

Recruitment phenology and pelagic larval duration in Caribbean amphidromous fishes

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Abstract: Amphidromous fishes are major components of oceanic tropical island stream ecosystems, such as those of the Caribbean island, Puerto Rico. Fishes with this life history face threats related to the requirement for connectivity between freshwater and marine environments during early life stages. Pelagic larval duration and recruitment phenology are 2 early life-history processes that are crucial for the biology, ecology, conservation, and management of amphidromous fishes. However, these processes are understudied in the Caribbean in general and have never been quantified in Puerto Rico. We quantified recruit abundance, recruitment phenology, and pelagic larval duration of several Caribbean amphidromous fish species in multiple rivers in Puerto Rico and explored the effects of environmental variables on recruit abundances. Two fish taxa—sirajo goby (*Sicydium* spp.) and River Goby (*Awaous banana*)—were exceptionally abundant as postlarvae and recruited to Caribbean rivers in pulsed migration episodes that were periodic at annual and lunar scales. Sirajo goby and River Goby recruit abundances varied among rivers, were greater at sunrise than at sunset, and were positively related to river discharge. The pelagic larval duration of 4 fish taxa ranged from a minimum of 28 d to a maximum of 103 d with means between 43 ± 7 d (SD) and 65 ± 11 d. We identified the last-quarter moon phase during the months of June through January as periods of maximum amphidromous fish recruitment to freshwater streams. The results and conclusions of our study can be applied to identify critical times to maintain river–ocean connectivity and stream flow for the benefit of the amphidromous fish population dynamics, stream ecology, and natural resources of the Caribbean.

Key words: fish recruitment, amphidromous, tropical island, pelagic larval duration, stream fish, phenology, flow regime

Amphidromous fishes face multiple threats related to a life history that requires freshwater–marine connectivity during early life stages (Kwak et al. 2016). Fishes with this life history spawn in freshwater streams, and the larvae drift to the ocean immediately after hatching. After an oceanic pelagic larval phase, they transition to postlarvae prior to river ingress (i.e., movement from the ocean into a river mouth). Once postlarvae reach a river, they typically undergo rapid metamorphosis to early juvenile stages during upstream migration to adult habitats (McDowall 2007, Keith et al. 2008). Anthropogenic threats to amphidromous fishes include in-stream barriers to migration (Holmquist et al. 1998, Cooney and Kwak 2013), streamflow alterations from water abstraction or hydroelectric operations (Brasher 2003, Smith and Kwak 2015, Kwak et al. 2016),

and habitat alteration by stream channelization (Engman and Ramírez 2012, Ramírez et al. 2012). Threats to amphidromous fish conservation are of special concern because these fishes are globally distributed, ecologically important, and culturally significant components of stream communities (Fitzsimons et al. 1996, Keith 2003, Feutry et al. 2012).

Amphidromous species are ubiquitous on oceanic tropical islands where the Gobiidae and Eleotridae families (suborder Gobioidae) typically dominate stream fish richness (Fitzsimons et al. 1996, McDowall 2004, Keith and Lord 2011, Feutry et al. 2012). They also are a major component of fish assemblages in streams on some continental tropical islands, temperate island chains, and in tropical coastal continental areas (McDowall 2004, 2010, Thuesen et al. 2011). Amphidromous fishes play key ecological roles in

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systems they inhabit. They occupy multiple levels of stream food webs, from primary consumer algivores (Schoenfuss and Blob 2007) to top predators that influence the distribution of other stream fauna (Hein and Crowl 2010). Moreover, amphidromous recruitment (i.e., river ingress by postlarvae) constitutes the upstream movement of biomass from marine to freshwater systems, which may have important ramifications for riverine and estuarine trophic ecology and production (Jenkins et al. 2010). Amphidromous fishes deliver valuable ecosystem services, including recreational and subsistence fisheries that target multiple life stages (Kwak et al. 2016). Artisanal fisheries that target postlarvae during river ingress are of particular interest from a research and conservation standpoint because these fisheries are widely practiced, culturally significant, and can be economically valuable (Bell 1999). Few investigators have estimated exploitation rates, and their sustainability is increasingly uncertain because of cumulative effects of decreased water quality, quantity, and the potential for overexploitation (Bell 1999, Castellanos-Galindo et al. 2011, Lefrançois et al. 2011).

In addition to the role of postlarval recruitment (i.e., river ingress) in ecosystem functions and services, recruitment is essential to the viability of amphidromous populations because it determines local and metapopulation dynamics in species with marine larval phases (Caley et al. 1996). To understand this key life-history process, the recruitment phenology, size- and age-at-recruitment, and recruit abundances of some amphidromous fish species have been examined (Bell 1997, Benbow et al. 2004, Maeda et al. 2007, Yamasaki et al. 2007, Iida et al. 2008, Shen and Tzeng 2008). The results of these studies have revealed interesting commonalities, including lunar and annual periodicity in the size, age, and abundance of recruiting postlarvae.

Despite the stressors faced by amphidromous fishes and their significance to streams and people, this life history remains less studied than other types of diadromy (Omori et al. 2012). Most prior studies on the early life history of amphidromous fishes have been conducted in the Indo-Pacific region, whereas published research on postlarval recruitment of Caribbean amphidromous fishes is scarce, despite the fact that most native stream fish richness in the region is composed of amphidromous gobioids (Keith 2003). In fact, with the exception of 2 descriptive notes (Clark 1905, Erdman 1961), 1 study on the island of Dominica represents the only research on amphidromous fish recruitment in Caribbean islands (Bell et al. 1995, Bell 1997). The lack of basic knowledge (i.e., abundance and phenology) about a key stage in the life history of a major component of stream ecosystems is a barrier to effective stream resource conservation and management in the Caribbean.

We quantified recruit abundance and recruitment phenology of the amphidromous fish assemblage on the Caribbean island of Puerto Rico. Specifically, we estimated the

annual and lunar periodicity of sirajo goby (*Sicydium* spp.) and River Goby (*Awaous banana*) postlarval recruit abundance and explored the effects of environmental variables and inter-river variability in sirajo goby and River Goby recruitment. In addition, we quantified the length- and age-at-recruitment and hatching dates of Puerto Rico's amphidromous fishes. The results and conclusions of our research are useful for stream and fisheries managers of Puerto Rico and the wider Caribbean region, and they improve the state of knowledge of tropical island stream and estuarine ecosystem ecology.

METHODS

Study systems

Puerto Rico is the smallest of the Greater Antilles and is located centrally in the Caribbean archipelago. Its streams harbor a typical oceanic tropical island fish assemblage. Native species richness is low and, with the exception of the American Eel (*Anguilla rostrata*), all of the native stream fish are amphidromous (Neal et al. 2009, Cooney and Kwak 2013). The freshwater amphidromous fish taxa of Puerto Rico include sirajo goby, River Goby, Bigmouth Sleeper (*Gobiomorus dormitor*), Smallscaled Spinycheek Sleeper (*Eleotris perniger*), Fat Sleeper (*Dormitator maculatus*), and Mountain Mullet (*Agonostomus monticola*) (Cooney and Kwak 2013). In Puerto Rico, the sirajo goby is a 4-species-complex that includes *Sicydium buski*, *Sicydium gilberti*, *Sicydium plumieri*, and *Sicydium punctatum*. These species are morphologically distinguishable only at the adult stage by microscopic examination of upper jaw dentition (Watson 2000). In addition to being ubiquitous in Puerto Rican streams, all of Puerto Rico's amphidromous fish species commonly occur in streams throughout the Caribbean region (Lord et al. 2010, Cooney and Kwak 2010, Nordlie 2012).

We selected 4 rivers that flow to the north coast of Puerto Rico as study systems. Two of the study rivers, the Río Grande de Arecibo and Río Grande de Manatí support artisanal amphidromous postlarvae fisheries. Fisher anecdotes suggest that postlarvae ingress to these rivers during mass recruitment episodes on the last quarter of the moon phase from June through January (Erdman 1961, personal communication). The Río Grande de Manatí and the Río Grande de Arecibo are adjacent drainages located in north-central Puerto Rico with headwaters in the volcanic Cordillera Central Mountain Range. They are 2 of the largest rivers in Puerto Rico by watershed area and flow through its karst geology region in their middle and lower reaches (Zamora et al. 1986). The other 2 study systems were the Mameyes River and the Sabana River. These adjacent drainages are in northeastern Puerto Rico, have headwaters in the volcanic Luquillo Mountain Range, and are largely situated in protected areas, including the El Yunque National Forest and

the Reserva Natural Corredor Ecológico del Noreste (Martinuzzi et al. 2007). These 2 river systems are of special conservation concern because they are considered among the least ecologically compromised systems on the island. For example, the Mameyes River is the only free-flowing river on the island with no artificial migration barrier (Cooney and Kwak 2013). The Mameyes and Sabana rivers harbor abundant and native-dominated fish assemblages (Kwak et al. 2007, 2013, Hein et al. 2011), but postlarvae are not harvested by people on these rivers.

Sampling protocol

We captured postlarvae of amphidromous fishes with a 1- × 1-m benthic kick net with 1-mm mesh, fitted with wooden brails and a bottom lead line enclosed in polyvinyl chloride (PVC). To sample fishes, a 2-person team pulled the net like a seine perpendicular to the bank with the net positioned at a 45° angle and the lead line ahead and lightly scraping the substrate. The net and sample were lifted into a 50-L tub placed onshore to collect the catch at the end of the net-haul. Captured fishes were separated from excess sediment and organic material and preserved in a 10% buffered formalin solution. We recorded the depth of the starting point of each net-haul and its distance from shore.

All sampling occurred at the river mouth of each study system—defined as the point where the river channel ends and ocean habitat begins. We sampled near the shore on the low-gradient bank side of the river mouth for feasibility and because recruiting postlarvae have been observed migrating in columns along the shallow banks of rivers (Clark 1905, Erdman 1961). Each sampling occasion comprised 5 net-hauls conducted over a 10- to 20-m section of the river mouth. We conducted the 1st net-haul at the downstream end of the sampling area and moved the location of subsequent net-hauls incrementally upstream. Occasionally, we had to conduct fewer than 5 net-hauls on a sampling occasion because of inclement weather or logistical constraints, but no fewer than 3 net-hauls ever constituted a sampling occasion.

In the laboratory, postlarvae of all 7 amphidromous fish taxa that are native to Puerto Rico were first sorted from other juvenile, postlarval, and larval fishes and crustaceans, which were sometimes present in preserved samples. Amphidromous fish postlarvae were identified and enumerated with an Olympus SZX7 stereomicroscope (Olympus). Typically, postlarvae could be distinguished at 10× magnification, but variable levels of magnification were used for identification.

A small number of samples contained so many individual amphidromous postlarvae that counting the total catch directly would have been impractical. The total catch of these 22 samples was estimated by subsampling. First, we weighed the entire sample (± 0.01 g). Then we placed the

entire sample in a bowl and used a tablespoon to mix the catch to ensure a homogeneous distribution of individuals. Next, we took 3 subsamples by filling a tablespoon once for each subsample. We weighed each subsample individually, counted all fish, and calculated the number of fish/g subsample of each species of interest. We then calculated the mean number of fish/g of each species from the 3 subsamples and multiplied by the total mass of the sample, which yielded an estimate of the total number of fish captured in the sample. We calculated the swept volume of each sample by approximating the area of a triangle with the depth and distance to shore measurements and multiplying that area by the width of the kick net. We calculated the catch-per-unit effort (CPUE) according to taxon of each sample by dividing the total number of fish captured in the sample by the swept volume.

Temporal sampling design

Our sampling schedule was designed to reveal patterns of postlarval ingress to river mouths at 2 temporal scales, the annual scale, which was defined by the 365-d year, and the lunar scale, which was defined by the 29.5-d cycle of the moon. We conducted all sampling during crepuscular hours, i.e., within 1 h of sunrise or sunset.

We conducted lunar-scale sampling on all 4 rivers. In 2013, we sampled the Sabana River and Río Grande de Manatí during the June–July lunar cycle only, and the Río Grande de Arecibo and Mameyes River from 18 June to 8 October (4 full lunar cycles). In 2014, we sampled all 4 rivers from 29 May through 17 October (5 full lunar cycles). In 2013, we sampled postlarvae twice per lunar quarter for a total of 8 sampling events per lunar month per river. In 2014, we generally conducted lunar-scale sampling 3 times per lunar quarter for a total of 12 sampling events per lunar month. We conducted additional sampling during the July 2014 lunar cycle, and we have included these samples in the data presented here.

We conducted annual-scale sampling on 2 rivers, the Río Grande de Arecibo and the Mameyes River, over a 23-mo period (June 2013–April 2015). Postlarvae were sampled on 2 d/mo during the last-quarter phase of the lunar cycle. We collected samples during all months of the sampling period except December 2013, February 2014, and April 2014. We selected the last-quarter moon phase based on evidence presented by Erdman (1961), fisher anecdotes, and because our initial lunar-scale sampling indicated that it was the period of maximum recruitment of sirajo goby and River Goby.

Determination of length- and age-at-recruitment

We examined recruiting postlarvae of all 4 native gobioid stream taxa to estimate their length (total length [TL], ± 0.1 mm) and age (d) at the time of recruitment.

We took samples of postlarvae for length and age determination concurrently with annual- and lunar-scale samples, typically at times when we observed high densities of postlarvae. We retained samples of postlarvae for length and age measurements on 2 dates at the Sabana River, 8 at the Mameyes River, 4 at the Río Grande de Manatí, and 31 at the Río Grande de Arecibo. In total, we sampled 499 individuals from the 4 taxa for length and age analyses. We captured and identified fishes as described above, but preserved them in 95% ethanol, rather than 10% formalin. We photographed each individual fish with a Lumenera Infinity digital camera (Lumenera Corporation, Ottawa, Canada) mounted to an Olympus SZX7 optical microscope (Olympus VMZ, Hamburg, Germany) and measured TL digitally with the aid of Image-Pro Insight 9 software (Media Cybernetics Inc., Rockville, Maryland).

We estimated the age (d) of individual postlarvae by enumeration of sagittal otolith increments. Daily increment formation on otoliths is widely accepted for age estimation in larval fishes under most growth conditions (Brothers et al. 1976, Jones 1992) and has been validated for tropical amphidromous gobioids (Hoareau et al. 2007). Procedures described by Bell et al. (1995) were generally followed, whereby otoliths were extracted with forceps and a scalpel, cleaned of any adhered tissue, and moved to a glass slide with the concave side of the otolith facing down. Our procedures differed from those of Bell et al. (1995) in that we used 95% ethanol to rinse the otoliths and did not mount the otoliths to slides. The extracted otoliths were always sufficiently translucent to view daily increments without sanding or polishing, but immersion oil was used to improve clarity (Sponaugle and Cowen 1994). We photographed each otolith at 400× magnification with the aid of the image analysis system described above after daily increments were enumerated.

We estimated ages of sampled postlarvae as described above, and calculated the mean and standard deviation of length- and age-at-recruitment of all individuals from each taxon. We estimated the earliest and latest observed hatching times in the annual cycle for all taxa by subtracting the age in days from the date sampled.

Modeling postlarval recruitment phenology

We adopted a periodic regression approach to model fluctuations in postlarval recruit abundances at river mouths over lunar and annual cycles. Periodic regression is a robust and sensitive method for modeling cyclic patterns in species abundance and has been applied to model amphidromous postlarval recruit abundance at the annual scale (Bell 1997, DeBruyn and Meeuwig 2001). Poisson generalized linear models were fit to sirajo goby and River Goby count data with a log-link. Effort (volume of water sampled) was included as an offset term in all models. We calculated mean CPUE (fish/m³) by lunar day for the 4 most numerous taxa

to identify which taxa exhibited possible patterns of recruit abundances that were related to the lunar cycle. We modeled recruitment phenology for sirajo goby and River Goby because these taxa were most abundant in our samples (Table 1).

For each analysis, we assigned the day a sample occurred to an angular equivalent (θ) by dividing the day of the cycle (0–28.5 for lunar and 0–364 for annual) by 2π (DeBruyn and Meeuwig 2001). Then, we developed 5 classes of models to describe periodicity in recruit abundances over both scales of interest: 1) models describing 1 peak in recruitment over the cycle using the terms $\sin(\theta)$ and $\cos(\theta)$ as independent variables, 2) models describing 2 even peaks in recruitment over the cycle using the terms $\sin(2\theta)$ and $\cos(2\theta)$ as independent variables, 3) models describing 2 uneven peaks in recruitment over the cycle using the terms $\sin(\theta)$, $\cos(\theta)$, and $\cos(2\theta)$ as independent variables, 4) models describing 2 uneven peaks in recruitment over the cycle using the terms $\sin(\theta)$, $\cos(\theta)$, and $\sin(2\theta)$ as independent variables, and 5) models describing no periodicity in recruit abundances.

We also considered 3 additional variables that were hypothesized to influence the abundances of recruiting postlarvae for model inclusion as environmental covariates. The environmental covariates were a categorical variable that identified whether a sample was taken at sunrise or sunset (SS), a categorical variable that identified the river of each sample (River), and the \log_{10} -transformed mean daily river discharge (Q) on the day of the sample. Q values were obtained from the lowest elevation US Geological Survey (USGS) gaging station present on each river (<http://nwis.waterdata.usgs.gov/nwis>). The station numbers used for each river were 50029000, Río Grande de Arecibo; 50038100, Río Grande de Manatí; 50065500, Mameyes River; and 50067000, Sabana River. The environmental covariates were considered for model inclusion in all possible combinations with each of the 5 classes of models.

We did not model interactions among terms. Thus, we developed a total of 40 candidate models for each species–temporal-scale combination. We used Akaike's Information Criterion (AIC) to select the best model from each suite of candidate models (Akaike 1974, Burnham and Anderson 2002). Once we selected a model, we used it to predict the density of postlarvae over the scale of interest while holding all other independent variables constant. We estimated a pseudo- R^2 value (calculated as $[1 - \text{selected model deviance}/\text{null model deviance}]$) as a measure of the predictive ability of each selected model (Cameron and Windmeijer 1996).

RESULTS

Postlarvae of all amphidromous fish taxa native to Puerto Rico were captured during both sampling schedules (Table 1). More River Goby postlarvae were caught in both

Table 1. The number of samples (*N*) and number of individuals of each taxon captured during each sampling schedule.

Sampling schedule	<i>N</i>	River Goby	Sirajo goby	Bigmouth Sleeper	Smallscaled Spinycheek Sleeper	Fat Sleeper	Mountain Mullet
Lunar-scale	1570	17,282	2240	1167	436	142	52
Year-scale	382	17,462	3012	102	526	26	31

annual- and lunar-scale samples than any other fish taxon. Sirajo goby was the 2nd-most abundant taxon. Relatively few Fat Sleeper and Mountain Mullet were captured, whereas intermediate numbers of Smallscaled Spinycheek Sleeper and Bigmouth Sleeper were sampled during both schedules. Plots of mean CPUE by lunar day of the 4 most abundant taxa revealed disproportionate abundances of sirajo goby and River Goby recruitment on specific days of the lunar cycle (Fig. 1A, B), whereas no such pattern was apparent for Smallscaled Spinycheek Sleeper and Bigmouth Sleeper (Fig. 1C, D). Moreover, the periods of elevated sirajo goby and River Goby recruitment coincided with the period of

the lunar month when annual sampling was conducted. Therefore, periodic regression models of the catch of sirajo goby and River Goby postlarvae were fit to determine annual and lunar periodicity in the recruit abundances of both taxa.

Lunar-scale recruitment phenology

AIC strongly favored model 3a (2 uneven recruitment peaks, all 3 environmental covariates) as the best model of both sirajo goby and River Goby catches from the lunar sampling schedule (Table 2). These models presented a substantial decrease in deviance from null models (sirajo

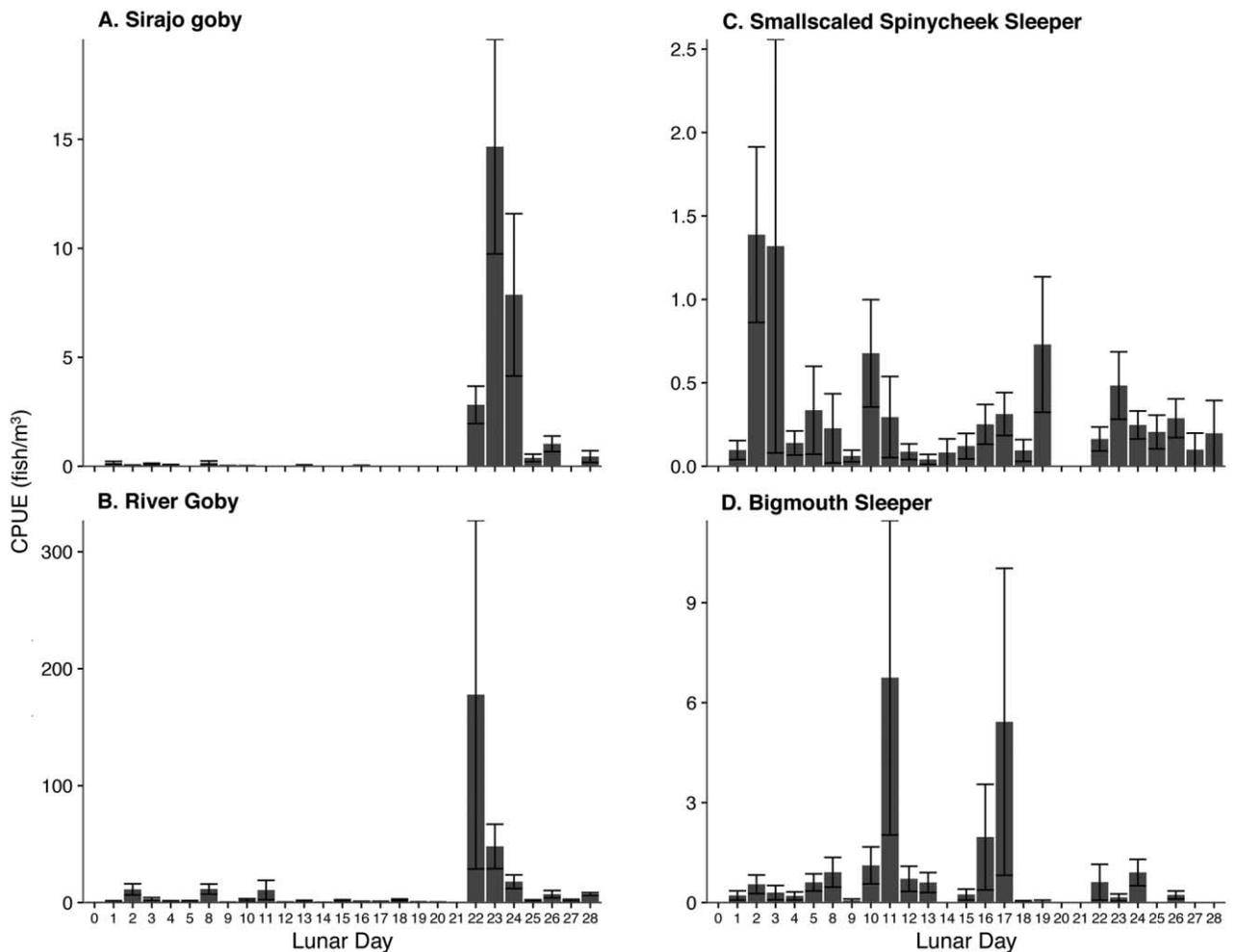


Figure 1. Mean (±SE) catch-per-unit-effort (CPUE) by lunar day of sirajo goby (A), River Goby (B), Smallscaled Spinycheek Sleeper (C), and Bigmouth Sleeper (D) in Puerto Rican rivers.

Table 2. The top 3 (based on Akaike's Information Criterion [AIC]) Poisson periodic regression models of postlarval recruit abundances for each taxon-scale combination that was modeled (see methods for further description). Only the top 3 models from a suite of 40 models that were considered are displayed because, in each instance, the top model held all of the AIC weight (w). In model descriptions, θ is either the lunar day in radians or the day of the year in radians, River is a factor that describes where sampling occurred, SS is a factor that identifies if samples were taken at sunrise or sunset, and Q is log-transformed mean daily river discharge.

Taxon	Scale	Model name	Model description	AIC _{<i>i</i>}	$\Delta_i(\text{AIC})$	$w_i(\text{AIC})$
Sirajo goby	Lunar	3a	$\cos(2\theta) + \cos(\theta) + \sin(\theta) + \text{River} + \text{SS} + Q$	7,132.77	0.00	1.00
		3b	$\cos(2\theta) + \cos(\theta) + \sin(\theta) + \text{River} + \text{SS}$	7,339.20	206.43	0.00
		3d	$\cos(2\theta) + \cos(\theta) + \sin(\theta) + \text{SS} + Q$	7,452.77	320.00	0.00
River Goby	Lunar	3a	$\cos(2\theta) + \cos(\theta) + \sin(\theta) + \text{River} + \text{SS} + Q$	7,3249.29	0.00	1.00
		3d	$\cos(2\theta) + \cos(\theta) + \sin(\theta) + \text{SS} + Q$	7,6952.93	3,703.64	0.00
		2a	$\cos(2\theta) + \sin(2\theta) + \text{River} + \text{SS} + Q$	7,7763.22	4,513.93	0.00
Sirajo goby	Annual	3a	$\cos(2\theta) + \cos(\theta) + \sin(\theta) + \text{River} + \text{SS} + Q$	7,701.42	0.00	1.00
		3b	$\cos(2\theta) + \cos(\theta) + \sin(\theta) + \text{River} + \text{SS}$	7,747.25	45.83	0.00
		4a	$\cos(\theta) + \sin(\theta) + \sin(2\theta) + \text{River} + \text{SS} + Q$	7,908.85	207.43	0.00
River Goby	Annual	3a	$\cos(2\theta) + \cos(\theta) + \sin(\theta) + \text{River} + \text{SS} + Q$	5,6320.41	0.00	1.00
		3b	$\cos(2\theta) + \cos(\theta) + \sin(\theta) + \text{River} + \text{SS}$	5,7243.68	923.26	0.00
		3d	$\cos(2\theta) + \cos(\theta) + \sin(\theta) + \text{SS} + Q$	57,397.73	1,077.32	0.00

goby: pseudo- $R^2 = 0.62$, River Goby: pseudo- $R^2 = 0.55$, respectively). All terms in the models of both taxa were statistically significant ($\alpha = 0.01$) (Table 3). Thus, these models indicate significant lunar periodicity in the catch of postlarvae of both goby taxa, and that goby postlarvae catch was related to the river in which sampling occurred, Q on the day of sampling, and whether the fish were sampled at sunrise or sunset.

The coefficients of model 3a fit to sirajo goby data indicated that, with other covariates held constant, recruitment would be expected to be highest at the Río Grande de Manatí, 2nd-highest at the Río Grande de Arecibo, 3rd-highest at the Mameyes River, and lowest at the Sabana River. This model also predicted greater recruit abundances at high mean daily Q and at sunrise (Table 3). The direction of the relationships between recruit abundances, mean daily Q , and sampling time described by model 3a fit to River Goby catches were the same as those for the sirajo goby model, but the relative expected abundances by river differed between the models of the 2 taxa. In the case of the River Goby model, if all other factors were held constant, the highest expected recruit densities would occur at the Sabana River, followed by the Río Grande de Arecibo, then the Mameyes River, and the lowest would occur at the Río Grande de Manatí.

The selected sirajo goby lunar-scale recruitment model describes 2 peaks in sirajo goby recruitment of very different amplitudes during each lunar cycle (Fig. 2A). The primary peak in sirajo goby recruitment is centered on the 23rd lunar day and spans days 20–28 of the lunar cycle. The location of the primary peak in recruitment agrees with nominal mean CPUE values, which were also greatest on the 23rd day of the lunar cycle and were relatively high

on days 22–26, and on day 28 (Fig. 1A). The maximum expected sirajo goby recruit abundances (at sunrise at each river's respective Q) were ~ 30 fish/m³ at the Río Grande de Arecibo and Río Grande de Manatí, almost 3 fish/m³ at the Mameyes River, and nearly 1 fish/m³ in the Sabana River. A secondary peak in sirajo goby recruitment is centered on the 6th lunar day and is much lower in amplitude than the primary peak. Expected recruit abundances at this point in the lunar cycle are < 1 fish/m³ at all rivers. Modeled sirajo goby recruit densities were near 0 at all times in the lunar cycle outside of these 2 peaks in recruitment. In this projection of sirajo goby abundances over the lunar cycle, the values at the Río Grande de Arecibo are slightly greater than at the Río Grande de Manatí, even though the coefficient for

Table 3. Model parameters and coefficients (SD) of sirajo goby and River Goby lunar-scale Poisson periodic regression models. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Parameter	Sirajo goby Model 3a	River Goby Model 3a
Intercept	-12.90 (0.46)***	-5.76 (0.08)***
Cos(θ)	5.52 (0.30)***	-0.29 (0.03)***
Sin(θ)	-1.91 (0.13)***	-0.96 (0.02)***
Cos(2 θ)	-5.14 (0.25)***	-2.10 (0.03)***
River: Mameyes	1.04 (0.38)**	-2.14 (0.09)***
River: Río Grande de Manatí	2.84 (0.37)***	-3.25 (0.09)***
River: Río Grande de Arecibo	2.51 (0.37)***	-0.83 (0.08)***
Sunrise–sunset: sunrise	3.54 (0.15)***	2.67 (0.04)***
Discharge	0.43 (0.03)***	1.08 (0.01)***
Pseudo- R^2	0.62	0.55

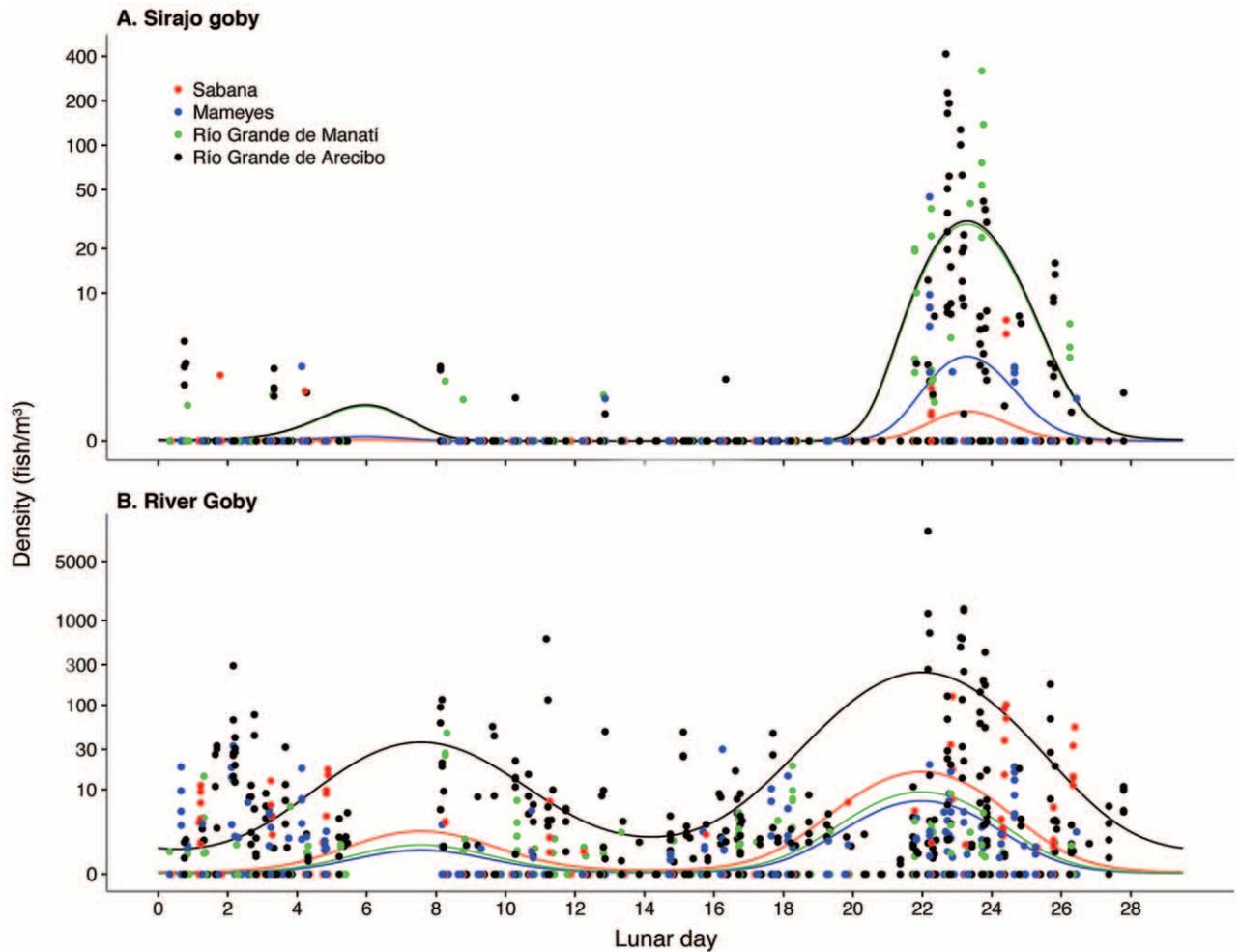


Figure 2. Modeled (lines) recruit abundances and observed catch-per-unit-effort (CPUE; points) for sirajo goby (A) and River Goby (B) over the lunar cycle for all 4 rivers. The model values are the expected catch from 1 m³ of water at sunrise at each river's respective mean discharge value.

the Río Grande de Manatí is slightly greater. This difference arose from differences in Q , which was greater in the Río Grande de Arecibo than in the Río Grande de Manatí.

The selected model of River Goby recruitment at the lunar scale describes a pattern similar to that of lunar-scale sirajo goby recruitment because there are 2 peaks in recruitment of very different amplitudes during each lunar cycle (Fig. 2B). However, both peaks were wider than those modeled for sirajo goby, and the expected mean recruit densities at the Río Grande de Arecibo were >1 fish/m³ throughout the lunar cycle. The primary peak in River Goby recruitment was centered on the 22nd lunar day. Maximum expected recruit abundances at the Río Grande de Arecibo were >200 fish/m³, ~ 15 fish/m³ at the Sabana River, and 8 fish/m³ at the Río Grande de Manatí. At the Mameyes River, the river with lowest predicted values at mean daily Q , recruit abundances were 6 fish/m³. The secondary peak in River Goby recruitment occurred between the 7th and 8th lunar day. During the secondary peak in re-

cruitment, expected recruit densities at the Río Grande de Arecibo were ~ 35 fish/m³, 2 fish/m³ at the Sabana River, and ~ 1 fish/m³ at the Mameyes River and the Río Grande de Manatí. When projected at mean daily Q values, the expected recruit abundances were highest for the Río Grande de Arecibo and were higher for the Río Grande de Manatí than the Mameyes River. This difference in the strength of the coefficients was a result of the effect of mean daily Q on the modeled values.

Annual-scale recruitment phenology

Model 3a also was selected by AIC as the best model to describe both sirajo goby and River Goby catch at the annual-scale. The pseudo- R^2 values of the annual-scale sirajo goby and River Goby models were 0.48 and 0.54, respectively, which indicated substantial predictive ability of these models (Table 4). All model terms for both species were significant ($\alpha = 0.01$), so the recruit abundances of

Table 4. Model parameters and coefficients (SD) of sirajo goby and River Goby annual-scale Poisson periodic regression models. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Parameter	Sirajo goby model 3a	River Goby model 3a
Intercept	-5.89 (0.32)***	-7.55 (0.12)***
Cos(2θ)	1.37 (0.05)***	2.88 (0.04)***
Cos(θ)	-0.10 (0.02)***	-1.24 (0.01)***
Sin(θ)	-2.11 (0.09)***	-5.50 (0.08)***
River: Río Grande de Arecibo	1.97 (0.10)***	1.83 (0.06)***
Sunrise–Sunset: Sunrise	4.31 (0.29)***	3.90 (0.08)***
Discharge	0.24 (0.04)***	0.48 (0.02)***
Pseudo- R^2	0.48	0.54

postlarvae of both goby taxa had significant annual periodicity and were affected by the river, whether samples were taken at sunrise or sunset, and mean daily Q values. The coefficients of these models indicated the same direction of effects of sunset vs sunrise and discharge on recruit abundances of both species that were found at the lunar scale. These models also predicted greater recruit abundances of both taxa at the Río Grande de Arecibo than at the Mameyes River.

The sirajo goby and River Goby annual-scale models described patterns of recruitment in which postlarval densities were relatively low from late January through June and relatively high from July through December. Modeled sirajo goby densities were <5 fish/m³ from day 27 (January 26) to day 152 (May 31) in the Río Grande de Arecibo and <1 fish/m³ from days 12 (January 12) to 166 (June 15) in the Mameyes River. River Goby densities were expected to be <5 fish/m³ from day 10 (January 11) to day 156 (June 4) in the Río Grande de Arecibo and <1 fish/m³ from days 361 (December 26) to 164 (June 13) in the Mameyes River. Models of both taxa described 2 distinct peaks of recruitment within the July–January period of elevated recruitment. The highest peak in recruitment of both taxa occurred during late July, and the secondary peak occurred during late December for sirajo goby and late November for River Goby. Maximum sirajo goby recruitment was modeled to occur on day 204 (July 23) with a mean density of sirajo goby postlarvae of 41 fish/m³ in the Río Grande de Arecibo and 3 fish/m³ in the Mameyes River. Maximum River Goby recruitment was modeled on day 207 (July 27) with a mean density of River Goby postlarvae of 567 fish/m³ in the Río Grande de Arecibo and 31 fish/m³ in the Mameyes River. The secondary peak in sirajo goby recruitment was centered on day 341 (December 7). The modeled mean density of sirajo goby postlarvae at this time was 34 fish/m³ at the Río Grande de Arecibo and almost 3 fish/m³ in the Mameyes River. The secondary peak in River Goby recruit-

ment was centered on day 330 of the year (November 25); the modeled mean density of River Goby postlarvae at this time was 64 fish/m³ in the Río Grande de Arecibo, and 3 fish/m³ in the Mameyes River.

The annual postlarval recruitment cycles of Puerto Rican gobies appeared to be associated with long-term precipitation. Mean daily rainfall in Puerto Rico is generally relatively high from April through December and is low through the rest of the year (Fig. 3A). Increases in recruitment of both gobies began ~60 to 90 d after a notable increase in mean daily rainfall. Recruitment began to taper shortly after mean daily rainfall began to decrease, and was low during the months of lowest rainfall (Fig. 3B, C).

Length- and age-at-recruitment

The length- and age-at-recruitment of 499 individuals from the 4 native gobioid taxa varied widely within and among taxa (Table 5). Sirajo goby was by far the largest of the 4 taxa at the time of recruitment (TL = 21.9 ± 1.8 mm [SD]); the minimum observed length of sirajo goby was greater than or equal to the maximum length of the other 3 taxa. Sirajo goby also varied the most in size. It had the largest standard deviation and largest size range of any taxon measured. Smallscaled Spinycheek Sleeper was the 2nd-largest taxon at recruitment (15.8 ± 0.7 mm), River Goby was 3rd largest (14.9 ± 0.8 mm), and Bigmouth Sleeper recruited at the smallest size (12.5 ± 0.6 mm). Smallscaled Spinycheek Sleeper was the oldest of the 4 taxa at recruitment (mean age = 65 ± 11 d). Their mean age-at-recruitment and range of ages at recruitment were similar to those of River Goby (64 ± 9 d). Sirajo goby was the 3rd oldest (59 ± 10 d) of the 4 taxa at the time of recruitment, and Bigmouth Sleeper recruited at the youngest age (43 ± 7 d).

The estimated hatch dates of individuals of all 4 taxa spanned a substantial period of the year, but the range of hatch day of year varied by taxon (Table 5). The earliest estimated hatch date was in May for all taxa except River Goby, and the latest estimated hatch date was in late November or early December for all taxa except Bigmouth Sleeper. The range of estimated hatch day of year was between 343 d for River Goby and 118 d for Bigmouth Sleeper. The ranges of estimated hatch day of year were intermediate for Smallscaled Spinycheek Sleeper (218 d) and sirajo goby (199 d).

DISCUSSION

We are the first investigators to quantify postlarval recruit abundances of all members of an island stream amphidromous fish assemblage while estimating the length- and age-at-recruitment of the most abundant taxa. Gobies exhibited strong annual and lunar periodicity in recruitment to rivers and were more abundant at the postlarval stage than other members of Puerto Rico's amphidromous

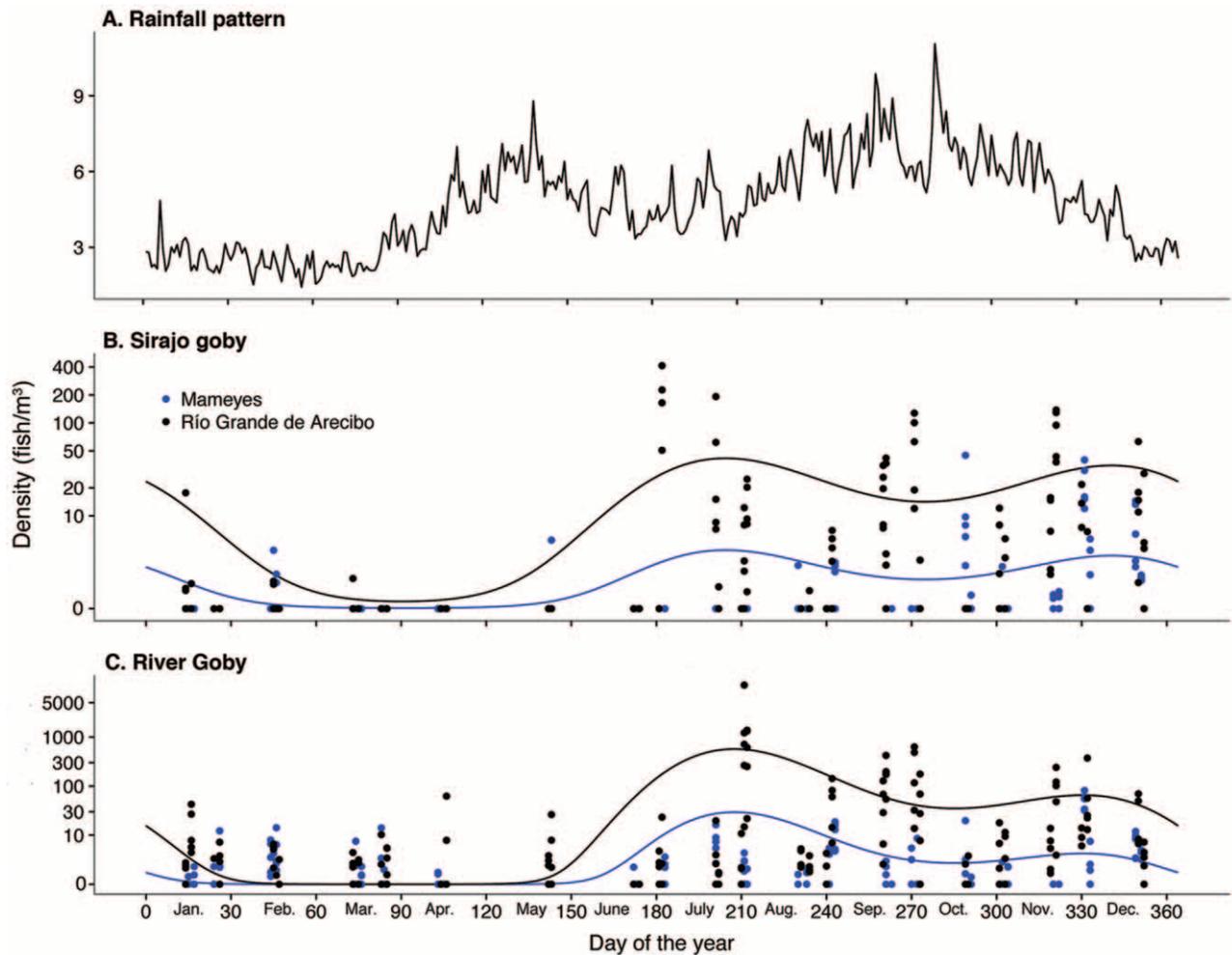


Figure 3. A. Mean daily rainfall for Puerto Rico averaged across all available gages from a historic record including 1950 to 2016 (Menne et al. 2012). Modeled (lines) recruit abundances and observed catch-per-unit-effort (CPUE; points) for sirajo goby (B) and River Goby (C) over 1 y for 2 rivers. The model values are the expected catch from 1 m³ of water at sunrise, at each river's respective mean discharge value.

fish assemblage. Length- and age-at-recruitment showed variation within and among amphidromous fish taxa, suggesting plasticity of pelagic larval duration.

Lunar-scale periodicity in recruit abundance

Maximum recruitment of both goby taxa occurred toward the end of the lunar cycle (days 21–28), during the time in the lunar cycle known as the last- or 3rd-quarter moon phase. A 2-peak model of lunar periodicity was the best fit to the sirajo goby recruitment data, but almost all sirajo goby recruitment occurred during the last-quarter moon phase, with maximum recruitment around the 22nd to 23rd lunar day. The secondary modeled peak in sirajo goby recruitment that occurred between the new and 1st-quarter moon phases was relatively small, and modeled recruitment at other times in the lunar cycle was near 0. The end of the lunar cycle also was clearly a major time

of recruitment for River Goby postlarvae, but recruitment of this species did not appear to be as restricted to the last-quarter moon phase as that of sirajo goby because the primary peak of River Goby recruitment spanned several days beyond the last quarter. Moreover, substantial River Goby recruit density was predicted at the Río Grande de Arcibo early in the 1st-quarter moon phase, and mean density of River Goby was not modeled to approach 0 at any point in the lunar cycle at this river.

These results corroborate the observations of Erdman (1961), who described mass recruitment episodes of Sirajo Goby postlarvae 2 d after the last lunar quarter began (i.e., 22nd and 23rd lunar day) in Puerto Rico. These findings also generally agree with those of Bell et al. (1995) on the Caribbean island of Dominica, which identified the last lunar quarter as the main period of recruitment for *Sicydium* spp. However, Bell et al. (1995) concluded that maximum *Sicydium* recruitment occurred at a slightly different time

Table 5. Length- and age-at-recruitment estimates including: mean, standard deviation (SD), minimum (min), and maximum (max) observed values for all 4 gobioid taxa. Also shown are the minimum and maximum estimated hatch dates (i.e., calendar dates) and day-of-year (DOY) of hatching.

Variable	River Goby (<i>N</i> = 266)		Sirajo goby (<i>N</i> = 140)		Smallscaled Spinycheek Sleeper (<i>N</i> = 36)		Bigmouth Sleeper (<i>N</i> = 57)	
	Mean (SD)	Min-max	Mean (SD)	Min-max	Mean (SD)	Min-max	Mean (SD)	Min-max
Age (d)	64 (9)	42-103	59 (10)	36-89	65 (11)	47-102	43 (7)	28-66
Length (mm)	14.9 (0.8)	12.9-16.7	21.9 (1.8)	17.8-26.1	15.8 (0.7)	14.3-17.9	12.5 (0.6)	11.4-13.8
Hatch date		2 Jan-11 Dec		15 May-30 Nov		10 May-14 Dec		5 May-31 Aug
Hatch DOY		2-345		135-334		130-348		125-243

in the lunar cycle than in our study of Puerto Rican fish. They observed maximum recruitment 4 d after the last lunar quarter, which is 3 d after the modeled and nominal-mean maxima presented here. The differences between these 2 studies may be attributable to small spatial or interisland variation in recruit timing or to differences in sampling methods (e.g., locations of traps deployed by Bell et al. 1995).

Our research expands on the few prior studies of amphidromous fish recruitment in the Caribbean in several ways. We quantitatively modeled lunar periodicity in recruit abundances, allowing for explicit predictions of migration and recruitment timing. Bell et al. (1995) quantified recruit abundances of *Sicydium* spp. and posited lunar cycling in this taxon, but did not fit a model of lunar periodicity. We also are the first to fit a lunar-periodic model of River Goby recruitment, which demonstrates synchronicity in the lunar periodicity of River Goby and sirajo goby and documents that River Goby postlarvae can reach even greater abundance than sirajo goby postlarvae over lunar and annual temporal scales. Furthermore, even with sufficient sampling, no obvious lunar cycling was revealed for other Caribbean gobioid species.

Lunar periodicity in postlarval recruitment has been established in other species of amphidromous gobies (Nishimoto and Kuamo'o 1997, Hoareau et al. 2007), catadromous eels (Sugeha et al. 2001, Jellyman and Lambert 2003), and coral reef fishes (McFarland et al. 1985, Robertson 1992, Sponaugle and Cowen 1994, Adamski et al. 2011). Plausible adaptive mechanisms of lunar-periodic recruitment include: 1) favorable tidal patterns during settlement, 2) reduced predation risk during nighttime migration on dark moon phases, and 3) reduced predation risk through predator swamping. None of these adaptive mechanisms are mutually exclusive, but we discuss in detail below the plausibility of each of the 3 as a mechanism of the observed lunar periodicity of Caribbean goby recruitment.

Caribbean amphidromous gobies recruit to rivers during neap tides (times of minimum differences between high and low tides), which occur on the first- and last-quarter moon phases. If adaptive mechanism 1 (tidal patterns) led to the lunar periodicities modeled here, then low tidal currents would confer greater recruitment success than high tidal currents. Recruiting when tidal currents are low could be adaptive if strong tidal currents interfere with postlarvae's ability to locate and navigate through a river mouth. Negative rheotaxis is thought to direct upstream migration by postlarvae to adult habitats (Bell 1994, Keith 2003, Keith and Lord 2011), and high flood tides could effectively dampen the river discharge signal that would cause negative rheotaxis, whereas strong ebbing tides may overwhelm the river discharge signal and cause gobies to swim toward shore but not necessarily navigate to a river mouth. The idea that rheotaxis plays a role in successful goby recruit-

ment is further supported by the coefficients of the periodic regression models, which indicate that densities increase with mean daily Q .

At first glance, adaptive mechanism 2 (reduced nighttime predation) seems unlikely to be related to the periodicity of Caribbean amphidromous goby recruitment because maximum ingress occurs when $\sim\frac{1}{2}$ of the moon is illuminated, rather than during the new moon when there is no lunar illumination. However, adaptive mechanism 2 could be partially responsible for the observed peaks in recruitment. For example, Sponaugle and Cowen (1994) speculated that mechanisms 1 and 2 may have worked in concert to yield maximum recruitment on the last-quarter moon phase in 2 reef gobies near Barbados. They reasoned that because the last-quarter moon rises later in the night than the first-quarter moon, coinciding darkness during early evenings and neap tides could create optimal conditions for settlement on reefs. Amphidromous goby recruitment was greater at sunrise than sunset in our study. Thus, more postlarvae probably make the transition from ocean to river habitats late in the night when the moon has already risen, which does not lend evidence to adaptive mechanism 2. However, if amphidromous gobies face substantial predation pressure from visual predators in nearshore areas of the ocean during an early-night approach to the river mouth, then adaptive mechanism 2 could lead to this lunar periodicity. Adaptive mechanism 2 also gains credence when one considers the migration of these gobies beyond river ingress. After ingress (i.e., entering a river mouth), goby postlarvae undergo rapid metamorphosis to juveniles and continue upstream migration to adult habitats, which can be as far as 84 km from the river mouth and 702 m asl in Puerto Rico (Kwak et al. 2007). The ideal habitats for goby species may be stream locations above natural barriers (e.g., waterfalls) that reduce or exclude predatory species (Cooney and Kwak 2013). Relatively little is known about the duration or diel patterns of upstream migration after river ingress, but if migration occurs at night over the 7 to 14 d following river ingress, then adaptive mechanism 2 could be influential because lunar illumination continues to decrease for ~ 1 wk, and maximum lunar illumination is not reached until 2 wk following peak ingress.

By parsimony, adaptive mechanism 3 (predator swamping) seems most likely to contribute to lunar synchrony because it would require only that the moon function as a cue for mass migration and a Hollings type-II interaction with river-mouth predators (Ims 1990). Moreover, diet sampling associated with our study (Engman 2017) and observations by other scientists (e.g., Clark 1905) indicate that goby postlarvae undergo intensive predation by wading birds and fishes. Fishes that were observed preying on goby postlarvae during these mass-recruitment episodes included Bigmouth Sleeper, American Eel, Mountain Mullet, Burro Grunt (*Pomadasys crocro*), and multiple species of snook

(*Centropomus* spp.). Possible freshwater invertebrate predators of amphidromous goby postlarvae include multiple species of predatory *Macrobrachium* shrimps and the Puerto Rican freshwater crab *Epilobocera sinuatifrons*.

Full understanding of the adaptive mechanisms that drive patterns of lunar periodicity in amphidromous goby recruitment would require additional investigation. However, regardless of the drivers of lunar periodicity, the conclusion is firm that the last-quarter moon phase is a key time for the population dynamics, conservation, and management of amphidromous fishes in Puerto Rico. Furthermore, the agreement among our study, the findings of Bell et al. (1995) on Dominica, and general fisher anecdotes (reviewed by Bell 1999) enable further generalization of this conclusion to state that the last-quarter moon phase is a key time for populations of amphidromous gobies throughout the Caribbean.

Annual-scale periodicity in recruit abundance

Our findings also demonstrate annual periodicity in the recruitment of amphidromous gobies to Puerto Rican rivers during the last-quarter moon phase. Sirajo goby and River Goby have a high-recruitment season from approximately June through January, whereas less recruitment occurs from late January to June. Annual periodic regression models described 2 local recruitment maxima for both taxa within the general recruitment season. For both taxa, the larger of the 2 maxima occurred in July. The secondary peak of recruitment was in December for sirajo goby and November for River Goby. These times might be periods of exceptionally high recruitment within a primary recruitment season, but they also might be simply manifestations of the variability in recruit abundances during last-quarter peaks over the 2 y during which we monitored postlarval densities.

The annual periodicity of Caribbean amphidromous fish recruitment demonstrated in our study corroborates and expands upon the observations by Erdman (1961) and the findings by Bell et al. (1995), who used fishery-dependent data (barrels landed of mixed-taxon catches of amphidromous postlarvae purportedly dominated by *Sicydium punctatum*) as a proxy for postlarval densities to fit an annual periodic regression model. Bell et al. (1995) did not consider multipeak models, but the model they fit and findings they presented described periods of low and high recruitment during approximately the same months as our models (i.e., relatively low recruitment from late January through June and relatively high recruitment from July through January). Similarly, Erdman (1961) described migration runs of postlarval sirajo goby from July through January with the largest runs occurring from September to November. Our results expand on the previous research by demonstrating annual periodicity in sirajo goby recruitment on Puerto Rico with a quantitative, fishery-independent data

set and by demonstrating similar annual periodicity in the recruitment of River Goby.

A probable mechanism underlying annual recruitment periodicity is related to annual patterns of precipitation. Periods of increased goby recruitment coincide with the rainy season in Puerto Rico (Fig. 3A–C). Moreover, a marked increase in recruitment occurred ~60 to 90 d following a notable increase in mean daily precipitation. The period approximates the typical pelagic larval duration of amphidromous gobies in Puerto Rico (Table 1). One reason for greater recruitment success during times of increased precipitation is that river mouths in Puerto Rico are susceptible to blockage by sand berms. For instance, we observed partial-to-complete blockage of the river mouths by sand berms on multiple occasions (especially between January and May) on the Mameyes and Sabana rivers and once on the Río Grande de Arecibo during our study. These berms are formed by ocean wave action and sand deposition and remain in place until a freshwater spate opens them (Negrón-Gonzalez and Cintrón 1979). River flows with sufficient magnitude to remove berms and maintain an open river mouth presumably are more frequent and of greater magnitude during periods of high precipitation. Thus, temporal matching of spawning and recruitment with high-rainfall periods enhances the probability that the river mouth will be open during larval export to the ocean and subsequent postlarval ingress to the river. The notion that river flow plays a role in successful recruitment migration is further supported by the significant, positive relationship between goby recruitment and mean daily Q in all periodic regression models presented here.

Length- and age-at-recruitment

Our study provides the first published estimates of the pelagic larval durations of River Goby, Bigmouth Sleeper, and Smallscaled Spinycheek Sleeper, and is the first in which the length- and age-at-recruitment of all gobioid members of an island fish assemblage were estimated simultaneously. River Goby and Smallscaled Spinycheek Sleeper had similar lengths- and ages-at-recruitment, and their pelagic larval durations appeared to be longer than the other gobioid taxa in Puerto Rico (Table 5). Sirajo goby exhibited faster overall larval growth rates than either River Goby or Smallscaled Spinycheek Sleeper because it recruited at younger ages, but larger sizes than River Goby and Smallscaled Spinycheek Sleeper. The observed differences in larval growth rates, lengths-, and ages-at-recruitment in Caribbean gobioids probably are a consequence of phylogenetic differences and follow patterns observed in other tropical island stream fish assemblages. For example, our observation that the pelagic larval duration of *Awaous* species in this Caribbean fish assemblage was greater than that of the sicydiine gobies is analogous to findings from Hawaii streams and estuaries where the

local *Awaous* species had a longer pelagic larval duration than *Lentipes concolor* (a sicydiine goby; Radtke et al. 2001).

Our results also enable direct comparisons with other studies of the pelagic larval duration of *Sicydium* gobies in the Caribbean. The pelagic larval duration of *Sicydium* spp. in our study (59 ± 10 d, range 36–89) is shorter than previous estimates of the pelagic larval durations of *Sicydium* species from Dominica and Guadeloupe. Bell et al. (1995) estimated the mean pelagic larval durations of *S. punctatum* and *Sicydium antillarum* in Dominica to be 83.4 ± 1.3 d (range 54–136) and 86.7 ± 3.4 d (range 63–139), respectively. In Guadeloupe, Lejeune et al. (2016) estimated mean larval duration for a single cohort of *S. punctatum* as 72.2 ± 10.5 d (range 54–102). One possible reason that mean pelagic larval durations in Puerto Rico are shorter than in Guadeloupe or Dominica is that physical oceanographic conditions near the Puerto Rican coast yield more frequent recruitment opportunities for larvae than conditions near smaller islands in the eastern Caribbean. Radtke et al. (2001) indicated that mesoscale circulation features or small-scale physical differences in the freshwater–marine interfaces probably would contribute to spatial variability in pelagic larval duration. Furthermore, Lejeune et al. (2016) suggested that sicydiine gobies may be able to delay recruitment until they reach a stream under optimal conditions, a suggestion supported by the consistent overlap and wide range of observed pelagic larval duration ranges in our study and other observations from throughout the Caribbean.

Conclusions and conservation implications

Our results and analyses identify the last-quarter moon phase during the months from June through January as especially critical periods for Caribbean amphidromous fish population dynamics. During these times, large pulses of amphidromous postlarvae form culturally valuable artisanal fisheries, represent a periodic food source for estuarine and riverine predators, and are a vector for the upstream transport of marine nutrients and energy. These temporal dynamics of fish recruitment clearly identify periods during the year and lunar-cycle when Caribbean natural resource managers could focus on protecting the integrity of stream ecosystems. One clear means to achieve ecosystem integrity during key recruitment periods is to set goals for natural (or similar) in-stream flows because they probably play a role in directing amphidromous migrations and maintaining open migration pathways, which are necessary to complete the complex amphidromous life cycle.

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manuscript preparation. TJK led funding and project administration, collaborated in study design, participated in field work, collaborated in data analysis and interpretation, and participated in manuscript preparation. JRF collaborated in study design, participated in fieldwork, directed and conducted laboratory analyses, compiled and processed data, collaborated in data analysis and interpretation, and participated in manuscript preparation.

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