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Movement of Bigmouth Sleeper, Gobiomorus dormitor, in the Río Cañas, Puerto Rico, revealed by radio telemetry, and a discussion of the species' amphidromous characterization

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MOVEMENT OF BIGMOUTH SLEEPER, *GOBIOMORUS DORMITOR*, IN THE RÍO CAÑAS, PUERTO RICO, REVEALED BY RADIO TELEMETRY, AND A DISCUSSION OF THE SPECIES' AMPHIDROMOUS CHARACTERIZATION

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Abstract: Bigmouth Sleeper, *Gobiomorus dormitor*, are tropical fish native to rivers of Puerto Rico. They are popular sport fish targeted by local anglers. They are considered as diadromous, but this characterization is controversial. The displacement of Bigmouth Sleeper in the Río Cañas, Puerto Rico, was examined using radio telemetry. Twenty fish were radio—tagged and monitored from January to November 2008. Fish were in the Río Cañas 69%, 62%, and 59% of the time before (January—May), during (June—August), and after (September—November) the spawning season, respectively. Average detected linear home range (within the river) for all tracking periods was 2.3 km, but varied from less than 0.1 km to 8.1 km. Detected linear home range was not related to weight class or sex. They may remain in freshwater as juveniles and adults, only spending their larval stage in estuarine or marine habitats (i.e., amphidromous diadromy). However, they can complete their larval stage in freshwater but appear to make periodic migrations to the marine environment as adults, as suggested by this study. The best descriptor of Bigmouth Sleeper is that of a facultative amphidromous euryhaline species. Fishery and habitat management for this fish should take into consideration their general migratory behavior and their plasticity with respect to this life history strategy.

KEY WORDS: amphidromy; eleotrid; euryhaline; migration

INTRODUCTION

Bigmouth Sleeper, *Gobiomorus dormitor*, is a tropical fish native to the Caribbean Basin and Central America (Gilmore 1992), where they play an important role in sport fishing. They are euryhaline and inhabit coastal lagoons and freshwater rivers (Gilmore 1992, Hernández—Saavedra et al. 2004). In Puerto Rico, Bigmouth Sleeper is the only native riverine fish species that grows well in artificial impoundments (Neal et al. 2009). The Puerto Rico Department of Natural and Environmental Resources (DNER) expressed interest in using Bigmouth Sleeper as a native alternative to the current introduced reservoir sport fish assemblage.

Information on life history characteristics and migratory behavior of Bigmouth Sleeper is limited and the data are conflicting. They have been classified as anadromous (Nordlie 1979), catadromous (Nordlie 1981, Gilmore and Hastings 1983), and amphidromous (Winemiller and Ponwith 1998). Hernández—Saavedra et al. (2004) were unable to determine spawning location for Bigmouth Sleeper in the Tecolutla estuarine system of Mexico. Smith and Kwak (2014) reported that most Bigmouth Sleeper in Puerto Rico rivers were amphidromous. However, a small proportion of Puerto Rico Bigmouth Sleeper deviated from classical amphidromy (Smith and Kwak 2014). Bacheler et al. (2004) reported a self—sustaining population in Carite Reservoir, Puerto Rico, and several researchers have indicated landlocked populations in natural lakes of Honduras (Darnell 1962) and Nicaragua (McKaye et al. 1979, Bedarf et al. 2001).

Management of a sport fishery requires detailed knowl-

edge of the species' life history. This is especially important for riverine species demonstrating diadromous behaviors in systems fragmented by artificial barriers (Cooney and Kwak 2013). Since the Bigmouth Sleeper has some degree of plasticity in their life history strategy, we hypothesize if freshwater habitats are limiting or become limited, the Bigmouth Sleeper might respond by spending a greater proportion of time in an adjacent marine habitat. The goal of this study was to describe movement patterns of Bigmouth Sleeper in a Puerto Rico river and to reconsider their diadromous characterization.

Materials and Methods

Study area

Puerto Rico is the smallest and easternmost island of the Greater Antilles. The Río Cañas is a non—navigable river that flows north to south through the coastal city of Ponce (Figure 1). This river was chosen for study because it has a known population of Bigmouth Sleeper and has a large waterfall at river kilometer (Rkm) 13. The waterfall effectively limits upstream movement and provides a manageable river reach for telemetry research. The river is shallow (~ 0.6 m deep on average, with some pools to 1.5 m) and narrow $\left($ ~20 m across at the mouth), with a mean \pm sd discharge of 14.4 x $10^6 \pm 6.09 \times 10^6 \text{ m}^3/\text{yr}$.

Transmitter implantation

Lotek model NTC—6—1 transmitters (22.4 x 9.1 mm; 2.8 g; 18 cm antenna) were used for this study. Four trans-

Figure 1. Map of the Río Cañas basin and watershed, and insert showing location on the south coast of Puerto Rico. Triangle is the location of a waterfall, which inhibits upstream fish passage. Black circle is the city of Ponce. River kilometer is indicated.

mitters broadcast on a single frequency, with five different frequencies represented among the 20 transmitters used in this study (Lotek Wireless, Newmarket, Ontario, Canada). Transmitter life was projected at 357 d with a 10 sec signal burst interval. This transmitter model had a mass less than 2% of fish body mass (Winter 1996, Bacheler 2002).

A tag retention study was conducted in July 2007 to validate the implantation protocol. Ten Bigmouth Sleeper (females = 3; males = 7) from the Río Cañas were tagged during the retention study. Fish were anesthetized using an 80 mg/L dose of buffered tricaine methanesulphonate. Each fish was sexed according to Bacheler (2002), measured (TL, mm) and weighed (g). Anesthetized fish were placed in a grooved tray and water was continuously passed over the gills. Betadine® was applied to the surgery site. A small incision (~1 cm) was made anterior to the anus between the ventral side of the fish and the lateral line. The incision site was chosen to avoid contact with the substrate, as they are benthic fish. Sham Lotek model NTC—6—1 transmitters were used for the retention study. Each transmitter was immersed in a Betadine® bath prior to implantation. Transmitters were implanted in the abdominal cavity through the incision. A separate exit site for the external antenna was

created by inserting a 16 gauge needle through the abdominal wall between the incision and the anus. The external antenna was threaded through the bore of the needle and consequently through the abdominal wall. The 16 gauge needle was then removed from the abdominal wall and slid off the external antenna. The incision was closed with three 3/0 Monoswift monofilament absorbable sutures using a 26 mm tapered needle. A biological adhesive was also applied to the wound. Surgical instruments were sanitized between surgeries (Winter 1996, Bacheler 2002). The mean weight of tagged fish was 224 ± 73.5 g and mean surgery time was 5.6 ± 1.4 min. Fish were held for 30 d during the tag retention study. After 30 d, there was a 20% tag loss rate. There were no mortalities during the tag retention study.

Specimens for the actual telemetry study were collected from 3 sites on the Río Cañas between Rkm 5 and 8 using backpack electrofishing on 12—17 December 2007. Fish were held at DNER's Maricao Fish Hatchery in two 1,552 L polyethylene tanks at half volume prior to and following transmitter implantation. Systems utilized flow—through water derived from the Maricao River. Radio transmitters were implanted in Bigmouth Sleeper (females = 5, males = 15) on 20 December 2007 using the protocol outlined above. Experimental fish had a mean weight of 250 ± 108 g and a mean TL of 316 ± 46 mm. All tagged fish were at least 200 mm TL, which is above the reported minimum length at maturation (Bacheler 2002). Fish were held at the Maricao Fish Hatchery for 14 d post—surgery and monitored for incision healing and tag retention. For convenience, the 20 fish were numbered 11 through 30.

Radio telemetry

On 4 January 2008, 5—8 tagged fish were randomly chosen for release at each of the original collection sites. Transmitters were operational in all 20 fish at the time of release. A tracking period was the 1—2 d interval during which the length of the river was searched for radio signals. Tracking was conducted during daylight hours, on foot, by slowly wading downstream from the upstream most location while scanning the appropriate radio frequencies. A Garmin GPS unit was used to determine the location of individuals as the fish were detected. The first tracking period was 7 January 2008. Tracking periods occurred about every other week from 7 January to 30 May 2008. Tracking periods occurred weekly during the presumed spawning season (June to August; Harris et al. 2012). Tracking periods reverted to a frequency of every other week from 12 September to 21 November 2008.

Non—detection of a radio signal could indicate transmitter failure, angler harvest of a tagged fish, a false non—detection (i.e., failure to detect the fish despite its presence in the Río Cañas), or fish movement out of the study area. A non—detection during one tracking period followed by detection during a subsequent tracking period would rule out transmitter failure or angler harvest. At a walking pace of about 1.6 km/hr and a transmitter range of about 0.7 km (based on the exponential model of Freund and Hartman (2002) and a maximum depth of 1.5 m in the Río Cañas), the tracker would be in transmitter range for ~52 min. The receiver scanned each of the 5 transmitter frequencies for 10 sec. The receiver would have had to miss the signal more than 70 times, while in range of the transmitter, to create a false non—detection during a tracking period. Few radio telemetry studies quantify rates of false non—detection, or conversely, rates of detection. Enders et al. (2007) reported detection rates of 99.3 \pm 2.2% and 96.9 \pm 6.5% for radio tagged juvenile Atlantic Salmon, *Salmo salar*, and Brown Trout, *Salmo trutta*, during two study periods in Stoney River, Newfoundland, Canada. The shallow nature of the Río Cañas, the absence of side channels in the study reach, the characteristics of the transmitters, the method of tracking, and reported radio telemetry detection rates all suggest that false non—detections did not strongly influence this study.

Radio transmitters have conductivity restrictions, but the signals should be clear in relatively shallow water (< 4 m) with conductivity < 800 μS/cm, but become less detectable after this conductivity threshold is reached (Peters et al. 2008). Measurements taken in February 2007 about 1.25 km upstream of the Río Cañas mouth indicated that conductivities were acceptable for radio signal transmission (583 μS/cm; C. Mace, Mississippi State University, unpublished data). Conductivity measurements at the Río Cañas mouth varied from 3,940 – 50,500 μS/cm in June—August of 2008 (Adelsberger 2009). It is most likely that signal non—detection during a tracking period indicated movement of a fish into high conductivity water near or seaward of the river mouth, rather than some other explanation. Data from this study were analyzed accordingly.

Data processing and analysis

Data for individual fish were truncated to include only the last detection of each fish and data from all preceding tracking periods. We refer to the length of time from release to last detection as the tracking duration. Non—detection during a specific tracking period within a truncated data set was interpreted as the fish being absent from the freshwater portion of the Río Cañas during that tracking period. The percent of time fish were present in the Río Cañas before, during, and after the presumed spawning season was estimated. We determined the average location of individual fish detected during each month of the study and then calculated the average location (in Rkm) of the group of fish during each month of the study. We also calculated the change in average location of the group between months of the study. Linear home ranges were calculated for each fish two ways. The detected linear home range represents the distance between the two farthest apart points where fish were actually observed. The presumed linear home range included Rkm 1 (where conductivity was too high for radio signal detection) for fish absent for at least one tracking period. Hence, the presumed linear home range represents the distance between the upstream most sites where fish were observed and Rkm 1. Fish were grouped by weight using 100 g intervals and sorted by sex. Detected and presumed linear home ranges were tested for normality with Shapiro—Wilkes test and homogeneity of variance with Levene's test (PROC UNIVARIATE; SAS Version 9.2) and data were rank transformed prior to further statistical analyses if they failed to meet these assumptions. The influences of weight class and sex on detected and presumed linear home ranges were examined using two—way analyses of variance (PROC ANO-VA; SAS Version 9.2). The interaction terms between the two main effects variables were also tested for significance. An alpha level of 0.05 was used to determine significance in these statistical tests.

RESULTS

Out of the 20 fish tagged in the study, 2 were lost within the first 4 months (Figure 2). Fish 24 was caught in mid— March by a freshwater angler who reported the harvest and returned the transmitter to DNER. No other fish were reported as harvested. Nine fish were detected as late as October and November of the study. The number of fish detected

Figure 2. Tracking duration frequency distribution for Bigmouth Sleeper during a radio telemetry study in Río Cañas, Puerto Rico. Tracking duration is the time (in months) from release to the last detection of a fish during any tracking period.

during a tracking period generally declined throughout the study (Figure 3). The mean number of fish detections per tracking period was 8.7 ± 4.1 fish. Only 3–4 fish were detected per tracking period between 12 September and 31 October. However, an increase in fish detected per tracking period occurred in the last two tracking periods.

All 20 fish were detected during some portion of the pre spawn period (January—May). These fish were in the Río Cañas an average of 69 ± 32% of the time (Figure 4). Of the 17 fish detected during some portion of the spawning season,

Figure 3. Number of Bigmouth Sleeper detections per tracking period during a radio telemetry study in Río Cañas, Puerto Rico. Each tracking period was a 2 d walking survey of the entire 13 km reach, during which detections and locations were recorded.

Figure 4. *Average percent of time Bigmouth Sleeper were present in the Río Cañas, Puerto Rico, before (January—May), during (June—September), and after (October—November) spawning. Error bars represent one standard deviation. Number above the error bar represents the sample size.*

fish spent an average of $62 \pm 26\%$ of the time in the Río Cañas. Nine fish were detected during the post—spawning period (September—November), and were in the Río Cañas an average of $59 \pm 19\%$ of the time.

Considered as a group, the fish showed little tendency to move up or down stream. The average location (in Rkm) of the group remained somewhat constant for the first 8 months of the study (Figure 5a). Between August and September, the average location of the group was displaced downstream about 3.6 km (Figure 5b). Between September and October, the average location of the group moved upstream about 1.5 km. No coordinated downstream movement by the group was detected during the presumed spawning period (Figure 5b).

Home ranges within the Río Cañas varied considerably among individuals throughout the study. Detected linear home range averaged 2.3 ± 2.2 km. The smallest detected linear home range was less than 0.1 km (Fish 19, Figure 6), but this individual was only tracked for a little more than 2 months. The largest detected home range was 8.1 km (Fish 26), occupied during 9 months of tracking. Presumed linear home range averaged 5.7 ± 2.4 km. The largest presumed linear home range was 8.2 km (Fish 30, Figure 6).

The distributions of detected and presumed linear home ranges were not normally distributed (Shapiro—Wilk, *W* = 0.0.84, p = 0.004 and *W* = 0.850, p = 0.005, respectively). Variances for detected and presumed linear home ranges were homogeneous among weight classes (Levene's test, $F_{2,17}$ = 1.70, p = 0.212 and $F_{2,17} = 0.84$, p = 0.448, respectively). Variances for detected and presumed linear home ranges were also homogeneous between the sexes (Levene's test, $F_{1,18}$) = 0.62, p = 0.442 and $F_{1,18}$ = 1.54, p = 0.230, respectively). The interaction term was not significant in either of the analyses of the effects of weight class and sex on detected and presumed linear home ranges. The interaction terms were removed from both models. The effect of weight class was insignificant in the analyses of detected and presumed linear home ranges, respectively (two—way ANOVA, $F_{2,16}$ = 0.86, p = 0.443 and $F_{2,16}$ = 0.20, p = 0.822). Likewise, the effect of sex was insignificant in the analyses of detected and presumed linear home ranges, respectively (two—way ANOVA, $F_{1,16}$ = 1.99, p = 0.178 and $F_{1.16} = 0.02$, p = 0.878).

Discussion

We failed to observe a coordinated movement by this group of tracked fish toward the mouth of the Río Cañas during the spawning season. Bigmouth Sleeper have been characterized as amphidromous (Winemiller and Ponwith 1998, Smith and Kwak 2014). Amphidromous species would presumably move downstream during the spawning season to facilitate rapid conveyance of eggs and larvae to the sea. We observed a downstream movement, but not until September, after the spawning season for Puerto Rico Bigmouth Sleeper identified by Harris et al. (2012). However, the spawning season might be longer than originally determined by Harris et al. (2012). Perhaps movements downstream were brief and episodic, and thus not observed during our 1—2 d tracking periods occurring weekly during the spawning season. Thus, our tracking data do not definitely prove the amphidromous characterization of this species.

The average detected linear home range was rather large for a stream fish. Home range studies of stream fish usually indicate little movement (30—122 m) with a trend showing larger home ranges for larger individuals (Gerking 1953). Gerking's work led him to develop the "restricted movement paradigm" in stream fish ecology (Gerking 1959), though the paradigm has been challenged for some larger mobile fishes (Gowan et al. 1994). Home ranges are larger for species that migrate to spawn, but we note that home ranges for Big-

Figure 5. Location of Bigmouth Sleeper in Río Cañas, Puerto Rico. a. Average location (in river km, Rkm) of all Bigmouth Sleeper by month of the study. Error bars represent one standard deviation. Numbers next to the diamond indicate the number of fish detected during the month b. The change in average location (km) between months of the study. Negative numbers represent downstream movement of the average location. The shaded portion indicates the presumed spawning season.

mouth Sleeper in the Río Cañas appear particularly large, because of presumptive movements outside of the spawning season. Furthermore, if they spent time in coastal or marine waters adjacent to the Río Cañas, as these telemetry data suggest, then home ranges were likely larger than characterized here.

The restricted freshwater range in the Río Cañas could have influenced frequency and duration of the use of marine and estuarine habitats. Two of the 5 rivers studied by Smith and Kwak (2014), the Río Grande de Añasco and the Río Grande de Manatí, were large systems, with watershed areas of 468 and 471 km², respectively, and main channel lengths of 155 and 224 Rkm, respectively. Conversely, the Río Cañas watershed is less than 24 km², with a main channel length of 23 Rkm, and only 13 Rkm of accessible habitat due to the waterfall that acts as a barrier to upstream movement. A Bigmouth Sleeper should be able to traverse the entire length of the river in only a few hours.

In addition to stream length, stream discharge may affect the life history strategy of Bigmouth Sleeper. Because the Río Grande de Añasco and the Río Grande de Manatí are larger systems, they have greater mean discharges. In addition, the Río Cañas drains the south coast of Puerto Rico, which is relatively dry compared to the rest of the island. For instance, the city of Ponce, which contains the lower portion of the Río Cañas, receives a mean annual rainfall of 97.7 cm/yr. By comparison, Mayagüez and Manatí, the cities at the mouths of the 2 largest rivers studied in Smith and Kwak (2014), receive mean annual rainfall amounts of 151.0 and 156.6 cm/yr, respectively (Current Results 2015). The Río Mameyes and the Río Sabana, the other 2 rivers studied by Smith and Kwak (2014), drain terrain that includes tropical rainforest. Although similar in watershed size and main channel length to the Río Cañas, these 2 systems likely experience more consistent base flow due to more consistent rainfall patterns. Thus, small size and irregular precipitation patterns may create variability in hydrology that is more pronounced in the Río Cañas than in these other Puerto Rico rivers. We note that daily discharge in the Río Cañas exceeded the average daily discharge plus 2 times the standard deviation 3 d in September and 7 d in October 2008. Such extreme flows could have displaced Bigmouth Sleeper from the river. When conditions in freshwater are not favorable (i.e., extreme low or high flow) and the distance to the marine environment is modest, it may be advantageous for fish to move to a more stable estuarine or marine habitat.

These data do not support a simple form of diadromy for Bigmouth Sleeper. Catadromous fishes spend their adult lives in freshwater and move to marine habitats to spawn. Anadromous fishes spend their adult lives at sea and move to freshwater to spawn (Myers 1949). Our data, though imperfect, suggest that Bigmouth Sleeper in the Río Cañas exhibited euryhaline salinity tolerance, spending the majority of their time in freshwater, but moving periodically between freshwater and estuarine or marine habitats.

Myers (1949) described amphidromy as a third form of diadromy where the migration from freshwater to marine

Figure 6. Detected (solid line) and presumed (solid line plus dashed line) linear home ranges of radio—tagged Bigmouth Sleeper. Number above home range is the number of months each fish was tracked.

habitat is "not for the purpose of breeding, but occurs regularly at some other definite stage of the life cycle." McDowall (2007) refined Myer's definition of amphidromy to include (a) spawning and hatching in freshwater, (b) rapid movement of larvae to sea, (c) feeding and growth at sea for a short period of time, (d) return to freshwater as a juvenile, and (e) feeding and growth in freshwater prior to maturity and spawning. Winemiller and Ponwith (1998) speculated that Bigmouth Sleeper and other Costa Rican eleotrids spent most of their time in freshwater but moved downstream to spawn in freshwater or upper estuarine habitats so that their larvae could occupy lower estuarine and marine habitats. This is consistent with McDowall's definition of amphidromy. Larval development of Bigmouth Sleeper is characteristic of marine pelagic development: undeveloped mouth, small size, large yolk sac, and unpigmented eyes (Harris 2007). Furthermore, larvae were collected only at the river mouth of the Río Cañas during larval sampling throughout a 9 km reach in June—August 2008 (Adelsberger 2009, Neal et al. 2011). All of these observations are consistent with an amphidromous characterization. However, data from this study suggested periodic movements into estuarine or marine habitats. Furthermore, Bigmouth Sleeper are known to spawn in freshwater systems, such as Carite Reservoir, Puerto Rico (Bacheler et al. 2004), and Lake Jiloá, Nicaragua (McKaye et al. 1979). Marine development of larvae is not possible in these systems due to fish passage barriers. Out of necessity or choice, some Bigmouth Sleeper exhibit behavior that does not reflect amphidromy.

Data from this study appear to support the notion that Bigmouth Sleeper practice partial migration. Chapman et al. (2012) reviewed the concept of partial migration where some fish exhibit migratory behavior while others within the same population do not. Chapman et al. (2012) described partial migration as a life—history polymorphism, such that there is a degree of plasticity in terms of reproductive life history strategy among individuals within a species. The proportion of individuals adopting a specific life history strategy could depend on environmental conditions or constraints encountered during the spawning season. Smith and Kwak (2014) used otolith microchemistry to characterize Bigmouth Sleeper from Puerto Rico rivers as amphidromous. Microchemistry analyses of otoliths suggested a marine larval phase, followed by a solely freshwater adult phase for 87% of the fish they examined. However, Smith and Kwak (2014) used the phrase semi—amphidromous to characterize the 9.3% of individuals with otolith microchemistry indicating a freshwater larval phase and the 3.7% of individuals with otolith microchemistry indicating movements to marine habitats during their adult phase. Smith and Kwak (2014) speculated that otolith microchemistry indicating adult movement to a marine habitat could also be explained by a marine diet while in freshwater, rather than from actual residence in a marine environment. Our Río Cañas data suggest that Bigmouth Sleeper periodically reside in marine habitats during their adult lives. The Río Cañas data do not contradict Smith and Kwak (2014), but they do indicate the proportion of fish moving between freshwater and marine or estuarine habitat during the adult phase is higher in the Río Cañas than the general estimate of 3.7% from Smith and Kwak (2014).

Exact characterization of the migratory behavior of Bigmouth Sleeper might be a matter of semantics. Smith and Kwak (2014) seem to be the first to use the term semi—amphidromous to describe them, citing Cronin and Mansueti (1971), Secor and Kerr (2009), and Whitfield (2005) for that terminology. Cronin and Mansueti (1971) refer to Striped Bass, *Morone saxatilis*, and White Perch, *M. americanus*, as semi—anadromous, stating, "Both of these are semi—anadromous fish, which move from saline water to, or almost to, freshwater for spawning." Secor and Kerr (2009) define semi—anadromous as "diadromous fishes that spend most of their lives in saline water and that migrate to, or almost to, freshwater for spawning" and cite Cronin and Mansueti (1971) for that terminology. Secor and Kerr (2009) define semi—catadromous as "diadromous fishes that spend most of their lives in freshwater and that migrate to the estuary to breed" and cite Whitfield (2005) for that terminology. Semi can mean "half" or it can mean "partially or incompletely." However, it is not clear from the phrase "semi—amphidromous" what part of the McDowall (2007) definition of amphidromy is or is not exhibited by semi—amphidromous fishes. Does the species spawn in freshwater, but not spend the larval phase in a marine habitat? Does a semi—amphidromous species spend the larval phase in a marine habitat, but does not spend its adult life solely in freshwater? Semi amphidromous could mean that half of the individuals are amphidromous and half are something else. The term is ambiguous.

Metcalfe et al. (2002) and McDowall (2007) used the term facultative, and Chapman et al. (2012) explicitly used the term "facultative amphidromy." The phrase facultative means "capable of but not restricted to a particular function or mode of life." Smith and Kwak (2014) reported that 87% of the Bigmouth Sleeper examined had otolith microchemistry indicating a marine larval phase followed by a solely freshwater adult phase. However, Smith and Kwak (2014) presented data suggesting that 3.7% of fish examined experienced marine or estuarine conditions during their adult phase. The telemetry data from the present study, though imperfect, suggest adult Bigmouth Sleeper do not remain solely in freshwater before, during, or after the spawning season. Adelsberger (2009) collected Bigmouth Sleeper larvae only at the moderately saline mouth of the Río Cañas. However, Smith and Kwak (2014) report that otolith microchemistry indicated that 9.3% of Bigmouth Sleeper examined had

freshwater larval phase. Carite Reservoir in Puerto Rico has juveniles that could not have spent their larval phase in marine water (Bacheler et al. 2004). These data lead us to favor the term facultative amphidromous euryhaline species to describe Bigmouth Sleeper.

This study suggests that Bigmouth Sleeper in the Río Cañas spent the majority of their time in the freshwater portion of the river. Nevertheless, they appeared to move between freshwater and estuarine or marine habitats throughout the year, and this movement has important consequences. First, fishery statistics, such as exploitation, should consider both marine and freshwater harvest by recreational anglers. Second, conservation efforts must

consider movement patterns and connectivity between the marine and freshwater habitats used by Bigmouth Sleeper. Natural impediments to movement, such as siltation at the river mouth, and anthropogenic impediments to movement, such as those described by Cooney and Kwak (2013), should be reduced or eliminated to allow migratory behavior of this and other Puerto Rico species. Finally, a careful examination of the landlocked population in Carite Reservoir might indicate whether that Bigmouth Sleeper population is merely exhibiting plasticity in its reproductive life history strategy, or if selective pressures are resulting in genetic changes towards a truly freshwater life history strategy.

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