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Threadfin shad *Dorosoma petenense* density and biomass of four Puerto Rico reservoirs – seasonal differences and comparison among temperate and tropical reservoirs

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Abstract. Threadfin shad, *Dorosoma petenense* (Günther, 1867) are the primary prey species for sport fish in many temperate and tropical reservoirs. However, quantification of density or biomass for threadfin shad is rare in the literature and limited in geographic scope. The objectives of this paper were to report seasonal threadfin shad biomass estimates from tropical reservoirs where this species has been introduced, and to compare tropical threadfin shad populations to temperate reservoirs where this species is native. Considerable variability was observed among Puerto Rico reservoirs for biomass ($F_{3,210}$=14.8, P<0.0001), with estimates ranging from 2.0 to 32.2 kg/ha. Within reservoirs, biomass fluctuated as much as 24-fold between seasonal sampling events (*CV* ranged 51–126%). Comparison to data from temperate reservoirs in the southern United States suggested that Puerto Rico reservoirs may have threadfin shad populations that are generally less dense with less biomass, calling into question the previous assumption that prey limitation was not an issue in tropical systems. This research also indicates that threadfin shad populations are under-evaluated in most temperate systems, and that current threadfin shad sampling strategies of single sampling event per year may not be adequate to provide accurate characterization of threadfin shad populations.

Key words. Trawl, sampling, variability, seasonal effect, Actinopterygi, Clupeiformes, *Dorosoma petenense*, Puerto Rico.

INTRODUCTION

Holistic fisheries management schemes based on trophic relationships within ecosystems are generally more effective than single-species approaches (Larkin 1979, May et al. 1979). This is because sport fish, which are usually predators in freshwater systems, are dependent on bottom-up influences affecting forage abundance and availability (Noble 1986). Whereas effective predator management requires accurate knowledge of prey availability and dynamics (Jenkins & Morais 1978), targeted sampling programs for prey species are critical to support sport fisheries management.

Threadfin shad, *Dorosoma petenense* (Actinopterygii: Clupeiformes: Clupeidae: Dorosomatinae) is pelagic species occupying freshwater and brackish subtropical waters of North and Central America. It is relatively small-size species with common length around 12 cm total length (TL), however, individuals up to 33 cm TL have been recorded. Maximal reported age is four years (see Froese & Pauly 2015). Although the life history characteristics of threadfin shad in temperate waters are well described, little is known about populations in tropical reservoirs, where this species has been introduced to (Prchalová et al. 2012). Stancil et al. (1997) reported that threadfin shad spawning occurs nearly year-round in Lucchetti Reservoir, Puerto Rico, with the exception of a short period from mid-August until mid-September. The same study reported that the maximum length (n=2,002) was only 8.6 cm TL and that the maximum age (n=124) was only 141 days. These data suggested that threadfin shad in tropical systems are a prolific and short-lived species.

For most reservoirs in the southern United States (US), gizzard shad (*Dorosoma cepedianum*) and threadfin shad are the principal prey species (Noble 1981). Despite the importance of these species, Neal & Prchalová (2012) concluded that abundance and biomass data on clupeid prey were lacking in the peer-reviewed literature. Furthermore, the few studies that addressed density or biomass largely relied on sampling strategies and methods that were biased or incomplete. Rotenone was the primary sampling method used in most pre-1980s studies, though this toxicant has been largely discredited for sampling pelagic prey (e.g., Hayne et al. 1967, Summers & Axon 1980, Davies & Shelton 1983). Trawling has proven much less biased (Boxrucker et al. 1995), but the handful of studies to use this method have ignored seasonal variability by sampling prey species only once per year, usually during the summer or fall (e.g., Siler 1986, Michaletz et al. 1995). Furthermore, many studies that address clupeid populations fail to distinguish between clupeid species in their reporting (e.g., Taylor et al. 2005).

Threadfin shad are the primary prey species for sport fish in many tropical reservoirs, particularly for largemouth bass (*Micropterus salmoides*) and butterfly peacock bass (*Cichla ocellaris*) (Alicea et al. 1997, Neal 2003). However, directed research has rarely quantified threadfin shad abundance or biomass in tropical systems (Neal & Prchalová 2012). Much of the research and management decisions for the sport fish in Puerto Rico have assumed that prey availability was not limiting (e.g., Alicea et al. 1997, Stancil et al. 1997, Neal et al. 2008), despite that conclusive data to this end have not been available. Furthermore, temporal dynamics of prey fish communities are poorly understood and complicated by the fact that tropical reservoirs do not experience the same magnitude of seasonal cues in physicochemical environment as temperate reservoirs (e.g., Dadzie & Aloo 1990, Gran 1995). Whereas effective sport fish management requires consideration of both predator and prey, improved understanding of threadfin shad population dynamics would enhance management for reservoirs in Puerto Rico and other tropical locations.

Recently, Prchalová and colleagues (2012) concluded that trawling was the most preferred method for sampling threadfin shad in steep-sided tropical reservoirs, and Neal & Prchalová (2012) recommended threadfin shad sampling protocols. Moreover, the latter study presented the first quantification of threadfin shad density in four Puerto Rico reservoirs. Building on those findings, the goal of this manuscript is to (1) provide much needed analysis of threadfin shad biomass in Puerto Rico, and (2) compare Puerto Rico threadfin shad populations to those in temperate US reservoirs. These data will improve biological understanding of trophic interactions and holistic sport fish management in tropical reservoirs, and provide a benchmark for comparisons of this species across its geographic range.

MATERIAL AND METHODS

In this paper, the available literature on threadfin shad density and biomass from Puerto Rico and the temperate USA was reviewed. The authors previously published estimates of threadfin shad density from four Puerto Rico reservoirs (Neal & Prchalová 2012), and use the raw data collected from that study to estimate biomass for comparisons in the current paper.

Study Sites

This research was conducted on four reservoirs located on the island of Puerto Rico. Reservoirs in Puerto Rico are generally mesotrophic to eutrophic, typically anoxic below 3–9 m depth, and depend on infrequent mixing events (Kröger et al. 2010). Surface water temperatures average around 27 °C, though this varies somewhat with altitude and season (Neal et al. 2009). The four study reservoirs were Lucchetti, Guajataca, Dos Bocas, and Carite, which range 108–360 ha in surface area. These reservoirs contain a mixture of fish species, with largemouth bass, threadfin shad, tilapia (*Oreochromis* and

Tilapia spp.), sunfishes (*Lepomis* spp.), ictalurids, and Amazon sailfin catfish (*Pterygoplichthys pardalis*) common to all four. Guajataca, Dos Bocas, and Carite Reservoir also contain butterfly peacock bass, and red devil cichlid (*Amphilophus labiatus*) has been collected from all four reservoirs, but is abundant only in Dos Bocas and Guajataca reservoirs.

Gear Specifications and Study Design

A custom frame fry trawl with a total length of 10.5 m was designed with frame aperture dimensions of 3×3 m, 6-mm mesh in the body of the trawl, and 4-mm in the cod-end. The tow rope between the trawler boat and the trawl was 100 m long. Each reservoir was divided into lower (near dam) and upper sections (Dos Bocas had two upper sections as it has two primary arms). Prior to trawling, three fixed transects were selected per reservoir section to provide three replicates each. At each transect location, up to three depth strata were sampled (0–3 m, 3–6 m, and 6–9 m). Depths deeper than 9 m were not sampled because most reservoirs in Puerto Rico are oligomictic, and anoxia is usually present at depths greater than 9 m. In the upper sections of each reservoir, only upper (0–3 m) and middle (3–6 m) depth strata were sampled due to insufficient depth for trawling. The trawl was flushed between depth samples to avoid cross contamination of biota. Only fishes gathered in the cod-end of the trawl were collected as a catch after each tow.

Sampling occurred within each reservoir at 3-month intervals for 1 year. The corresponding seasonal data were spring (April), summer (June), fall (October), and winter (January). All trawling was conducted at night. Trawl tow duration was held at 2 min with average speed of 3.6 km/h, resulting in a trawled distance of approximately 120 m, and a sampled volume of approximately 1,080 m^3.

All fishes retained were measured for total length (TL, mm) and weighed to the nearest 0.01 g. Sub-sampling was performed when necessary. Weights of non-weighted individuals from sub-samples were calculated using length-weight relationships specific for a given campaign. Overview of recorded lengths of threadfin shad can be found in Prchalová et al. (2012).

Data Processing and Analysis

Threadfin shad biomass estimates (g/1,000 m^3, all threadfin shad including larvae) were calculated for individual tows and then averaged across replicates to obtain section-depth averages. All depth strata from each section were averaged to produce section means, and sections were averaged assuming a 1:1 areal ratio between upper and lower reservoir sections to produce the seasonal reservoir mean. Threadfin shad biomass estimates for Puerto Rico were compared among seasons and reservoirs using analysis of variance (ANOVA; PROC GLM, SAS Version 9.2; $\alpha=0.05$). Estimates were transformed using $\log_e(X + 1)$, where X=biomass, to normalize data and stabilize variances. For significant comparisons, differences between variables were determined using the least squares means procedure (LSMEANS; SAS Version 9.2; $\alpha=0.05$).

Seasonal reservoir biomass estimates were converted from g/1,000 m^3 to kg/ha for comparison to other studies by summing depth strata estimates and expanding area. Seasonal biomass and density estimates were averaged across the year to provide the annual mean biomass. Statistical comparisons between Puerto Rico and temperate reservoirs were not feasible because of many differences in sampling gears and designs, insufficient data availability in the literature, and limitations in the format used for data reporting. Instead, a descriptive approach was used to compare temperate and tropical reservoirs and highlight limitations in threadfin shad sampling in all habitats.

RESULTS AND DISCUSSION

Puerto Rico Population Dynamics

Biomass estimates differed significantly among Puerto Rico reservoirs ($F_{3,210}=14.8$, $P<0.0001$; Table 1). Lucchetti Reservoir displayed the greatest annual mean biomass (32.2±18.7 kg/ha), but this value was heavily influenced by a large winter estimate (86.9±11.4 kg/ha). Dos Bocas Reservoir exhibited the greatest biomass in 3 out of 4 seasons. Carite Reservoir consistently displayed the least threadfin shad biomass across seasons (ranged 0.2–4.7 kg/ha), with an annual mean of 2.0±1.2 kg/ha (Fig. 1).

Within individual Puerto Rico reservoirs, threadfin shad biomass displayed significant variability among seasons (Table 1; $F_{3,210}=25.7$, $P<0.0001$). Whole lake mean biomass estimates varied as much as 24-fold between samples, and coefficients of variation ranged from 51 to 122%. Dos Bocas Reservoir had the least seasonal variability in mean biomass (51%) followed by Guajataca Reservoir (CV=68%). Conversely, biomass was most variable in Carite Reservoir (122%) followed by Lucchetti Reservoir (CV=116%).

Neal & Prchalová (2012) reported that threadfin shad density varied across spatiotemporal gradients in tropical reservoirs, with high between-reservoir variability (more information on

Table 1. Threadfin shad biomass estimates for four Puerto Rico reservoirs from spring 2010 to winter 2011. Mean standing biomass (g/1,000m^3) ± one *SE* for each depth stratum by reservoir section, and overall biomass estimates (kg/ha) by season and year are presented. Carite Reservoir was added to the sampling efforts in summer 2010. The two upper arms of Dos Bocas Reservoir were sampled independently, but the average for each depth stratum is presented

season	longitudinal section	depth strata (m)	mean biomass by depth strata (g/1,000 m^3)			
			Dos Bocas[a]	Guajataca	Lucchetti	Carite
spring	upper	0–3	825.5±205.7	371±71.5	673.9±76.8	n/a
		3–6	326.6±107.8	18.8±4.8	32.8±13.1	n/a
	lower	0–3	567.2±249.6	139.1±51.0	573.5±114.1	n/a
		3–6	206.1±139.6	11±5.6	110.3±21.2	n/a
		6–9	21.9±4.3	77.9±30.0	1.5±0.3	n/a
spring estimated biomass		kg/ha	35.1±5.0	11.1±2.4	25.1±5.2	n/a
summer	upper	0–3	428.2±156.7	129.1±38.6	113.3±41.5	6.4±2.6
		3–6	62.8±10.5	142.8±23.5	4.8±2.3	0.4±0.4
	lower	0–3	624.5±46.0	43.6±13.3	375.3±24.9	1.6±1.5
		3–6	80.5±25.9	2.2±0.7	24.5±16.4	0.0±0.0
		6–9	40.2±16.5	2.4±1.0	1.1±1.1	0.0±0.1
summer estimated biomass		kg/ha	22.3±4.2	5.8±1.1	9.3±2.5	0.2±0.0
fall	upper	0–3	36.6±11.2	85.8±8.3	254.3±96.6	19.9±5.4
		3–6	31.1±7.5	82.4±13.6	7.6±2.9	30.2±18.8
	lower	0–3	262.7±118.7	75.9±23.8	140.4±3.2	96.3±34.9
		3–6	55.8±13.7	4.5±3.1	11.1±4.7	96.1±0.1
		6–9	30.1±11.5	0.1±0.1	2.2±1.4	18±2.6
fall estimated biomass		kg/ha	7.5±1.7	4.5±0.7	7.5±1.8	4.7±0.6
winter	upper	0–3	366.9±55.8	296±40.4	2,053.8±837.4	14.7±2.9
		3–6	103.1±30.5	527.8±100.5	694.2±125.7	14.9±1.1
	lower	0–3	1,204.5±398.4	195.8±56.0	1,020.4±181.6	11.7±3.7
		3–6	67.1±11.4	83.5±62.4	961.9±307.8	13.6±1.2
		6–9	13.4±1.2	14.3±3.8	97.3±20.5	1.3±0.6
winter estimated biomass		kg/ha	31.6±8.0	20.1 ±3.2	86.9±11.4	1.0±0.1
annual mean biomass		kg/ha	24.1±6.2	10.4±3.6	32.2±18.7	2.0±1.2

spatiotemporal pattern can be found in that study itself). Not surprisingly, threadfin shad biomass varied similarly across reservoirs in the current study. The observed variability was likely due to the relationship of primary productivity and hydraulic retention time. Carvajal-Zamora (1979) noted that Carite was one of the least productive reservoirs in Puerto Rico, which was reflected by threadfin shad biomass reported here. Furthermore, when analyzed for phosphate (PO_4) and nitrate (NO_3) content (Kröger et al. 2010), Dos Bocas exhibited the highest nutrient levels (PO_4=0.057 0.012 ppm; NO_3=0.378±0.105 ppm), followed by Lucchetti Reservoir (PO_4=0.017±0.000 ppm; NO_3=0.080±0.004 ppm), and Guajataca Reservoir (PO_4=0.014±0.002; NO_3=0.050±0.002 ppm). Water quality data were not available for Carite Reservoir. Neal and Prchalová (2012) reported hydraulic retention times for these reservoirs to vary considerably, ranging from 16 (Dos Bocas Reservoir) to 453 days (Guajataca Reservoir). This suggests that although Dos Bocas Reservoir is considerably more nutrient-rich than the other reservoirs, these nutrients may be flushing out of the reservoir before they are fully utilized by biota (Kennedy & Walker 1990). Carite Reservoir and Lucchetti Reservoir were intermediate (312 d and 231 d, respectively), but would likely be more similar to Guajataca Reservoir.

Threadfin shad reproduction and recruitment have been shown to vary widely across the annual cycle in Puerto Rico (Stancil et al. 1997, Neal & Prchalová 2012), and this episodic production combined with rapid growth and high mortality commonly produces peaks and troughs in estimated biomass across seasons. This variability has both biological and management consequences. Biologically, seasonal variation in threadfin shad biomass implies that prey availability to sport fish also will vary seasonally, with potential effects on sport fish growth, survival, and recruitment. In

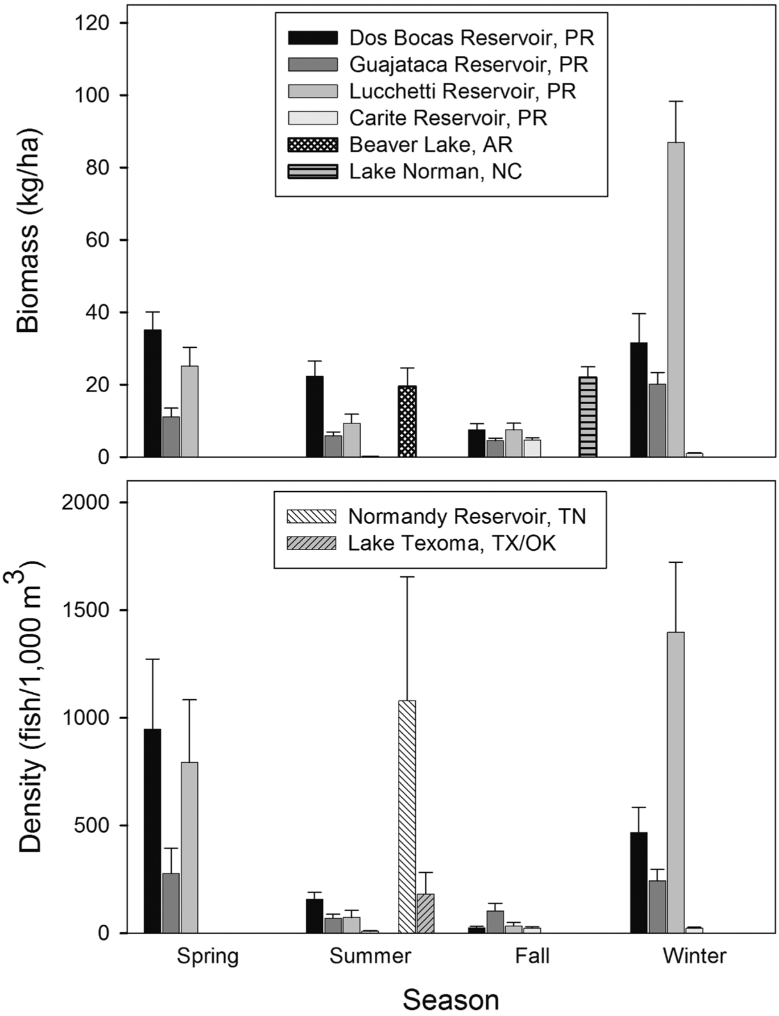

Fig. 1. Comparison of mean seasonal biomass (top; kg/ha) and density (bottom; fish/1,000 m^3) of threadfin shad among four Puerto Rico reservoirs and four temperate reservoirs. Puerto Rico systems from darkest to lightest are Dos Bocas, Guajataca, Lucchetti, and Carite (this study); temperate reservoirs are Lake Norman, NC (biomass; Siler 1986), Beaver Lake, AR (biomass; Rainwater & Houser 1982, Fourt et al. 2002), Normandy Reservoir, TN (density; Sammons et al. 1998), and Lake Texoma, TX/OK (density; Michaletz et al. 1995). Error bars represent one *SE*. Legend for PR reservoirs is valid for both biomass and density plots.

Table 2. Comparison of threadfin shad biomass (kg/ha) and density (fish/1,000 m^3) estimates among temperate and tropical reservoirs. Unless otherwise noted, values are displayed with ± one *SE*. Sampling methods used were cove rotenone (CR), frame trawl (FT), neuston net (NN) and Tucker trawl (TT). Superscripts description: a – *SE* presented for annual means in Puerto Rico represents variability across seasons, b – these data were presented with 95% *CI*, not with *SE*, c – no measure of variability was provide in the source publication, and d – these data were collected from a reservoir that was subject to frequent winterkill of threadfin shad

reservoir/site (year)	seasonal estimate				annual	gear	source
	spring	summer	fall	winter	mean		
Puerto Rico	mean biomass estimates (kg/ha)						
Dos Bocas Reservoir (2010–2011)	35.1±5.0	22.3±4.2	7.5±1.7	31.6±8.0	24.1±6.2[a]	FT	this study
Guajataca Reservoir (2010–2011)	11.1±2.4	5.8±1.1	4.5±0.7	20.1±3.2	10.4±3.6[a]	FT	this study
Lucchetti Reservoir (2010–2011)	25.1±5.2	9.3±2.5	7.5±18	86.9±11.4	32.2±18.7[a]	FT	this study
Carite Reservoir (2010–2011)		0.2±0.0	4.7±0.6	1.0±0.1	2.0±1.2[a]	FT	this study
North Carolina							
Lake Norman (1979)			16.5±3.5[b]			TT	Siler (1986)
Lake Norman (1980)			26.3±5.8[b]			TT	Siler (1986)
Lake Norman (1981)			23.3±4.9[b]			TT	Siler (1986)
Arkansas							
Beaver Lake (1966)		5.3[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1967)		0.0[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1968)		23.1[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1969)		48.3[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1970)		0.6[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1971)		20.7[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1972)		30.4[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1973)		7.5[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1974)		81.5[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1975)		58.3[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1976)		14.2[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1979)		0.1[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1980)		0.2[c]				CR	Rainwater & Houser (1982)
Beaver Lake (1995)		13.1[c]				CR	Fourt et al. (2002)
Beaver Lake (1996)		4.2[c]				CR	Fourt et al. (2002)
Beaver Lake (1997)		16.8[c]				CR	Fourt et al. (2002)
Beaver Lake (1998)		29.2[c]				CR	Fourt et al. (2002)
Beaver Lake (1999)		4.0[c]				CR	Fourt et al. (2002)
Beaver Lake (2000)		12.5[c]				CR	Fourt et al. (2002)

Table 2. (continued)

reservoir/site (year)	seasonal estimate				annual	gear	source
	spring	summer	fall	winter	mean		
Puerto Rico	mean density estimates (fish/1,000 m^3)						
Dos Bocas Reservoir (2010–2011)	947.7±325.3	157.8±32.4	24.9±6.9	467.9± 116.2	399.6±204.9^{a}	FT	this study
Guajataca Reservoir (2010–2011)	277.2±116.8	69.9±17.9	103.4±35.6	242.6± 53.3	173.2±51.0^{a}	FT	this study
Lucchetti Reservoir (2010–2011)	792.1±291.1	72.3±33.4	32.9±16.9	1,397.0±325.4	573.5±325.3^{a}	FT	this study
Carite Reservoir (2010–2011)		8.4±4.1	22.6±7.8	22.3±5.0	25.1±9.0^{a}	FT	this study
Tennessee							
Normandy Reservoir (1992)		237^{c,d}				NN	Sammons et al. (1998)
Normandy Reservoir (1993)		634^{c,d}				NN	Sammons et al. (1998)
Normandy Reservoir (1994)		3,296^{c,d}				NN	Sammons et al. (1998)
Normandy Reservoir (1995)		178^{c,d}				NN	Sammons et al. (1998)
Normandy Reservoir (1996)		1,052^{c,d}				NN	Sammons et al. (1998)
Texas/Oklahoma							
Lake Texoma/Central Pool (1991)		50.4±4.0				FT	Michaletz et al. (1995)
Lake Texoma/Little Mineral (1991)		148.8±26.9				FT	Michaletz et al. (1995)
Lake Texoma/Big Mineral (1991)		548.1±83.5				FT	Michaletz et al. (1995)
Lake Texoma/Central Pool (1991)		44.6±5.5				TT	Michaletz et al. (1995)
Lake Texoma/Little Mineral (1991)		116.5±24.2				TT	Michaletz et al. (1995)
Lake Texoma/Big Mineral (1991)		565±206.2				TT	Michaletz et al. (1995)

terms of management, seasonal variability of key prey species can affect many factors, including the success of supplemental stocking of sport fishes and the utility of fish sampling designs.

Comparison of Puerto Rico to US Reservoirs

A review of the literature confirmed that data on threadfin shad populations are limited, as only five studies on four reservoirs were found to have quantified adult threadfin shad biomass or density. These studies examined populations in Arkansas (Rainwater & Houser 1982, Fourt et al. 2002), North Carolina (Siler 1986), Tennessee (Sammons et al. 1998), and Texas/Oklahoma (Michaletz et al. 1995) (Table 2). Biomass estimates in Beaver Lake, Arkansas ranged from 0.0 to 81.5 kg/ha (median=13.1 kg/ha, mean=19.8 kg/ha). Biomass estimates in Lake Norman, North Carolina ranged from 16.3 to 26.3 kg/ha, with median value of 23.3 kg/ha and mean of 22.0 kg/ha. Density estimates in Normandy Reservoir, Tennessee ranged from 178 to 3,296 fish/1,000 m^3, with median value of 634 fish/1,000 m^3 and mean of 1,079 fish/1,000 m^3. Density estimates in Lake Texoma, Texas/Oklahoma ranged from 44.6 to 565.0 fish/1,000 m^3, with median value of 132.7 fish/1,000 m^3 and mean of 245.6 fish/1,000 m^3.

All threadfin shad biomass or density estimates found in the literature for temperate reservoirs were based on a single sampling event per year. All estimates also were generated during summer months except for Lake Norman, North Carolina, which used fall sampling. If temperate reservoirs are subject to the same extreme seasonal variability as observed in tropical reservoirs, these instantaneous estimates of biomass will not provide a complete picture of threadfin shad populations. For the purposes of comparison, it was assumed that seasonal patterns in temperate reservoirs were similar in pattern and magnitude to tropical reservoirs, and that seasonal estimates from the continental USA can be compared to the appropriate seasonal data from Puerto Rico.

Comparisons of biomass estimates from Puerto Rico were possible with two temperate reservoirs (Fig. 1). Beaver Lake, Arkansas, exhibited numerically greater mean biomass across its sampling history than all Puerto Rico reservoirs except Dos Bocas Reservoir during summer. The Dos Bocas Reservoir summer mean (22.3 kg/ha) was slightly greater than the Beaver Lake mean (19.5 kg/ha), but was almost one quarter of the maximum observed biomass in Beaver Lake (81.5 kg/ha). The other Puerto Rico reservoirs displayed summer biomass estimates that were, at most, only about half of the Beaver Lake mean biomass.

The Beaver Lake samples were collected using cove rotenone, while Puerto Rico estimates were derived from open water trawls. Several studies have shown the difficulties of extrapolating cove rotenone data to open water (Hayne et al. 1967, Summers & Axon 1980, Davies & Shelton 1983). Furthermore, threadfin shad have been observed to be denser in open-water habitats than in littoral-zone habitats, which suggested that the Beaver Lake cove rotenone data may have underestimated reservoir-wide biomass. Perhaps a more valid comparison can be made between the Puerto Rico frame trawl estimates and the Tucker trawl estimates from Lake Norman, North Carolina (Siler 1986). These samples were collected in the fall and averaged 22.0 kg/ha across three years. When compared to the fall Puerto Rico data, the Lake Norman biomass estimates were 290–490% greater than each tropical reservoir.

Two temperate reservoirs reported seasonal threadfin shad density estimates that could be compared to season densities in Puerto Rico. Normandy Reservoir, Tennessee, reported a mean density of 1,079 fish/1,000 m^3 during summer across 5 sampling years. This mean density was considerably greater than the summer densities found in Puerto Rico reservoirs, which ranged from 8.4 to 157.8 fish/1,000 m^3. The Normandy Reservoir data also were collected using cove rotenone sampling and subject to the same biases previously described. Furthermore, this reservoir was subject to frequent episodes of threadfin shad winterkill. For these reasons, the Normandy Reservoir data also may have underestimated reservoir-wide biomass carrying capacity.

Conversely, data from Lake Texoma, Texas/Oklahoma, were collected using similar sampling gear as this Puerto Rico study, so direct within-season comparison should be valid. Threadfin shad density estimates from Lake Texoma averaged 245.6 fish/1,000 m^3 during summer 1991 across three different reservoir arms using two types of trawls (frame trawl and Tucker trawl; Michaletz et al. 1995). Lake Texoma displayed considerable spatial heterogeneity, with spatially explicit estimates ranging 44.6–565 fish/1,000 m^3 depending on the embayment sampled. All Puerto Rico systems displayed summer threadfin shad densities less than the mean Lake Texoma threadfin shad density, but three reservoirs were within the range of estimates reported for Lake Texoma. Carite Reservoir, however, had considerably lower threadfin shad density than all Lake Texoma mean estimates.

The comparisons presented have potential limitations. One confounding issue is that the sampling gears varied, and similar gears were deployed in a variety of ways. This consideration is especially true for sampling depth. In the Puerto Rico study, all depths between the surface and 9 m were sampled systematically and each depth was accounted for in the calculation of threadfin shad densities and biomasses. The Lake Norman study indicated that multiple depths were sampled, but did not provide detailed descriptions on the actual depths sampled or how depth was factored into estimates. The Lake Texoma trawling study similarly sampled from the surface to depths of 7 m, but did not provide a description of shad densities by depth.

The comparison of Puerto Rico and temperate reservoir estimates is further confounded by the fact that threadfin shad are the sole pelagic herring (Clupeidae) species in Puerto Rico, but are found in conjunction with other herring species in the comparison lakes. This is often why threadfin shad density or biomass is not estimated independently in temperate reservoirs (e.g., Taylor et al. 2005). Instead, species of the family Clupeidae are often estimated jointly, yielding estimates of "shad" or "forage fishes" that are not directly comparable. It is unknown if the co-existence of threadfin shad with other species such as gizzard shad and alewife (*Alosa pseudoharengus*) will result in niche partitioning and compensatory decrease in density and biomass. A number of studies have suggested that the presence of threadfin shad can cause displacement of gizzard shad in reservoir systems (Noble 1981, Shelton et al. 1982, Stiefvater & Malvestuto 1987). Sammons with colleagues (1998) reported that catch of gizzard shad larvae was inversely related to biomass and density of adult threadfin shad in Normandy Reservoir, suggesting that the carrying capacities of these two species were not mutually exclusive. Furthermore, Armstrong and colleagues (1998) concluded that larval gizzard shad and threadfin shad are similar relative to gape morphology and feeding ecology, and thus, direct competition is likely.

If the presence of other Clupeids does indeed reduce a reservoir carrying capacity for threadfin shad, it is arguable that the threadfin shad biomass in Puerto Rico and other reservoirs that do not contain additional Clupeid species should be greater than in reservoirs containing multiple Clupeid species. This was not the case, as most Puerto Rico reservoirs displayed comparatively less biomass or density than temperate reservoirs. However, Guest and colleagues (1990) did not find a decrease in threadfin shad biomass when gizzard shad were introduced in small ponds, which suggested that the ecological displacement may be one-way.

All four reservoirs in Puerto Rico are generally considered mesotrophic to eutrophic (Carvajal--Zamora 1979), and should be similar to the temperate reservoirs in trophic status. For example, Lake Norman, North Carolina, has been classified as slightly eutrophic (EPA 1975) and Normandy Reservoir, Tennessee, is classified as eutrophic (Sammons et al. 1998). Lake Texoma has been classified as eutrophic overall (EPA 1977, Franks et al. 2001), with individual reaches ranging mesotrophic to hypereutrophic (Sager et al. 2011). Beaver Lake, Arkansas, is generally less productive, with the eutrophic conditions in the headwaters (Haggard et al. 1999) quickly declining to oligotrophic conditions near the dam (ADPCE 1992). Thus, Puerto Rico reservoirs were within the range of trophic states of the temperate reservoirs, and should be capable of producing comparable threadfin shad populations.

In general, most of the Puerto Rico reservoirs sampled in this study displayed threadfin shad populations that were fewer by number and weight than the temperate reservoirs used for comparison. Though the comparisons between these systems must be approached cautiously, the implications of potentially reduced threadfin shad availability in Puerto Rico are significant, particularly in terms of sport fish management. Managers of these reservoirs have historically followed management schemes created for temperate reservoirs (e.g., Neal et al. 2008), yet these systems may behave less like temperate reservoirs than previously thought. If threadfin shad populations in Puerto Rico are not comparable to those in temperate systems, then it is unreasonable to expect sport fish populations to mirror reservoirs in the southern USA.

Neal & Prchalová (2012) first reported that threadfin shad populations in the USA and elsewhere may be understudied and more poorly understood than previously thought. The authors found only five instances in the literature where threadfin shad biomass or density was estimated for aquatic systems, and only a handful of gizzard shad estimates (e.g., Michaletz et al. 1995, Schramm & Pugh 2005, Schaus et al. 1997, 2002). Many of these estimates were based on rotenone sampling, which can be considerably biased (Hayne et al. 1967, Summers & Axon 1980, Davies & Shelton 1983). The Lake Texoma series of studies, popularly known as the Shad-a-thon and overviewed by Boxrucker and colleagues (1995), was a major step forward in sampling shad in southern US reservoirs. However, although sampling during that effort and the few subsequent studies have used gears that are less biased, sampling in these studies has always been conducted in a single season. Data from Puerto Rico reservoirs revealed that tropical threadfin shad populations display marked changes seasonally, with changes in biomass of up to 2,400 % within a 3-month sampling window. If similar patterns are present in temperate reservoirs, the single instantaneous measures of shad biomass or density would have limited utility in supporting fisheries management decisions.

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