

## A capture–recapture model of amphidromous fish dispersal

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Adult movement scale was quantified for two tropical Caribbean diadromous fishes, bigmouth sleeper *Gobiomorus dormitor* and mountain mullet *Agonostomus monticola*, using passive integrated transponders (PITs) and radio-telemetry. Large numbers of fishes were tagged in Río Mameyes, Puerto Rico, U.S.A., with PITs and monitored at three fixed locations over a 2.5 year period to estimate transition probabilities between upper and lower elevations and survival probabilities with a multistate Cormack–Jolly–Seber model. A sub-set of fishes were tagged with radio-transmitters and tracked at weekly intervals to estimate fine-scale dispersal. Changes in spatial and temporal distributions of tagged fishes indicated that neither *G. dormitor* nor *A. monticola* moved into the lowest, estuarine reaches of Río Mameyes during two consecutive reproductive periods, thus demonstrating that both species follow an amphidromous, rather than catadromous, migratory strategy. Further, both species were relatively sedentary, with restricted linear ranges. While substantial dispersal of these species occurs at the larval stage during recruitment to fresh water, the results indicate minimal dispersal in spawning adults. Successful conservation of diadromous fauna on tropical islands requires management at both broad basin and localized spatial scales.

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Key words: Caribbean; diadromy; migration; passive integrated transponder; telemetry.

### INTRODUCTION

Diadromous fauna pose unique challenges for conservation because they migrate extensively between wide ranging habitats. As they migrate between marine and fresh waters, diadromous organisms cross jurisdictional borders, perform important ecological functions and are often the target of high value fisheries (McDowall, 1992). Characterizing the spatial scale of migration is a critical component in defining the most effective management units for diadromous fisheries (McDowall, 1999); however, migratory scale is poorly understood for many diadromous species.

Much of the native freshwater fauna found on tropical islands throughout the world follows a diadromous life cycle termed amphidromy (Myers, 1949; McDowall, 1988).

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Amphidromous organisms complete the majority of their life in fresh water, and only larvae experience estuarine or marine conditions after hatching in fresh water and being passively transported downstream (McDowall, 1988; Keith, 2003). After a period of estuarine or marine development which may last up to 6 months in some species (Bell, 1994; Keith & Lord, 2011), metamorphosing larvae recruit to freshwater habitats, where they develop, grow and remain as adults. Diadromous migrations may be important sources of longitudinal nutrient and energy transport (Flecker *et al.*, 2010), and amphidromous recruitment migrations are the target of locally important artisanal fisheries (Erdman, 1961; Bell, 1999; Castellanos-Galindo *et al.*, 2011). Amphidromous recruitment migration at the basin scale, ranging from the estuary to stream headwaters, has been documented across taxa (Keith, 2003; Kikkert & Crowl, 2009; Keith & Lord, 2011). Furthermore, interbasin and even interisland recruitment is known to occur (Cook *et al.*, 2010). In contrast, the scale of amphidromous fish migration after recruitment into fresh water, whether adults are sedentary, mobile or migrate for spawning, remains uncertain. Evidence indicates that amphidromous fish in Hawaii, U.S.A. [*Awaous guamensis* (Valenciennes 1837)] (Kido & Heacock, 1992) and Australia (*Prototroctes maraena* Günther 1864) (Koster *et al.*, 2013) make annual reproductive migrations to the estuary, and otolith microchemistry suggests that another group of Pacific freshwater gobies, *Sicyopterus* spp., may undergo adult migrations between upper and lower river reaches (Lord *et al.*, 2011). Little is otherwise known about amphidromous fish dispersal after recruitment into fresh waters or how migratory patterns are structured within amphidromous fish assemblages.

Native Caribbean stream fishes, bigmouth sleeper *Gobiomorus dormitor* Lacépède 1800 and mountain mullet *Agonostomus monticola* (Bancroft 1834), have each been considered amphidromous or catadromous (*i.e.* migrating to the ocean for spawning; Myers, 1949) by different authors over the years (Anderson, 1957; Nordlie, 1981; McDowall, 1988; Phillip, 1993; Winemiller & Ponwith, 1998). *Agonostomus monticola* migratory patterns were an example of the ambiguity in the distinction between catadromy and amphidromy in Myers' (1949) description of diadromous migration and life histories. The critical distinction between catadromy and amphidromy lies in the scale of movement of adults during the spawning season. Do they migrate to the estuary or beyond to the ocean? If they do migrate to the ocean, their life history is consistent with catadromy; if not, they should be categorized as amphidromous. Evidence to support reproductive migrations to lower river reaches has been anecdotal, indirect and sparse (Anderson, 1957; Nordlie, 1981; McDowall, 1988; Phillip, 1993; Winemiller & Ponwith, 1998), and no investigator has documented the dispersal patterns of adults using a direct method.

Therefore, the ambiguity in the diadromy mode of two Caribbean fishes was resolved by directly estimating the spatial scale of movement with a tagging investigation. The scale of dispersal of *G. dormitor* and *A. monticola* was directly estimated with a multistate capture–recapture model and fish tagging data from passive integrated transponders (PITs) and radio-telemetry in a free-flowing Caribbean island river. Tagged fishes were monitored and resampled using a combination of PIT arrays and electrofishing recaptures over 2.5 years and weekly radio-telemetry relocations over a reduced period. The multistate model allowed estimation of survival probabilities and transition probabilities between spatial strata based on empirical field data. In the application presented here, transition probabilities indicated the likelihood of fishes moving from higher to lower elevations (*i.e.* downstream

migration), and estimates of linear ranges from fine-scale radio-telemetry results indicated the scale of dispersal in adult *G. dormitor* and *A. monticola*.

## MATERIALS AND METHODS

### STUDY SYSTEM

Río Mameyes is a fourth-order, free-flowing river that drains the Luquillo Mountains of north-eastern Puerto Rico, U.S.A., the smallest and eastern-most island of the Greater Antilles in the Caribbean Sea. The Luquillo Mountains are of volcanic origin and reach heights >1000 m within 20 km of the island coast (Pike *et al.*, 2010). The steep topography interacts with north-easterly trade winds and frequent tropical storms to produce extremely high rainfall (averaging nearly 5 m year<sup>-1</sup>; Lugo *et al.*, 2012) and flood-dominated rivers, typical in hydrology to other Antillean rivers. Río Mameyes is one of only a few undammed rivers in Puerto Rico (Cooney & Kwak, 2013) with continuous aquatic connectivity from the headwaters to the ocean. It has a steep, short drainage, with an origin 850 m above sea level, flowing 12 km north into the Atlantic Ocean. The upper watershed consists of protected secondary forest within the El Yunque National Forest, and the lower watershed contains primarily secondary forest, agricultural land and small urbanized areas, including the villages of La Vega, Palmer and Fortuna (Martinuzzi *et al.*, 2007; Fig. 1). Río Mameyes's unrestricted connection to the ocean, condensed length and generally undeveloped watershed render it an ideal system to study tropical lotic fish populations with minimal anthropogenic influence.

Native diadromous fauna dominates Puerto Rico freshwater streams with uninterrupted connectivity to the estuary (Holmquist *et al.*, 1998; Kwak *et al.*, 2007; Cooney & Kwak, 2013). Thus, native diadromous fishes and shrimp fauna are the primary aquatic community inhabitants in the free-flowing Río Mameyes (Kwak *et al.*, 2007). Río Mameyes may be considered representative of the undeveloped streams found on tropical islands throughout the Caribbean and the world, with native diadromous fish assemblages experiencing high rates of flood disturbance, and findings may be applicable to the broad-scale conservation of tropical diadromous fish assemblages.

### FISH TAGGING AND RECAPTURE

Fishes were captured, PIT tagged and recaptured during 13 sampling periods over 2.5 years (2009–2011; Fig. 2). Sampling periods were 1 month in duration and were selected to compare early (May to July) and late (August to September) fish spawning seasons to a non-spawning period (February to March). Spawning season was determined by an annual time series of gonadal development in *G. dormitor* and *A. monticola* in Puerto Rico, which indicated that spawning for *G. dormitor* and *A. monticola* occurred from late spring through to early autumn (Smith, 2013). Populations of PIT-tagged fishes were sampled using backpack electrofishing at both random and fixed locations and PIT arrays at fixed locations in the coastal plain, foothills and mountains (Fig. 1). Fishes were tagged with PITs during each sampling period until August 2011. PIT arrays were deployed and populations were resampled by a backpack electrofisher during each sampling period after March 2009.

Fish populations were sampled by pulsed direct-current backpack electrofisher (Smith-Root Model LR-24; www.smith-root.com; 400 V, 30% pulse width, 0.2–0.3 A) from nine 100–150 m reaches during each sampling period, five randomized reaches in the coastal plain (2–6.5 river km) and four upper elevation reaches (6.5–10.2 river km). Upper elevation river access is limited, so sampling occurred among 10 fixed sites by a backpack electrofisher in the foothills and mountains. Assuming that capture and tagging caused some degree of stress to fishes, reaches were not resampled in consecutive sampling periods. Sampling was conducted either by three passes in 100 m reaches [in sites used to estimate fish density, Smith (2013)] or two passes in 150 m reaches.

Tagging protocols were designed to minimize fish stress by tagging only adult fishes (Bateman & Gresswell, 2006), sterilizing all tagging equipment, briefly anaesthetizing fishes

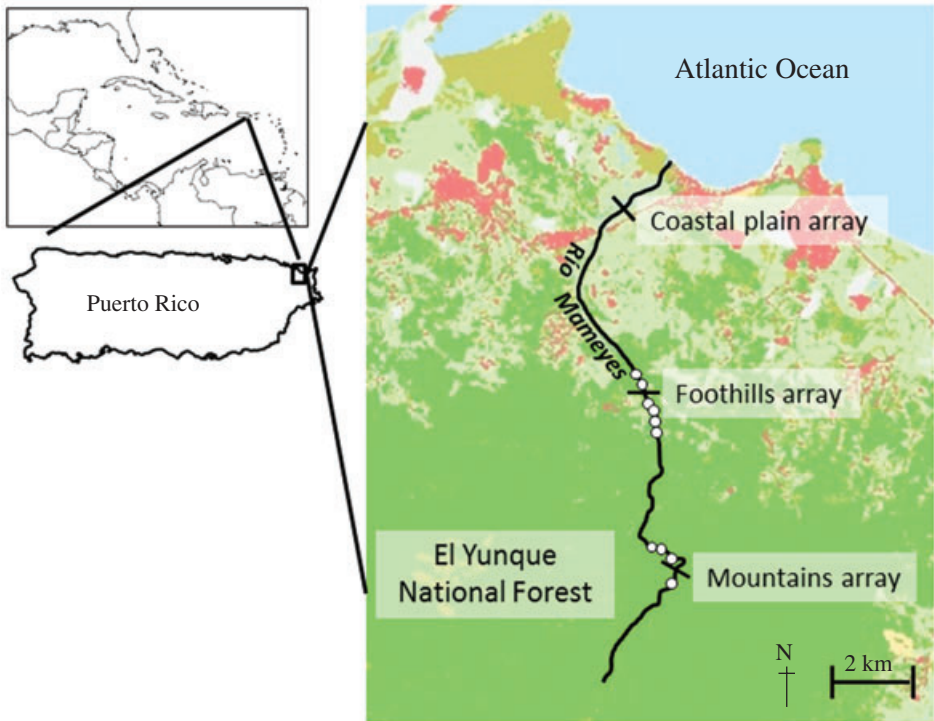


FIG. 1. Land cover map of the Río Mameyes, Puerto Rico, catchment showing locations of remote passive integrated transponder (PIT) arrays and upper elevation electrofishing sites. The coastal plain array was located 2.2 km upstream of the ocean (2.2 river km) [2 m above sea level (a.s.l.)]; the foothills array was located at 6.4 river km (42 m a.s.l.) and the mountain array was located at 9.9 river km (117 m a.s.l.). —, PIT arrays; ○, high elevation electrofishing locations; ■, forested; ■, mangrove; ■, agricultural; ■, urban.

during tagging and minimizing the total handling time of each fish. Only *A. monticola* of > 120 mm total length ( $L_T$ ) and *G. dormitor* of > 130 mm  $L_T$  were implanted with PIT tags or radio-transmitters. Most of the female *A. monticola* mature by 113 mm  $L_T$ , and males do not commonly reach sizes greater than or equal to the minimum size at tagging (Smith, 2013). Most of the *G. dormitor* mature by 144 mm  $L_T$ ; thus, most of the tagged fishes were assumed to have reached reproductive maturity. Fishes receiving a PIT tag were lightly anaesthetized in aerated river water containing  $80 \text{ mg l}^{-1}$  tricaine methane sulphonate (MS-222) for 2 min before transfer to a tank containing a maintenance level of anaesthetic ( $30 \text{ mg l}^{-1}$  MS-222).

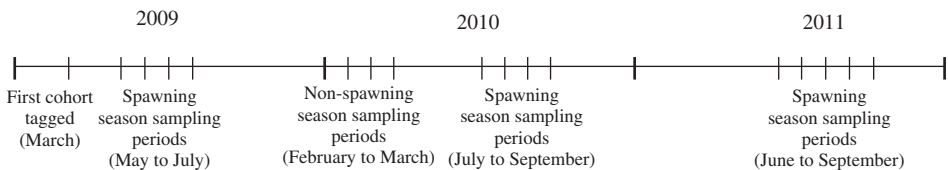


FIG. 2. Sampling chronology showing fish capture–recapture periods. | indicate the beginning and end of each sampling period; | delineate years.

$L_T$ , mass, sex and capture location were recorded for each fish. PIT tags (Texas Instruments; [www.ti.com/rfid](http://www.ti.com/rfid); 23 mm, half-duplex, 0.6 g) were implanted intra-abdominally *via* a 4 mm incision posterior to the pelvic fin (Baras *et al.*, 1999). Fishes of >250 mm  $L_T$  were implanted with larger 32 mm tags (0.8 g). Before each implantation, all equipment and PIT tags were disinfected in a solution of Benzall surgical disinfectant. Each PIT tag implantation lasted *c.* 1 min, and total sedation time was 7.5 min on average, after which fishes recovered in a 30 l live well, with flowing river water for 1–2 h before release. Only fishes in apparently good condition were released. The short-term mortality rate associated with the capture and tagging process was estimated by holding a sub-set of each species for 16 h in live wells at densities not greater than 15 fish per live well. Tagging procedures resulted in a small scar that was visible on all recaptures of previously tagged fishes. Before tagging, all fishes were examined for this scar in order to assess the potential for tag loss.

During the final sampling periods (June to September 2011), a small sample of large *G. dormitor* and *A. monticola* were fitted with radio-transmitters. Fishes implanted with radio-transmitters were captured and allowed to recover after surgery following the same procedures for PIT tagging. Fishes receiving a radio-transmitter were anaesthetized for 4 min in 80 mg l<sup>-1</sup> MS-222. Radio-transmitters required a 12 mm incision, and each surgery lasted for *c.* 10 min. Water containing 30 mg l<sup>-1</sup> MS-222 was circulated over the gills using a hand siphon while a small radio-transmitter (Advanced Telemetry Systems; [www.atstrack.com](http://www.atstrack.com); Model F1545, 0.9 g) and a 23 mm PIT tag were implanted intra-abdominally, including the trailing antenna (not inserted through body wall). Incisions were closed with two sterile sutures.

## TAGGED FISH DETECTION

PIT-tagged fishes were monitored continuously at three fixed points in Río Mameyes in the coastal plain, the foothills and the mountains (Fig. 1), with pairs of automated PIT antennas (PIT arrays). PIT antennas spanned the entire river channel and recorded the unique tag identification number and time at which tagged fishes passed stationary points in the river. Two antennas were placed 2–3 m apart at each site to improve the probability that tagged fishes would be detected when present at array sites, and data were combined from the two antennas. Each antenna was connected to a series of capacitors and a multiplex PIT reader and automated data logger (Oregon RFID; [www.oregonrfid.com](http://www.oregonrfid.com)).

Antennas were firmly secured to the river bed with concrete anchors and mounds of small boulders in a horizontal pass-over design for protection against high velocity flood waters. Vertical pass-through antenna designs yield greater PIT detection efficiencies but are more vulnerable to damage during flooding compared to pass-over designs (Nunnallee *et al.*, 1998; Greenberg & Giller, 2000). Shorter antennas tend to have greater read ranges and less surface area to create drag during periods of high water velocity, and pass-over antenna designs are most effective when animal movement is restricted to a narrow range of depths. Therefore, PIT array sites were selected to maximize detection efficiency by reducing total array length (river width) and water depth. Antennas were each 1 m wide and 17, 11 and 18 m in length in the coastal plain, foothills and mountains, with respective read ranges of 0.38, 0.50 and 0.25 m. Based on the depth profile at each site, these read ranges were sufficient to cover >90% of the river channel under base flow conditions.

Radio-telemetered fishes were manually located at weekly intervals through September 2011. Individual fish locations were recorded with a hand-held GPS device, and fish locations were also described relative to previous locations and prominent stream features or landmarks. Fish locations were converted to linear position in the river (river km) using Google Earth software ([www.google.com/earth](http://www.google.com/earth)). A curvilinear path was delineated through the Río Mameyes channel, and fish locations were assigned to the closest point on the river path.

## MULTISTATE MODEL

A multistate Cormack–Jolly–Seber model (Seber, 1982; Brownie *et al.*, 1993; Kery & Schaub, 2011) was used to estimate the time-specific probabilities of moving from upper elevations (foothills and mountains) to lower elevations (coastal plain) and the probabilities of moving from lower to upper elevations, while accounting for apparent

TABLE I. Parameters, indices and data of the multistate model

Parameters of the state model	Definition
$M$	Monthly rate of natural mortality
$\psi_{s,t}$	Probability of moving out of state $s$ ( <i>i.e.</i> emigrating) during sampling period $t$
$z_{i,t}$	Latent variable for state of individual $i$ at time $t$
$d$	Probability of mortality due to capture and tagging
Parameters of the observation model	
$\alpha_{j,t}$	PIT array observation probability at PIT array $j$ during sampling period $t$
$\beta$	Electrofishing observation probability
Indices	
$i$	Individual ( $i = 1, \dots$ , total number tagged)
$j$	PIT array index ( $j = 1, 2, 3$ )
$s$	State [ $s = 1$ (alive and downstream), $s = 2$ (alive and upstream), $s = 3$ (unobserved or dead)]
$t$	Sampling period ( $t = 1, \dots, 13$ )
Data	
$y_{i,t}$	Observed state of individual $i$ at time $t$
$f_i$	Sampling occasion in which individual $i$ was first encountered
$g_t$	Number of months between sampling period $t$ and $t - 1$
$m$	Number of mortalities during a short-term experiment to estimate $d$
$n$	Total sample size of a short-term experiment to estimate $d$

PIT, passive integrated transponder.

survival and observation probabilities. Bayesian multistate models were fit separately to *G. dormitor* and *A. monticola* PIT data. The multistate model is an extension of the Cormack–Jolly–Seber model (Seber, 1982) that estimates survival and observation probabilities over time in an open population of tagged animals. In addition to the probability of surviving or dying, the multistate model adds the probability of transitioning between a second category of states, defined in the model as a spatial state, the state of being downstream or the state of being upstream. Thus, tagged fishes could be observed alive and downstream ( $y_{i,t} = 1$ ), alive and upstream ( $y_{i,t} = 2$ ) or unobserved or dead ( $y_{i,t} = 3$ ). Parameters, indices and data of the multistate model are described in Table I. The multistate model consisted of two hierarchical components, a state equation describing how individual states,  $z_{i,t}$ , evolve over time, conditional on individual states during the previous sampling occasion and an observation equation linking the probability of observations conditional on individual states.

A categorical latent variable,  $z_{i,t}$ , indicating true states was estimated for each individual during each monthly sampling occasion. Values of  $z_{i,t}$  were assumed to be assigned to a captured individual's state without error during the period of initial capture,  $f_i$ . Subsequent to  $f_i$ , each  $z_{i,t}$  was categorically distributed, with three possible outcomes [alive and downstream ( $z_{i,t} = 1$ ), alive and upstream ( $z_{i,t} = 2$ ) or dead ( $z_{i,t} = 3$ )], and conditional on survival and spatial state during the previous sampling occasion,  $z_{i,t} \sim \text{categorical}(\Omega)$ , where  $\Omega$  was a state transition probability matrix with columns corresponding to past states and rows corresponding

to current states,

$$\Pr(z_{i,t} = s) = \begin{array}{c} \begin{array}{ccc} \text{State at time } t - 1 \\ \hline s = 1 & s = 2 & s = 3 \\ \hline \end{array} \\ \begin{bmatrix} \phi_{t-1} \times (1 - \psi_{1,t-1}) & \phi_{t-1} \times \psi_{2,t-1} & 0 \\ \phi_{t-1} \times \psi_{1,t-1} & \phi_{t-1} \times (1 - \psi_{2,t-1}) & 0 \\ 1 - \phi_{t-1} & 1 - \phi_{t-1} & 1 \end{bmatrix} \\ \begin{array}{l} s = 1 \\ s = 2 \\ s = 3 \end{array} \end{array} \quad \text{State at time } t$$

for all individuals alive at  $t - 1$ .  $\phi_t$  was the discrete probability of surviving  $t$ , and  $\psi_{s,t}$  was the probability of transitioning out of state  $s$  (*i.e.* emigrating). The first two columns contained the probabilities of moving between spatial states, conditional on survival. The last column contained the probabilities of state transitions after death. Individuals estimated to have died remained dead with probability = 1.

$\phi_t$  was a function of fixed monthly rate of instantaneous mortality,  $Z$ , and the number of months between sampling occasions,  $g_t$ ,  $\phi_t = e^{-Z \times g_t}$ .  $Z$  was composed mostly of natural mortality,  $M$ , and a very small quantity of fishing mortality,  $F$ .  $g_t$  was used to adjust survival probabilities between uneven sampling occasions. Annual survival rate was calculated by setting  $g$  equal to 12. Some tagged fishes may have died due to the capture and tagging process, so survival during the initial period after tagging was adjusted to account for this additional mortality.  $d$  was the probability of mortality due to capture and tagging, estimated empirically by tagging and holding a sub-set of fishes *in situ* in flow-through live wells for 16 h after tagging. The number of mortalities over the holding period,  $m$ , was binomially distributed, with probability,  $d$ , and sample size equal to the number held in live wells after tagging,  $n$ ,  $m \sim \text{binomial}(d, n)$ .

To account for tagging mortality, a reduced survival probability,  $\phi_{\text{initial}}$  was assigned to each individual's initial sampling period,  $\phi_{\text{initial}} = (1 - d) \times \phi_t$ .

Heterogeneity in the exact time at large during the initial period after tagging was accounted by reducing individual mortality rates during the initial period of tagging by the fraction of the initial sampling period that passed before the individual was tagged.

Observations of individuals,  $y_{i,t}$ , could take three possible values, corresponding to the three possible values of  $z_{i,t}$  [observed downstream ( $y_{i,t} = 1$ ), observed upstream ( $y_{i,t} = 2$ ) or unobserved ( $y_{i,t} = 3$ )]. Observations occurred at PIT arrays and at randomized electrofishing locations. The probability of observation at PIT array  $j$ ,  $\alpha_{j,t}$ , was estimated separately for each sampling period to account for time-specific factors that may have influenced observation probability, such as variation in stream discharge and periods when PIT arrays were disabled. The probability of observation during electrofishing samples,  $\beta$ , was held constant across all sampling occasions and locations because all electrofishing samples were standardized by area and effort. Observations of individuals,  $y_{i,t}$ , were categorically distributed,  $y_{i,t} \sim \text{categorical}(\Theta)$ , where  $\Theta$  was an observation probability matrix with rows corresponding to true states and columns corresponding to observed states,

$$\Pr(y_{i,t} = s) = \begin{array}{c} \begin{array}{ccc} \text{Observed state at time } t \\ \hline s = 1 & s = 2 & s = 3 \\ \hline \end{array} \\ \begin{bmatrix} p_{\text{observation}} & 0 & 0 \\ 0 & p_{\text{observation}} & 0 \\ 1 - p_{\text{observation}} & 1 - p_{\text{observation}} & 1 \end{bmatrix} \\ \begin{array}{l} s = 1 \\ s = 2 \\ s = 3 \end{array} \end{array} \quad \text{True state at time } t$$

Observation probabilities,  $p_{\text{observation}}$ , were equal to  $\alpha_{j,t}$  or  $\beta$ .

Uninformative prior distributions were assumed for all model parameters (Table II), and OpenBUGS software (v. 3.2.1; Lunn *et al.*, 2009) was used to sample the posterior distribution of each parameter. Model code can be found in Appendix S1 (Supporting information). Movement probabilities >0.5 indicated high probabilities of fishes leaving longitudinal strata

TABLE II. Prior distributions for all multistate model parameters

Parameter	Distribution	Prior
$M$	Gamma	(0.001,0.001)
$\psi_{s,t}$	Beta	(1,1)
$d$	Beta	(1,1)
$\alpha_{j,t}$	Beta	(1,1)
$\beta$	Beta	(1,1)

(*i.e.* emigrating), while movement probabilities  $<0.5$  indicated low probabilities of emigration (*i.e.* sedentary behaviour). Estimates with 95% credible intervals that did not include 0.5 indicated that sufficient information was collected to estimate movement probabilities and to infer migratory or sedentary behaviour. Significant probabilities of moving from upper to lower elevations during the spawning season were interpreted as evidence of the potential for a downstream spawning migration. Direct estimates of natural mortality [ $-\ln$  (apparent survival)] from tagging were compared to estimates of natural mortality generated using the Lorenzen (1996) method, based on the range of body masses observed in tagged fishes. The Lorenzen (1996) method estimates natural mortality using a non-linear regression model and body mass. This method is among the most commonly applied life-history techniques to indirectly estimate natural mortality in the absence of direct information from tagging. The range of Lorenzen (1996) natural mortality estimates corroborated tagging estimates of natural mortality if Lorenzen (1996) estimates overlapped the credible intervals of tagging estimates.

Multistate model estimates of dispersal (movement probabilities) were compared to observed long-distance dispersal. Long-distance dispersal was quantified by calculating linear ranges. Long-distance dispersal was defined as any movement  $>4$  km, the approximate distance required to traverse between physiographic regions in Río Mameyes. Linear ranges were calculated as the maximum distance between any two encounter locations (Hayne, 1949), assuming that dispersal occurred at the time of the second encounter. Linear ranges were also calculated for all radio-telemetered fishes, and mean linear range values for each species, based on radio-telemetry, were assumed to represent the average scale of dispersal. Linear range estimation was the primary use of radio-telemetry data. Telemetry data were not incorporated into the multistate model likelihood because they were not replicated throughout each sampling period.

## RESULTS

Large numbers of fishes were PIT tagged, generating a great quantity of coarse information about movement and survival, and a small number of fishes were located using radio-telemetry, generating complementary, fine-scale movement data. From March 2009 to September 2011, 1455 *G. dormitor* and 784 *A. monticola* were PIT tagged. A total of 264 PIT-tagged *G. dormitor* and 241 PIT-tagged *A. monticola* were detected at PIT arrays, and 162 PIT-tagged *G. dormitor* and 63 PIT-tagged *A. monticola* were recaptured in electrofishing samples. From June to August 2011, 15 *G. dormitor* and 13 *A. monticola* were tagged with radio-transmitters and later relocated at least four times before death or battery expiration.

Low annual rates of apparent survival were estimated by the multistate model for both *G. dormitor* and *A. monticola* (Table III); however, few PIT-tagged fishes died during short-term mortality trials. Of the 102 *G. dormitor* tagged and held for 16 h, only four died, and of the 55 tagged *A. monticola*, only one died. Multistate



TABLE III. Modelled population parameters estimated by multistate capture–recapture models for two diadromous tropical fish species. Annual mortality was composed of natural mortality and a very small but unknown quantity of fishing mortality. Natural mortality was also estimated using the Lorenzen (1996) mass-based method, using the range of masses of all tagged fishes of each species

Parameter	Estimate	s.d.	95% c.i.
<i>Gobiomorus dormitor</i>			
Annual mortality rate ( $Z$ )	1.06	0.08	0.91–1.22
Annual natural mortality rate, Lorenzen (1996) method	0.86–1.16	–	–
Annual apparent survival rate ( $S$ )	0.35	0.03	0.29–0.40
<i>Agonostomus monticola</i>			
Annual mortality rate ( $Z$ )	1.19	0.09	1.02–1.38
Annual natural mortality rate, Lorenzen (1996) method	0.76–1.33	–	–
Annual apparent survival rate ( $S$ )	0.30	0.03	0.25–0.36

model estimates of natural mortality were similar to natural mortality estimated using the Lorenzen (1996) method. Movement probability estimates were generally low or not significant, indicating sedentary behaviour of PIT-tagged *G. dormitor* and *A. monticola* and low rates of migration between high and low elevations [Fig. 3(a), (b), (d), (e)]. Observed patterns of long-distance dispersal (linear ranges) also indicated sedentary behaviour [Fig. 3(c), (f)]. A small number of *G. dormitor* dispersed downstream during the early spawning season of 2011 and the late spawning season of 2011; however, the majority of all observed dispersal was local. A significant exception to the local movement patterns of *A. monticola* occurred during the late spawning season of 2011, when a large number of *A. monticola* were observed in upper elevations after emigrating from lower elevations. Emigration probability was estimated at 0.78 (95% c.i. = 0.62–0.90) for lower elevation *A. monticola* during this period, which followed a major flood disturbance event (Smith, 2013). Sedentary behaviour was also observed in radio-telemetered fishes. Linear ranges of radio-telemetered *G. dormitor* were variable among individuals, with a mean  $\pm$  s.d. =  $0.30 \pm 0.36$  km (range = 0.03–1.39 km). Linear ranges of radio-telemetered *A. monticola* also varied, with a mean  $\pm$  s.d. =  $0.53 \pm 0.34$  km (range = 0.16–1.27 km). No radio-telemetered individual of either species was observed moving between upper and lower elevation strata.

## DISCUSSION

Direct evidence presented here demonstrates a low probability of downstream dispersal, from upper to lower elevations, for both *G. dormitor* and *A. monticola* in Río Mameyes during two spawning seasons, indicating that spawning occurs in freshwater riverine habitats. Furthermore, the period of greatest long-distance dispersal for both species during September 2011 was subsequent to a major flood disturbance, the most likely cause of adult dispersal observed during the study.

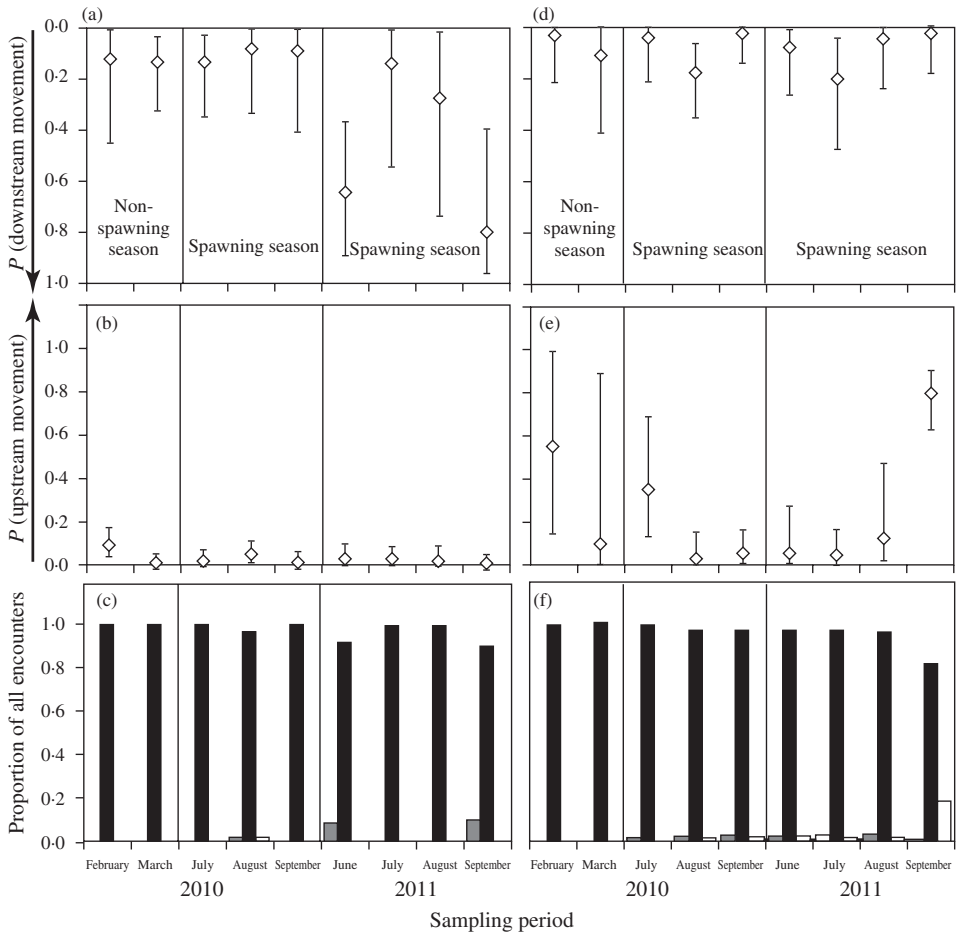


FIG. 3. (a, b, d, e) Movement probabilities estimated by a multistate model fit to all observations of PIT-tagged fishes and (c, f) observed long-distance dispersal for (a–c) PIT-tagged *Gobiomorus dormitor* and (d–f) *Agonostomus monticola*. (a, d)  $P$  (downstream movement) indicates the probability of moving from the foothills and mountains to the coastal plain and (b, e)  $P$  (upstream movement) indicates the probability of moving from the coastal plain to the foothills and mountains. (c, f) Long-distance dispersal is defined as movement  $>4$  km, the approximate distance required to traverse between physiographic regions in Río Mameyes. ■, long-distance downstream dispersal; ■, local dispersal; □, long-distance upstream dispersal.

Thus, it is concluded that neither *G. dormitor* nor *A. monticola* are catadromous in this system, resolving any ambiguity related to previous indirect, speculation based on anecdotal observations in other systems (Anderson, 1957; Nordlie, 1981; Phillip, 1993; Winemiller & Ponwith, 1998). The movement patterns observed are consistent with an amphidromous life history with spawning completed within fresh waters, directly confirming this presumption by previous investigators (Cruz, 1987; McDowall, 1988).

Estimates of survival rates, movement probabilities and observation probabilities could each be biased by violations of the Cormack–Jolly–Seber model assumptions

(Seber, 1982). Therefore, field sampling and modelling protocols were designed to maximize adherence to model assumptions and accounted for heterogeneity in survival probabilities and time at large during the initial period after tagging. The capture and tagging of fishes was the process most likely to result in systematic heterogeneity of survival probabilities (Arnason & Mills, 1987), so measures were taken to enhance the condition of each fish after capture during tagging, sedation and recovery. Furthermore, short-term survival of the capture and tagging process was accounted by tagging and holding a sub-set of fishes for a short time to empirically estimate tagging mortality, and tagging mortality estimates were used to reduce individual survival probabilities during the initial period after tagging. Just as mortality from capture creates a smaller pool of tagged fishes available for later recapture, so too can the loss of tags, generating negative bias in survival estimates (Seber, 1982). The surgical implantation of PIT tags in *G. dormitor* and *A. monticola* resulted in a secondary mark, a small scar from the incision. This scar was visible on all electrofished recaptured fishes, and no fishes were observed with a scar and no PIT tag. This finding was interpreted as anecdotal evidence of low tag loss, similar to that measured in other PIT-tagging studies (Gries & Letcher, 2002; Bateman & Gresswell, 2006; Isermann & Carlson, 2008). Permanent emigration from the study area can bias survival estimates and temporary emigration can bias estimates of observation probabilities (Seber, 1982); however, the restricted linear ranges of radio-telemetered *G. dormitor* indicated that emigration of any sort was generally unlikely. The high probability of *A. monticola* migration estimated by the multistate model during the final sampling period, based on only PIT-tagged *A. monticola*, suggested that survival probabilities for this species may have been biased low due to upstream migration into inaccessible regions of Río Mameyes; however, this migratory period was associated with unusual environmental conditions, the most significant flood disturbance event during the study. Furthermore, it occurred at the end of the study, and emigration during this period would not have affected survival estimates.

Earlier studies concluding that *G. dormitor* (Nordlie, 1981; Winemiller & Ponwith, 1998) and *A. monticola* (Anderson, 1957; Phillip, 1993) migrate to the estuary or ocean for spawning and are thus catadromous were based entirely on indirect, anecdotal evidence derived from studies not designed to comprehensively assess movement patterns. Phillip (1993) and Winemiller & Ponwith (1998) found ripe females in the estuary but not in fresh water; however, freshwater sample sizes in both studies were small. It is not clear that Nordlie (1981) sampled throughout the spawning season or actually assessed reproductive condition. Anderson (1957) found *A. monticola* post-larvae at sea, a considerable distance from the nearest possible freshwater source but never observed adults or spawning activity. While he concluded that the patterns observed were consistent with a catadromous life history, they were also consistent with an amphidromous life history that may include a marine larval dispersal phase (McDowall, 1988; Keith, 2003), which was poorly understood at the time. These findings are among the first direct evidence of movement patterns in adults of any amphidromous fish species and the first direct evidence for Caribbean amphidromous fishes. The direct tagging method allowed individual movements to be tracked through the spawning season, and tagging large numbers of fishes allowed robust statistical comparisons within the spawning season and among seasons. Counter to the conclusions of previous studies, direct estimates from this research

indicate that *G. dormitor* and *A. monticola* were sedentary with relatively low probabilities of long-distance dispersal or dispersal between upper and lower elevations. One exception to this general rule was documented in a radio-telemetered *A. monticola* that moved 1.25 km downstream after a brief, intense spate but returned to its activity centre within 2 days. Major flood disturbance events may result in some temporary, downstream displacement but not in population-scale movements to lower river reaches.

These findings also include the first estimates of survival rates for adults of any amphidromous fishes. Apparent survival estimates indicated that only 30–35% of adult *G. dormitor* and *A. monticola* populations in Río Mameyes survive from 1 year to the next. Assuming that these rates approximate the level of natural mortality experienced by *G. dormitor* and *A. monticola* populations, natural mortality estimates were similar to other fish populations with similar average body sizes (Lorenzen, 1996). While illegal harvest of *G. dormitor* is known to occur in Río Mameyes (W. E. Smith, pers. obs.), illegal fishing is unlikely to remove a large proportion of the adult population, but this has not been investigated and is difficult to measure. Only minimal harvest of either *G. dormitor* or *A. monticola* was observed in lower reaches of the river, and the upper river is closed to fishing within the El Yunque National Forest. Thus, it is concluded that the estimates of total mortality presented here approximate natural mortality rates in this system.

The predominant cause of high mortality rates in Río Mameyes is probably the intense disturbance regime that characterizes lotic ecosystems in this region. The El Yunque National Forest receives nearly 5 m of rainfall annually (Lugo *et al.*, 2012), including brief periods of intense rainfall during tropical cyclones. One tropical cyclone, Hurricane Irene, struck Puerto Rico during this study and resulted in a 10% reduction in mean fish density in Río Mameyes (Smith, 2013). Flood disturbances of Hurricane Irene's magnitude (>250 cm of rain in 24 h; U.S. National Weather Service; [water.weather.gov/precip](http://water.weather.gov/precip)) occur only approximately every 4 years, but chronic flood disturbances of lesser intensity are characteristic of Puerto Rico watersheds (Ramírez *et al.*, 2009; Pike *et al.*, 2010). Repeated exposure of fish populations to discrete, minor mortality events may have an additive effect, resulting in considerable mortality at an annual scale.

## CONSERVATION IMPLICATIONS

Evidence presented here and in related research (Smith, 2013; Smith & Kwak, 2014) suggests the following amphidromous model of *G. dormitor* and *A. monticola* migratory life history. Adult fishes spawn in freshwater lotic habitat, and after hatching in fresh water, larvae are passively transported downstream to marine or estuarine habitats. After a period of development, post-larvae actively return to fresh water, often in large aggregate migrations, where they find suitable habitat and remain for the duration of their lives and spawn as adults. Periodically, flood disturbances may spatially and demographically redistribute fishes, but even subsequent to major flooding, most of the adults remain sedentary. The sedentary behaviour of adult *G. dormitor* and *A. monticola* suggests that management of adult amphidromous fishes at the local site or reach scale may be an effective approach, contrasted with broad, basin-scale management. In contrast, amphidromous larvae spawned in lotic habitat require access to marine waters, and post-larvae migrate

from the estuary to the head waters (Keith, 2003; Kikkert & Crowl, 2009; Keith & Lord, 2011); thus, management of amphidromous fish recruitment requires consideration of the entire basin. This model of amphidromous life history suggests that basin characteristics, such as the geology, land cover and number and spatial location of dams of a watershed, influence the recruitment of juveniles into local habitats. After recruitment, more sedentary amphidromous adults are influenced by localized factors, such as exploitation and instream habitat quality.

The low apparent survival rates estimated here suggest that adult *G. dormitor* and *A. monticola* populations may be able to withstand substantial harvest rates, given adequate recruitment. In general, adding low to moderate additional mortality (*i.e.* fishing) when natural mortality rates are very high has little effect on fish populations (*i.e.* compensatory, rather than additive effects; Allen *et al.*, 1998; Winemiller, 2005). Information about juvenile survival, growth rate, size at maturation and fecundity, however, are necessary to fully characterize the harvest potential and population dynamics of these species. Furthermore, the metapopulation dynamics of amphidromous species are not fully understood, and the proportion and abundance of larvae emigrating from and immigrating to other systems has not been quantified. Models of amphidromous populations that can explicitly test population sensitivity to harvest at different life stages are not feasible with currently available information; thus, future research focused on migration and mortality of early life stages is warranted. While additional adult mortality may have little influence on the sustainability of *G. dormitor* and *A. monticola* populations, the effects of additional juvenile mortality remain to be determined.

These findings represent the first comprehensive, direct elucidation of movement and mortality in adult amphidromous fishes, with implications for the management of tropical aquatic resources. The model of migratory life history developed here is based on direct quantitative evidence and suggests that management of amphidromous fauna should be approached from two spatial scales: a broad basin scale that influences recruitment and a local scale that influences adults and potential fishery resources. Future research will enhance this understanding for other amphidromous species and life stages to inform conservation and management of tropical insular lotic ecosystems.

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### Supporting Information

Supporting Information may be found in the online version of this paper:  
APPENDIX S1. OpenBUGS code for the multistate capture–recapture model for riverine diadromous fish dispersal.

## References

- Allen, M. S., Miranda, L. E. & Brock, R. E. (1998). Implications of compensatory and additive mortality to the management of selected sportfish populations. *Lakes and Reservoirs: Research and Management* **3**, 67–79.
- Anderson, W. W. (1957). Larval forms of the fresh-water mullet (*Agonostomus monticola*) from the open ocean off The Bahamas and South Atlantic coast of the United States. *Fishery Bulletin* **120**, 415–425.
- Arnason, A. N. & Mills, K. H. (1987). Detection of handling mortality and its effects on Jolly–Seber estimates for mark–recapture experiments. *Canadian Journal of Fisheries and Aquatic Sciences* **44** (Suppl. 1), 64–73.
- Baras, E., Westerloppe, L., Mélard, C., Philippart, J. C. & Bénech, V. (1999). Evaluation of implantation procedures for PIT-tagging juvenile Nile tilapia. *North American Journal of Aquaculture* **61**, 246–251.
- Bateman, D. S. & Gresswell, R. E. (2006). Survival and growth of age-0 steelhead after surgical implantation of 23-mm passive integrated transponders. *North American Journal of Fisheries Management* **26**, 545–550.
- Bell, K. N. I. (1994). Life cycle, early life history, fisheries and recruitment dynamics of diadromous gobies of Dominica, W.I., emphasizing *Sicydium punctatum*. PhD Thesis, Memorial University of Newfoundland, St. John's, NF, Canada. Available at <http://www.ucs.mun.ca/~kbell/pubs/PDFpapers/Thes94.html/>
- Bell, K. N. I. (1999). An overview of goby-fry fisheries. *Naga* **22**, 30–36.
- Brownie, C., Hines, J. E., Nichols, J. D., Pollock, K. H. & Hestbeck, J. B. (1993). Capture–recapture studies for multiple strata including non-Markovian transitions. *Biometrics* **49**, 1173–1187.
- Castellanos-Galindo, G. A., Carlo-Sanchez, G., Beltran-Leon, B. S. & Zapata, L. (2011). A goby-fry fishery in the northern Colombian Pacific Ocean. *Cybium* **35**, 391–395.
- Cook, B. D., Pringle, C. M. & Hughes, J. M. (2010). Immigration history of amphidromous species on a Greater Antillean island. *Journal of Biogeography* **37**, 270–277.
- Cooney, P. B. & Kwak, T. J. (2013). Spatial extent and dynamics of dam impacts on tropical island freshwater fish assemblages. *BioScience* **63**, 176–190.
- Cruz, G. A. (1987). Reproductive biology and feeding habits of cuyamel, *Joturus pichardi* and tepemechin, *Agonostomus monticola* (Pisces; Mugilidae) from Rio Platano, Mosquitia, Honduras. *Bulletin of Marine Science* **40**, 63–72.
- Erdman, D. S. (1961). Notes on the biology of the gobiid fish, *Sicydium plumieri*, in Puerto Rico. *Bulletin of Marine Science of the Gulf and Caribbean* **11**, 448–456.
- Flecker, A. S., McIntyre, P. B., Moore, J. W., Anderson, J. T., Taylor, B. W. & Hall, R. O. (2010). Migratory fishes as material and process subsidies in riverine ecosystems. *American Fisheries Society Symposium* **73**, 559–592.
- Greenberg, L. A. & Giller, P. S. (2000). The potential of flat-bed passive integrated transponder antennae for studying habitat use by stream fishes. *Ecology of Freshwater Fish* **9**, 74–80.
- Gries, G. & Letcher, B. H. (2002). Tag retention and survival of age-0 Atlantic salmon following surgical implantation with passive integrated transponder tags. *North American Journal of Fisheries Management* **22**, 219–222.
- Hayne, D. W. (1949). Calculation of the size of home range. *Journal of Mammalogy* **30**, 1–18.
- Holmquist, J. G., Schmidt-Gengenbach, J. M. & Yoshioka, B. B. (1998). High dams and marine-freshwater linkages: effects on native and introduced fauna in the Caribbean. *Conservation Biology* **12**, 621–630.
- Isermann, D. A. & Carlson, A. J. (2008). Initial mortality and retention associated with using passive integrated transponders in black crappies. *North American Journal of Fisheries Management* **28**, 1157–1159.
- Keith, P. (2003). Biology and ecology of amphidromous Gobiidae of the Indo-Pacific and the Caribbean regions. *Journal of Fish Biology* **63**, 831–847.
- Keith, P. & Lord, C. (2011). Tropical freshwater gobies: amphidromy as a life cycle. In *The Biology of Gobies* (Patzner, R. A., Van Tassell, J. L., Kovacic, M. & Kapoor, B. G., eds), pp. 243–277. Enfield, NH: Science Publishers.

- Kery, M. & Schaub, M. (2011). *Bayesian Population Analysis Using WinBUGS*. Waltham, MA: Academic Press.
- Kido, M. H. & Heacock, D. E. (1992). The spawning ecology of o'opu-nakea (*Awaous stamineus*) in Wainiha River. In *New Directions in Research Management and Conservation of Hawaiian Freshwater Stream, Biology and Fisheries Management* (Devick, W., ed), pp. 142–157. Honolulu, HI: Hawaii Department of Aquatic Resources.
- Kikkert, D. A. & Crowl, T. A. (2009). Upstream migration of amphidromous shrimps in the Luquillo Experimental Forest, Puerto Rico: temporal patterns and environmental cues. *Journal of the North American Benthological Society* **28**, 233–246.
- Koster, W. M., Dawson, D. R. & Crook, D. A. (2013). Downstream spawning migration by the amphidromous Australian grayling (*Prototroctes maraena*) in a coastal river in south-eastern Australia. *Marine and Freshwater Research* **64**, 31–41.
- Lord, C., Tabouret, H., Claverie, F., Pécheyrán, C. & Keith, P. (2011). Femtosecond laser ablation ICP-MS measurement of otolith Sr:Ca and Ba:Ca composition reveal differential use of freshwater habitats for three amphidromous *Sicyopterus* (Teleostei: Gobioidi: Sicydiinae) species. *Journal of Fish Biology* **79**, 1304–1321.
- Lorenzen, K. (1996). A simple von Bertalanffy model for density-dependent growth in extensive aquaculture, with an application to common carp (*Cyprinus carpio*). *Aquaculture* **142**, 191–205.
- Lugo, A. E., Waide, R. B., Willig, M. R., Crowl, T. A., Scatena, F. N., Thompson, J., Silver, W. L., McDowell, W. H. & Brokaw, N. (2012). Ecological paradigms for the tropics. In *A Caribbean Forest Tapestry* (Brokaw, N., Crowl, T. A., Lugo, A. E., McDowell, W. H., Scatena, F. N., Waide, R. B. & Willig, M. R., eds), pp. 3–41. New York, NY: Oxford University Press.
- Lunn, D., Spiegelhalter, D., Thomas, A. & Best, N. (2009). The BUGS project: evolution, critique, and future directions. *Statistics in Medicine* **28**, 3049–3067.
- Martinuzzi, S., Gould, W. A. & Ramos-González, O. M. (2007). Land development, land use, and urban sprawl in Puerto Rico integrating remote sensing and population census data. *Landscape and Urban Planning* **79**, 288–297.
- McDowall, R. M. (1988). *Diadromy in Fishes, Migrations Between Freshwater and Marine Environments*. London: Croom Helm.
- McDowall, R. M. (1992). Particular problems for the conservation of diadromous fish. *Aquatic Conservation: Marine and Freshwater Ecosystems* **2**, 351–355.
- McDowall, R. M. (1999). Different kinds of diadromy: different kinds of conservation problems. *ICES Journal of Marine Science* **56**, 410–413.
- Myers, G. S. (1949). Usage of anadromous, catadromous, and allied terms for migratory fishes. *Copeia* **1949**, 89–97.
- Nordlie, F. G. (1981). Feeding and reproductive biology of eleotrid fishes in a tropical estuary. *Journal of Fish Biology* **18**, 97–110.
- Nunnallee, E. P., Prentice, E. F., Jonasson, B. F. & Patten, W. (1998). Evaluation of a flat-plate PIT tag interrogation system at Bonneville Dam. *Aquacultural Engineering* **17**, 261–272.
- Phillip, D. T. (1993). Reproduction and feeding of the mountain mullet, *Agonostomus monticola*, in Trinidad, West Indies. *Environmental Biology of Fishes* **37**, 47–55.
- Pike, A. S., Scatena, F. N. & Wohl, E. E. (2010). Lithological and fluvial controls on the geomorphology of tropical montane stream channels in Puerto Rico. *Earth Surface Processes and Landforms* **35**, 1402–1417.
- Ramírez, A., De Jesús-Crespo, R., Martínó-Cardona, D. M., Martínez-Rivera, N. & Burgos-Caraballo, S. (2009). Urban streams in Puerto Rico: what can we learn from the tropics? *Journal of the North American Benthological Society* **28**, 1070–1079.
- Seber, G. A. F. (1982). *The Estimation of Animal Abundance and Related Parameters*. Caldwell, NJ: Blackburn Press.
- Smith, W. E. (2013). Reproductive ecology of Caribbean amphidromous fishes. PhD Thesis, North Carolina State University, Raleigh, NC, U.S.A. Available at <http://repository.lib.ncsu.edu/ir/handle/1840.16/8322/>
- Smith, W. E. & Kwak, T. J. (2014). Otolith microchemistry of tropical diadromous fishes: spatial and migratory dynamics. *Journal of Fish Biology* **84** (in press).

- Winemiller, K. O. (2005). Life history strategies, population regulation, and implications for fisheries management. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 872–885.
- Winemiller, K. O. & Ponwith, B. J. (1998). Comparative ecology of eleotrid fishes in Central American coastal streams. *Environmental Biology of Fishes* **53**, 373–384.

### Electronic Reference

- Kwak, T. J., Cooney, P. B. & Brown, C. H. (2007). Fishery Population and Habitat Assessment in Puerto Rico Streams: Phase 1 Final Report. *Federal Aid in Sportfish Restoration Project F-50 Final Report*. Marine Resources Division, Puerto Rico Department of Natural and Environmental Resources, San Juan, U.S.A. Available at [www.drna.gobierno.pr/biblioteca/publicaciones/tecnicas/Kwak\\_et\\_al\\_2007\\_PR\\_Streamms\\_PrintView.pdf](http://www.drna.gobierno.pr/biblioteca/publicaciones/tecnicas/Kwak_et_al_2007_PR_Streamms_PrintView.pdf) (accessed on 23 November 2012).