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Reproduction of a Landlocked Diadromous Fish Population: Bigmouth Sleepers *Gobiomorus dormitor* in a Reservoir in Puerto Rico

NATHAN M. BACHELER*[1], J. WESLEY NEAL[1,2], AND RICHARD L. NOBLE[1]

[1]*Department of Zoology Box 7617, North Carolina State University, Raleigh, NC 27695-7617.*
[2]*Present address: Aquaculture/Fisheries Center of Excellence, 1200 North University Drive, P.O. Box 4912, University of Arkansas at Pine Bluff, Pine Bluff, AR 71611, *Corresponding author: nate_bacheler@ncsu.edu*

ABSTRACT.—The bigmouth sleeper *Gobiomorus dormitor* is thought to be diadromous, requiring both fresh and saltwater at different stages of its life cycle. This unique life history has rendered them sensitive to hydrologic alterations, which are ubiquitous throughout their range and widespread in Puerto Rico. Previous research in Puerto Rico documented extirpations of bigmouth sleepers above dams without spillway discharge. However, a moderate population size of bigmouth sleepers in Carite Reservoir provides one glaring exception. Our goal was to determine if true landlocking, where fish have no hydrologic pathway into or out of the reservoir, was occurring in Carite Reservoir. We collected bigmouth sleepers between 33 and 399 mm TL, and estimated a total population size of 1,783 (± 921) in 2000 and 3,353 (± 1,788) the following year in Carite Reservoir. Bigmouth sleepers were ripe and mature in early summer. Moreover, absence of bigmouth sleepers in samples from La Plata Reservoir and the La Plata River downstream of Carite Reservoir supports the hypothesis of successful reproduction within Carite Reservoir. These results suggest that anthropogenic changes to a river have led to the landlocking of a normally diadromous species of fish and that the resultant landlocked population appears to be flourishing. This research adds to the understanding of Puerto Rico's most unique and important native freshwater fisheries, and contributes to the understanding of bigmouth sleeper biology and ecology across their geographic range.

KEYWORDS.—life cycle, fisheries, Carite, oocyte

INTRODUCTION

The bigmouth sleeper *Gobiomorus dormitor* (Eleotridae) is a poorly known fish found in tropical coastal habitats throughout the Caribbean and the southern portion of the Gulf of Mexico (Lindquist 1980; Gilmore 1992). Bigmouth sleepers are typically considered obligatorily diadromous, thought to require both fresh and salt water at different stages off its life cycle (Darnell 1962; Kelso 1965; Nordlie 1981; Winemiller and Ponwith 1998). Most of their lifetime is spent in freshwater rivers, but adults are thought to either undertake a migration to the sea for breeding purposes (i.e., catadromy), or instead let their eggs or larvae be carried to the ocean, after which juveniles then travel back upriver (i.e., amphidromy) (McDowall 1987). The unique hydrologic requirements of this species have rendered it sensitive to alterations in its habitat. As a consequence, Musick et al. (2000) suggested that bigmouth sleepers should be listed as a 'vulnerable' species.

There is one possible published exception to the paradigm of obligate diadromy in bigmouth sleepers. McKaye (1977) and McKaye et al. (1979) documented reproductive behavior, egg laying and brood guarding via direct observation in Lake Jíloa, Nicaragua, a natural freshwater lake, but made no comment as to the success of these reproductive attempts. The reasons for the presence of bigmouth sleepers in Lake Jíloa are therefore unknown; possible explanations include inputs of juveniles or adults into the lake by humans, introduction of larval fish by birds or other animals, or natural colonization and successful reproduction of the species in the lake.

In Puerto Rico, nearly all rivers contain barriers that appear to restrict the movement of native, riverine organisms (Benstead et al. 1999; Pringle 2001). A complete loss of native fish was documented in riv-

ers above barriers that lacked spillway discharge in Puerto Rico (Holmquist et al. 1998). A drastic reduction of native fish diversity and abundance above barriers with spillway discharge was also noted (Holmquist et al. 1998).

Yet on rare occasions bigmouth sleepers were collected in creel, gillnet, and electrofishing samples from 4 of 13 major manmade reservoirs in Puerto Rico (Rivera-Gonzales 1976; Corujo 1989; Churchill et al. 1995; Corujo 1999; Neal et al. 1999, 2001). However, catch rates of this species were extremely low in all reservoirs except Carite Reservoir, which supported a moderate population (Neal et al. 2001). This contrasts with Erdman (1984), who considered reservoirs in Puerto Rico unsuitable environments for native river fishes. Erdman (1984) found that, after the construction of the first four dams on the island, only three species of native fishes, the bigmouth sleeper, mountain mullet *Agonostomus monticola*, and river goby *Awaous tajasica*, were reported in reservoirs, and none established successfully reproducing populations (Erdman 1984). Today in Carite Reservoir, however, recreational fishermen frequently target, catch, and consume bigmouth sleepers.

Thus, the goal was to determine if true landlocking, where fish have no potential hydrologic pathway into or out of the reservoir, was indeed occurring in Carite Reservoir. We collected information on the biology and ecology of bigmouth sleepers in Carite Reservoir that would help understand their landlocking situation. In particular, we documented their population abundance and size structure, and we determined reproductive characteristics including age at maturation, reproductive seasonality, and oocyte size. We also examined hydrologic pathways out of the reservoir, as well as the fish communities downstream. With this research we intended to add to the understanding of Puerto Rico's most unique and important native freshwater fisheries, and contribute to the understanding of bigmouth sleeper biology and ecology across their geographic range.

Materials and Methods

Study site

Bigmouth sleepers were studied from January 2000 to October 2001 in Carite Reservoir, a 124-hectare impoundment located near the town of Cayey in mountainous south-central Puerto Rico (Fig. 1). The reservoir is situated at 18°04′N, 66°05′W at 543.6 m above sea level. Carite Reservoir was impounded in 1913 by construction of an earthen dam (Erdman 1984), and is the uppermost of a series of impoundments on the La Plata River. Carite Reservoir is one of the least productive reservoirs in Puerto Rico and catch rates of all fishes in the past have been consistently low (Neal et al. 2001). The water level fluctuated 4 m during this study, which is far less than the extreme fluctuations observed in other reservoirs on the island (e.g., up to 17 m annually in Lucchetti Reservoir; Neal et al. 1999).

Population biology.—We used the Lincoln-Petersen population model (± 95% CI) with the Chapman (1951) modification to estimate adult (i.e., > 200 mm total length (TL)) and total bigmouth sleeper population size in Carite Reservoir in the winters of 2000 and 2001. The estimator is:

$$\hat{N} = ((n_1 + 1)(n_2 + 1)/(m_2 + 1)) - 1$$

where $\hat{N}$ is the estimated population size, n_1 is the number of fish caught, marked, and released in the marking period, n_2 is the number of fish caught in the recapture period, and m_2 is the number of marked fish caught in the recapture period. The variance for $\hat{N}$ was estimated as:

FIG 1. Map of Puerto Rico showing the location of Carite Reservoir and its outflow stream, the La Plata River.

$$var\ (\hat{N}) = ((n_1 + 1)(n_2 + 1)\ (n_1 - m_2)\ (n_2 - m_2))/((m_2 + 1)^2\ (m_2 + 2))$$

(Seber 1970).

We collected fish by slowly (i.e., < 1 km h^{-1}) boom electrofishing the entire shoreline, using a boat-mounted boom shocker that delivered 3 – 4 A and 60 pps DC, during marking and recapture periods. Bigmouth sleepers strongly associate with shoreline habitats (N. Bacheler unpublished data); thus shoreline sampling with electrofishing gear was assumed representative of the entire Carite Reservoir population. All fish were measured (mm TL) during the marking and recapture period, and weights were recorded to the nearest g during the marking period only. During each marking period, bigmouth sleepers less than 200 mm TL received an anal fin mark and fish over 200 mm TL were marked with a pelvic fin clip. To differentiate between years, we used left pelvic fin clips in 2000 and right clips in 2001. Recapture sampling for each population estimate was conducted approximately 4 weeks following marking.

Reproduction.—To study aspects of bigmouth sleeper reproductive ecology, we collected specimens eight times between 14 October 2000 and 20 October 2001 in Carite Reservoir. Bigmouth sleepers were captured using boom electrofishing as previously described. All fish were immediately euthanized by anesthetic (MS-222) overdose and placed on ice until processing, which took place 3-6 h after collection. In the laboratory, each fish was measured (mm TL) and weighed to the nearest 0.01 g.

Bigmouth sleeper gonads were dissected from individual fish and weighed to the nearest 0.01 g, and stomach contents were removed and weighed. The sex of each fish was noted by gonadal examination. The gonadosomatic index (GSI), an index of relative maturity stage, was calculated for each fish using the following formula:

$$GSI = \text{gonad weight}/(\text{body weight} - \text{stomach contents weight}) * 100$$

Reproductive periodicity was determined based on seasonal changes in mean GSI. A maximum nonreproductive gonad state was computed for both males and females based upon the highest individual GSI values observed during the nonreproductive season. The smallest mature male and female collected during the study was considered the length at which sexual maturation occurs in Carite Reservoir.

Oocyte diameters were measured for 40 females that ranged from 178 to 328 mm TL collected April – June 2001. Subsamples of eggs from ripe females were taken from the ovaries and measured. Diameters of oocytes from each female were measured to the 0.01 mm using an ocular micrometer on a dissecting scope. Oocytes less than 0.20 mm were designated as primary oocytes; those more than 0.20 mm were considered maturing oocytes. Only maturing oocytes were analyzed in this study. We measured 25 eggs each from the anterior, medial, and posterior regions of the ovary (n = 75 total oocytes per fish) to make positional comparisons of oocyte size. Measurement was accomplished according to West (1990), orienting the follicle axis parallel to the micrometer.

All analyses were made using parametric statistics. Significance was accepted at the a $\alpha \leq 0.050$ level.

RESULTS

Population biology.—The population estimate sampling conducted in 2000 and 2001 totaled 65.1 h of electrofishing and collected 907 bigmouth sleepers, or 13.9 fish h^{-1}. Bigmouth sleepers ranged from 33 – 399 mm TL in 2000 and 35 – 385 mm TL in 2001 (Fig. 2). Most fish captured in 2000 were between 240 – 360 mm TL, while in 2001 the majority of fish captured were between 80 – 180 mm TL. The 2001 length-frequency distribution revealed a multimodal population suggesting several distinct age-classes, while the 2000 size structure was less defined.

Total population size was estimated at 1,783 (± 921) individuals in 2000 and 3,353 (± 1,788) the following year (Table 1). No statistically significant difference in popu-

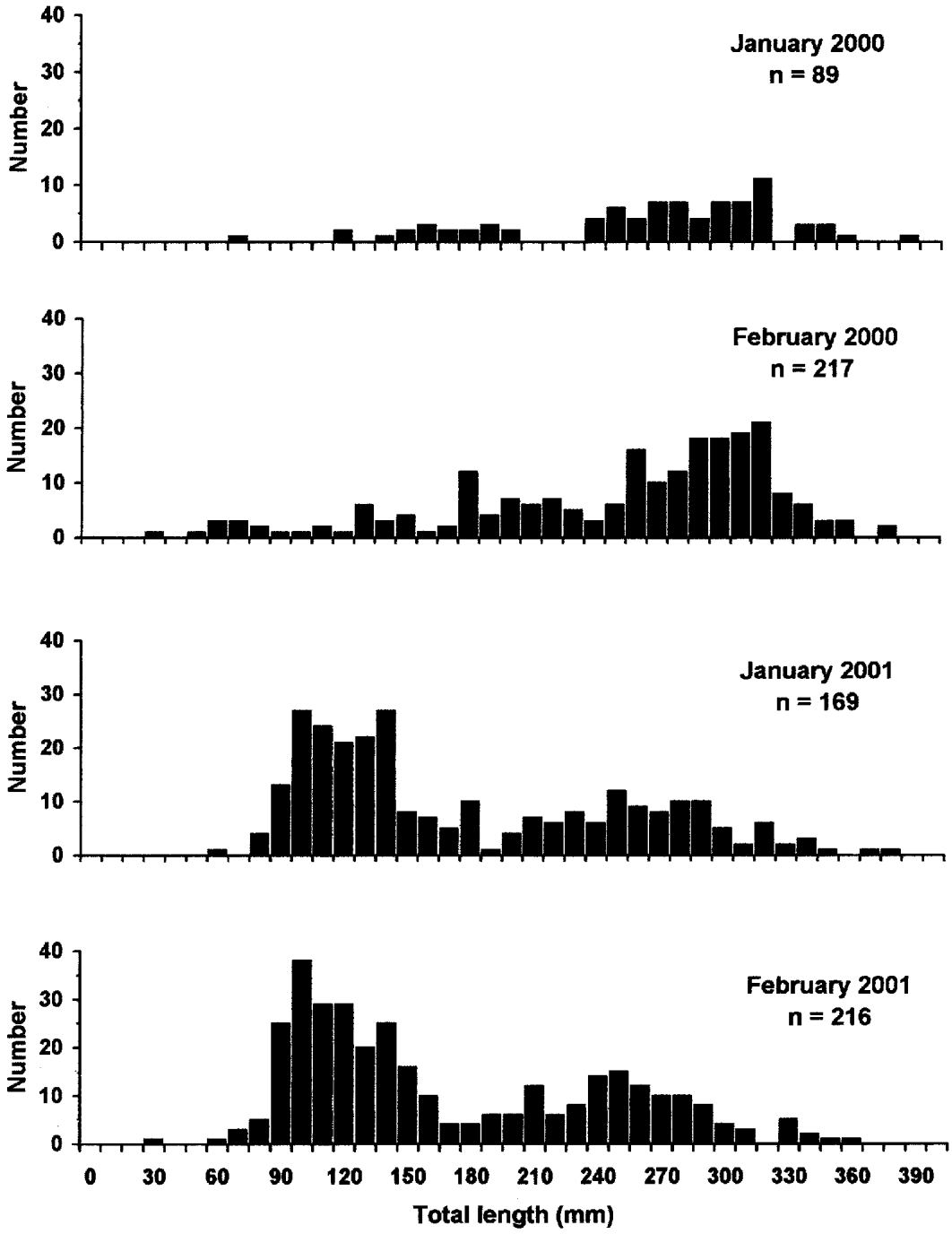

FIG 2. Length frequencies of bigmouth sleepers *Gobiomorus dormitor* in Carite Reservoir, Puerto Rico, captured during the marking (January) and recapture (February) periods of 2000 and 2001.

TABLE 1. Population estimates for adult and total bigmouth sleepers *Gobiomorus dormitor* for 2000 and 2001 in Carite Reservoir, Puerto Rico. Fish larger than 200 mm TL were classified as adults.

Date	Population	Marked	Captured	Recaptured	Pop. size	95% CI
2000	All Fish	89	217	10	1,783	± 921
2000	Adults Only	73	170	8	1,405	± 795
2001	All Fish	169	216	10	3,533	± 1,788
2001	Adults Only	102	117	8	1,349	± 769

lation size was detected between years (Standard Normal Test: $Z = -0.78$; $p = 0.22$). Adult bigmouth sleeper population size was 1,405 (± 795) and 1,349 (± 769) in 2000 and 2001, respectively. Adult populations were also not significantly different in the two years (Standard Normal Test: $Z = 0.05$; $p = 0.48$). Total biomass of bigmouth sleepers in Carite Reservoir in 2001 was 1.5 kg ha^{-1}.

Reproduction.—Two-hundred forty-eight bigmouth sleepers were collected during electrofishing efforts targeting fish for reproductive analyses. Male (n = 117) and female (n = 131) total length was not significantly different (Student's t-test; $t = 1.95$, $df = 246$, $p = 0.052$), but the difference in weight of males and females was significant ($t = 2.40$, $df = 246$, $p = 0.017$), with females being heavier than males. Moreover, the length-weight relationship was not significantly different between males and females in slope ($t = 0.77$, $df = 1$, $p > 0.05$) or intercept ($t = 0.79$, $df = 1$, $p > 0.05$).

Mean GSI values were considerably higher for females (mean = 1.64) than males (mean = 0.34) in Carite Reservoir. Average GSI for males and female bigmouth sleepers was quite variable throughout the year, and a cycle of reproductive development was apparent (Fig. 3). Average GSI of both males and females was low in January and February, increased in April, peaked in May and June, and decreased in October. No difference in reproductive seasonality was apparent among size classes of fish.

Individual GSI values during January and February were always less than 0.30 for males and 1.0 for females (see Fig. 3); these values were used as threshold values above which individuals were considered mature. The smallest male with a GSI higher than 0.30 was a 159 mm TL fish with a GSI of 0.46 captured on 20 October 2001 (Fig. 4a). The smallest female with a GSI higher than 1.0 was a 178 mm fish with a GSI of 1.54 captured on 11 June 2001 (Fig. 4b).

Frequency distributions of oocytes in female ovaries during the reproductive season typically fell into two size groups: primary oocytes (≥ 0.20 mm) and maturing oocytes (0.20 mm). Maturing oocyte size range peaked at 0.51-0.55 mm diameter, and smaller oocytes disappeared as the spawning season progressed (Fig. 5). Larger oocytes ranged from 0.66 to 0.70 mm diameter in 5 females. No significant difference occurred in oocyte diameters among positions within the ovary (ANOVA: $F = 3.04$, $df = 2$, $p = 0.054$).

DISCUSSION

This research is the first comprehensive attempt to document a suite of biological and ecological characteristics of bigmouth sleepers. These results suggest that anthropogenic changes to a river have led to the landlocking of a normally diadromous fish, and the resultant landlocked population appears to be self-sustaining. The wide size range and multimodal size distribution observed during this study indicate that the population is comprised of multiple age classes, and that juveniles recruit to the population on a regular basis. Although larval sampling has not been performed in this system, individuals as small as 24 mm TL have been collected (Neal et al. 2001).

This study was the first to attempt system-wide abundance estimates for bigmouth sleepers in any environment. Similarity of population estimates of adult bigmouth sleepers in 2000 and 2001 suggests that population size is moderately large and relatively stable. A large cohort of

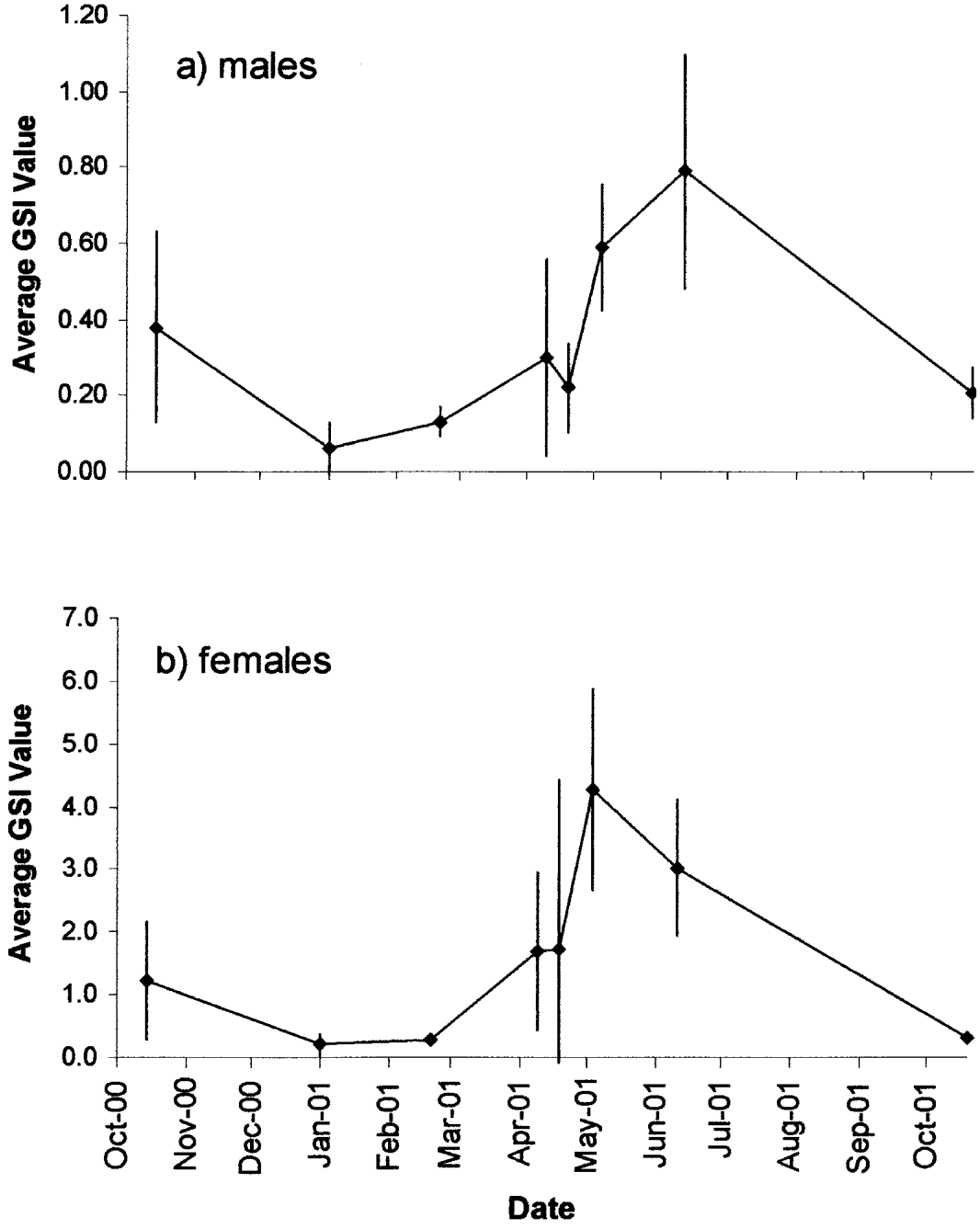

FIG 3. Average gonadosomatic index (GSI) for male (a) and female (b) bigmouth sleepers *Gobiomorus dormitor* from October 2000 to October 2001 in Carite Reservoir, Puerto Rico. Error bars denote 95% confidence intervals.

juvenile fish was detected in 2001, providing evidence of substantial reproduction within the reservoir during the previous year. Furthermore, bigmouth sleeper abundance estimates were as high as those reported for largemouth bass *Micropterus salmoides* in Carite Reservoir during the same period (Neal et al. 2001). Largemouth bass

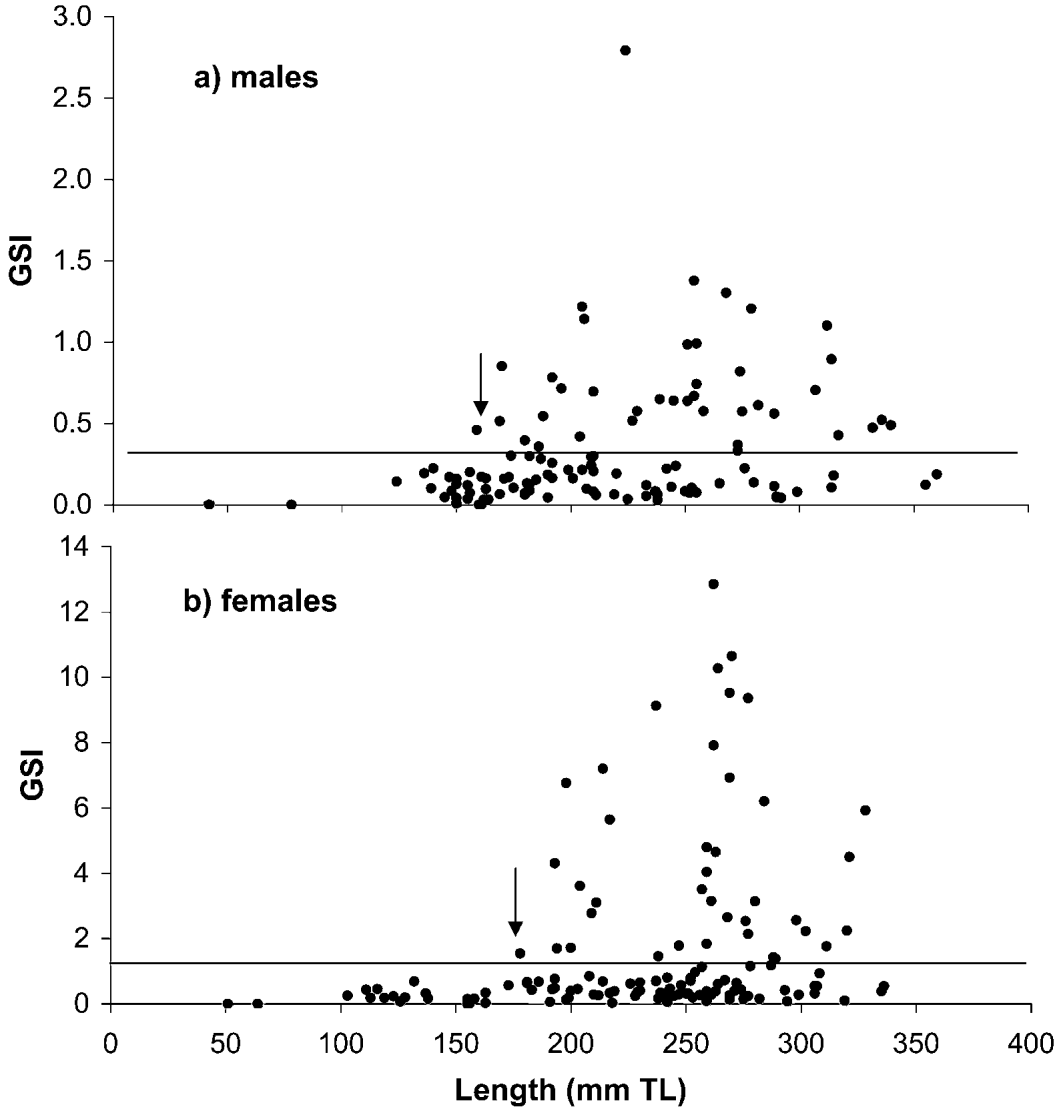

FIG 4. Gonadosomatic index (GSI) for each male (a) and female (b) bigmouth sleeper *Gobiomorus dormitor* collected between October 2000 and October 2001, all seasons combined, in Carite Reservoir, Puerto Rico. Baseline nonreproductive GSI values were always below 0.3 for males and 1.0 for females during the nonreproductive season, denoted by the horizontal line. The smallest male and female with a GSI above this baseline value are denoted by the vertical arrows.

were introduced in Puerto Rico to create reservoir fisheries in the absence of native species (Erdman 1984).

Perhaps the most convincing evidence supporting within-reservoir reproduction of bigmouth sleepers is the hydrologic isolation of Carite Reservoir. This impoundment is the uppermost in a chain of reservoirs that includes one major and two minor reservoirs downstream. La Plata Reservoir, one of the largest artificial lakes in Puerto Rico, is the lowest reservoir in the chain and is impounded by a large and impassable concrete dam. Hence, adult bigmouth sleepers migrating to the estuary and juvenile fish migrating up river

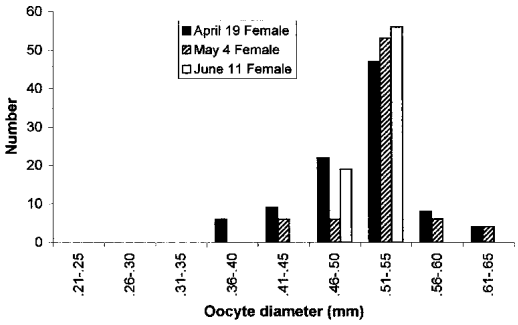

FIG 5. Oocyte diameter length frequency for three randomly selected female bigmouth sleepers *Gobiomorus dormitor* caught in April, May, and June, 2001, in Carite Reservoir, Puerto Rico.

would need to traverse four dam structures in each direction. The complete absence of bigmouth sleepers in electrofishing samples from La Plata Reservoir (Neal et al. 2001) and the La Plata River downstream of Carite Reservoir (N. Bacheler unpublished data) does not support such an unlikely feat.

Analysis of GSI supports the idea that bigmouth sleepers are reproductively active in Carite Reservoir. We observed highest gonadal development values between April and June, and a few individuals were ripe or ripening in October. No ripe fish were found in January or February. In addition, small bigmouth sleepers were frequently captured in year-round sampling efforts in Carite Reservoir (Neal et al. 2001), indicating a prolonged spawning season by adults. Year-round occurrence of juveniles was likely not a function of slow juvenile growth rates, because young bigmouth sleepers apparently hatched in spring-summer 2000 were as large as 160 mm TL by the 2001 population sample (Fig. 2).

Spawning season of bigmouth sleepers in Carite Reservoir was similar to that reported from lagoon and natural lake environments. For instance, Kelso (1965) collected gravid bigmouth sleeper females during May in Tortuguero Lagoon, Costa Rica. In Lake Jíloa, Nicaragua, 90% of bigmouth sleeper nesting activity was observed in May, with the remainder in April (McKaye 1977). In contrast, Winemiller and Ponwith (1998) found some individuals in Costa Rica with ripe or ripening gonads, as well as small juveniles (15 – 30 mm), during each of the 10 months of their study period (March – December), suggesting nearly year-round reproduction by at least some population segments.

Large, developed oocytes in bigmouth sleepers also suggested the presence of reproductively active fish. Ripe or ripening female bigmouth sleepers in Carite Reservoir had one group of primary oocytes and one group of developing oocytes. Oocytes of 0.51 – 0.55 mm diameter were the most common for ripe females, and eggs larger than 0.55 mm were rarely found. This size distribution suggests that female bigmouth sleepers typically release eggs of this size class (0.50 – 0.55 mm) during reproduction. Larger oocytes were likely swollen mature oocytes that were not spawned and await resorption (i.e., atresia).

Maximum oocyte diameter recorded in this study was twice as large (0.70 mm: 0.35 mm) as the maximum diameter reported by Winemiller and Ponwith (1998) for bigmouth sleepers from Tortuguero Lagoon, Costa Rica. It is unlikely that this discrepancy resulted from their failure to collect ripe females with mature oocytes, especially since they collected numerous mature fish over a 10 month period. Hence, it appears that oocyte sizes differ between these two reproductive populations. Variation in maximum oocyte diameter implies either that this trait is phenotypically variable, local adaptation has occurred in Carite Reservoir since damming, or that Puerto Rico and Costa Rica populations may be different species or subspecies. Further evaluations must be conducted to resolve this discrepancy.

This research indicates strongly that successful reproduction of bigmouth sleepers is occurring in Carite Reservoir. The existence of a self-sustaining landlocked bigmouth sleeper population in Carite Reservoir offers unique opportunities to both managers and ecologists. Currently, Carite Reservoir is the only place in Puerto Rico where bigmouth sleepers are capable of completing their life cycle in freshwater. This indicates that physical and biological conditions within Carite Reservoir differ significantly from other Puerto Rico reser-

voirs. If these conditions can be identified, improvements in bigmouth sleeper conservation and management should be possible. Better understanding of bigmouth sleeper ecology could lead to increased importance of this native species as a fisheries resource, reducing the dependence on introduced species in sport fisheries management. Native fisheries management can provide unique native angling opportunities while simultaneously contributing to the environmental integrity of native freshwater resources of Puerto Rico.

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