

Reproductive and Feeding Characteristics of Threadfin Shad in a Puerto Rico Reservoir

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Abstract: Although threadfin shad (*Dorosoma petenense*) have been widely introduced as forage fish, little is known about their natural history in tropical reservoirs. Gonadosomatic index (GSI) analysis of threadfin shad from Lucchetti Reservoir, Puerto Rico, indicated that most spawning occurred from January to June and again in October, but some spawning occurred year-round, except from mid-August to mid-September. Aging of sagittal otoliths indicated that total length (TL) increased with age ($r^2 = 0.36$). Maximum length was 86 mm TL ($N = 2,002$) and maximum age was 141 days ($N = 124$). Hatch date distribution corroborated GSI data regarding spawning periodicity. Diet analysis indicated that detritus and insects were the primary foods. Inconsistencies in threadfin shad dynamics among reservoirs suggest that system-level approaches should be employed in predator-prey management when threadfin shad comprise an important part of the prey base.

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Stocking forage fish to enhance sport fishing is a common reservoir management practice throughout North America (Noble 1981). Threadfin shad are often used in management of reservoirs (DeVries and Stein 1990) and have been introduced into reservoirs far beyond their native range, which encompasses portions of the Gulf of Mexico drainage from northern Guatemala to Florida (Carlander 1969). Included in the range extension of threadfin shad has been their introduction into Puerto Rican reservoirs (Erdman 1984). The effects of threadfin shad on sport fisheries are diverse and management recommendations disparate (e.g., Noble 1981, DeVries and Stein 1990). Therefore, predicting the role of threadfin shad populations

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and their effects on biotic communities based on previous studies may be inadequate.

Although the natural history of threadfin shad in temperate waters is well described, little is known about populations in tropical reservoirs. Irwin and Bettoli (1995) found that clupeid reproduction could not be predicted based on latitude, so system-specific examination should occur. Reviews of threadfin shad studies from North America indicate that spawning occurs over a wide range of temperatures, and spawning seasons vary both in time of year and duration (Carlander 1969, Jenkins and Burkhead 1994). Likewise, diet studies indicate that threadfin shad consume a wide variety of food and are capable of planktivory and benthivory (e.g., Haskell 1959, Baker and Schmitz 1971).

During a 3-year study of sport fish recruitment in Lucchetti Reservoir, Puerto Rico (Churchill et al. 1995), threadfin shad were continually represented in forage base assessments and comprised a significant proportion of the diet of juvenile largemouth bass (*Micropterus salmoides*) (Alicea 1995). We wanted to learn more about the reproduction, growth, and diet of threadfin shad to better understand trophic relationships so we could make more-informed management decisions.

Our objectives were to determine 1) the spawning season and size at maturation of threadfin shad by analyzing gonads, 2) hatching periodicity, longevity, growth rates, and age at maturation from length and age data, and 3) the primary foods of threadfin shad and trends related to variations in size and season.

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Methods

Lucchetti Reservoir, an 108-ha impoundment located in the mountains of southwestern Puerto Rico, was created when a dam impounding the Yauco River and 3 smaller tributaries was completed in 1952. Mean depth is 11.6 m and maximum depth is 54.3 m (Pérez-Santos 1994). The reservoir is considered mesotrophic (Pérez-Santos 1994) to eutrophic (Puerto Rico Environ. Quality Board 1992). Surface water temperatures ranged from 24 to 30 C during the 3-year study and water level fluctuated up to 17 m annually (Churchill et al. 1995). Lucchetti Reservoir has traditionally been popular for recreational fishing (Corujo-Flores 1989) with largemouth bass as the principal sport fish. Threadfin shad were first stocked in Puerto Rico in 1963 (Erdman 1984) and were introduced into Lucchetti Reservoir during the mid 1980s.

Nighttime electrofishing was conducted using a 260-volt, direct current, hand-held probe (Jackson and Noble 1995) at 3-week intervals from March 1992 to December 1994 to assess the littoral fish community. Five sites, representative of the littoral

habitat available and individually comprising approximately 5% of the shoreline at conservation pool, were sampled throughout the 3-year period (Churchill et al. 1995). Although no attempt was made to collect shad as a quantitatively-representative part of the littoral community due to their schooling behavior and attraction to light, a sample target of 10 shad was established at each site for a target of 50 shad per sampling period. Shad were placed on ice in the field and subsequently pooled by collection date and stored in alcohol.

Excess alcohol was blotted off prior to weighing individual shad to the nearest 0.1 g and measuring total length to the nearest millimeter. After shad were weighed, gonads, sagittal otoliths, and digestive tracts were removed. Excess alcohol was blotted off gonads and weight determined to the nearest 0.1 g. We determined sex by examining gonads with a dissecting microscope and quantified sexual development using GSI defined as $(\text{gonad weight} / \text{total weight}) \times 100 \%$.

We analyzed temporal trends in reproductive state by combining data from shad collected in 1993 and 1994 and grouping the data by month. To examine the relationship between total length and GSI, we grouped shad into 5-mm length classes. Due to insufficient samples for 1992, only data from 1993 and 1994 were used in reproductive analysis.

Otoliths were stored dry and prepared for aging using techniques described by Secor et al. (1991). Otoliths were embedded in epoxide resin blocks and sectioned in the transverse plane (1-mm thick sections) using an Isomet saw equipped with diamond blades. Sections were glued onto pieces of microscope slides and ground to the nucleus on both sides using 20-, 1-, and 0.3- μ grit on a sanding wheel.

Daily otolith rings were counted in the dorsal field 4 times each by 2 readers at a magnification of 400 X or 1,000 X using a compound microscope. We averaged the median values of each counter's 4 readings and analyzed agreement between readers using CVs. If the CV was $\geq 10\%$, the first set of readings was disregarded and the otolith was read 4 additional times by each reader. If the CV was still $\geq 10\%$, the otolith was discarded from further consideration. To determine age from time of hatching, we added 4 days to the mean daily ring count based on findings by Davis et al. (1985) and Valido (1976) regarding ring formation in early life history stages. Hatching dates for each shad were estimated by subtracting age from collection date.

Initially there were 129 readable otoliths; 5 otoliths were discarded after the second set of readings, yielding 124 acceptable otoliths. Otoliths from 116 shad 22–56 mm TL (mean 40.6 mm) collected throughout the sampling period were selected to determine hatch date distribution. At least 8 of these shad were collected during each calendar month. Otoliths from 8 shad ≥ 70 mm TL collected during 8 different sampling events were aged additionally and included in determination of longevity and growth. We used regression analysis to determine the precision of our age estimates.

We analyzed gut contents of 428 threadfin shad collected from 1992 to 1994. A dissecting microscope was used to examine gizzards, where most food items occurred. Contents were classified as detritus, insects, vegetation, bivalves, and empty. Food habits were quantified using the frequency of occurrence of each category.

Results

We collected 2,002 threadfin shad from March 1992 to December 1994. Total lengths ranged from 21 to 86 mm with a mean of 52 mm (Fig. 1). Weights ranged from 0.1 to 6.1 g with a mean of 1.3 g.

Reproduction

We examined gonads of 681 shad from 1993 ($N = 316$) and 1994 ($N = 365$); of these, sex was distinguishable for 514 fish (75.5%). There were 344 females and 170 males, yielding a 2:1 sex ratio. Eggs were visible with a dissecting microscope in females as small as 29 mm TL; only 2 spent females were encountered.

GSI values were calculated for 344 females and 170 males from 1993 and 1994. With the exception of 1 fish (42 mm TL), no females < 45 mm TL had GSI values > 2.5% (Fig. 2). Therefore, for purposes of analysis, we established 45 mm TL as the minimum length and 2.5% as the minimum GSI value for female maturity.

GSI values varied among females of the same size for each year and within each sample. Shad of the same size class collected together varied markedly in GSI levels; small shad often had higher GSI values than larger ones from the same sample. Some large females (> 70 mm TL) had GSI values < 2.5% but had developing ovaries, while smaller females (< 50 mm TL) had GSI values > 8.0%. Differences in GSI levels between shad of different sizes were not necessarily due to when they were collected, but reflected the high variability in GSI levels throughout the sampling period.

Mean GSI values and percent of females with GSI values $\geq 2.5\%$ gradually increased up to the 60- to 64-mm length class (mean GSI = 5.2%; 62% with GSIs \geq

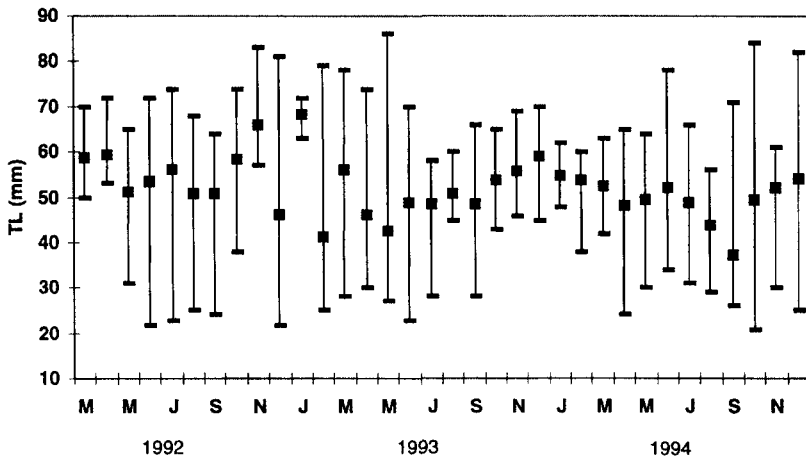


Figure 1. Monthly mean total lengths (TL) and length ranges for threadfin shad collected by shoreline electrofishing, Lucchetti Reservoir, Puerto Rico, 1992–1994.

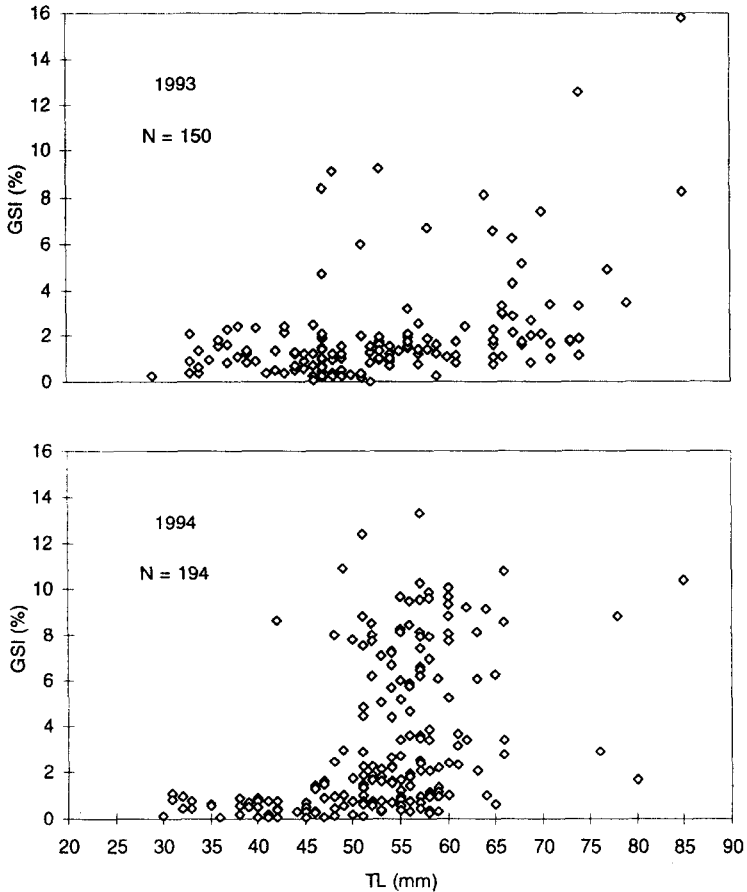


Figure 2. GSI values for female threadfin shad as a function of total length, Lucchetti Reservoir, Puerto Rico, 1993 and 1994.

2.5%) before declining in the next 2.5-mm length classes. Females ≥ 75 mm TL ($N = 8$) had the highest mean GSIs (7.0%) and percent GSIs $\geq 2.5\%$ (88%).

One or more females with a GSI value $\geq 3.5\%$ were present in every month except August. Mean GSI values and percent GSIs $\geq 2.5\%$ were highest from January to June and in October (Fig. 3). There was a substantial decrease in mean GSI from June to July, coupled with a decrease in percent GSIs $\geq 2.5\%$; mean GSI decreased from 4.3% to 0.9% while percent GSIs $\geq 2.5\%$ decreased from 54% to 3%. Maximum GSI values from January to June ranged from 8.1% to 15.8%. Maximum GSI values for July–December were $< 3.8\%$ for each month except September (8.5%) and October (10.8%).

Male GSI values followed the same trends as female GSIs (Fig. 3). Only males ≥ 40 mm TL were used to analyze monthly trends and we established 1.0% as the minimum GSI value for maturity. Monthly mean GSI values for males ranged from

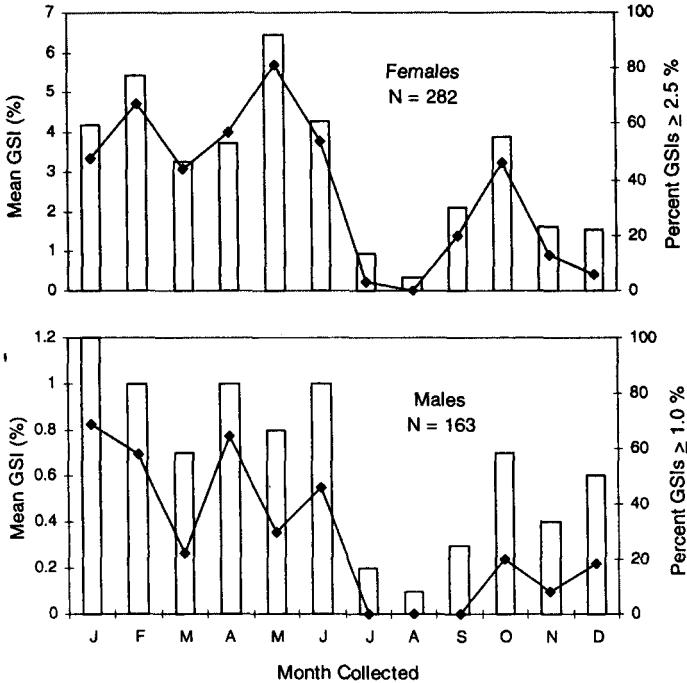


Figure 3. Monthly trends in GSI values of female (≥ 45 mm TL) and male (≥ 40 mm TL) threadfin shad, Lucchetti Reservoir, Puerto Rico, 1993 and 1994. Mean GSI values represented by columns, percent mature values by lines.

0.1% in August to 1.2% in January. Values were highest from January to June with monthly means ranging from 0.7% to 1.2% and percent GSIs $\geq 1.0\%$ ranging from 22% to 69%. For the remainder of the year, mean GSI value and percent GSIs $\geq 1.0\%$ were highest for October (0.7% and 20%, respectively).

Aging

Agreement between the 2 readers' age estimates was strong. Average CV among multiple readings for 124 otoliths was 2.5% while the mean difference between the 2 readers' median counts of individual otoliths was 3.3 days.

Of 116 shad aged, 5 or more were hatched in each month of the year and most months produced newly-hatched shad in more than 1 year (Table 1). However, no hatch dates were detected between mid-August and mid-September, corresponding to the low GSI period (Fig. 3).

In an attempt to establish confidence in the daily aging process, we examined the relationship between total length and calculated age in days. The equation was significant ($r^2 = 0.36$; $P < 0.01$) and indicated a mean growth rate of 0.38 mm/day (Fig. 4). The 8 largest shad (≥ 70 mm TL) had faster mean growth rates (0.65 mm/day) and reduced the r^2 value. Minimum age at maturity for females (45 mm TL)

Table 1. Hatch date distribution for threadfin shad collected, from March 1992–December 1994, Lucchetti Reservoir, Puerto Rico.

Month	1991	1992	1993	1994	Total
Jan			11	2	13
Feb			5	7	12
Mar			6	5	11
Apr		3	3	4	10
May				7	7
Jun				16	16
Jul			1	5	6
Aug				5	5
Sep		3	5	2	10
Oct		3	4	2	9
Nov	3	1	1		5
Dec		9	3		12
Total	3	19	39	55	116

was estimated to be 106 days using the regression equation. Growth rates did not differ ($P = 0.51$) between females (0.44 mm/day; $N = 47$) and males (0.46 mm/day; $N = 17$). The 2 oldest shad (a 48-mm male and an 80-mm female) were only 141 days, indicating a very short life span.

Diet

Most shad gizzards contained food; maximum occurrence of empty gizzards was 7% in 1994 (Table 2). Annual frequency of occurrence for each year ranged from

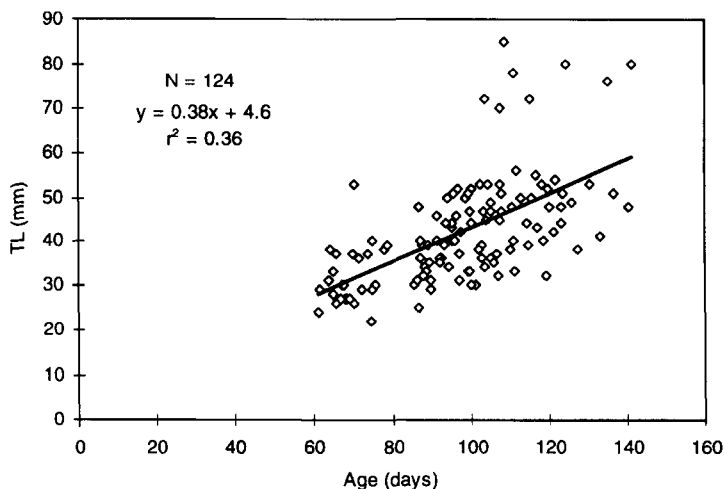


Figure 4. Relation between total length and age determined from otoliths for threadfin shad, Lucchetti Reservoir, Puerto Rico, 1992–1994.

Table 2. Frequency of occurrence of food items in threadfin shad gizzards, March 1992–1994, Lucchetti Reservoir, Puerto Rico. Winter = January–March; Spring = April–June; Summer = July–September; Fall = October–December.

Collection period	N	Frequency of occurrence				
		Empty	Detritus	Insects	Vegetation	Bivalves
Winter 1992	13		0.54	0.92	0.15	
Spring 1992	12		0.92	0.25		
Summer 1992	24		0.83	0.17		
Fall 1992	31	0.03	0.94	0.06		0.03
Winter 1993	59	0.02	0.95	0.07		
Spring 1993	61	0.02	0.93	0.05		
Summer 1993	0					
Fall 1993	25		0.40	0.76		
Winter 1994	75	0.07	0.75	0.29	0.01	
Spring 1994	57	0.04	0.75	0.23		
Summer 1994	6		1.00			
Fall 1994	65	0.12	0.45	0.55		0.06
All dates	428	0.04	0.76	0.28	0.01	0.01

0.66 to 0.85 for detritus and 0.18 to 0.35 for insects. Annual frequency of occurrence for all other categories was ≤ 0.03 for each year. Detritus occurred most frequently on 21 of 27 sample dates; insects occurred most often in the remaining 6 samples. Detritus occurred most frequently in all seasons except winter 1992 and fall 1993 and 1994, when insects occurred more frequently (Table 2). Frequency of occurrence values for detritus were ≥ 0.40 for all samples, while values for insects ranged from 0.00 to 0.92. Insect taxa, in decreasing frequency, were dipterans (mostly chironomids), unidentifiable winged insects, hemipterans, and hymenopterans. We did not detect any difference in diet related to shad size.

Discussion

Threadfin shad collected from Lucchetti Reservoir differed in many ways from those in temperate systems of the continental United States. Maximum total length was only 86 mm, much less than in the southeastern United States, where threadfin shad typically exceed 120 mm TL (Table 3). Small shad were collected throughout the majority of the sampling period, characteristic of an extended spawning season, and aging verified that shad were produced in every month. Shad in Lucchetti Reservoir consumed detritus and insects, which indicates benthic feeding, in contradiction with the majority of available literature.

Threadfin shad from Lucchetti Reservoir matured at a small size (45 mm TL) and a young age (106 days). Ten shad 42–50 mm TL had GSI values $\geq 2.5\%$ and 5 of these had GSIs $\geq 8.0\%$. Early maturation is probably due to continuous high water temperatures. Threadfin shad are best adapted to warm water temperatures while cold temperatures can cause winter kills in areas north of their native range (McLean et al. 1985). Most studies indicate that threadfin shad mature at a larger size and a

Table 3. Threadfin shad maximum age, maximum length, and spawning season characteristics.

Citation	Study site	Maximum age	Maximum TL	Spawning season
Baker and Schmitz (1971)	Bull Shoals Reservoir, Ark. Beaver Reservoir, Ark.		160 mm 150 mm	
Bryant and Houser (1969)	Bull Shoals Reservoir, Ark.	4 years	161 mm	
Davis and Foltz 9191	Jocassee Reservoir, S.C.	2 years	144 mm	
Heidinger and Imboden (1974)	Lake of Egypt, Ill.		144 mm	May–Aug
Irwin and Bettoli (1995)	Dale Hollow Reservoir, Tenn.		129 mm	May–Aug
Johnson (1970, 1971)	Salt River Reservoirs, Ariz.	4 years	174 mm	Apr–Jun
Lambou (1965)	Bogue Falaya, La. Clear Lake, La. Lake Bistineau, La.		203 mm 127 mm 114 mm	
McLean et al. (1985)	Watts Bar Reservoir, Tenn.		159 mm	
Swingle (1969)	ponds, Ala.			May–Jun
Present study	Lucchetti Reservoir, Puerto Rico	141 days	86 mm	year-round

later age than those from Lucchetti Reservoir (Carlander 1969, Jenkins and Burkhead 1994). However, there is limited evidence of threadfin shad maturing at sizes and ages comparable to the population from Lucchetti Reservoir. Johnson (1971) reported mature females as small as 49 mm in an Arizona reservoir. Heidinger and Imboden (1974) found female threadfin shad that were mature < 4 months after hatching in an Illinois reservoir.

GSI values indicated that most spawning occurred from January to June, but a secondary peak occurred in October. Females with high GSI values were collected in all months except August, indicating some spawning nearly year-round. Spawning seasons of threadfin shad in temperate systems do not exceed 4 months and occur in late spring and summer (Table 3). Spawning is regulated by water temperatures (Burns 1966, Irwin and Bettoli 1995) and usually occurs at 14–27 C (Carlander 1969, Jenkins and Burkhead 1994). Irwin and Bettoli (1995) reported that threadfin shad GSI values in a Tennessee reservoir were highest when surface water temperatures were 22–26 C; Swingle (1969) indicated that spawning began in May at 24.4 C. In Lucchetti Reservoir, surface temperatures ranged from 24 C in January to 30 C in July and August (Churchill et al. 1995). Therefore, water temperatures were high enough to support spawning year-round, but summer temperatures may have surpassed the optimal spawning range, causing spawning to subside.

Our GSI and hatch date distribution data gave similar results regarding spawning activity. Hatch date distribution indicated the presence of hatching, but did not indicate the proportion of the population hatching at a given time. If threadfin shad development is similar to that of gizzard shad (*D. cepedianum*) which hatch in 3 days at 19 C (Davis et al. 1985), spawning season and hatch date duration are practically the same. GSI data showed that each month except August had a female with a GSI value $\geq 3.5\%$. Hatch date distribution indicated that shad were hatched in each month of the year with only a 1-month gap between mid-August and mid-September.

Age estimates indicated that large shad from Lucchetti Reservoir were not older than smaller shad, but appeared instead to grow at faster rates. Age estimates for shad ≥ 70 mm were similar to estimates for shad ≤ 56 mm. Maximum age of threadfin shad in other systems can be as much as 4 years (Bryant and Houser 1969), but most do not reach 2 years (Johnson 1970, Davis and Foltz 1991). Berry et al. (1956) observed threadfin shad spawning mortality in 2 Florida lakes; similar mortality could account for the short life span of shad from Lucchetti Reservoir. Only 0.6% of the shad in our study had spent ovaries; all others had maturing ovaries and the eggs appeared to be at the same state of development. This could suggest that post-spawning mortality occurred, resulting in individuals spawning only once. However, without direct observation we could not determine if the act of spawning limited longevity.

Our study indicated that threadfin shad were benthic feeders that fed primarily on detritus and insects. Low incidence of empty stomachs suggested that food resources were available throughout the year. Gizzard contents are usually well masticated (Burns 1966), which may have inhibited our ability to identify some stomach contents. Zooplankton was absent from our diet samples, which is surprising based on research elsewhere. Although threadfin shad are usually considered planktivores, previous studies indicate that this assessment is not always accurate. Numerous studies have documented planktivory (e.g., Davis and Foltz 1991, DeVries et al. 1991), but there is also evidence for benthic feeding. In a lab study, Ingram and Ziebell (1983) demonstrated that threadfin shad would feed on individual chironomids in a sand substrate in the absence of daphnids. Haskell (1959) and Baker and Schmitz (1971) determined that threadfin shad fed on phytoplankton and zooplankton in the limnetic zone but also fed in the benthic zone. Darnell (1961), Baker and Schmitz (1971), and Hendricks and Noble (1979) documented detritivory by threadfin shad and Valido (1976) determined that threadfin shad in Guajataca Reservoir, Puerto Rico, fed on zooplankton and detritus.

Zooplankton abundance in Lucchetti Reservoir during our study was low and dominated by rotifers. Even at their highest densities, which approached 25 organisms per liter, Cladocera and Copepoda only contributed 13% and 32%, respectively, of the total number of zooplankters collected (Churchill et al. 1995). Low abundance of large-bodied zooplankton and low zooplankton species diversity for reservoirs throughout the tropics have been attributed to consistent high temperatures, predation from fish, and lack of suitable food in reservoirs dominated by blue-green algae (Fernando 1980, Collado et al. 1984). Therefore, factors in addition to predation by threadfin shad are likely responsible for low zooplankton densities in Lucchetti Reservoir. The lack of zooplankton in diets may affect shad condition and could account for their short life span and total length. However, other factors, such as temperature or top-down factors, could play more prominent roles. Due to the paucity of research in tropical reservoirs, it is difficult to discern the various influences of abiotic and biotic factors on the zooplankton community of Lucchetti Reservoir.

Several researchers have expressed concern that threadfin shad may compete with larval and juvenile sport fishes by impacting the zooplankton community. Threadfin shad have reduced zooplankton densities (Ziebell et al. 1986, Guest et al.

1990) and reduced the proportion of larger zooplankters (Prophet 1985). Our study did not include larval fish diets, so interaction between larval threadfin shad and larval sport fishes is uncertain. Although zooplankton was occasionally found in age-0 largemouth bass stomachs, insects and fish were much more common (Alicea 1995). Rapid growth rates of 1 mm/day of age-0 largemouth bass as well as diet analysis indicated that adequate food resources were available for largemouth bass in Lucchetti Reservoir and suggested that threadfin shad should not negatively impact largemouth bass recruitment.

Peaks in spawning activity of largemouth bass and threadfin shad in Lucchetti Reservoir were similar; thus the latter provided a ready source of prey for young bass. As for threadfin shad, adult largemouth bass GSI values were highest from late January to early June 1993 (Gran 1995), and highest abundance of young bass occurred in spring (Churchill et al. 1995). Although fecundity analysis and hatch date distribution indicated limited largemouth bass spawning activity in late October and early November 1993 (Churchill et al. 1995), substantial fall spawning of largemouth bass did not typically occur to take advantage of shad reproduction which peaked again in October. Fall stocking of fingerling largemouth bass is being considered to make better use of this shad forage base (Churchill et al. 1995).

Characteristics of threadfin shad from Lucchetti Reservoir are not representative of all Puerto Rican reservoirs. Although threadfin shad collected in most Puerto Rico reservoirs are small, males and females recently collected by daytime electrofishing from Cidra Reservoir, Puerto Rico, ranged from 133 to 160 mm TL and averaged 141 mm ($N = 19$). We aged 3 shad from Cidra Reservoir (134–142 mm TL) and found them to be 150–186 days old. Diet analysis indicated that threadfin shad from Cidra Reservoir fed on detritus but, in contrast to Lucchetti Reservoir shad, also consumed large numbers of cladocerans and ostracods. Due to our lack of zooplankton and fish community data from Cidra Reservoir and possible effects of daytime vs. nighttime electrofishing, we cannot draw any conclusions about the effects of threadfin shad on the zooplankton community and its subsequent effects on sport fishes. However, these incidental data indicate that threadfin shad in tropical reservoirs can reach sizes typical of the species in the continental United States. A more thorough study of Cidra Reservoir may increase our understanding of trophic relations in tropical reservoirs.

Based on our study and juvenile largemouth bass diet analysis (Alicea 1995), we feel that the threadfin shad population in Lucchetti Reservoir is beneficial to the largemouth bass population. To assess the suitability of a forage fish, Ney (1981) identified 6 criteria: prolific, stable in abundance, trophically efficient, vulnerable to predation, non-emigrating, innocuous. Threadfin shad from Lucchetti Reservoir spawned throughout most of the year, which maintained a stable population and provided piscivores with forage of a wide size range year-round. The small maximum size ensured that they did not grow too large to be preyed upon by largemouth bass. Analysis of food habits indicated that shad had a continual food supply, and did not compete with sport fishes for food resources in the size range analyzed. This information can help fisheries managers to better evaluate the appropriateness of threadfin

shad as a forage fish in similar systems as well as refine current management practices such as timing of supplemental stocking of game species.

Species are often introduced into areas outside of their native ranges without knowing how their reproduction, growth, diet, and other characteristics will change in a different environment and what effects the introduction will have on the fish community. Assessing the role of threadfin shad in the fish community of Lucchetti Reservoir based on information from the continental United States would have been a mistake. Our findings agreed with Irwin and Bettoli (1995) that clupeid reproductive strategies differ on the system level, and indicated flexible foraging by threadfin shad. To better understand impacts on predator-prey relationships between threadfin shad and sport fishes, threadfin shad populations must be evaluated for the environmental conditions present in the system of concern.

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