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Climbing for dummies: recommendation for multi- specific fishways for the conservation of tropical eels and gobies

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Abstract :

Dams and other man-made barriers impair upstream fish migration and thus threaten fish populations that need access to upper river reaches to complete their life cycle. For many years, fishways have been used to mitigate this impact. Fishways around the globe are typically built based on recommendations made for northern hemisphere species, particularly salmonids. These recommendations do not consider the locomotor characteristics and skills of other species, especially those living in the tropics. Among tropical species, freshwater eels and gobies of the Sicydiinae subfamily are important cultural and economic species that are particularly sensitive to the impact of man-made barriers. Our experimental study aimed to test different substrates and slopes for ramp-like fishways adapted to tropical eels and sicydiines. Among the five substrates tested for 368 eels Anguilla marmorata, elastomer pins appeared to be the most efficient. Elastomer pins also appeared to be more efficient than the fine concrete which is currently used in fishways for sicydiines (Sicyopterus lagocephalus, N = 1797, and Cotylopus acutipinnis, N = 1303). The slope had a lesser effect on the climbing success of sicydiines compared to substrate type, except for gradients greater than 50° that induced a slight decrease in success. Our results indicated that ramp-like fishways fitted with 1.0 cm diameter elastomer pins, positioned in staggered rows with a diagonal spacing of 1.3 cm, wetted with low-flow and angled less than 50°, are well adapted to accommodate the different locomotor characteristics and skills of tropical eels and sicydiines.

Keywords : amphidromy, catadromy, dam, fish migration, river continuum, upstream passage, fishways, eels

Introduction

The fragmentation of river ecosystems by dams and other man-made barriers has been reported as a major threat for freshwater biodiversity (Vörösmarty et al., 2010). Additionally, human population growth and economic development increase water demand for energetic, agricultural and domestic purposes. Consequently, more than 30,000 major dams (Chen et al., 2016), and many smaller ones, were constructed over the past decades and more than 3,000 are currently planned or under construction (Zarfl et al., 2015). These dams are of particular threat to fish species that need access to upper river reaches to complete their life cycles. A common conservation measure to mitigate the impact of dams and other barriers on fish populations is the construction of fishways (Larinier et al., 1992). However, globally, most fishways were designed for salmonids. As these fishways do not consider the various locomotor styles and performance of other species (Birnie-Gauvin et al., 2019), they are generally less efficient for non-salmonid species (Noonan, Grant, & Jackson, 2012). Consequently, fishways specifically adapted to the locomotor capacities of the non-salmonid species have been developed (Baker & Boubée, 2006; Romão et al., 2017; Bao et al., 2019). Fishways for eels provide a well-documented example of fishways adapted to locomotor specificities (Porcher, 2002; Solomon & Beach, 2004). These fishways consist of an inclined ramp fitted with a wetted climbing substratum adapted to eel crawling behaviour. The efficiency of fishways for eels has recently been under scrutiny both in experimental (Vowles et al., 2015; Watz et al., 2019) and in situ studies (Drouineau et al., 2015). However, most of these studies focused on the northern hemisphere and/or temperate eel species, whereas southern hemisphere and/or tropical species have received little attention (Jellyman, Bauld, & Crow, 2017).

Indigenous freshwater fish species inhabiting small tropical islands are particularly sensitive to dams and other barriers (Franklin & Gee, 2019). Most of these species migrate from the sea to freshwater at a specific stage of their anadromous, catadromous or amphidromous life cycle (Augspurger, Warburton, & Closs, 2016). Anadromous species spawn in freshwater, and their juveniles migrate to the sea where they mature before returning to spawn in freshwater. Catadromous adults reproduce in the sea and their juveniles grow in rivers until they mature. Amphidromous adults reproduce in rivers, their larvae grow in the sea and juveniles return to rivers to grow and mature (McDowall, 1988). The fragmentation of riverine habitat may severely impair these populations by limiting their access to their growing and/or spawning habitats (March et al., 2003). Catadromous eels (*Anguilla* spp.) and the amphidromous gobies of the Sicydiinae subfamily are abundant in small tropical islands (Kwak, Engman, & Lilyestrom, 2018; Lagarde et al., 2020a). These freshwater fish species are economically and culturally important at both the local and international scales (Bell, 1999; Robinet et al., 2008; Jacoby et al., 2015). These species have specific locomotor ("climbing") capacities that allow them to pass migration barriers several meters high. Eels can crawl to climb barriers, as their adherence to the substrate can be maintained by friction and surface tension even when the slope of the obstacle is very steep (Legault, 1988). They also use substrate roughness to support their movement (Larinier et al., 1992). While climbing, sicydiines alternate undulatory movement to progress, and rest when they adhere their ventral sucker to the substrate (Schoenfuss & Blob, 2003). Species of the *Sicyopterus* genus have also been documented to use their mouth to attach to the substrate when climbing (Blob et al., 2019). Further, when climbing, eels and sicydiines use areas where the water layer is only a few millimetres deep. Despite the strong migration capacities of eels and sicydiines, dams have been reported to severely impact their populations as a limited number of individuals are able to pass structures of more than approx. 10 m high (Cooney & Kwak, 2013; Lagarde, Borie, & Ponton, 2020b).

In Reunion Island (southwestern Indian Ocean), freshwater fish assemblages are dominated by two sicydiine species: the cosmopolitan *Sicyopterus lagocephalus* and the endemic *Cotylopus acutipinnis*, and one eel species, the cosmopolitan *Anguilla marmorata* (Teichert et al., 2014a; Lagarde et al., 2020a). Fishways specifically adapted to the climbing behaviour of sicydiines were developed by Voegtlé, Larinier & Bosc (2002). These authors recommended building a ramp covered with fine concrete and with a longitudinal slope of 50° (120%). Dams constructed between 2000 and 2010 are equipped with such fishways. However, recent studies demonstrated that eels were not able to pass these specific fishways (Lagarde et al., 2015a) and only sicydiine individuals with the highest climbing performance could climb over them (Lagarde et al., 2020b). These observations highlight the need to adapt the existing fishways to facilitate the passage for both eels and sicydiines, as these species colonise the same reaches within watersheds.

Consequently, we aimed to test different substrates and ramp longitudinal slopes to allow eels to successfully climb the ramps while facilitating the climbing of sicydiines. Our results will be useful in implementing new multi-specific fishways designed specifically for tropical eels (especially *A. marmorata*) and sicydiines (especially *S. lagocephalus* and *C. acutipinnis*).

Material and Methods

Fish sampling and experimental arena

Fish were sampled using a Hans Grassel IG 200-2 portable electro-shocker during low flow conditions in 2015 and 2016 following the recommendation of permit N° 15–024 DEAL/SEB/UPEMA delivered by the Direction de l’Environnement, de l’Aménagement et du Logement de la Réunion. This permit allowed for the annual sampling of a maximum of 200 eels, 1,500 *C. acutipinnis* and 2,000 *S. lagocephalus*. Eels smaller than 15–20 cm total length (TL) were not fully pigmented and consequently could not be identified at the species level (Keith et al., 2006). However, *A. marmorata* represents more than 90% of eel individuals in Reunion Island (Robinet et al., 2007) and fully pigmented individuals captured during this study were all identified as *A. marmorata*.

It was thus assumed that all eels sampled during this study were *A. marmorata*. *Sicyopterus lagocephalus* and *A. marmorata* were sampled in the downstream reach of St Etienne River, the closest river to the experimental facilities. *Cotylopus acutipinnis* were sampled in the downstream reach of Marsouins River which hosts the largest population of the species (Olivier, Valade, & Bosc, 2004; Ocea Consult', 2014). After capture, all fish were transported to the experimental facilities in an aerated bucket filled with stream water.

The experimental arena consisted of three 2.5 m long, 0.5 m wide ramps placed between two 90 L tanks (Fig. 1A). Each ramp was fed by a low flow (0.5 $L.s^{-1}$ or 1,800 $L.h^{-1}$). It had a transversal slope of 6° (10%) insuring the presence of a water layer a few millimetres deep which is used by eels and sicydiines for climbing. One ramp was covered with fine concrete, the substrate used for ramps specific to sicydiines (Voegtlé et al., 2002; Lagarde et al., 2015a). The two other ramps were fitted with different substrates commonly used to build fishways for European eels: a) concrete or elastomer studs, b) 1.0 cm and 0.6 cm wide elastomer pins (Fig1B). The aligned concrete studs (Evergreen, Sobutéma) were 4.5 cm high, 5.5 cm in diameter, and 4.0 cm from each other. Lines of studs were separated by lines of holes with the same dimension as the studs. This type of substrate was proven to work and adapted to build fishways for small (TL <15 cm) European eels (Voegtlé et al., 2002). The three other substrates were developed specifically for European eels with an elastomer resin resistant to collisions and abrasion (available at www.montaison-anguille.fr). Resistance appears particularly important in the context of tropical rivers where cyclonic floods can carry huge quantities of sand, pebbles and even boulders over the fishways. The elastomer studs were 3.0 cm high and 3.0 cm in diameter with a minimum distance of 2.0 cm between them. The elastomer pins were 1.0 cm and 0.6 cm in diameter, and 5 cm and 2 cm high with a minimum distance of 1.3 cm and 1.3 cm between them, respectively. Elastomer pins and studs were not aligned but positioned in staggered rows. Each substrate was tested with three longitudinal ramp slopes: 30° (60%), 50° (120%) as recommended in ramps for sicydiines (Voegtlé et al., 2002) and 70° (280%). The 30° slope was selected as the 50° slope recommended for ramps for sicydiines is slightly steeper than the maximal slope recommended for ramps for European eels (45°, Voegtlé & Larinier, 2000). Finally, a steep 70° slope was also tested; and if proven efficient for *A. marmorata* and sicydiines, it might be a good solution to reduce the dimension of fishways and their construction costs.

Fig. 1

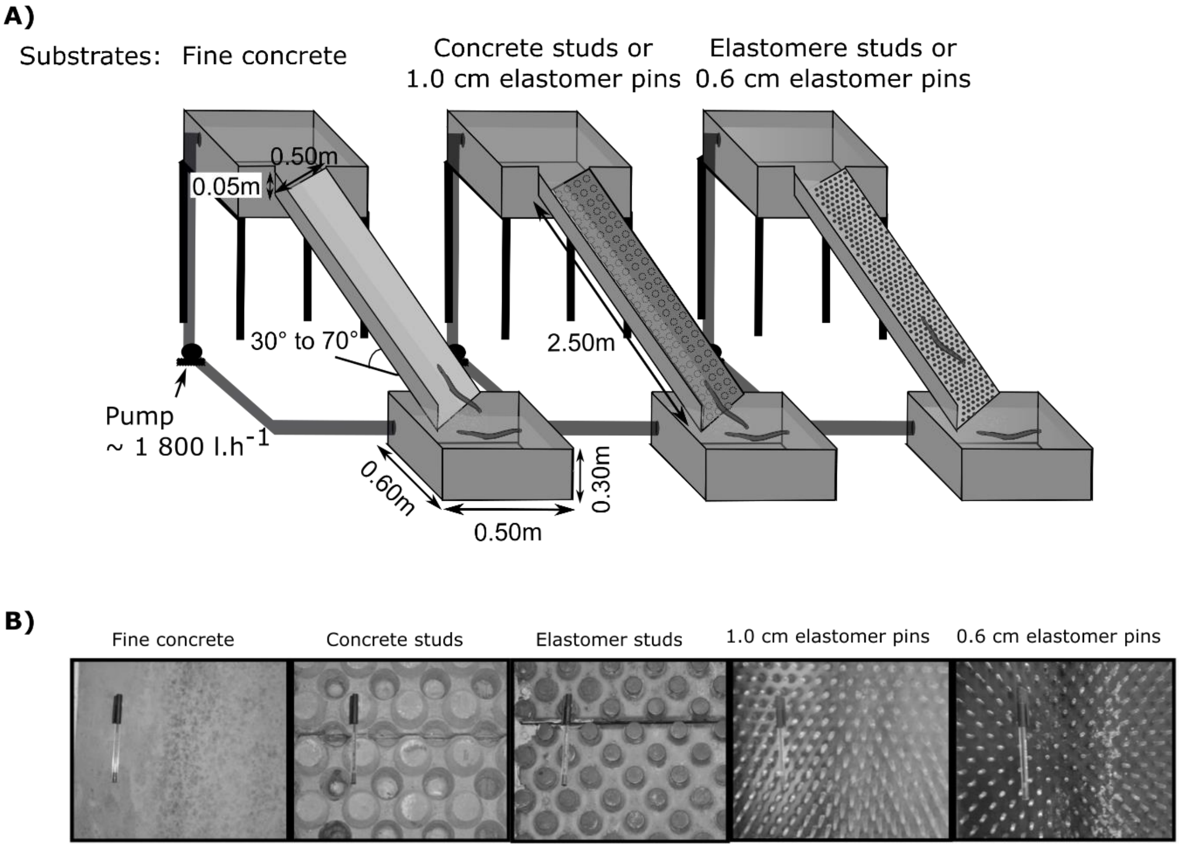

Figure 1: Schematic representation of the experimental arena used to evaluate the ability of *A. marmorata*, *S. lagocephalus* and *C. acutipinnis* to climb ramps with different substrates and longitudinal slopes (A). Photographs illustrating the different substrates (B). The pencil depicted is 14 cm long.

Climbing experiments

A five-step climbing test was conducted for each of the three species. First, the three ramps were set to the same angle, and each ramp was fitted with a different substrate. Second, a pre-defined number of fish was introduced in the lower tank of each experimental system and allowed acclimate for a minimum of two hours. Third, fish climbing behaviour was stimulated with flowing water (approx. 1,800 L.h^{-1}) pumped from the lower tank to the upper tank of each ramp. The discharge was selected to stimulate the climbing behaviour and was not selected to simulate natural conditions. As a reference, the natural discharge flow over ramps is usually> 300,000 L.h^{-1} (Lagarde et al., 2015b). However, independent of the discharge, fish climb in a water layer of only a few millimetres deep that limits the effect of discharge on their climbing success. Fourth, the fish that had climbed to the upper tank, referred to as "climbers" hereafter, were collected several times during the test depending on the species (see below for details), and held in aerated buckets of water until the end of the test. Those that were still climbing the ramps, or those that remained in the lower tank, referred to as "non-climbers", were collected at the end of the climbing test and held. Finally, all climbers and non-climbers were anesthetized in 0.3 ml.L^{-1} of clove oil solution (diluted at 30% in alcohol), counted and measured (TL) to the closest mm.

In 2015, three climbing experiments were performed for *A. marmorata*, at slopes of 30°, 50° and 70° with 3 substrates: fine concrete, concrete studs and elastomer studs. In 2016, three climbing experiments were performed at the same slopes with 2 substrates: 1.0 cm and 0.6 cm elastomer pins. As eels are known to primarily migrate during the night (Jellyman, 1977), their climbing behaviour was stimulated over two two-hour periods, from 18:00 to 20:00 and from 4:00 to 6:00, during the first two nights after capture (two tests per night). Due to the limited number of *A. marmorata* available, the same 50–70 individuals were used in the four consecutive tests for each slope (Table 1). *A. marmorata* were randomly divided between the tested substrates before each climbing test. Preliminary observations showed that the climbing success of *A. marmorata* on fine concrete was null. Consequently, only a few individuals (42–66) were tested with this substrate to confirm this observation. *A. marmorata* present in the upper tanks were removed every 15 min and kept in a bucket until TL could be measured in order to prevent their escape from the upper tanks. Across all experiments, less than ten *A. marmorata* were observed escaping the upper tank.

For *S. lagocephalus* and *C. acutipinnis*, three climbing experiments were performed in 2016 at slopes of 30°, 50° and 70° with three different substrates: the fine concrete (considered as control because it is used to build fishways for sicydiines) and the 1.0 cm and 0.6 cm elastomer pins, which were the two most efficient substrates for *A. marmorata* (see results). As many *S. lagocephalus* and

C. acutipinnis were available, groups of 200-250 individuals were established and used for a single test. Each group was randomly divided into three sub-groups (one per substrate). Each slope was tested using three groups of *S. lagocephalus* and two groups of *C. acutipinnis* separately (Table 1), and each group was randomly divided into three sub-groups (one sub-group per tested substrate). As both species climb primarily during the afternoon (Lagarde et al. 2015a) with a slower climbing speed than *A. marmorata* (Blob et al. 2019, personal observations), their climbing behaviour was stimulated over a four-hour period, from 14:00 to 18:00 the day of capture. *Sicyopterus lagocephalus* and *C. acutipinnis* present in the upper tanks were removed every hour and kept in a bucket until TL could be measured. No *S. lagocephalus* and *C. acutipinnis* were observed escaping from the upper tank.

The room that housed the experimental arena was maintained at approximately 24°C, a temperature frequently observed in Reunionese rivers (Teichert et al., 2014b; Hoarau et al., 2019), in a 12:12h light/dark cycle. The three species were kept unfed during the experiment. All individuals were released at their capture site the day following the end of the experiment.

Statistical analysis

Fish length is an important factor affecting climbing performance of eels (Legault, 1988) and sicydiines (Lagarde et al., 2018a). Their mass-specific power production decreases with their body size while the constraints of drag from flowing water and the force of gravity increase (Blob et al., 2007). Consequently, a preliminary analysis consisted of comparing TL distributions between all fish, climbers and non-climbers, for each ramp slope and substrate using kernel density estimates (Langlois et al., 2012). As TL distributions differed between groups for all species (see results and Fig. S1), TL was integrated as an explanatory variable in climbing success analyses.

For each species, climbing success was considered as a binary variable; where climbers were assigned a score of one, and non-climbers a score of zero. Climbing success was analysed using logistic general additive models (GAMs) with three explanatory variables: one continuous, a smooth penalised splines function of TL, and two categorical, the ramp substrate and slope. For *A. marmorata*, the four different tests were not independent as they were performed with the same groups of individuals. Consequently, the tests cannot be considered as true replicates and the four GAMs were constructed and interpreted separately. This procedure guaranteed that individuals were only considered once per GAM analysis in order to avoid pseudo-replication. For these GAMs, the significance of TL, ramp substrate and slope on climbing success was assessed with a Chi² test. For *S. lagocephalus* and *C. acutipinnis,* between two and three groups of individuals were tested for each slope. These groups were independent and thus can be considered as true replicates. A unique GAM was constructed for each species with the test identifier as a random effect. The significance of the fixed effect of TL, ramp substrate and slope on climbing success was assessed with a Chi² test. All statistical analyses were performed using the open source R v. 3.6.0 software (R Core Team, 2018), packages *Kernsmooth* (Wand, 2015) and *sm* (Bowman & Azzalini, 2014) were used for for TL distribution comparison, and *gamm4* (Wood & Scheipl, 2014) was used for GAMs analyses with and without random effects.

Results

General results

Climbing tests were performed on 368 *A. marmorata*, 1,797 *S. lagocephalus* and 1,303 *C. acutipinnis*. The TL of *A. marmorata* ranged from 72 mm to 577 mm, with most individuals measuring between 100 mm and 250 mm (Table 1, Fig. S1 A). For *S. lagocephalus,* TL ranged from 30 mm to 117 mm, with most individuals measuring between 30 mm and 60 mm. For *C. acutipinnis*, TL ranged from 21 mm to 90 mm, with most individuals measuring between 25 mm and 50 mm. TL distributions of tested individuals differed significantly between ramp slope and substrate for the three species (Kernel density estimates, band width = 50 mm for *A. marmorata* and 5 mm for *S. lagocephalus* and *C. acutipinnis,* $p<0.001$). Consequently, TL was considered as an explanatory variable in further analyses. The percentage of *A. marmorata,* which successfully climbed the ramps, varied between 0% for fine concrete at all slopes, and more than 55% for 1.0 cm elastomer pins at 70° (Table 1). This percentage varied between 19% for fine concrete at 70° and 68% for 1.0 cm elastomer pins at 50° for *S. lagocephalus* and between 4% for fine concrete at 70° and 71% for 1.0 cm for *C. acutipinnis* (Table 1).

Table 1: Number (N) of *A. marmorata* (N = 368), *S. lagocephalus* (N = 1797) and *C. acutipinnis* (N = 1303) tested during the climbing experiment, number of individuals which successfully climbed the ramps (N_climb) and the mean climbing success for all tests (%success). For both groups the size range (TL) is specified in parenthesis. For *A. marmorata*, all individuals from the four climbing tests performed during the two first nights were grouped. Consequently, each *A. marmorata* is counted four times. For *S. lagocephalus* and *C. acutipinnis*, the three and two groups of 200-250 fish tested were grouped, respectively. Consequently, each *S. lagocephalus* and *C. acutipinnis* is counted only once. "-" indicates concrete and elastomer studs were not tested for *S. lagocephalus* and *C. acutipinnis* in 2016, as 2015 and 2016 experiments demonstrated that *A. marmorata* performed better with elastomer pins.

		A. marmorata			*S. lagocephalus*			*C. acutipinnis*		
Substrate	Slope	N (TL)	N_climb (TL)	% success	N (TL)	N_climb (TL)	% success	N (TL)	N_climb (TL)	% success
Fine concrete	30°	43 (78-354)	0	0%	189 (34-104)	76 (34-95)	40%	135 (26-75)	44 (26-67)	33%
	50°	42 (75-421)	0	0%	231 (35-115)	73 (36-109)	32%	131 (25-83)	43 (25-83)	33%
	70°	66 (82-482)	0	0%	160 (30-112)	30 (30-84)	19%	140 (21-72)	5 (31-42)	4%
Concrete studs	30°	87 (66-352)	8 (110-271)	9%	-	-	-	-	-	-
	50°	85 (72-570)	16 (202-436)	19%	-	-	-	-	-	-
	70°	109 (82-557)	0	0%	-	-	-	-	-	-
Elastomer studs	30°	92 (69-347)	27 (74-347)	29%	-	-	-	-	-	-
	50°	90 (72-582)	34 (131-431)	38%	-	-	-	-	-	-
	70°	100 (83-550)	32 (152-339)	32%	-	-	-	-	-	-
1.0 cm elastomer pins	30°	118 (94-492)	63 (94-353)	53%	204 (35-117)	86 (35-106)	42%	139 (26-90)	51 (27-73)	37%
	50°	128 (82-409)	35 (137-341)	27%	232 (35-114)	157 (35-96)	68%	139 (26-86)	99 (26-86)	71%
	70°	115 (89-377)	63 (89-336)	55%	182 (30-109)	54 (32-91)	30%	145 (24-74)	78 (27-60)	54%
0.6 cm elastomer pins	30°	122 (93-488)	57 (93-354)	47%	215 (33-102)	113 (36-98)	53%	151 (27-76)	91 (27-68)	60%
	50°	124 (90-410)	41 (105-316)	33%	221 (35-106)	135 (41-100)	61%	152 (25-75)	105 (25-75)	69%
	70°	124 (91-379)	59 (98-307)	48%	163 (30-93)	40 (31-66)	25%	169 (25-79)	64 (25-62)	38%

Effect of TL, ramp substrate and slope on climbing success

For *A. marmorata*, almost 70% of successful climbing events were observed during the two climbing tests performed on the first night, probably because fatigue and stress due to multiple handling and climbing tests limited the climbing success during the second night. Consequently, only the results concerning the tests performed during the first night are presented (Fig. 2A-B and Table 2); the results concerning the two tests performed during the second night are provided as supplementary materials for information only (Fig. S2 and Table S1). The two GAMs fitted separately for the first and second climbing tests performed during the first night explained a moderate proportion of the total variance in climbing success of *A. marmorata* (24% and 27%, respectively). The effect of the ramp slope on *A. marmorata* climbing success was not significant for the two GAMs fitted separately for two climbing tests performed during the first night (Table 2, Fig. 2A-B). Conversely, the ramp substrate had a significant effect on *A. marmorata* climbing success in all GAMs analyses with the 1.0 cm and 0.6 cm elastomer pins, and, to a lesser extent the elastomer studs associated with the highest climbing success rates (Table 2, Fig. 2A-B). This effect was consistent among the three independent groups of eels tested each year and for each substrate at 30°, 50° and 70° slopes. The climbing success increased with TL, reaching a maximum at approximately 200-300 mm and decreasing steadily for larger individuals (Fig. 2A-B and S2A-B).

Fig. 2

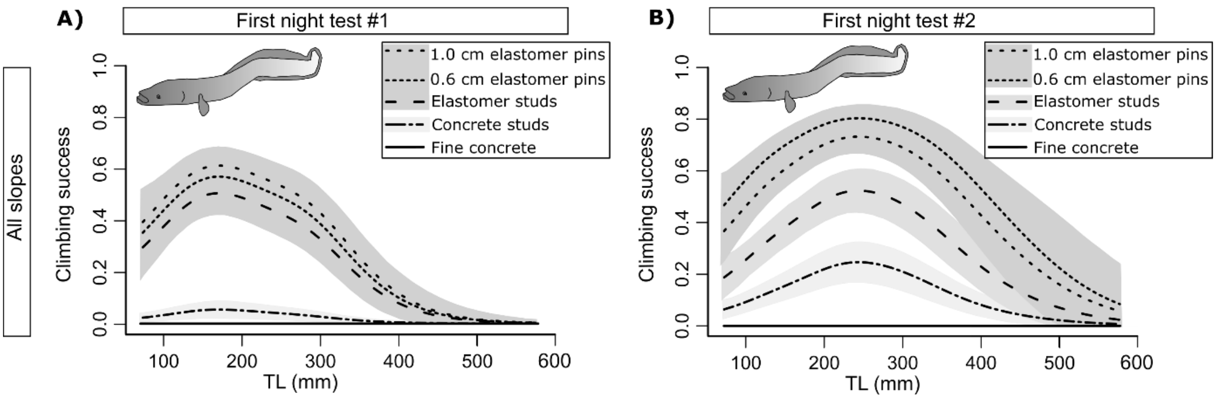

Figure 2: Climbing success probability of *A. marmorata* during the first night test#1 (A) and test#2 (B) with respect to their size (TL) and for the five different substrates tested. The grey shaded areas represent the standard error predictions.

Table 2: Summary of the GAM models predicting *A. marmorata* climbing probability with the ramp substrate (Substrate), its slope (Slope) and a smoothing function of the total length (s(TL)) as explanatory variables. Two models were built separately for the first night test#1 and #2.

	Variable	df	Chi²	p
First night test#1	Substrate	4.0	27.8	<0.001
	Slope	2.0	0.8	0.664
	s(TL)	2.7	12.3	0.008
First night test#2	Substrate	4.0	27.6	<0.001
	Slope	2.0	1.2	0.542
	s(TL)	2.7	14.5	0.002

As the 1.0 cm and 0.6 cm elastomer pins were the most efficient substrates to facilitate *A. marmorata* climbing, the efficiency of these two substrates was compared to those of fine concrete for *S. lagocephalus* and *C. acutipinnis* in 2016. The aim was to assess the potential of ramps equipped with elastomer pins for the three species. For *S. lagocephalus*, the fixed effects of the mixed GAMs explained a low proportion (11%) of the total variance in their climbing success. For *C. acutipinnis*, it explained a moderate proportion (23%) of the total variance in their climbing success. For *S. lagocephalus* and *C. acutipinnis*, the effects of ramp substrate, slope and TL were significant (Table 3, Fig. 3 and 4). For both species the climbing success rate was higher for the 1.0 cm and 0.6 cm elastomer pins compared to the fine concrete (Fig. 3 and 4). This rate was slightly lower at 70° compared to 30° and 50°, and decreased with fish TL (Fig. 3 and 4).

Table 3: Summary of the fixed effects of the mixed GAM models predicting *S. lagocephalus* and *C. acutipinnis* climbing probability with the ramp substrate (Substrate), its slope (Slope) and a smoothing function of the total length (s(TL)) as explanatory variables. The climbing tests were considered as a random effect.

	Variable	df	Chi²	p
S. lagocephalus	Substrate	2.0	70.0	<0.001
	Slope	2.0	47.5	<0.001
	s(TL)	1.0	77.1	<0.001
C. acutipinnis	Substrate	2.0	120.9	<0.001
	Slope	2.0	13.4	0.001
	s(TL)	2.8	259.7	<0.001

Fig. 3

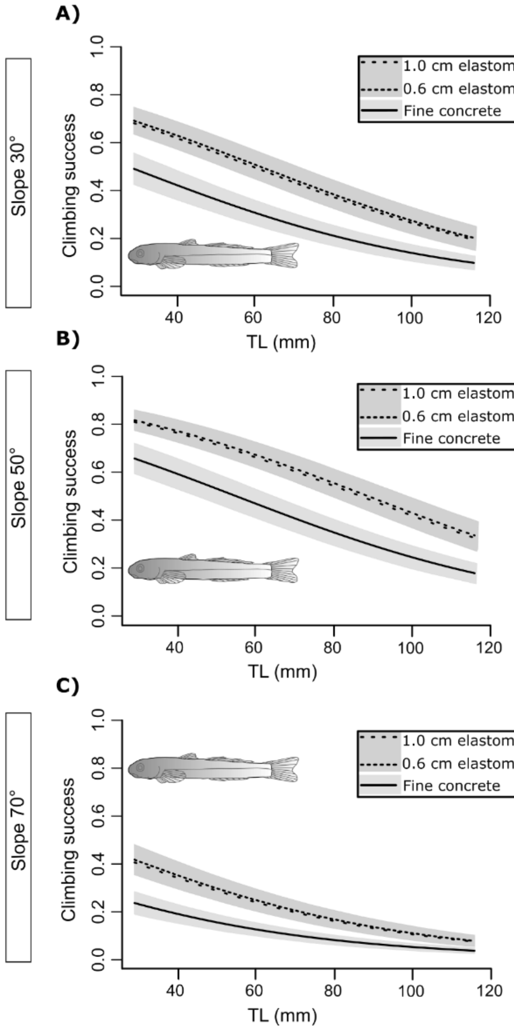

Fig. 4

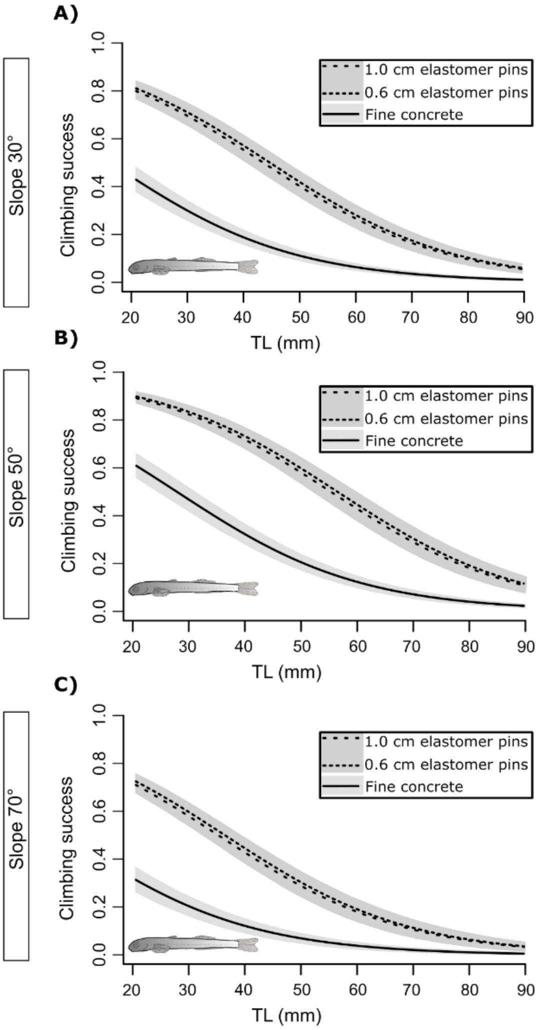

Figure 3 : Climbing success probability of *S. lagocephalus* with respect to their size (TL) and for the three different substrates tested with ramp slopes of 30° (A), 50° (B) and 70° (C). The grey shaded areas represent the standard error predictions.	Figure 4 : Climbing success probability of *C. acutipinnis* with respect to their size (TL) and for the three different substrates tested with ramp slopes of 30° (A), 50° (B) and 70° (C). The grey shaded areas represent the standard error predictions.

Discussion

Overall, our study provides new recommendations for the construction of fishways specifically adapted to tropical eels and sicydiines. Specifically, these fishways should consist of a ramp with a maximal longitudinal slope of 50° fitted with elastomer pins positioned in staggered rows with a diagonal spacing of 1.3 cm. Even if our results indicated that climbing success of the three species was comparable between the 0.6 cm and 1.0 cm elastomer pins, the larger diameter of the 1.0 cm elastomer pins makes them more resistant to shocks and abrasion during floods. In the context of tropical islands, the 1.0 cm elastomer pins appear more adapted than the smaller ones. The ramp should have a transversal slope to ensure the presence of a water layer measuring a few millimetres in depth, to allow eels and sicydiines to climb. Although our study was conducted on one species of eel (*A. marmorata*) and two species of sicydiines (*S. lagocephalus* and *C. acutipinnis*), the morphological and climbing behaviour similarities among eel and sicydiine species should make our results applicable to other species in these groups.

Ideally, a perfect ramp substrate should ensure the climbing success of the target species for the entire size range of migrating individuals. The 1.0 cm and 0.6 cm elastomer pins nearly meet this objective. The two substrates were the most efficient for *A. marmorata* and more efficient than fine concrete for *S. lagocephalus* and *C. acutipinnis*. Their high efficiency is probably partly explained by their elevated surface roughness that reduces the velocity of the water flowing over the ramp and which also increases flow heterogeneity (Baker & Boubée, 2006; Jellyman et al., 2017). Although the concrete and elastomer studs used in our experiment probably increase energy dissipation, reduce water velocity and increase flow heterogeneity, their effect is less important due to their lower density and thus lower roughness. The reduced water velocity limits the constraints of drag from the flowing water and the increased flow heterogeneity provides many resting areas for climbing fish, thereby reducing their effort (Maie, Schoenfuss, & Blob, 2007; Ditsche & Summers, 2014). Another hypothesis which may explain the efficiency of elastomer pins compared to the other studied substrates is related to the climbing behaviours of eels and sicydiines. *Anguilla* spp. are known to climb obstacles by crawling (Jellyman, 1977; Legault, 1988). When crawling, their body needs to be in contact with several points of the substrate (Solomon & Beach, 2004). With a distance of only 1.3 cm between two elastomer pins, eels can be in contact with several different pins that probably help them to climb. Sicydiine species can climb smooth substrates with the help of their ventral and/or oral sucker (Blob et al., 2019; Lagarde et al., 2018a). Additionally, during this study, we observed individuals pushing on the pins with their tails and fins while climbing. As a similar observation was made for the Hawaiian sicydiine *Lentipes concolor* (Blob et al., 2006), it can reasonably be assumed that this behaviour facilitates climbing among sicydiines. However, the narrow 1.3 cm space between two pins can also limit the climbing success for individuals with a larger body width. This size constraint may explain why the climbing probabilities of eels decreased for individuals with a TL longer than 300 mm. Another explanation for this decrease may be that larger individuals weighed more, resulting in an increase in climbing effort. This latter hypothesis better explains why the climbing success of sicydiines also decreased with size for two elastomer pin substrates while their body width is narrower than 1.3 cm. Nonetheless, in the context of small tropical islands such as Reunion Island, upstream migration is mainly undertaken by small-sized individuals. The eels are less than 200 mm TL (Robinet, 2004) with a body width narrower than 1.0 cm. Sicydiine juveniles are less than 55 mm TL (Lagarde et al., 2015a) with a body width narrower than 0.8 cm. Consequently, the space between two pins would be large enough for these individuals, which recently arrived from the ocean, especially for sicydiines for which only individuals longer than 100 mm TL have a body width larger than 1.3 cm. In larger rivers on continents, these species can migrate hundreds of kilometres upstream (Harrison, 1993; Lyons, 2005; Hanzen et al., 2020) and thus have time to grow. In continental watersheds, fishways thus need to accommodate larger individuals in upstream reaches and our recommendation need to be adjusted to a larger size range of fishes. In this context, increasing the variety of pin dimensions, and inter-pin spacing, could facilitate the climbing of a greater number of fish size classes.

The ramp slope is another critical factor affecting eels and sicydiines as climbing success is supposed to decrease with steeper slopes (Voegtlé et al., 2002; Jellyman et al., 2017). Our results only partially confirmed this expectation. The climbing success of the sicydiines slightly decreased for the steepest slope (i.e. 70°) whereas the climbing success of eels did not decrease with slopes varying from 30°-70°. The increase of the gravity constraint on climbing individuals, and the energy requirement for climbing the ramps would explain why the climbing success of the two sicydiine species was lower for the steeper slopes. This had already been observed by Voegtlé et al. (2002) who described lower climbing success of *S. lagocephalus* at 70° and 90° slopes compared to 50° and by Lagarde et al., (2018a) who observed that small *C. acutipinnis* juveniles failed to climb a plastic gutter angled at 70°. Surprisingly, and despite the observation made for other eel species such as *Anguilla australis* (Jellyman et al., 2017) or *Anguilla anguilla* (Watz et al., 2019), the climbing success of *A. marmorata* did not decrease when ramp slopes became steeper. This absence of effect has to be interpreted with caution as only one group of *A. marmorata* was tested per slope. However, beyond this methodological consideration, the absence of effect of the ramp slope on the climbing success of *A. marmorata* may be explained by their behaviour. Although still poorly understood, the behavioural factors influencing fish entrance and progression in fishways likely play an important role in determining the efficiency of fishways (Castro-Santos, Cotel, & Webb, 2009; Silva et al., 2017). These behavioural factors probably explain why our GAMs models performed moderately in explaining eels and sicydiines climbing probabilities. Turbulent flows have been documented to better attract and stimulate the climbing behaviour of *A. anguilla* (Piper, Wright, & Kemp, 2012). Therefore, elevated turbulence at the foot of the ramps may have positively attracted eels and stimulated their climbing behaviour. The velocity of water flow increased with the slope, generating greater turbulence when the water reached the lower tank. These intense turbulences in the lower tank may have increased eels' attraction and stimulated their climbing behaviour, counterbalancing the expected lower climbing success on steeper ramps. This hypothesis could have been confirmed by enumerating the number of climbing attempts made for each substrate and each slope (Watz et al., 2019). Unfortunately, we did not have the equipment necessary to record the lower section of the three ramps, especially in the dark. Understanding the factors influencing the climbing behaviour of eels and sicydiines is another crucial step for properly designing the entry of fishways (hydraulic exit).

The diadromous life cycle of eels and sicydiines makes these species particularly sensitive to the impact of instream barriers (Han et al., 2008; Rolls, 2011). Many dams and other manmade structures impede their migrations throughout their distribution range (Holmquist, Schmidt-Gengenbach, & Yoshioka, 1998; Lagarde et al., 2020b; Lin et al., 2017). Most fishways at dams focus on upstream passage, but diadromous species have a life cycle that also requires downstream passage. Our recommendations for designing ramp-like fishways fitted with 1.0 cm elastomer pins, positioned in staggered rows with a diagonal spacing of 1.3 cm, wetted with low flow and angled less than 50° will help to improve the design of fishways to restore the upstream migration of tropical eels and sicydiines. However, when water is impounded in dams, this will also greatly impact the downstream migration of eel future genitors and sicydiine larvae (March et al., 2003). Traditional mitigation measures to restore downstream migration of temperate eels involve the building of screening systems to prevent eels from being diverted with the water and to then guide them toward a bypass (Larinier & Travade, 2002; Gosset et al., 2005). These methods can easily be adapted to tropical eels. Conversely, the small size of sicydiine larvae (about 2 mm long) prevents the use of physical barriers to guide their migration (Lagarde et al., 2017). Moreover, their stochastic seasonal and diel migration dynamics limits the efficiency of water diversion shutdown (Lagarde et al., 2018b). Methods to mitigate the impact of dams on the downstream migration of sicydiine (and other amphidromous species) larvae are urgently needed and this key research gap must be central in applied research concerning these species (Jarvis & Closs, 2019).

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Data availability statement

Survey data cannot be made public for legal reasons but they are available upon request from the authors and data producers.

Authors contribution statement

RL, DC and DP conceived and designed the study. RL; HG and LF performed the field work. RL analysed the data. RL wrote the manuscript; other authors provided editorial advice.

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References:

Augspurger, J. M., Warburton, M., & Closs, G. P. (2016). Life-history plasticity in amphidromous and catadromous fishes: a continuum of strategies. *Review in Fish Biology and Fisheries* 27, 177–192.

Baker, C. F., & Boubée, J. a. T. (2006). Upstream passage of inanga *Galaxias maculatus* and redfin bullies *Gobiomorphus huttoni* over artificial ramps. *Journal of Fish Biology* 69, 668–681.

Bao, J., Li, W., Zhang, C., Mi, X., Li, H., Zhao, X., Cao, N., Twardek, W. M., Cooke, S. J., & Duan, M. (2019). Quantitative assessment of fish passage efficiency at a vertical-slot fishway on the Daduhe River in Southwest China. *Ecological Engineering* 141, 105597.

Bell, K. N. I. (1999). An overview of goby-fry fisheries. *Naga, the ICLARM Quarterly* 22, 30–36.

Birnie-Gauvin, K., Franklin, P., Wilkes, M., & Aarestrup, K. (2019). Moving beyond fitting fish into equations: Progressing the fish passage debate in the Anthropocene. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29, 1095–1105.

Blob, R. W., Rai, R., Julius, M. L., & Schoenfuss, H. L. (2006). Functional diversity in extreme environments: effects of locomotor style and substrate texture on the waterfall-climbing performance of Hawaiian gobiid fishes. *Journal of Zoology* 268, 315–324.

Blob, R. W., Wright, K. M., Becker, M., Maie, T., Iverson, T. J., Julius, M. L., & Schoenfuss, H. L. (2007). Ontogenetic change in novel functions: waterfall climbing in adult Hawaiian gobiid fishes. *Journal of Zoology* 273, 200–209.

Blob, R. W., Lagarde, R., Diamond, K. M., Keeffe, R. M., Bertram, R. S., Ponton, D., & Schoenfuss, H. L. (2019). Functional diversity of evolutionary novelties: Insights from waterfall-climbing kinematics and performance of juvenile gobiid fishes. *Integrative Organismal Biology* 1, 1–8.

Bowman, A. W., & Azzalini, A. (2014). R package “sm”: non parametric smothing method R package version 2.2-5.4.

Castro-Santos, T., Cotel, A., & Webb, P. (2009). Fishway evaluations for better bioengineering: an integrative approach. *American Fisheries Society Symposium* 69, 557–575.

Chen, J., Shi, H., Sivakumar, B., & Peart, M. R. (2016). Population, water, food, energy and dams. *Renewable and Sustainable Energy Reviews* 56, 18–28.

Cooney, P. B., & Kwak, T. J. (2013). Spatial extent and dynamics of dam impacts on tropical island freshwater fish assemblages. *BioScience* 63, 176–190.

Ditsche, P., & Summers, A. P. (2014). Aquatic versus terrestrial attachment: Water makes a difference. *Beilstein Journal of Nanotechnology* 5, 2424–2439.

Drouineau, H., Rigaud, C., Laharanne, A., Fabre, R., Alric, A., & Baran, P. (2015). Assessing the efficiency of an elver ladder using a multi-state mark–recapture model. *River Research and Application* 31, 291–300.

Franklin, P., & Gee, E. (2019). Living in an amphidromous world: Perspectives on the management of fish passage from an island nation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29, 1424–1437.

Gosset, C., Travade, F., Durif, C., Rives, J., & Elie, P. (2005). Tests of two types of bypass for downstream migration of eels at a small hydroelectric power plant. *River Research and Applications* 21, 1095–1105.

Han, M., Fukushima, M., Kameyama, S., Fukushima, T., & Matsushita, B. (2008). How do dams affect freshwater fish distributions in Japan? Statistical analysis of native and non native species with various life histories. *Ecological Research* 23, 735–743.

Hanzen, C., Lucas, M. C., O'Brien, G., Calverley, P., & Downs, C. T. (2020). Surgical implantation of radio tags in three eel species (*Anguilla* spp.) in South Africa. *Journal of Fish Biology* 96, 847–852.

Harrison, I. J. (1993). The West African sicydiine fishes, with notes on the genus *Lentipes* (Teleostei: Gobiidae). *Ichthyological Exploration of Freshwaters* 4, 201–232.

Hoarau, P. E., Courtecuisse, E., Treilhes, C. R., Lagarde, R., Teichert, N., & Valade, P. B. (2019). Reproductive biology of a small amphidromous shrimp *Atyoida serrata* on Reunion Island, south-west Indian Ocean. *Limnologica* 76, 41–47.

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.

Jacoby, D. M. P., Casselman, J. M., Crook, V., DeLucia, M.-B., Ahn, H., Kaifu, K., Kurwie, T., Sasal, P., Silfvergrip, A. M. C., Smith, K. G., Uchida, K., Walker, A. M., & Gollock, M. J. (2015). Synergistic patterns of threat and the challenges facing global anguillid eel conservation. *Global Ecology and Conservation* 4, 321–333.

Jarvis, M. G., & Closs, G. P. (2019). Water infrastructure and the migrations of amphidromous species: impacts and research requirements. *Journal of Ecohydraulics* 4, 4–13.

Jellyman, D. J. (1977). Summer upstream migration of juvenile freshwater eels in New Zealand. *New Zealand Journal of Marine and Freshwater Research* 11, 61–71.

Jellyman, P. G., Bauld, J. T., & Crow, S. K. (2017). The effect of ramp slope and surface type on the climbing success of shortfin eel (*Anguilla australis*) elvers. *Marine and Freshwater Research* 68, 1317–1324.

Keith, P., Marquet, G., Valade, P., & Vigneux, E. (2006). Atlas des poissons et des crustacés d'eau douce des Comores, Mascareignes et Seychelles. Paris: Muséum national d'Histoire naturelle. 250 p.

Kwak, T. J., Engman, A. C., & Lilyestrom, C. G. (2018). Ecology and conservation of the American eel in the Caribbean region. *Fisheries Management and Ecology* 26, 42–52.

Lagarde, R., Teichert, N., Boussarie, G., Grondin, H., & Valade, P. (2015a). Upstream migration of amphidromous gobies of La Réunion Island: implication for management. *Fisheries Managment and Ecology* 22, 437–449.

Lagarde, R., Teichert, N., Courret, D., & Grondin, H. (2015b). Etude et suivi du fonctionnement des dispositifs de franchissement pour les Cabots bouche-ronde mis en place sur les captages d'eau ILO des rivières du Mât et de Fleurs Jaunes. Etang Salé : ARDA. 87 p.

Lagarde, R., Teichert, N., Grondin, H., Magalon, H., Pirog, A., & Ponton, D. (2017). Temporal variability of larval drift of tropical amphidromous gobies along a watershed in Réunion Island. *Canadian Journal of Fisheries and Aquatic Sciences* 74, 948–957.

Lagarde, R., Borie, G., Blob, R. W., Schoenfuss, H. L., & Ponton, D. (2018a). Intra- and inter-specific morphological diversity of amphidromous gobies influences waterfall-climbing performance. *Journal of Zoology* 306, 243–251.

Lagarde, R., Teichert, N., Faivre, L., Grondin, H., Magalon, H., Pirog, A., Valade, P., & Ponton, D. (2018b). Artificial daily fluctuations of river discharge affect the larval drift and survival of a tropical amphidromous goby. *Ecology of Freshwater Fish* 27, 646–659.

Lagarde, R., Teichert, N., Valade, P., & Ponton, D. (2020a). Structure of small tropical island freshwater fish and crustacean communities: A niche-or dispersal-based process? *Biotropica* published online.

Lagarde, R., Borie, G., & Ponton, D. (2020b). Dams select individual morphology but do not modify upstream migration speed of tropical amphidromous gobies. *River Research and Applications* 36, 57–67.

Langlois, T. J., Fitzpatrick, B. R., Fairclough, D. V., Wakefield, C. B., Hesp, S. A., McLean, D. L., Harvey, E. S., & Meeuwig, J. J. (2012). Similarities between line fishing and baited stereo-video estimations of length-frequency: novel application of kernel density estimates. *PLoS ONE* 7, e45973.

Larinier, M., & Travade, F. (2002). Downstream migration: problems and facilities. *Bulletin Français de la Pêche et de la Pisciculture* 364, 181–207.

Larinier, M., Travade, F., Porcher, J. P., & Gosset, C. (1992). Passes à poissons : expertise et conception des ouvrages de franchissement. Paris: CSP. 336 p.

Legault, A. (1988). Le franchissement des barrages par l'escalade de l'anguille. Etude en Sèvre Niortaise. *Bulletin Français de la Pêche et de la Pisciculture* 308, 1–10.

Lin, H.-Y., Jupiter, S. D., Jenkins, A. P., & Brown, C. J. (2017). Impact of anthropogenic disturbances on a diverse riverine fish assemblage in Fiji predicted by functional traits. *Freshwater Biology* 62, 1422–1432.

Lyons, J. (2005). Distribution of *Sicydium* Valenciennes 1837 (Pisces: Gobiidae) in Mexico and Central America. *Hidrobiologica* 15, 239–243.

Maie, T., Schoenfuss, H. L., & Blob, R. W. (2007). Ontogenetic scaling of body proportions in waterfall-climbing Gobiid fishes from Hawai'i and Dominica: implications for locomotor function. *Copeia* 2007, 755–764.

March, J. G., Benstead, J. P., Pringle, C. M., & Scatena, F. N. (2003). Damming tropical island streams: problems, solutions, and alternatives. *BioScience* 53, 1069–1078.

McDowall, R. M. (1988). Diadromy in fishes: migration between freshwater and marine environments. Croom Helm. London.

Noonan, M. J., Grant, J. W. A., & Jackson, C. D. (2012). A quantitative assessment of fish passage efficiency. *Fish and Fisheries* 13, 450–464.

Ocea Consult'. (2014). Suivi 2014 des éléments biologiques "poissons et macro-crustacés" des rivières du bassin Réunion. Saint Denis : OLE. 243 p.

Olivier, J.-M., Valade, P., & Bosc, P. (2004). Analyse des données du réseau de suivi piscicole de La Réunion : Etude de faisabilité d'un outil d'expertise de la qualité des peuplements piscicoles et de la fonctionnalité des milieux aquatiques associés. Etang Salé: ARDA. 55 p.

Piper, A. T., Wright, R. M., & Kemp, P. S. (2012). The influence of attraction flow on upstream passage of European eel (*Anguilla anguilla*) at intertidal barriers. *Ecological Engineering* 44, 329–336.

Porcher, J. P. (2002). Fishways for eels. *Bulletin Français de la Pêche et de la Pisciculture* 364, 147–155.

R Core Team. (2018). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Robinet, T., Réveillac, E., Kuroki, M., Aoyama, J., Tsukamoto, K., Rabenevanana, M. W., Valade, P., Gagnaire, P.-A., Berrebi, P., & Feunteun, E. (2008). New clues for freshwater eels (*Anguilla* spp.) migration routes to eastern Madagascar and surrounding islands. *Marine Biology* 154, 453–463.

Robinet, T., Feunteun, E., Keith, P., Marquet, G., Olivier, J.-M., Réveillac, E., & Valade, P. (2007). Eel community structure, fluvial recruitment of *Anguilla marmorata* and indication for a weak local production of spawners from rivers of Réunion and Mauritius islands. *Environmental Biology of Fishes* 78, 93–105.

Robinet, T. (2004). Mécanismes de persistance des assemblages piscicoles en eau douce : des bassins côtiers continentaux aux îles océaniques. La Rochelle. 253 p.

Rolls, R. J. (2011). The role of life-history and location of barriers to migration in the spatial distribution and conservation of fish assemblages in a coastal river system. *Biological Conservation* 144, 339–349.

Romão, F., Quaresma, A. L., Branco, P., Santos, J. M., Amaral, S., Ferreira, M. T., Katopodis, C., & Pinheiro, A. N. (2017). Passage performance of two cyprinids with different ecological traits in a fishway with distinct vertical slot configurations. *Ecological Engineering* 105, 180–188.

Schoenfuss, H. L., & Blob, R. W. (2003). Kinematics of waterfall climbing in Hawaiian freshwater fishes (Gobiidae): vertical propulsion at the aquatic-terrestrial interface. *Journal of Zoology* 261, 191–205.

Silva, A. T., Lucas, M. C., Castro-Santos, T., Katopodis, C., Baumgartner, L. J., Thiem, J. D., Aarestrup, K., Pompeu, P. S., O'Brien, G. C., Braun, D. C., Burnett, N. J., Zhu, D. Z., Fjeldstad, H.-P., Forseth, T., Rajaratnam, N., Williams, J. G., & Cooke, S. J. (2017). The future of fish passage science, engineering, and practice. *Fish and Fisheries* 19, 340–362.

Solomon, D. J., & Beach, M. H. (2004). Fish pass design for eel and elver (*Anguilla anguilla*) (R&D Technical report No. W2- 070/TR1). Bristol: Environment Agency. 92 p.

Teichert, N., Valade, P., Lim, P., Dauba, F., Labonne, J., Richarson, M., Bosc, P., & Gaudin, P. (2014a). Habitat selection in amphidromous Gobiidae of Reunion Island: Sicyopterus lagocephalus (Pallas, 1770) and Cotylopus acutipinnis (Guichenot, 1863). *Environmental Biology of Fishes* 97, 255–266.

Teichert, N., Valade, P., Fostier, A., Lagarde, R., & Gaudin, P. (2014b). Reproductive biology of an amphidromous goby, *Sicyopterus lagocephalus,* in La Réunion Island. *Hydrobiologia* 726, 123–141.

Voegtlé, B., & Larinier, M. (2000). Etude sur les capacités de franchissement des civelles et anguilette. Site hydroélectrique de Tuilières sur la Dordogne (24). Barrage estuarien d'Arzal sur la Vilaine (56) (RAPPORT GHAAPPE RAOO .05 / MIGADO G15-00-RT). 126 p.

Voegtlé, B., Larinier, M., & Bosc, P. (2002). Étude sur les capacités de franchissement des cabots bouche-rondes (*Sicyopterus lagocephalus*, Pallas, 1770) en vue de la conception de dispositifs adaptés aux prises d'eau du transfert Salazie (île de La Réunion). *Bulletin Français de la Pêche et de la Pisciculture* 109–120.

Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S. E., Sullivan, C. A., Liermann, C. R., & Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature* 467, 555–561.

Vowles, A. S., Don, A. M., Karageorgopoulos, P., Worthington, T. A., & Kemp, P. S. (2015). Efficiency of a dual density studded fish pass designed to mitigate for impeded upstream passage of juvenile European eels (*Anguilla anguilla*) at a model Crump weir. *Fisheries Management and Ecology* 22, 307–316.

Wand, M. (2015). KernSmooth: functions for kernel smoothing supporting Wand & Jones (1995). R package version 2.23-15.

Watz, J., Nilsson, P. A., Degerman, E., Tamario, C., & Calles, O. (2019). Climbing the ladder: an evaluation of three different anguillid eel climbing substrata and placement of upstream passage solutions at migration barriers. *Animal Conservation* 22, 452–462.

Wood, S., & Scheipl, F. (2014). gamm4: Generalized additive mixed models using mgcv and lme4. R package version 0.2-3.

Zarfl, C., Lumsdon, A. E., Berlekamp, J., Tydecks, L., & Tockner, K. (2015). A global boom in hydropower dam construction. *Aquatic Sciences* 77, 161–170.