20	197.69	246.80	446.42
3-1-3-2	2.12	2.65	5.53	60.65	83.61	184.78	72.58	98.88	213.54	173.19	236.85	465.26	54.21	72.90	161.10	36.13	48.33	106.35	340.36	424.94	768.81
3-1-3-3	3.26	4.07	8.50	66.01	91.00	201.16	83.82	114.19	246.63	200.00	273.51	537.32	140.51	188.82	415.73	39.81	53.26	117.09	374.45	468.79	853.68
3-2-1-1	0.08	0.10	0.21	6.42	8.93	20.56	3.58	4.90	10.82	5.02	6.86	13.69	0.03	0.04	0.09	2.06	2.76	6.10	1.05	1.39	2.99
3-2-1-2	0.12	0.15	0.31	7.19	10.01	23.05	4.88	6.68	14.72	8.33	11.39	22.63	0.35	0.47	1.05	8.12	10.87	23.97	1.87	2.47	5.31
3-2-1-3	0.18	0.23	0.48	7.61	10.60	24.39	5.63	7.71	17.01	9.57	13.09	26.01	1.00	1.35	3.00	9.28	12.41	27.34	2.55	3.38	7.34
3-2-2-1	0.43	0.53	1.13	11.46	15.95	36.71	13.69	18.73	41.39	24.43	33.40	66.60	0.42	0.56	1.24	2.75	3.69	8.14	4.50	5.96	12.78
3-2-2-2	0.61	0.77	1.61	12.84	17.88	41.15	18.66	25.55	56.32	40.53	55.41	110.12	5.06	6.81	15.24	10.83	14.49	31.96	7.98	10.56	22.68
3-2-2-3	0.96	1.20	2.53	13.59	18.92	43.56	21.56	29.52	65.09	46.59	63.69	126.58	14.53	19.51	43.41	12.37	16.55	36.45	10.88	14.45	31.34
3-2-3-1	0.79	0.98	2.08	16.50	22.97	52.86	23.81	32.57	71.96	55.40	75.75	151.06	1.69	2.27	5.02	3.44	4.61	10.17	12.05	15.93	34.19
3-2-3-2	1.13	1.42	2.98	18.49	25.74	59.26	32.44	44.41	97.93	91.94	125.69	249.78	20.51	27.59	61.72	13.54	18.11	39.95	21.36	28.25	60.67
3-2-3-3	1.78	2.22	4.67	19.57	27.25	62.73	37.49	51.32	113.17	105.67	144.46	287.11	58.83	79.03	175.82	15.46	20.68	45.56	29.11	38.67	83.85
3-3-1-1	0.02	0.02	0.05	2.87	4.04	9.68	3.27	4.47	9.90	1.74	2.38	4.87	0.01	0.01	0.02	0.33	0.44	0.97	0.28	0.39	0.91
3-3-1-2	0.03	0.04	0.08	3.19	4.50	10.78	4.49	6.15	13.59	3.33	4.55	9.29	0.06	0.08	0.18	1.44	1.93	4.28	0.52	0.70	1.65

(continued)

Table 1. (continued)

Population parameters	Flathead catfish			White bass			Striped bass			Saugeye			Largemouth bass			Blue catfish			White crappie		
	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High	Low	Medium	High
3-3-1-3	0.05	0.06	0.14	3.37	4.74	11.36	5.18	7.10	15.70	3.81	5.21	10.62	0.19	0.25	0.58	1.84	2.46	5.45	0.79	1.08	2.54
3-3-2-1	0.09	0.11	0.25	5.12	7.21	17.28	12.50	17.11	37.89	8.45	11.56	23.68	0.18	0.24	0.55	0.44	0.58	1.30	1.22	1.65	3.87
3-3-2-2	0.17	0.21	0.45	5.70	8.03	19.24	17.17	23.52	51.99	16.20	22.16	45.20	1.59	2.15	5.02	1.92	2.57	5.71	2.21	3.00	7.03
3-3-2-3	0.27	0.34	0.73	6.01	8.47	20.29	19.84	27.17	60.07	18.53	25.34	51.69	5.33	7.20	16.65	2.45	3.28	7.26	3.38	4.60	10.83
3-3-3-1	0.17	0.21	0.45	7.37	10.38	24.88	21.73	29.74	65.88	19.16	26.21	53.71	0.44	0.59	1.35	0.54	0.73	1.62	3.25	4.42	10.36
3-3-3-2	0.31	0.39	0.82	8.21	11.56	27.71	29.85	40.90	90.39	36.75	50.27	102.52	3.88	5.26	12.25	2.40	3.21	7.13	5.91	8.03	18.81
3-3-3-3	0.51	0.63	1.35	8.66	12.19	29.22	34.49	47.24	104.44	42.02	57.48	117.25	13.00	17.56	40.61	3.06	4.10	9.08	9.04	12.32	28.98

needed to meet predator demand on day 60 when mortality was low. Therefore, for each simulation, the nine estimates (three growth rates × three fecundity values) for the low, medium and high gizzard shad non-predation mortalities were averaged. The resulting averages represent low, medium and high categories of gizzard shad productivity.

Monte Carlo simulations indicated that predator demand frequently exceeded sustainable gizzard shad abundance (Fig. 4). The gizzard shad biomass required to support seven piscivores exceeded the 50th percentile of published age-0 gizzard shad biomass in 69% of the simulations. Monte Carlo simulations exceeded the 95th percentile of published gizzard shad abundance in 18% of the simulations.

Comparisons with detailed estimates

Estimates of annual consumption for individual piscivores based on the simplified low, medium or high categorisation system were similar to the more detailed estimated values reported for Norris Reservoir, TN and Smith Mountain Lake, VA (Table 2). Estimates produced by the three-category method were all within 4 kg ha^{-1} when study populations could be assigned to a single simulation category and between 0 and 21 kg ha^{-1} when study parameters fell midway between categories. These discrepancies are relatively small compared with the range of predator demand values resulting from different piscivore population characteristics (e.g. Table 1).

Discussion

The simple low-medium-high categorisation system provided estimates of sustainable predator demand for age-0 gizzard shad similar to more refined estimates for two different reservoirs. Although additional validation is warranted, the similarity in estimates between the current study and these two previous studies suggests that the outputs from this study (Table 1) provide fisheries managers with a tool that can be used for rapid estimation of the gizzard shad biomass required to sustain a piscivore community with specific population attributes (i.e. meeting certain management objectives for growth rate and population size). This tool does not require detailed piscivore population measurements; rather, selecting low, medium or high for each parameter to reflect whether the parameter is likely to be closest to the 10th, 50th or 90th percentile for the parameter is sufficient (benchmark values of each parameter level for all species are provided in Tables S2–S8). Because of the approach used, the model output is not constrained by the prey abundance of the system but simply calculates the amount of
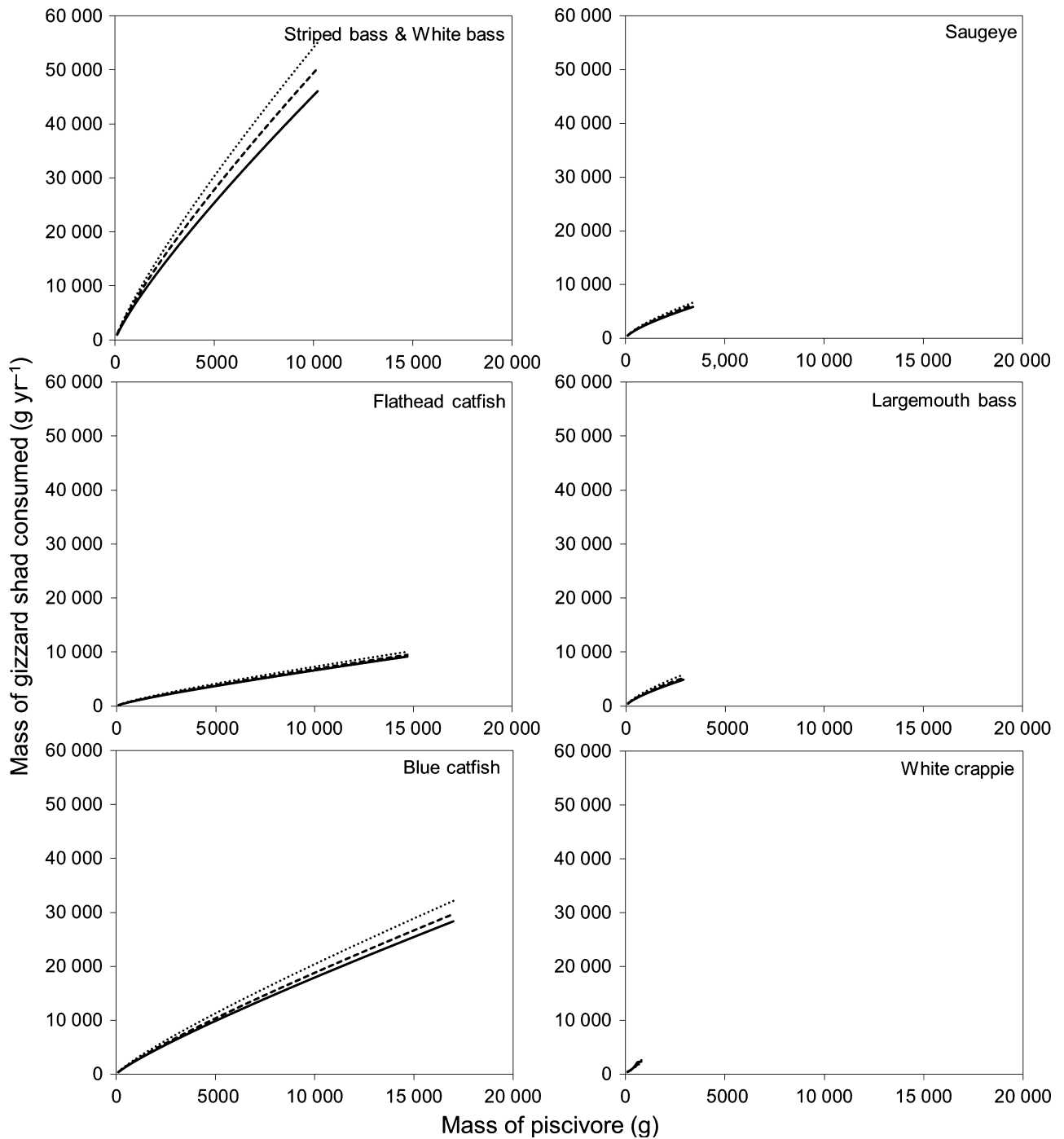
Figure 2. Consumption estimates of age-0 gizzard shad from the bioenergetics models for blue catfish, flathead catfish, largemouth bass, saugeye, striped bass and white crappie under southern latitude (Lake Buchanan, TX; short dash line), central latitude (Possum Kingdom Reservoir, TX; long dash line) and northern latitude (Kentucky Lake, KY; solid line) temperature regimes from the southern USA. All species were modelled with starting mass of individuals = 100 g, population size = 1 individual, no mortality and diet = 100% gizzard shad. White bass follows same trajectory as striped bass.

age-0 gizzard shad that must be consumed by piscivores to maintain the species with the selected population attributes. This allows managers not only to assess the

current demand of their system but also to see what gizzard shad biomass levels would be needed to meet hypothetical population characteristics related to management
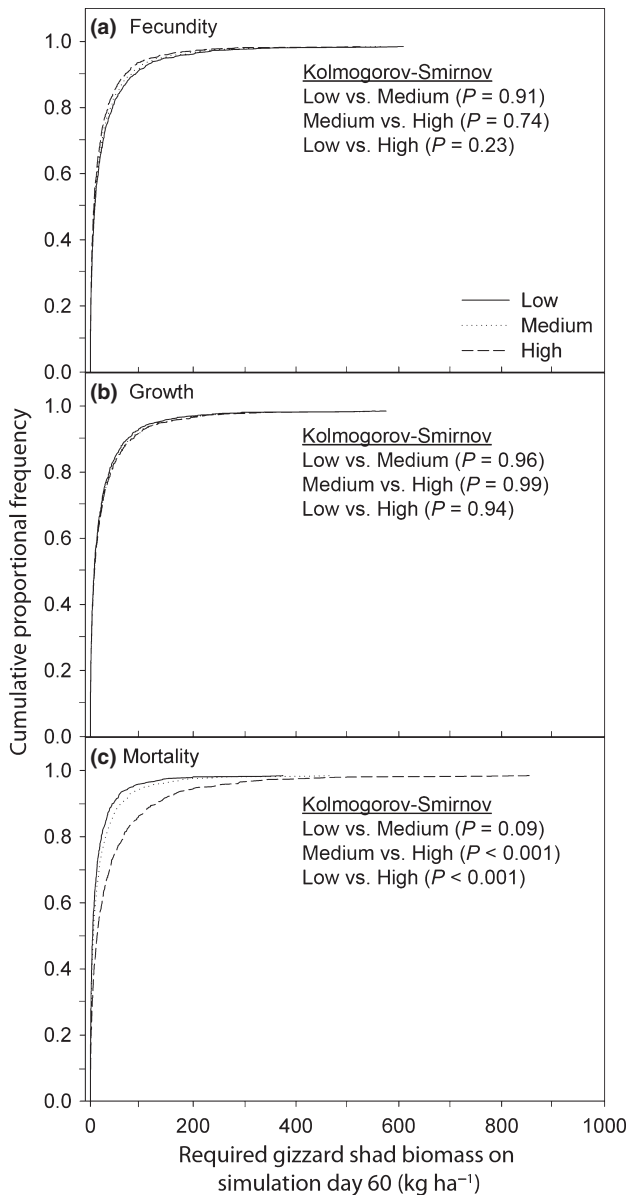
Figure 3. The frequency (from 100 000 warm-temperature bioenergetics Monte Carlo simulations) of age-0 gizzard shad biomasses (kg ha^{-1} on simulation day 60) required to meet predator demand parameterized under different levels of gizzard shad fecundity, growth and non-predation mortality.
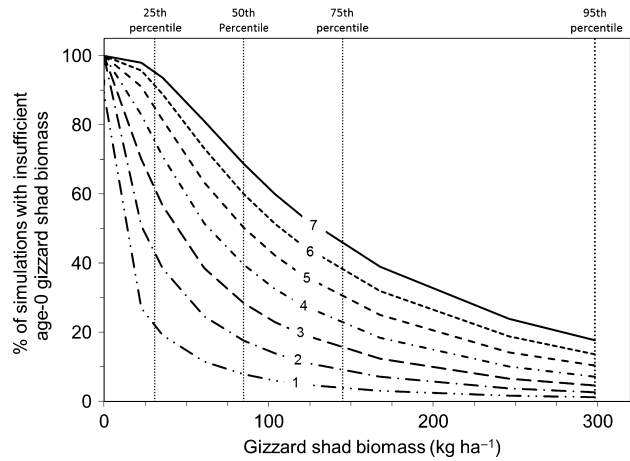

Figure 4. Percent of warm-temperature-regime Monte Carlo simulations in which age-0 gizzard shad biomass was insufficient to meet predator demand at different published late summer age-0 gizzard shad abundances (vertical dotted lines). Numbers associated with the lines indicate the number of piscivores.

Table 2. Comparison of estimated annual consumption of gizzard shad (kg ha^{-1}) in the current study with those estimated in Norris Reservoir, TN (Raborn *et al.* 2002, 2007) and Smith Mountain Lake, VA (Cyterski *et al.* 2002). Population parameters were categorised from data provided in referenced publications to match the model output ranking system where parameters were numerically coded in order as growth-mortality-initial population size-percent by weight gizzard shad; low (1), medium (2) and high (3) parameters corresponded with the 10th percentile, median and 90th percentile of published values for each piscivore species (see Tables S2–S8 for published values that correspond with each parameter level for each species)

	Original study consumption estimate (kg ha^{-1})	Input parameter coding	Current study consumption estimate (kg ha^{-1})
Norris Reservoir, TN			
Largemouth bass	23	2-3-3-3	19
Striped bass	49	3-3-2-3	46
Walleye	38	3-1-1-3	38
Smith Mountain Lake, VA			
Largemouth bass	23	3-2-2-2	19
Striped bass	49	1-1-2-1–2-1-2-1	28–49

goals. However, managers should be aware that the model results are for systems in prey supply equilibrium (i.e. modelled under the assumption that gizzard shad maintain steady-state population abundances via stable reproduction, recruitment and growth).

The Monte Carlo simulation results quantitatively support the traditional logic (Axon & Whitehurst 1985; Ney 1990; Michaletz 1997) that piscivore populations in systems with average or below-average age-0 gizzard shad abundances are prey limited as a consequence of inadequate age-0 gizzard shad abundance. Only when age-0 gizzard shad biomass was above the 75th percentile did all seven piscivores have a > 50% probability of not being gizzard shad prey resource limited. This was true despite accounting for alternative prey usage. Therefore, managers should have realistic expectations in systems with many piscivores and should only consider adding new piscivores (e.g. stocking non-reproducing species such as hybrid striped bass or saugeye) in systems with

high prey biomasses [i.e. those exceeding the 75th percentile of published gizzard shad abundances (145 kg ha^{-1})].

Estimates of prey demand from this study (Table 1) should be considered minimum requirements; actual prey demand could be higher in some situations. The modelling approach described in this study used the range of published population attributes to estimate consumption. Therefore, even the highest consumption estimates would fall short of the predator demand (and growth potential) of unconstrained feeding. The model parameters corresponding to the greatest predator demands are based on the 90th percentile of published values. Therefore, some populations could exist that would exceed the highest estimates. Second, predation by non-game species (which were not modelled due to insufficient data) would increase total piscivore demand. However, the consumption by non-game piscivores should be low given their low biomass in most systems [e.g. of 72 lake and year combinations sampled by the Oklahoma Department of Wildlife Conservation (ODWC) from 2009 to 2012, only 2.3% of the piscivorous fish species captured in gillnets were non-game species; K. Kuklinski, ODWC, unpublished data]. Therefore, managers should recognise the total predator demand estimates generated using Table 1 are approximate and may underestimate the prey abundance required in their system, especially if their system has unusually large or fast-growing populations or a high non-game piscivore biomass.

Practitioners using the model proposed in this study should also keep in mind that this model is reductionistic in its approach, but natural systems have complex interactions and feedback loops that could lead to unexpected changes. For example, if the diversity of piscivores in a system is altered (e.g. stocking of hybrid striped bass and saugeye is suspended), the proportion of gizzard shad in the diet of the remaining piscivores may change if competitive release allows for an expansion of the realised niche of one or more remaining piscivore. Additionally, a change in one model parameter for a given species may result in alteration to other model parameters for that population. For example, increasing the population size may result in slowed growth or higher mortality for a population, even if sufficient prey resources exist to meet the higher prey demand, if other resources became the limiting factor for the population. The model parameters are derived from a large number of different populations encompassing a wide range of environmental conditions and fish communities. As such, the parameters probably encompass the majority of conditions under which the model results could be applied. However, if the model is used to predict future prey consumption that might result from a possible management change, the model cannot provide reliable results unless the parameter values selected for each piscivore species are end values expected to result from the management change.

Responses to insufficient prey and management implications

Piscivores likely respond dynamically to insufficient prey resources in lakes depending on the extent and duration of prey resource limitation. Piscivores can theoretically respond via long-term responses such as niche partitioning. However, this type of response typically occurs over evolutionary time intervals that exceed the duration of most sport fish management regulations and frequently the service lifetimes of reservoirs (Moermond 1979; Raborn *et al.* 2007). Moreover, partitioning of gizzard shad prey is further doubtful due to the lack of spatial and temporal separation between gizzard shad and piscivores in reservoirs (Jester & Jensen 1972; Downey & Toetz 1983; Cyterski & Ney 2005). Although piscivores may be spatially separated by habitat preferences, gizzard shad populations likely roam throughout reservoirs as they are commonly found in littoral (Gelwick & Matthews 1990; Bailey & Gerow 2005) as well as pelagic habitat (Degan & Wilson 1995; Gido 2001). Spatial separation of piscivores, therefore, does not partition gizzard shad prey. Piscivores are more likely to respond via short-term responses including reduced consumption (Rice & Cochran 1984) and diet shifts (Jenkins 1979; Venturelli & Tonn 2006), usually leading to decreased growth (Muth & Wolfert 1986; Weatherley 1990) or decreased population abundance and biomass (Ploskey & Jenkins 1982). Thus, short-term responses influence sport fish populations in ways that are typically counterproductive to management objectives. Managers must, therefore, set achievable management objectives that are consistent with the prey availability of the systems they manage and be willing to alter their management objectives and strategies if necessary. The model outputs (Table 1) provide fisheries managers with benchmarks that aid in evaluating the sufficiency of prey (standing stock in August) to support increased piscivore production.

Alternative prey use

Simulations were performed in accordance with the premise that clupeids, particularly gizzard shad, often account for the majority of the prey base in US lakes (Noble 1981; Storck 1986; Johnson *et al.* 1988). Many pelagic piscivore species feed almost exclusively on age-0 gizzard shad or other clupeids of similar size, as few alternative prey fishes occur in the pelagic habitat (Cyterski *et al.* 2003; Raborn *et al.* 2007), and gizzard shad constitute a

large proportion (typically over 50%) of many littoral piscivores' diets [Horton & Gilliland 1990; Pope *et al.* 2001; Tables S2–S8 and the citations therein (Table S1)], suggesting that gizzard shad prey abundance is a primary limiting factor to piscivore growth. However, the bioenergetics approach used in this study did account for alternative prey use via the input parameter for percent gizzard shad in the piscivore diet. Therefore, some proportion of alternative prey were being eaten by the piscivores in the simulations, so the gizzard shad consumption estimates assume alternative prey are being eaten to some extent at the same time gizzard shad are being consumed. Because of this, the output (Table 1) assumes there will always be sufficient biomass of alternative prey types to meet predator demand. Therefore, in systems with limited alternative prey, managers should use the highest level for the percent-of-gizzard-shad-in-the-diet parameter to minimise the chance of forage depletion.

Temperature effects

The effects of temperature on prey demand were small relative to changes in piscivore population parameters for a given species or difference in consumption estimates among species. The temperature regimes were chosen because of their relative latitude, spanning much of the perceived climate variation within the southern United States. However, the mean of daily temperature differences between the warmest and coolest temperature regime, on any given simulation day, was only 4.3 °C; a magnitude of differences in temperatures that is, especially at moderate temperatures, not expected to influence bioenergetics estimates as much as more extreme temperature differences (Bajer *et al.* 2004; Petersen & Paukert 2005). This suggests the results should be applicable to a wide geographical range and should only be moderately affected by interannual differences in temperature cycles. This is further supported by the accuracy with which the simplified categorisation system used in this study (low, medium or high for each parameter) matched more detailed annual piscivore consumption data without using the actual detailed temperature regime from the studied systems. Additionally, the relatively small effects of temperature on consumption estimates suggest that the predictions from the current study should still be realistic even if some fish spend most of their time at deeper depths than those where the modelled temperature profiles were measured. Most southern reservoirs only have a few Celsius degree difference from the surface to the thermocline (e.g. OWRB 2007), which would produce only relatively small effects on consumption compared with the effects of different population parameters (e.g. Table 1).

Conclusions and future research needs

This study combined bioenergetics and prey population modelling to provide a simple tool that estimates predator demand in southern US reservoirs. Using simple categorical descriptors (i.e. low, medium or high) of growth, mortality, population size and percent of gizzard shad in the diet of each species of interest, biologists can use the model output to estimate total predator demand by piscivore communities composed of any combination of the piscivores studied. In some cases, practitioners could estimate predator demand by additional species using the model output of a closely related species, assuming they are willing to accept the potential trade-off in the accuracy of the estimate; for example, black crappie, *Pomoxis nigromaculatus* (Lesueur), could not be modelled in the current study because there is no published bioenergetics model for this species; the output for white crappie provides estimates that probably are similar to what might be consumed by a black crappie population, but this remains untested. This bioenergetic estimate of predator demand can then be compared to measured gizzard shad biomass in late summer to determine whether prey limitation exists under the assumed, and modelled, population characteristics for each piscivore. The results of the Monte Carlo simulation using these outputs suggested a high probability that prey availability limits piscivore growth in most reservoirs, which is consistent with the findings of field-based studies (Hale 1996; Michaletz 1997; Venturelli & Tonn 2006). Future research on factors affecting gizzard shad population dynamics is needed to enable age-0 prey production and management strategies to be developed that complement the sport fish focused management strategies currently being used.

References

Aumen N.G., Crist C.L., Miller D.E. & Meals K.O. (1992) Particulate organic carbon supply and trophic dynamics in a Mississippi flood-control reservoir dominated by gizzard shad (*Dorosoma cepedianum*). *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 1722–1733.

Axon J.R. & Whitehurst D.K. (1985) Striped bass management in lakes with emphasis on management problems. *Transactions of the American Fisheries Society* **114**, 8–11.

Bachmann R.W., Jones B.L., Fox D.D., Hoyer M., Bull L.A. & Canfield D.E. Jr (1996) Relations between trophic state indicators and fish in Florida (U.S.A.) lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **53**, 842–855.

Bailey P.E. & Gerow K.G. (2005) Seining effort needed to estimate species richness of small littoral zone fishes: a simulation study in three Wyoming reservoirs. *North American Journal of Fisheries Management* **25**, 1310–1314.

Bajer P.G., Hayward R.S., Whitledge G.W. & Zweifel R.D. (2004) Simultaneous identification and correction of systematic error in bioenergetics models: demonstration with a white crappie (*Pomoxis annularis*) model. *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 2168–2182.

Berry F.H. (1957) Age and growth of the gizzard shad (*Dorosoma lacepede*) (Lesueur), in Lake Newnan, Florida. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners* **11**, 318–331.

Blanc T.J. & Margraf F.J. (2002) Effects of nutrient enrichment on channel catfish growth and consumption in Mount Storm Lake, West Virginia. *Lakes & Reservoirs: Research and Management* **7**, 109–123.

Bodola A. (1955) *The Life History of the Gizzard Shad*, Dorosoma cepedianum *(LeSueur), in Western Lake Erie*. PhD thesis, Columbus, OH: The Ohio State University, 129 pp.

Bonds C.C. (2000) *Assessment of the Response of Piscivorous Sportfishes to the Establishment of Gizzard Shad in Claytor Lake, Virginia*. MSc Thesis, Blacksburg, VA: Virginia Polytechnic Institute and State University, 110 pp.

Buynak G.L., Hale R.S. & Mitchell B. (1992) Differential growth of young-of-year gizzard shad in several Kentucky reservoirs. *North American Journal of Fisheries Management* **12**, 656–662.

Byrd I.B. (1952) Depth distribution of the bluegill, *Lepomis macrochirus* Rafinesque, in farm ponds during summer stratification. *Transactions of the American Fisheries Society* **81**, 162–170.

Clayton D.L. & Maceina M.J. (2002) Trophic state differences in population characteristics of gizzard shad in two Tennessee River impoundments. *Lake and Reservoir Management* **18**, 109–117.

Cyterski M.J. & Ney J.J. (2005) Availability of clupeid prey to primary piscivores in Smith Mountain Lake, Virginia. *Transactions of the American Fisheries Society* **134**, 1410–1421.

Cyterski M., Ney J. & Duval M. (2002) Predator demand for clupeid prey in Smith Mountain Lake, Virginia. *Fisheries Research* **59**, 1–16.

Cyterski M., Ney J. & Duval M. (2003) Estimation of surplus biomass of clupeids in Smith Mountain Lake, Virginia. *Transactions of the American Fisheries Society* **132**, 361–370.

Degan D.J. & Wilson W. (1995) Comparison of four hydroacoustic frequencies for sampling pelagic fish populations in Lake Texoma. *North American Journal of Fisheries Management* **15**, 924–932.

Dennerline D.E. & Van Den Avyle M.J. (2000) Sizes of prey consumed by two pelagic predators in US reservoirs: implications for quantifying biomass of available prey. *Fisheries Research* **45**, 147–154.

Dicenzo V.J., Maceina M.I. & Stimpert M.R. (1996) Relations between reservoir trophic state and gizzard shad population characteristics in Alabama reservoirs. *North American Journal of Fisheries Management* **16**, 888–895.

Downey P. & Toetz D. (1983) Distribution of larval gizzard shad (*Dorosoma cepedianum*) in Lake Carl Blackwell, Oklahoma. *American Midland Naturalist* **109**, 23–33.

Eggleton M.A. & Schramm H.L. Jr (2002) Caloric densities of selected fish prey organisms in the lower Mississippi River. *Journal of Freshwater Ecology* **17**, 409–414.

Eggleton M.A. & Schramm H.L. Jr (2004) Feeding ecology and energetic relationships with habitat of blue catfish, *Ictalurus furcatus*, and flathead catfish, *Pylodictis olivaris*, in the lower Mississippi River, U.S.A. *Environmental Biology of Fishes* **70**, 107–121.

Evans N.T. (2009) *Age-0 Gizzard Shad Supply and Predator Demand: Analysis of the Trophic Support Capacity of Southern U.S. Reservoirs*. MSc Thesis, Stillwater, OK: Oklahoma State University, 109 pp.

Gelwick F.P. & Matthews W.J. (1990) Temporal and spatial patterns in littoral-zone fish assemblages of a reservoir (Lake Texoma, Oklahoma-Texas, USA). *Environmental Biology of Fishes* **27**, 107–120.

Gido K.B. (2001) Feeding ecology of three omnivorous fishes in Lake Texoma (Oklahoma-Texas). *The Southwestern Naturalist* **46**, 23–33.

Hale R.S. (1996) Threadfin shad use as supplemental prey in reservoir white crappie fisheries in Kentucky. *North American Journal of Fisheries Management* **16**, 619–632.

Hale R.S., Degan D.J., Renwick W.H., Vanni M.J. & Stein R.A. (2008) Assessing fish biomass and prey availability in Ohio reservoirs. In: M.S. Allen, S. Sammons & M.J. Maceina (eds) *Balancing Fisheries Management and Water Uses for Impounded River Systems*. Bethesda, MD: American Fisheries Society, Symposium 62, pp. 517–541.

Hartman K.J. & Brandt S.B. (1995) Comparative energetics and the development of bioenergetics models for sympatric estuarine piscivores. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 1647–1666.

Horton R.A. & Gilliland E.R. (1990) Diet overlap between saugeye and largemouth bass in Thunderbird Reservoir, Oklahoma. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* **44**, 98–104.

Houser A. & Netsch N.F. (1971) Estimates of young-of-year shad production in Beaver Reservoir. In: G.E. Hall (ed.) *Reservoir Fisheries and Limnology*. Bethesda, MD: American Fisheries Society, Special Publication 8, pp. 359–370.

Irwin B.J., DeVries D.R. & Wright R.A. (2003) Evaluating the potential for predatory control of gizzard shad by largemouth bass in small impoundments: a bioenergetics approach. *Transactions of the American Fisheries Society* **132**, 913–924.

Jenkins R.M. (1979) Predator-prey relations in reservoirs. In: R.H. Stroud & H. Clepper (eds) *Predator-Prey Systems in Fisheries Management*. Washington, DC: Sport Fisheries Institute, pp. 123–134.

Jester D.B. & Jensen B.L. (1972) *Life History and Ecology of the Gizzard Shad*, Dorosona cepedianum *(LeSueur) with Reference to Elephant Butte Lake*. New Mexico State

University Agricultural Experiment Station Research Report 218. 56 pp.

Johnson B.M., Stein R.A. & Carline R.F. (1988) Use of a quadrat rotenone technique and bioenergetics modeling to evaluate prey availability to stocked piscivores. *Transactions of the American Fisheries Society* **117**, 127–141.

Kitchell J.F., Stewart D.J. & Weininger D. (1977) Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* **34**, 1922–1935.

Kubecka J. & Wittingerova M. (1998) Horizontal beaming as a crucial component of acoustic fish stock assessment in freshwater reservoirs. *Fisheries Research* **35**, 99–106.

Michaletz P.H. (1997) Influence of abundance and size of age-0 gizzard shad on predator diets, diet overlap, and growth. *Transactions of the American Fisheries Society* **126**, 101–111.

Michaletz P.H. (1998a) Population characteristics of gizzard shad in Missouri reservoirs and their relation to reservoir productivity, mean depth, and sport fish growth. *North American Journal of Fisheries Management* **18**, 114–123.

Michaletz P.H. (1998b) Effects on sport fish growth of spatial and temporal variation in age-0 gizzard shad availability. *North American Journal of Fisheries Management* **18**, 616–624.

Miranda L.E. (1983) Average ichthyomasses in Texas large impoundments. *Annual Proceedings of the Texas Chapter, American Fisheries Society* **6**, 58–67.

Moermond T.C. (1979) Resource partitioning: a dynamic competitive balance. In: R.H. Stroud & H. Clepper (eds) *Predator-Prey Systems in Fisheries Management*. Washington, DC: Sport Fishing Institute, pp. 303–309.

Moore C.M. (1988) *Food Habits, Population Dynamics, and Bioenergetics of Four Predatory Fish Species in Smith Mountain Lake, Virginia*. PhD thesis, Blacksburg, VA: Virginia Polytechnic Institute and State University, 218 pp.

Muth K.M. & Wolfert D.R. (1986) Changes in growth and maturity of walleyes associated with stock rehabilitation in western Lake Erie, 1964-1983. *North American Journal of Fisheries Management* **6**, 168–175.

Ney J.J. (1981) Evolution of forage-fish management in lakes and reservoirs. *Transactions of the American Fisheries Society* **110**, 725–728.

Ney J.J. (1990) Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. *Reviews in Aquatic Sciences* **2**, 55–81.

Noble R.L. (1981) Management of forage fishes in impoundments of the southern United States. *Transactions of the American Fisheries Society* **110**, 738–750.

Olmstead L.L. (1974) *The Ecology of Largemouth Bass (*Micropterus salmoides*) and Spotted Bass (*Micropterus punctulatus*) in Lake Fort Smith, Arkansas*. PhD thesis, Fayetteville, AR: University of Arkansas, 134 pp.

Ostrand K.G., Schramm H.L. Jr, Kraai J.E. & Braeutigam B. (2001) Effects of intensive stocking of hybrid striped bass on the population structure of gizzard shad in a west Texas impoundment, a case study. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* **55**, 324–333.

Overholtz W.J., Fast A.W., Tubb R.A. & Miller R. (1977) Hypolimnion oxygenation and its effects on the depth distribution of rainbow trout (*Salmo gairdneri*) and gizzard shad (*Dorosoma cepedianum*). *Transactions of the American Fisheries Society* **106**, 371–375.

OWRB (2007) *2007 Report of the Oklahoma Beneficial Use Monitoring Program*. Oklahoma Water Resources Board. 653 pp. Available at: http://www.owrb.ok.gov/quality/monitoring/bump/pdf_bump/archives/BUMPLakesReport.pdf (accessed 8 April 2013)

Petersen J.H. & Paukert C.P. (2005) Development of a bioenergetics model for humpback chub and evaluation of water temperature changes in the Grand Canyon, Colorado River. *Transactions of the American Fisheries Society* **134**, 960–974.

Pierce R.J. (1977) *Life History and Ecological Energetics of the Gizzard Shad* (Doromosa cepedianum) *in Acton Lake, Ohio*. PhD thesis, Oxford, OH: Miami University, 125 pp.

Ploskey G.R. & Jenkins R.M. (1982) Biomass model of reservoir fish and fish-food interactions, with implications for management. *North American Journal of Fisheries Management* **2**, 105–121.

Pope K.L., Brown M.L., Duffy W.G. & Michaletz P.H. (2001) A caloric-based evaluation of diet indices for largemouth bass. *Environmental Biology of Fishes* **61**, 329–339.

Raborn S.W., Miranda L.E. & Driscoll M.T. (2002) Effects of simulated removal of striped bass from a southeastern reservoir. *North American Journal of Fisheries Management* **22**, 406–417.

Raborn S.W., Miranda L.E. & Discoll M.T. (2004) Diet overlap and consumption patterns suggest seasonal flux in the likelihood for exploitative competition among piscivorous fishes. *Ecology of Freshwater Fish* **13**, 276–284.

Raborn S.W., Miranda L.E. & Driscoll M.T. (2007) Prey supply and predator demand in a reservoir of the southeastern United States. *Transactions of the American Fisheries Society* **136**, 12–23.

Rice J.A. & Cochran P.A. (1984) Independent evaluation of a bioenergetics model for largemouth bass. *Ecology* **65**, 732–739.

Rice J.A., Breck J.E., Bartell S.M. & Kitchell J.F. (1983) Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. *Environmental Biology of Fishes* **9**, 263–275.

Roell M.J. & Orth D.J. (1993) Trophic basis of production of stream-dwelling smallmouth bass, rock bass, and flathead catfish in relation to invertebrate bait harvest. *Transactions of the American Fisheries Society* **122**, 46–62.

Sammons S.M., Bettoli P.W. & Fiss F.C. (1998) Effect of threadfin shad density on production of threadfin shad and gizzard shad larvae in a Tennessee reservoir. *Environmental Biology of Fishes* **53**, 65–73.

Schramm H.L. Jr & Pugh L.L. (1996) *Gizzard Shad Stock Estimate for Lake Apopka, Florida, 1996*. Special Publication SJ97-SP11, St. Johns River Water Management District. 47 pp.

Schulze T., Baade U., Dörner H., Eckmann R., Haertel-Borer S.S., Hölker F. *et al.* (2006) Response of the residential piscivorous fish community to introduction of a new predator type in a mesotrophic lake. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 2202–2212.

Sebring S.H. (2002) *Development and Application of a Bioenergetics Model for Gizzard Shad*. MSc Thesis, Lubbock, TX: Texas Tech University, 83 pp.

Smith W.A. Jr (1959) Shad management in reservoirs. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners* **12**, 143–147.

Stein R.A., DeVries D.R. & Dettmers J.M. (1995) Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* **52**, 2518–2526.

Storck T.W. (1986) Importance of gizzard shad in the diet of largemouth bass in Lake Shelbyville, Illinois. *Transactions of the American Fisheries Society* **115**, 21–27.

Tisa M.S. (1988) *Compatibility and Complementarity of Alewife and Gizzard Shad as Forage Fish in Smith Mountain Lake, Virginia*. PhD thesis, Blacksburg, VA: Virginia Polytechnic Institute and State University, 240 pp.

Vatland S. & Budy P. (2007) Predicting the invasion success of an introduced omnivore in a large, heterogeneous reservoir. *Canadian Journal of Fisheries and Aquatic Sciences* **64**, 1329–1345.

Vatland S., Budy P. & Thiede G.P. (2008) A bioenergetics approach to modeling striped bass and threadfin shad predator-prey dynamics in Lake Powell, Utah-Arizona. *Transactions of the American Fisheries Society* **137**, 262–277.

Venturelli P.A. & Tonn W.M. (2006) Diet and growth of northern pike in the absence of prey fishes: initial consequences for persisting in disturbance-prone lakes.

Transactions of the American Fisheries Society **135**, 1512–1522.

Weatherley A.H. (1990) Approaches to understanding fish growth. *Transactions of the American Fisheries Society* **119**, 662–672.

Zweifel R.D. (2000) *Development and Evaluation of a Bioenergetics Model for White Crappie*. MSc Thesis, Columbia, MO: University of Missouri, 176 pp.

Zweifel R.D., Landis A.M.G., Hale R.S. & Stein R.A. (2010) Development and evaluation of a bioenergetics model for saugeye. *Transactions of the American Fisheries Society* **139**, 855–867.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Literature sources and number of populations used to obtain bioenergetics input parameters (growth, mortality, initial population size and percent gizzard shad in diet) for the seven piscivore species.

Table S2. Largemouth bass input parameters used in bioenergetics simulations.

Table S3. White bass input parameters used in bioenergetics simulations.

Table S4. Striped bass input parameters used in bioenergetics simulations.

Table S5. White crappie input parameters used in bioenergetics simulations.

Table S6. Flathead catfish input parameters used in bioenergetics simulations.

Table S7. Blue catfish input parameters used in bioenergetics simulations.

Table S8. Saugeye input parameters used in bioenergetics simulations.