

# Big runs of little fish: first estimates of run size and exploitation in an amphidromous postlarvae fishery

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**Abstract:** Amphidromous postlarvae fisheries (APFs) constitute a globally widespread and distinctive class of fishery that is largely unknown to fisheries science. APFs harvest ocean-to-river migrating fishes at smaller sizes and younger ages than any other class of fishery. No quantitative estimates of run size and exploitation exist, which are needed to evaluate APF sustainability. Migrating amphidromous fishes are vectors of marine nutrients to estuaries and rivers, and run size quantification is needed to reveal the magnitude of this ecosystem function. We present a novel adaptation of trapezoidal area under the curve methods, which we apply in a Caribbean case study to yield the first simultaneous estimates of an APF run size and harvest. Run size estimates ranged 7.3–9.4 million postlarvae (926–1184 kg), and exploitation estimates (5.8%–7.0%) indicated low harvest in the Río Grande de Arecibo, Puerto Rico. Our representative run size estimates reveal that amphidromous postlarvae transport hundreds of kilograms of biomass per month to an estuary and river, the first empirical evidence that amphidromous migrations are large-magnitude material subsidies of lotic ecosystems.

**Résumé :** Les pêches aux post-larves de poissons amphidromes (PPA) constituent une catégorie de pêches distincte répandue dans le monde entier qui demeure méconnue en sciences halieutiques. Les PPA exploitent des poissons migrant de l'océan vers des rivières de tailles et d'âges moindres que dans toute autre catégorie de pêches. Aucune estimation quantitative de la taille des migrations et du taux d'exploitation n'existe, de telles estimations étant pourtant nécessaires à l'évaluation de la pérennité des PPA. Les poissons amphidromes migrateurs sont des vecteurs de nutriments marins vers les estuaires et les rivières et la quantification de la taille des migrations est nécessaire pour établir la magnitude de cette fonction écosystémique. Nous présentons une adaptation novatrice de la méthode des trapèzes pour déterminer l'aire sous la courbe, que nous appliquons à une étude de cas caraïbéenne pour obtenir les premières estimations simultanées de la taille de la migration et des prises d'une PPA. Les estimations de la taille de la migration vont de 7,3 à 9,4 millions de post-larves (926–1184 kg) et les estimations des taux d'exploitation (5,8 % – 7,0 %) indiquent de faibles prises dans le Río Grande de Arecibo (Puerto Rico). Nos estimations représentatives de la taille de la migration révèlent que les post-larves amphidromes transportent des centaines de kilogrammes de biomasse par mois vers un estuaire et une rivière et constituent ainsi les premières preuves empiriques des importants apports de matières dans les écosystèmes lotiques que représentent les migrations amphidromes. [Traduit par la Rédaction]

## Introduction

Amphidromous postlarvae fisheries (APFs) are globally widespread and harvest fish at smaller sizes and younger ages than any other class of fishery. APFs target 15- to 50-mm total length (TL) gobioid and galaxiid postlarvae at mean ages of 2–7 months during lunar- and annual-cyclic ocean-to-river mass-recruitment events (Bell et al. 1995; Hoareau et al. 2007; Lejeune et al. 2016; Engman 2017). APFs occur where amphidromous fishes are prevalent — a global distribution that includes the rivers and streams of tropical islands, major island archipelagos such as Japan and New Zealand, and the steep-sloped coastal regions of South and Central America and Australia (McDowall 2007). In contrast with the small size of the target taxa, APF harvests and economic and cultural value can be large. For example, a total harvest of 20 000 t·year<sup>-1</sup> was estimated for a widespread gobioid APF in the Philippines (Bell 1999), galaxiid whitebait in New Zealand sell for up to NZ\$145·kg<sup>-1</sup> (McDowall 2007), and postlarvae are commonly a

delicacy food item associated with local cultural identity (e.g., Collazo et al. 2019).

Despite their unique nature, global occurrence, and cultural importance, APFs are largely unknown to fisheries science. APFs have been labeled unsustainable (Keith 2003), but without any previous quantification of exploitation rates or stock assessments, it remains unknown whether these unique, largely artisanal fisheries appreciably deplete fish populations. A limited number of descriptive studies and estimates of total harvest in specific APFs have been published (Bell 1999; Castellanos-Galindo et al. 2011; Jiménez-Prado 2014), but no quantitative estimates of the total abundance of an amphidromous fish mass-recruitment event (i.e., run size) appear in the literature. Simultaneous quantitative estimates of harvest and run size are required to estimate exploitation rates, determine the impact of APFs on populations, and to set appropriate regulations for sustainable harvests.

Quantification of postlarvae run sizes is also needed to determine the role of amphidromous migrations in ecosystem functioning.

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The cross-ecosystem nutrient biotransport function of postlarval migration was recently demonstrated (Engman et al. 2018), and the apparent magnitude of mass-recruitment events implies that this influx of biomass from the ocean could subsidize estuary, river, and stream food webs (Jenkins et al. 2010). Postlarval recruits are an important forage for American eel (*Anguilla rostrata*) and other freshwater and estuarine predator fishes during mass-migration events. However, quantitative estimates of the magnitude of amphidromous fish migrations (i.e., biomass) are needed to determine their importance as a material subsidy to inland aquatic ecosystems (Flecker et al. 2010; Engman 2017; Engman et al. 2017a).

The trapezoidal area under the curve method (TAUC) has been widely used to estimate salmon spawner abundance (i.e., run size) and escapement. The application of this method has never been extended beyond salmon fisheries to other exploited diadromous fishes, and a method to estimate these parameters for APFs is needed. The first step of the TAUC method is to develop an abundance curve by plotting abundance data (i.e., periodic visual spawner counts in the case of salmon) over time (i.e., sampling day for spawner counts). The abundance curve can also be modeled as a Gaussian or Poisson distribution or as a multimodal smooth curve using regression splines, which produces a measure of the precision of the total abundance estimate (Millar and Jordan 2013). Next, the area under the abundance curve (AUC) is calculated by summing the area of a series of trapezoids, defined by linear interpolation of the periodic counts or model-predicted abundances on the abundance curve. The total abundance of a run is then obtained by dividing the AUC by the product of the residence time in the sampling area and an estimate of observer efficiency.

In this study, we present the adjustments necessary to apply the TAUC method to estimate the numerical abundance and biomass of an amphidromous postlarvae fish mass-migration event. Our methodology is illustrated through a case study that applies fishery-independent and -dependent data from a key river for the Puerto Rico APF to produce the first simultaneous estimates of escapement, run size, and exploitation of an APF. This methodology could be applied by other researchers to obtain valid estimates of amphidromous fish run size and fishery exploitation, which will serve to reveal the ecosystem functions and services of a group of globally prevalent, but largely overlooked, diadromous species.

**Methods**

**Introduction to TAUC**

The TAUC method estimates the number of upstream-migrating fish that escape a downstream fishery by approximating the integral of the curve of fish abundance over the migration period in a study area (English et al. 1992). The fish abundance curve comes from periodic counts of fish in the area of interest over the entire migration period, and the integral is approximated (i.e., AUC) with linear interpolation between observations ( $t_i, c_i$ ), where  $t_i$  is a survey time (typically expressed as a day for salmon) and  $c_i$  is the count of fish at the  $i$ th sample time (Fig. 1; Millar and Jordan 2013):

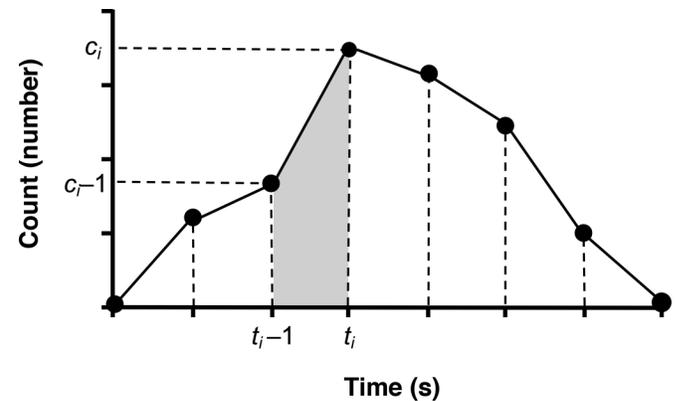
$$(1) \quad \hat{F}_T = \sum_{i=2}^{n-1} (t_i - t_{i-1}) \frac{c_i + c_{i-1}}{2}$$

where  $\hat{F}_T$  denotes TAUC, which is the number of fish-unit-of-time (usually fish-days for salmon). To estimate escapement ( $\hat{E}$ ), we adjusted the AUC for residence time, defined as the number of units of time that a fish is alive ( $l$ ) in the area of interest and, when available, fish detection probability, which is often referred to as observer efficiency ( $v$ ):

$$(2) \quad \hat{E} = k\hat{F}$$

where  $k = 1/(lv)$ .

**Fig. 1.** Generalized postlarval run curve, in which  $t$  is the survey time,  $c$  is count of postlarvae at a given survey time, and the shaded area is one trapezoidal area under the abundance curve in postlarvae-seconds.  $\hat{F}_T$  is the summation of all trapezoidal areas. The quotient of  $\hat{F}_T$  and residence time yields an estimate of escapement ( $\hat{E}$ , the number of postlarvae to ascend the river).



Several adjustments were made to the parameter estimations used in past studies of salmon fisheries to adapt the TAUC method to estimate the escapement of an APF. First, a distinct time step was required because of inherent differences in run duration, migration behavior, and sampling methods used for the two taxa. Salmon runs may last for 100 days or more, and counts come from visual surveys that estimate the number of fish in an area of interest on a given day, resulting in  $F_T$  calculations in the unit of fish-days (Hilborn et al. 1999). Time steps of hours or seconds are more appropriate for amphidromous fishes because amphidromous postlarvae runs can occur over time scales as short as 1 to 3 days, and abundances vary widely over short periods of time (Engman et al. 2017b). Visual surveys to count postlarvae are impractical because of their small size and transparent bodies, so active or passive capture gears are used to obtain counts of fish in an area of interest. The active capture gear utilized in this study yields a nearly instantaneous estimate of fish abundance so the time points ( $t_i$ ) are expressed in seconds, and the estimates of  $F_T$  are in the unit of fish-seconds, rather than fish-days. Migrating amphidromous postlarval fishes are best sampled where they are continuously moving upstream through the freshwater-marine transition zone. Therefore, the residence time ( $l$ ) in the area of interest was estimated by directly measuring swimming speed in the river. Further, because no estimates of the capture probability of gears used to sample amphidromous fishes is available,  $v$  is assumed to equal 1, and the correction factor ( $k$ ) is simply  $1/l$ .

An escapement estimate and its precision can also be obtained by developing a model where abundance is the response variable and time is a predictor variable. The abundance curve is constructed by modeling the structural signal of the counts over time with a smooth curve, such as a Gaussian or more flexible regression splines. With this approach, the variability of the escapement estimate can also be estimated from the variability of the model (Millar and Jordan 2013). The area under the modeled curve can be calculated with eq. 1, where  $c_i$  is a model-expected count over the entire time period of the run. Each model-predicted count has an associated error estimate  $\widehat{\text{var}}(c_i)$ , and the precision of the overall escapement estimate can be determined with

$$(3) \quad \widehat{\text{var}}(\hat{F}_T) = 0.25 \sum_{i=2}^{n-1} (t_i - t_{i-1})^2 \widehat{\text{var}}(c_i)$$

Amphidromous fish run curves are often multimodal and asymmetric with extreme changes in abundance over short timescales,

so modelling using flexible regression splines and overdispersed error distributions are broadly appropriate.

### Study system

This study was conducted at the mouth of the Río Grande de Arecibo (RGA), Puerto Rico (18.473°N, 66.711°W; Fig. 2A), the location where this single-channeled river flows into the Atlantic Ocean. The RGA watershed is ~997 km<sup>2</sup>, and its geology is mixed karst and volcanic origin (Zamora et al. 1986). The RGA river mouth location experiences mixed semidiurnal tides (tidesandcurrents.noaa.gov). The RGA receives regular and relatively large mass-recruitment pulses, or runs, of sirajo goby (*Sicydium* spp.) that are tightly synchronized with the lunar cycle. Specifically, 2- to 3-day duration sirajo goby postlarvae runs occur during the last quarter moon phase in rivers throughout the Caribbean, recruitment is annually cyclic, and the largest recruitment events occur from June through January (Engman et al. 2017b).

The RGA mouth is one of the most important locations for the Puerto Rico APF. The city of Arecibo identifies itself as “The Capital of Ceti” with roadside signs, ceti being the colloquial term for goby postlarvae. Puerto Rican ceti fishers prefer sirajo goby postlarvae over the other native gobioids because of their relatively large size (E. Camello, artisanal fisher, personal communication, 2014). They target sirajo goby at river mouths, a pinch-point for migrating postlarvae, and on the adjacent beach habitat. The most commonly used gears in this fishery are made from fine-mesh mosquito netting, which is typically pulled like a seine by two people, or fashioned into a dip net with a frame and handle for solo fishing.

### Postlarvae abundance

Sirajo goby postlarvae were sampled at the RGA river mouth throughout the duration of the July 2015 mass-recruitment event (ceti run). Prior knowledge and experience with sirajo goby postlarvae run timing was used to design a sampling schedule that provided full coverage of the run with sufficient sample frequency to accurately describe changing densities. Sampling began at 0600, 8 July 2015, and was conducted again at 1900; then from 0030, 9 July to 0630, 11 July sampling occurred every 3 h. On each sampling occasion, five net haul samples were collected for a total of 21 sampling occasions and 105 individual samples of postlarvae abundance over 72 h.

The sampling location and methods were selected to accurately quantify postlarvae abundance throughout the run. The sampling area was a 20 m section of the shallow and low-gradient side of the river mouth, chosen because rather than using the entire river cross-section, recruiting postlarvae are known to migrate in columns along shallow banks of rivers (Erdman 1961; Fig. 2A). The sampling area was located adjacent and directly upstream of the ceti fishery to minimize interference of fishing activities with samples of postlarvae density and to ensure that our estimates of escapement accounted for fishery harvest. Postlarvae were sampled with a 1 m × 1 m benthic kick net with 1 mm nylon mesh, fitted with wooden brails and a bottom lead line. For each sample, a two-person team pulled the net toward shore perpendicular to the bank with the net positioned at a 45° angle and the lead line ahead lightly scraping the substrate (Fig. 2B). The depth of the starting point of each net haul and its distance from shore were measured to calculate the two-dimensional swept area of the water column using the equation for the area (*A*) of a triangle, where the distance from shore is the height (*h*) and the depth (*b*) of the starting point is the base:

$$A = 0.5bh$$

The total volume of water sampled (i.e., sampling effort) was obtained by multiplying *A* by the width of the kick net (1 m). This method was shown to be an effective and accurate way to quantify the abundance of migrating postlarvae by Engman et al. (2017b). Furthermore, because kick-net samples of postlarvae were

conducted rapidly, they allow for efficient estimation of changing densities at a fine temporal scale, which was critical to this study. The first net haul of each sampling occasion was conducted at the downstream end of the sampling area, and subsequent net-haul starting locations were moved incrementally upstream with no overlap between net-haul sweeps. Captured fishes were separated from excess sediment and organic material and preserved in a 10% buffered formalin solution for further processing and identification as described by Engman et al. (2017b).

### Sirajo goby residence time

Sirajo goby residence time was determined from in situ measurements of swimming speed. A GoPro camera (HD 1080p resolution) with a macro lens was used to record video (30 frames·s<sup>-1</sup>) of migrating sirajo goby at the RGA mouth. The camera was oriented perpendicular to the river bed so it filmed the fish laterally as they swam through the sample area, and a ruler was fixed in placed in the back of the frame for length reference. Frame-by-frame video playback was used to measure the swimming speeds of 50 individuals that moved through the field of view. The distance traveled (mm) in the field of view was estimated from the ruler using a correction factor approach to account for parallax error (Stephens et al. 2019). Swimming duration in the field of view was converted to seconds and swimming speeds were calculated. Sirajo goby migrate through the river mouth as a continuously moving column, so residence time was estimated directly from the mean of the measured swimming speeds. Residence time was expressed as the average duration (s) to swim upstream, across the swath of a kick-net sample, which was 1 m (Fig. 2B).

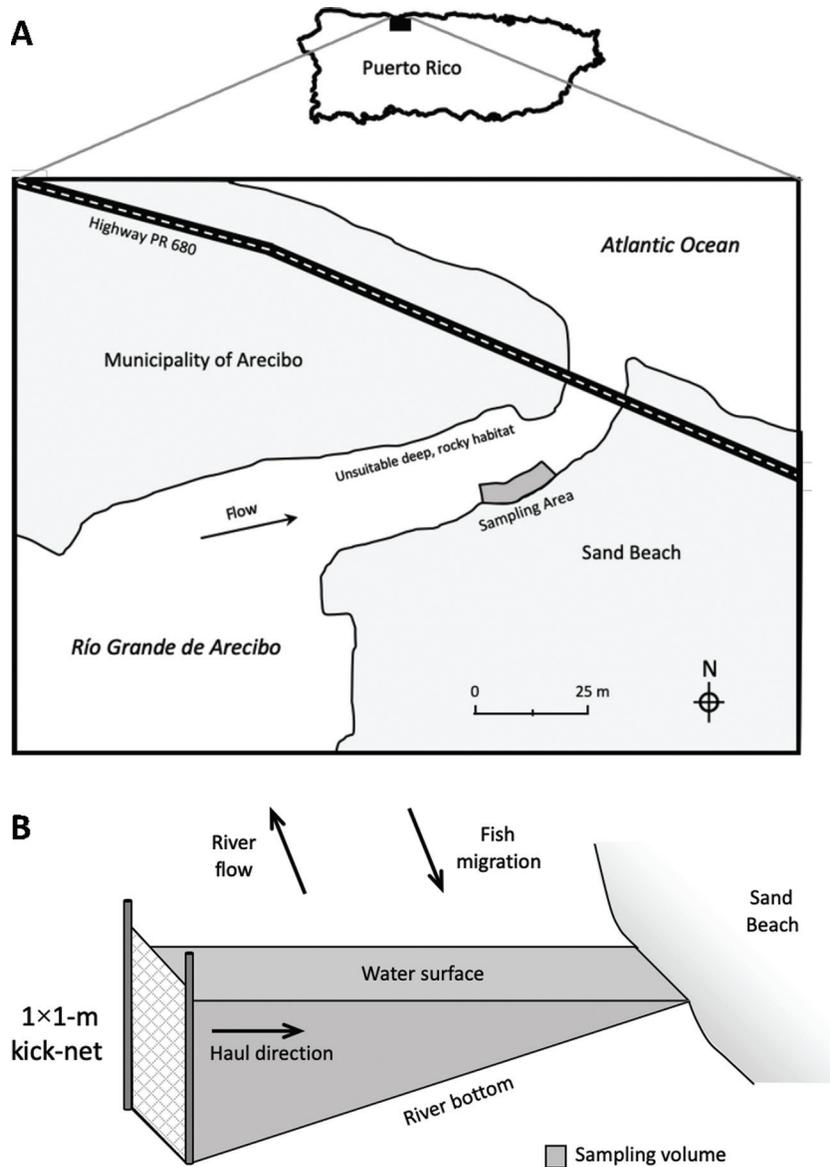
### Harvest census

The number of fishery participants, individual group size, group effort (h), and harvest of ceti (kg) were observed and measured using access-point surveys (Jones and Pollock 2012). Participants in the RGA ceti fishery use a single access point to reach the river mouth and adjacent beach fishing locations. Fishers were observed continuously from the access point from the arrival of the first fishers (0418, 9 July 2015) until the departure of the last fisher at 0630, 11 July 2015. The start and end times of each fishing trip were recorded for each group or individual ceti fisher to determine fishing effort (h). The total wet weight of the catch was measured to the nearest 0.1 kg at the termination of each fishing trip. Samples of the catch were obtained from four of the fishing groups to determine the ratio of whole catch wet weight to the number of individual sirajo goby harvested. Each sample was weighed to the nearest 0.01 g, preserved, and enumerated following the methods used for our kick-net catch, detailed by Engman et al. (2017b). To estimate the total number of sirajo goby individuals harvested, we summed and multiplied all catches by the mean number of sirajo goby per gram wet weight of the catch samples.

### Escapement and run size

The areas under two abundance curves were calculated: one from the observed kick-net catch per unit effort (CPUE, fish·m<sup>-3</sup> of water sampled) data and another from a thin-plate regression spline model. To develop abundance curves, we aggregated (summed) catch and effort each by sampling occasion. This step provided a comprehensive assessment of postlarval abundance in the sampling area, without adding variance due to sampling error and spatial variation. The observed data abundance curve was constructed by plotting the CPUE (i.e., summed catches divided by the total effort) against the median time of each sampling occasion. Then eq. 1 was applied to estimate *F<sub>T</sub>* (i.e., AUC, fish·seconds), where *c<sub>i</sub>* was the CPUE value (count of fish·m<sup>-3</sup>) and *t<sub>i</sub>* was the median time of the 21 sampling occasions.

**Fig. 2.** (A) Map of the Río Grande de Arecibo river mouth with the location of the postlarvae kick-net sampling upstream of the area of the active postlarvae fishery identified (map modified from Google Earth; Google Earth 2020). (B) Diagram depicting the postlarvae kick-net sampling procedure, with the sampling volume (dark gray area) calculated as one-half of the product of the water depth and distance from shore at the haul starting point (see Methods for additional detail); residence time was determined from measured swimming speeds and was calculated as the time for a postlarva to cross the 1 m swath of the kick net.



The regression spline abundance curve was derived from a generalized additive model (GAM) in which the aggregated sirajo goby kick-net catch was modeled as a smooth function ( $s$ ) of time with an offset of effort, which was the  $\log_e$  of the total volume of water sampled per sampling occasion:

$$(4) \quad \text{Catch} \sim s(\text{time}) + \text{offset}(\text{effort})$$

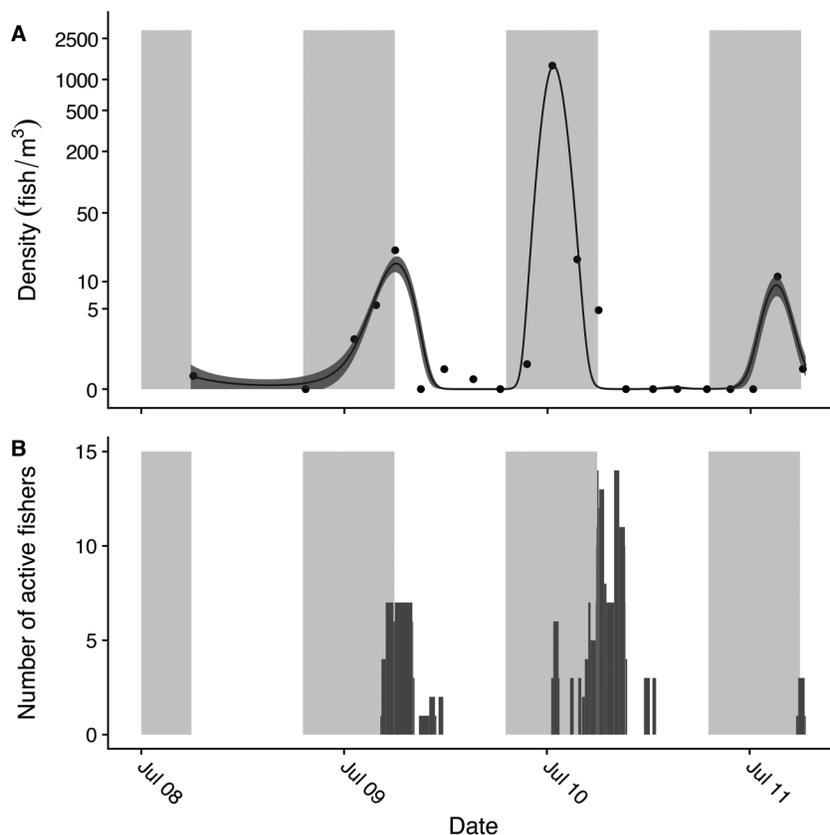
Sirajo goby postlarvae catch data were over-dispersed and were modeled with a quasi-Poisson error distribution and a log-link function in R software (version 3.3.1; R Core Team 2016) using the package “mgcv” (Wood 2015), which produces maximum likelihood estimates of the optimal smoothing parameters for thin plate splines. The resulting GAM was used to predict the expected catch in a  $1 \text{ m}^3$  sample at 1 s intervals over the entire sampling period. The mgcv package also yields error estimates of each

predicted value from the Bayesian posterior variance–covariance matrix. The resulting series of  $c_i$  (the expected catch) and  $\text{var}(c_i)$  (the corresponding expected variance) were used to estimate  $F_T$  and its total standard error. The areas under the abundance curves (fish-seconds) were calculated with the auc function in the “mess” package of R, which applies eq. 1 (Ekström 2019).

Escapement was estimated using the  $F_T$  values detailed above, the in situ measurements of swimming speed, and by extrapolating estimates to the maximum volume of water sampled. The total abundance of sirajo goby that migrated through a  $1 \text{ m}^3$  volume of the channel was calculated by dividing  $F_T$  by the residence time. The maximum volume of water sampled with a kick-net haul was  $2.9 \text{ m}^3$ , and sirajo goby postlarvae were captured in that sample. Thus, it was conservatively assumed that this river channel volume represented the entire migration corridor utilized

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**Fig. 3.** July 2015 Río Grande de Arecibo sirajo goby postlarvae run and fishery activity. Shaded columns represent nighttime periods. (A) Sirajo goby postlarvae abundance. Points represent observed catch per unit effort as an estimate of density from kick-net sampling, and the smooth curve is the regression spline model-predicted abundance. The shaded area around the curve represents standard error of the model. The y axis is on the  $\log_{10}$  scale for ease of interpretation. (B) Temporal allocation of postlarvae fishing effort. Dark bar height represents the total number of active fishers present at the time interval encompassed by bar width.



by sirajo goby (Fig. 2), and total escapement was calculated by extrapolating the  $1 \text{ m}^3$  estimates to  $2.9 \text{ m}^3$ . No estimate of the sampling efficiency of our gear is available, so 100% capture efficiency was assumed. Wet-weight escapement biomass was calculated by multiplying escapement estimates by the mean sirajo goby wet weight. The run size was calculated by summing harvest and escapement estimates.

## Results

### Run timing and abundance curves

The July 2015 RGA sirajo goby postlarvae run occurred over three nights, 8–9, 9–10, and 10–11 July, for a total duration of  $\sim 72$  h (Fig. 3). The multimodal abundance curve reveals a clear diel cycle of ingress; sirajo goby density peaked each night between midnight and sunrise, sharply decreased around sunrise, and was low or zero through the middle of the day. The model explained 98.9% of the deviance in the catch data and the smooth term was significant ( $p < 0.001$ ). Sirajo goby density was greatest around midnight (0042) on 10 July, when the CPUE was  $1353.1 \text{ fish}\cdot\text{m}^{-3}$ . Modeled and observed peaks in recruitment occurred  $\sim 4.8$  h after the nighttime high tide on the first night of the run and  $\sim 1.5$  h before the nighttime high tide on the second night of the run and coincided with the nighttime high tide on the third night of the run (Table 1).

### Harvest

The cetí fishery was active over the 50 h period of the three nights of the run, and fishers harvested a total 64.7 kg of sirajo goby postlarvae. Fishing began at 0418 on 9 July, the last catch was made by 2130 on 10 July, and all fishing effort concluded at

0630 on 11 July. Fishing was conducted by single fishers or groups of two to four fishers (mean  $\pm$  SD group size =  $2.3 \pm 0.9$  fishers), a total of 26 group fishing trips were observed with a mean effort of  $1.46 \pm 1.22$  h and a mean catch of  $2.49 \pm 5.63$  kg. All fishers allowed us to measure their catch. The greatest catch of a single trip was 21.0 kg by a group of three who fished for 4.42 h beginning at 0454 on 10 July. The second greatest catch of a single trip was 18.0 kg by a group of three who fished for 52 min beginning at 0031 on 10 July. We counted a mean of  $7.9 \pm 0.2$  sirajo goby per gram of catch ( $0.13 \pm 0.0$  g mean weight per postlarva) and estimated that 512 278 sirajo goby postlarvae were harvested during this run (Table 2).

Fishing effort at the RGA mouth was intermittent with effort allocated disproportionately to periods of greatest abundance. Fishing trips were most frequently initiated in dark hours between sunset and sunrise, and fishers often terminated trips if they perceived relatively low catch rates. This behavior resulted in 50% (13 of 26) of trips terminated with no catch. Between trips on the RGA, fishers reported that they rested or visited adjacent rivers, such as the Río Grande de Manatí, where they also fished for sirajo goby postlarvae.

### Residence time

Sirajo goby mean  $\pm$  SD swimming speed was  $202 \pm 97 \text{ mm}\cdot\text{s}^{-1}$ , and the median speed was  $182 \text{ mm}\cdot\text{s}^{-1}$ . The residence time in our 1 m wide sampling area was 4.9 s. In situ observations and review of video indicated that sirajo goby generally swam in a straight line, and there was no indication that fish altered their swimming speed as they passed a laterally placed camera.

**Table 1.** Times of the nocturnal and diurnal high and low tides, respectively, and peaks in postlarvae recruitment as indicated by the time of maximum observed sirajo goby catch per unit effort (CPUE) and model-predicted maximum sirajo goby densities for three nights of a postlarvae mass-recruitment event.

Date	Nighttime high tide		Daytime low tide		Peak recruitment time	
	Time	Mean level (m)	Time	Mean level (m)	Modeled	CPUE
9 July	0123	0.26	0801	-0.22	0607	0600
10 July	0214	0.15	0847	-0.25	0042	0034
11 July	0307	0.17	0934	-0.28	0302	0311

**Table 2.** Estimates of sirajo goby escapement and total run size expressed as the number of individual fish and total biomass obtained using two abundance curves: one from observed catch per unit effort (CPUE) and the other modeled using thin-plate regression splines.

Estimator	Escapement		Run size		Harvest		
	No. of individuals	Biomass (kg)	No. of individuals	Biomass (kg)	No. of individuals	Biomass (kg)	Exploitation (%)
CPUE	8 865 773	1 119.7	9 378 051	1 184.4			5.8
Model	6 821 780 (2 536)	861.6 (0.3)	7 334 058	926.3	512 278	64.7	7.0

**Note:** Harvest was estimated by a census of all participating fishers and are independent of the escapement estimates. Fishery exploitation rates were calculated separately from the two estimators (i.e., CPUE and model). Numbers in parentheses are standard error values.

### Escapement, exploitation, and run size

The July 2015 RGA sirajo goby run was of large magnitude, and most of the run escaped the fishery (Table 2). The escapement estimate derived from CPUE data was 23% higher than the estimate from the GAM, but both methods resulted in similarly high-magnitude run size estimates and low-magnitude exploitation rates. The CPUE-derived escapement estimate was nearly nine million individual sirajo goby and just over 1000 kg of biomass, while the estimates derived from the GAM were close to seven million individuals and just under 900 kg biomass. The GAM model escapement estimate was very precise, with standard error estimates of ~2.5 thousand individuals and 0.3 kg biomass. Both estimation methods resulted in exploitation rates less than 10%; specifically, estimates derived from CPUE and the GAM were 5.8% and 7.0%, respectively. Using both escapement estimates as bounds for an overall run size estimate, it can be surmised that between 7.3 and 9.4 million sirajo goby, representing between 900 and 1200 kg of biomass, migrated through the mouth of the RGA within a 72 h period during the July 2015 migration event.

### Discussion

Though amphidromous postlarval migrations and salmon spawning migrations are fundamentally similar, until this study, the accepted and often used analytical methods developed for estimating salmon run size (TAUC and its variants) have not been adapted to estimate amphidromous fish run size. Two main modifications were necessary to apply this method to data on an amphidromous fish migration, which resulted in differences in the way parameters were estimated. First, the run was modeled as a continuously moving band of migrants, which allowed for estimates of residence time by directly measuring swimming speed. The other distinction is that our abundance data were obtained from a capture gear rather than visual counts of individuals. Thus, our counts came from multiple kick-net samples and were standardized by area, and our time steps were expressed in seconds, rather than days. Despite these differences in the way parameters were estimated, our data provided quantitative estimates of the magnitude and dynamics of abundance of fish in the river over time, which is fundamentally what is needed to estimate escapement. The methods and analyses employed here should be broadly applicable to estimating run size and harvest of other APFs in globally distributed locations. Similar to sirajo goby, all amphidromous fishes exhibit a continuous upstream migration behavior through river mouths; thus, calculating residence time from swimming speeds should be broadly valid. In relatively small river systems with narrow mouths, like the RGA, the use of a kick net or other active sampling gear to estimate abundance across the

entire migration corridor is likely to be feasible. In larger systems, passive gears such as those used for sampling glass eels (Harrison et al. 2014) may be more appropriate. Finally, the application of GAM and other flexible modelling techniques is especially suitable for application of the AUC method to APFs, because amphidromous postlarvae runs are often multimodal.

Through this adaptation of AUC methodology, we produced the first quantitative abundance estimate for an amphidromous postlarvae fish run, revealing evidence that amphidromous migrations may be large-magnitude material subsidies to inland aquatic ecosystems. Sirajo goby was identified as a biotransport vector of marine nutrients to freshwater ecosystems by Engman et al. (2018), and the current study demonstrates that the biomass moving from the donor (marine) to the recipient (freshwater) ecosystem is relatively large. In an island-wide Puerto Rico survey, Kwak et al. (2013) observed a mean total freshwater stream fish biomass of 76.7 kg·ha<sup>-1</sup>. The estimates presented here indicate that over a 3-day period, greater than 10 times the mean total biomass of all fish in a hectare of river area in Puerto Rico entered the mouth of the RGA. Prior research indicates that the run detailed here was of typical magnitude. Models, developed from 2 years of repeated sample data, predict mean lunar peak densities of sirajo goby within an hour of sunrise at the RGA of ~30 fish·m<sup>-3</sup> (Engman et al. 2017b), which is similar to or greater than the values observed and modeled for that time of day in the present study. Engman et al. (2017b) also demonstrated annual cycles of sirajo goby recruitment and found that relatively large runs of sirajo goby occur from June through January and vary by less than an order of magnitude over this time. Therefore, sirajo goby recruitment is a predictable, large-magnitude (near 1000 kg) pulse of marine biomass to the RGA that occurs on a monthly basis for over half of each calendar year.

The conclusion that the magnitude of upstream migrating biomass was very large relative to fish biomass in the receiving ecosystem holds, even when uncertainty in estimates and potential violations of the assumptions used in calculating our estimates are considered. Our estimate of the standard error of the escapement estimate was very low, and a 95% confidence interval would be less than 1% of the magnitude of the estimate. This estimate of error would be higher if samples of abundance were not aggregated by sampling occasion. However, an error estimate from unaggregated samples would be inflated by sampling error and spatial variation. As with any study that employs the AUC method, our conclusions are sensitive to the estimates of the residence time parameter (i.e., they are directly proportional). However, as recommended by English et al. (1992), our residence

time estimate comes from system-specific empirical measurements that temporally correspond to the run being estimated. The assumption that sirajo goby only migrated where we sampled is reasonable and necessary, because based on our observations and other accounts (Erdman 1961), sirajo goby migrations proceed along the shallow margins of the channel, so extrapolating to the entire channel would likely result in an overestimate of total abundance. If this assumption was violated and a portion of the sirajo goby run migrated through an area of the channel that we did not sample, then we underestimated the magnitude of this run. Violation of our assumption of 100% capture efficiency would also result in underestimation of the run size. Therefore, the results that we presented here should be considered conservative, minimum estimates of the potential magnitude of material subsidy provided by amphidromous fish migrations.

The unprecedented level of detail that we applied to describe this amphidromous postlarvae run allows us to generate hypotheses about the adaptive importance of this mass-migration behavior. Our intensive sampling design captured the entire, multimodal sirajo goby abundance curve, and our flexible modelling method revealed a clear diel pattern of sirajo goby ingress. Density peaks after midnight and low to zero density during daylight suggest preference for river mouth ingress in the latter half of nighttime periods. This temporal pattern of migration could indicate a trade-off between optimizing survival and reducing energy expenditure. River mouths are high-risk areas for migrating postlarvae because they must pass through a restricted area with a predator gauntlet (Engman et al. 2017a). Lunar synchronous migration has been postulated as a mechanism to reduce mortality by predator swamping (Engman 2017), and nocturnal movements could further reduce risk, because low light conditions reduce foraging efficiency of visual predators (Furey et al. 2016). However, the darkest conditions during the last-quarter moon phase occur between the end of twilight and midnight (time of moon rise), so this single hypothesis does not explain why peaks in ingress did not occur until midnight or later. Peak ingress in the latter half of the night might be explained by selective tidal stream transport, an energy-saving strategy known to be employed by other migratory postlarvae such as anguillid glass eels during approach to the river mouth (Harrison et al. 2014). Our data support this hypothesis because we observed peak ingress near or following the nighttime high tide on all three nights. Nonetheless, further research is warranted to confirm whether amphidromous gobies utilize tidal stream transport as an energy saving mechanism.

Our estimates of APF fishery exploitation on the RGA allow for a quantitative assessment of harvest impact. Given our relatively low estimates of total exploitation, even when model uncertainty and variation in results from the two estimation methods applied are considered, it is unlikely that fishing at this rate is significantly depleting the sirajo goby population. APFs are distinct from most other classes of fisheries because they harvest an early life stage, when fish are generally most likely to experience density-dependent mortality (Stige et al. 2019). Thus, the level of fishing mortality at the postlarval stage that we observed may even be compensatory with natural mortality and minimally affect total mortality for the sirajo goby population (Allen et al. 1998). However, no stock assessment model has been developed for sirajo goby or any other amphidromous fish stock, so we may speculate, but not definitively conclude, that this fishery is sustainable. Comparison with analogous fishery types also indicates relatively low exploitation and a potentially sustainable harvest rate in the RGA APF. Exploitation rates of anguillid glass eel fisheries are known to range from 30% to 75% or greater, and rates of 30%–50% have been postulated to have little actual effect on yellow or silver eel production when elver mortality rate is high (Lin et al. 2017).

The artisanal nature of the Puerto Rico APF (i.e., low-technology fishing gear, intermittent fishing pressure, a relatively low number

of participants) and a portfolio approach are likely explanations for high escapement and a potentially sustainable harvest. The mosquito-net seines and dipnets used in this fishery are hand-made, hand-deployed, require considerable skill, and have a limited total haul size. Fishers using these gears allow escapement even during active fishing periods because they must expend time sorting their catch into buckets or processing pits far from the water's edge after each successful haul. The allocation of fishing effort on the RGA also results in periods where the harvest was below the maximum potential of the fishery. Although fishers attempted to focus effort on the highest-density periods of the run, they did not predict peak densities exactly (Fig. 3). For example, on 9 July (the first night of the run), harvest began ~4 h after sirajo goby density sharply increased, and there were fewer active fishers around 0100 on 10 July (during the maximum peak in sirajo goby density) than there were later in the same day when sirajo goby density had already declined. Although there are no accurate statistics on the number of cetí fishers in Puerto Rico, the population appears to be small, and fishers reported that they distribute their fishing effort across a portfolio of rivers. They described a cooperative phone network through which they reported the apparent abundance of simultaneous runs at several rivers in North-Central and Northwest Puerto Rico. Fishers reported selecting a river to fish based on information from the phone network. In addition to the RGA, the portfolio that fishers reported includes the Río Grande de Añasco, Río Grande de Manatí, Camuy, and Culebrinas rivers.

Despite the indications that the fishery appears sustainable at current exploitation rates, management agencies may consider approaches to conserve Caribbean APF resources in an uncertain future. One tool to inform management is monitoring, an action that is not currently in place for any Caribbean island APF. Monitoring would allow further assessment of fishing pressure and harvest, and data collected could be useful for developing stock assessment models to quantify the impact of fishing on sirajo goby populations. Managers may also consider implementing regulations that maintain the artisanal nature of the fishery. The small-scale and low-technology aspects of this fishery are why fishing is likely currently at a sustainable level. As in all fisheries, changes in market demand could lead to increased harvest-related impacts through shifts in technology or fishery participation (Sethi et al. 2010). For this fishery, a shift to the use of mechanical methods (e.g., boats, winches, lifts) or a large increase in the number of fishers could quickly increase exploitation. Harvest could be limited to the current level by restricting gears to those that are deployed by hand, prohibiting the use of large weirs, requiring a license, and controlling the number of licenses issued. Instream barriers to migration are considered the most severe threat to amphidromous fish populations (Cooney and Kwak 2013). Addressing habitat loss due to instream barriers and other non-fishing-related threats, such as habitat degradation due to urban impacts (Ramírez et al. 2012), instream flow alterations (Engman et al. 2017b), and pollution (Kwak et al. 2016; Buttermore et al. 2018), is likely to be the most impactful form of amphidromous fish conservation. The findings presented here may guide management of artisanal, sustainable APFs that provide a healthy and culturally valuable food source to the people of Caribbean islands for years to come.

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