



HAL
open science

Predation pressure in amphidromous gobies: how their morphology is selected by predator species

R. Lagarde, Dominique Ponton

► **To cite this version:**

R. Lagarde, Dominique Ponton. Predation pressure in amphidromous gobies: how their morphology is selected by predator species. *Journal of Zoology*, 2022, 319 (1), pp.32-41. <10.1111/jzo.13021>. <hal-04732136>

HAL Id: hal-04732136

<https://hal.science/hal-04732136v1>

Submitted on 8 Dec 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY 4.0 - Attribution - International License

Predation pressure in amphidromous gobies: how their morphology is selected by predator species

Lagarde R. ^{1,*}, Ponton D. ²

¹ Environnements Méditerranéens, Centre de Formation et de Recherche sur les Universités de Perpignan Via Domitia – CNRS Perpignan France

² ENTROPIE, IRD-Université de La Réunion-CNRS-Université de la Nouvelle-Calédonie-IFREMER, c/o, Institut Halieutique et des Sciences Marines (IH.SM) Université de Toliara Toliara Madagascar

* Corresponding author : R. Lagarde, email address : raphael.lagarde@univ-perp.fr

Abstract :

The morphology of an individual can improve its ability to escape predators and ultimately its chances of survival. Sicydiine fishes reproduce in rivers, and their larvae develop in the sea. Once juveniles arrive in rivers, they face numerous predatory fish species. Some juveniles can climb above the first waterfall where the abundance of predatory species is reduced. For individuals that do not climb waterfalls, survival only depends upon their ability to avoid predation. While the factors that affect climbing performance of sicydiines have been extensively described, the information is scarce concerning their predator escape performance. Our experimental study aimed to describe how the predation pressure imposed by three predatory fish species (*Eleotris klunzingerii*, *Kuhlia rupestris*, and *Anguilla marmorata*) affects the individual morphology of juveniles of two sicydiine species from Reunion Island (*Cotylopus acutipinnis* and *Sicyopterus lagocephalus*). Individuals which survived predation had a more streamlined body and larger and/or longer pectoral fins for the two sicydiine species, whereas other morphological variables differed with the predator species. Body form of individuals that survived predation also differed from the body form of individuals that climbed waterfalls. The different prey's body forms under selection by the three predator species should be considered in further studies that could address the tradeoff in sicydiines between climbing waterfalls and escaping predation in the field. For example, a careful description of the predator community would help to understand which predator(s) sicydiines juveniles need to escape in downstream reaches and how this particular predation pressure can select body forms.

Keywords : fish, diadromy, phenotype, predation pressure, selection, body shape, morphology, sicydiines

13 Introduction

14 As in many animal taxa, predation is a key driver in fish population dynamics. Direct impacts
15 correspond to prey mortality rates whereas indirect impacts are prey phenological adaptations to the
16 risk of predation (Johansson, Turesson & Persson, 2004; Kotrschal *et al.*, 2017). To decrease the risk
17 of predation, prey fishes can develop anti-predator traits such as body colors that reduce detection
18 (Donnelly & Whoriskey, 1991), changes in foraging behavior (Brown, 1999), morphological features
19 that limit the risk of ingestion (ex. deep body, spines, Domenici *et al.*, 2008), or increased escape
20 performance (Domenici, 2010; Gerry, Robbins & Ellerby, 2012). Body form plays a particularly
21 important role in a fish's ability to avoid predation. Narrower and shorter prey appear less
22 conspicuous, reducing their detectability, whereas deeper and/or longer prey have higher fast-start
23 swimming performance limiting their risk of capture (Domenici & Blake, 1997). Consequently, prey
24 body form, i.e. its size and shape, is among the traits selected by the pressure of predation
25 (Scharnweber *et al.*, 2013). However, the relationship between a prey's form and the likelihood it will

1 escape predation varies during ontogeny (Diamond *et al.*, 2019), between environments, and
2 depends on predatory species (Januszkiewicz & Robinson, 2007). Disentangling the relative
3 influences of these factors is necessary to describe 1) the ability of prey to escape predation and 2)
4 how predation pressure influences the demography of prey populations.

5 Gobies of the Sicydiinae sub-family are amphidromous (McDowall, 1988). These species
6 reproduce in rivers (Teichert *et al.*, 2013). Their larvae drift to the sea (Lagarde *et al.*, 2017, 2018b)
7 where they develop during several months (Teichert *et al.*, 2012, 2016) before returning to rivers
8 where individuals grow and reproduce (Teichert *et al.*, 2014a, 2014b). Their amphidromous life cycle
9 explains the elevated gene flow among populations due to larval mixing at sea (Berrebi *et al.*, 2005;
10 Hoareau *et al.*, 2007, Moody *et al.*, 2015). After their arrival in rivers, sicydiine juveniles face
11 numerous predators (Lagarde *et al.*, 2021b). Among them, *Eleotris* spp., which are ambush predators
12 with a strike/suction feeding strategy (Maie *et al.*, 2014), *Kulhia* spp., which actively chase their prey,
13 and *Anguilla* spp., which use both chasing and ambushing strategies. One remarkable behavior of the
14 sicydiine juveniles, allowing them to escape from predation, is their waterfall climbing behavior
15 (Schoenfuss & Blob, 2003; Blob *et al.*, 2019). Sicydiines use their pelvic and oral suckers to attach the
16 substrate while climbing (Schoenfuss & Blob, 2003). Once above the first waterfalls, sicydiine
17 juveniles encounter an environment with lower predation risks as only a few *Anguilla* spp. individuals
18 are capable of climbing waterfalls (Diamond *et al.*, 2021; Lagarde *et al.*, 2021a).

19 Sicydiines are good model species to study the response of individual body form to several selective
20 pressures, especially predation (Blob *et al.*, 2007; Schoenfuss & Blob, 2007). Indeed, before reaching
21 upstream reaches where predation risk is lower, the survival of sicydiine juveniles depends on their
22 ability to avoid predation in downstream areas (Blob *et al.*, 2010). Interestingly, some sicydiine
23 individuals do not migrate upstream; they grow and mature in downstream reaches (Teichert *et al.*,
24 2018). For these individuals, predation pressure will occur throughout their life and predation
25 avoidance ability plays a central role in their survival. For sicydiine species, no clear strategy

1 decreasing individual detectability by predators, or morphological features limiting the risk of
2 ingestion, has been ever observed despite extensive field observations. Consequently, it appears
3 likely that their main predator avoidance strategy relies on their ability to escape predator strikes.

4 Numerous studies have demonstrated that the waterfall climbing performance of sicydiine
5 juveniles imposes a selection on an individuals' morphology (Blob *et al.*, 2008; Kawano *et al.*, 2013;
6 Moody *et al.*, 2017; Lagarde *et al.*, 2018a, Lagarde, Borie & Ponton 2020). These studies also
7 highlighted that body forms associated with better climbing performance differed between species
8 depending on their climbing mode. To the best of our knowledge, the only study that focuses on the
9 effect of predation pressure on sicydiine juveniles was conducted in Hawaii with one species of
10 predator (*Eleotris sandwicensis*) and one sicydiine (*Sicyopterus stimpsoni*, Blob *et al.*, 2010). These
11 authors demonstrated that the selective pressures imposed by climbing and by predation differed.
12 Overall, fish that escaped predation had a greater body depth than the control group, and fish that
13 successfully passed the climbing trial had a narrower body. Blob *et al.* (2010) suggested the existence
14 of a trade-off between climbing waterfalls and escaping predation, in *S. stimpsoni*. However, the
15 existence of a trade-off remains unexplored for other sicydiine species subjected to the predation
16 pressure of multiple predatory species. This question is of interest as downstream reaches of tropical
17 rivers are populated by several predatory species (Lagarde *et al.* 2021b). An improved understanding
18 for how an individual's morphology can enhance its escape performance and capacity to climb
19 waterfalls would be pivotal to understand the possibility for each individual to grow and reproduce.
20 Eventually, it would help improve the population dynamic models for sicydiines (Artzrouni, Teichert
21 & Mara, 2014).

22 In this context, our experimental study aimed to describe how the predation pressure
23 imposed by three predatory species (*Eleotris klunzingerii*, *Kulhia rupestris* and *Anguilla marmorata*)
24 impacted the individual morphology of juveniles from two sympatric sicydiine species (*Cotylopus*
25 *acutipinnis* and *Sicyopterus lagocephalus*). Specifically, we proposed two hypotheses: (i) The effect of

1 predation pressure on morphology will be similar between the two closely related sicydiine species
2 and (ii), the morphologies selected by the predation pressure will differ between predators' species.

3

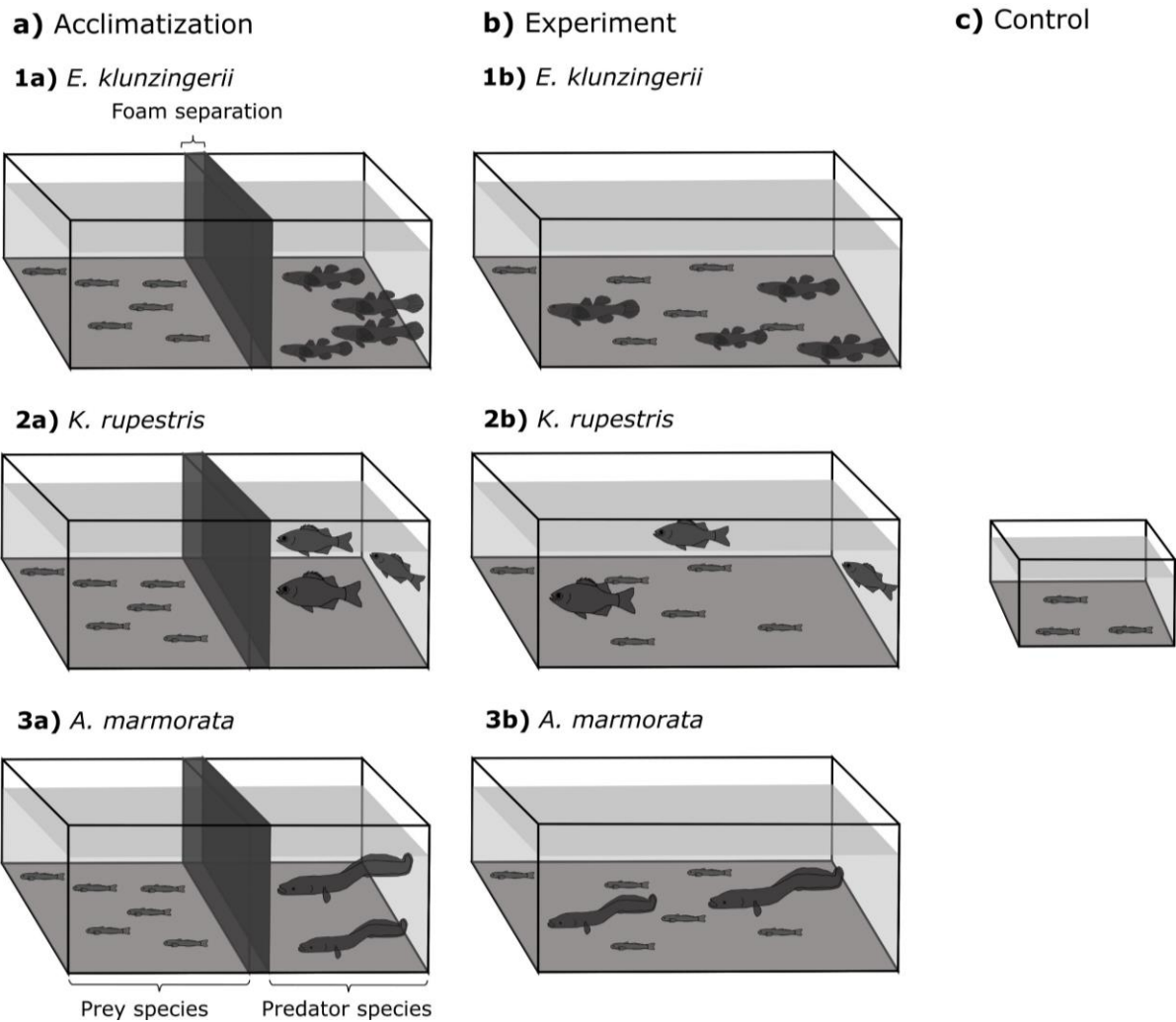
4 **Materials and methods**

5 Fish capture and predation experiments

6 Fish capture and predation experiments were conducted under permit N°16-019/DEAL/SEB/UPEMA
7 issued by the Direction de l'Environnement de l'Aménagement et du Logement de La Réunion.
8 Predator individuals were collected in the downstream reach of the Saint-Etienne River (Reunion
9 Island 21.0°S-55.5°E) using an IG 200-2 (Hans Grassl, Germany) portable electro-shocker. Individual
10 sizes (total length, L_T) ranged from 7.5 to 13.1 cm for *E. klunzingerii*, from 25.6 to 36.8 cm for *A.*
11 *marmorata* and from 14.4 to 17.6 cm for *K. rupestris*. For all individuals, the approximate gape size
12 (distance between the upper and lower jaws when the mouth is fully open) was more than 1 cm,
13 thus larger than the maximum body depth observed in prey (0.5 cm). After capture, fish were
14 transported to the laboratory and acclimated in three separated (one per species) 150 L aquaria. The
15 water temperature in the room was set at approximately 24°C, a temperature frequently recorded in
16 Reunionesse rivers (Teichert *et al.*, 2014a; Hoarau *et al.*, 2019). Fish were fed live tilapia (*Oreochromis*
17 spp.) from a local fish farm for a period of at least five days. They were starved for 48h before the
18 start of the experiment.

19 Freshly recruited juveniles with low pigmentation (stage J1, according to Keith *et al.* [2008])
20 *C. acutipinnis* (N=620) and *S. lagocephalus* (N=442) were collected immediately after their arrival in
21 freshwater at the mouth of the Saint-Etienne River using the same electro-shocker. The collection
22 site was located several kilometers downstream to the first waterfall in an area where the
23 abundance of predators was very low (personal observation). These young juveniles have thus
24 undergone very little selection pressure from predation and none from having to climb a waterfall.
25 All fish were collected and transported to the laboratory within a four-hour period to limit the effect

1 of prolonged captivity. Fish used in the four following experiments were collected during four
2 separate dates within a one-month period (from 5 December 2016 to 2 January 2017, Table S1) to
3 limit the differences in fish size among experiments. Depending on the period of the year that the
4 fish arrived in freshwater, the size, and thus morphology, of individuals of both species varied, 17-
5 23 mm L_T for *C. acutipinnis* (Teichert *et al.*, 2012), and 27-37 mm L_T for *S. lagocephalus* (Teichert *et*
6 *al.*, 2016b). Two experiments were performed with each predator-prey couple except for *C.*
7 *acutipinnis* and *A. marmorata* for which only one experiment was performed because all *A.*
8 *marmorata* died from a pathogen just before the first experiment. The protocol used in predation
9 experiments was similar to the one used by Blob *et al.* (2010). In short, upon arrival at the laboratory,
10 fish were randomly divided into “control” and “treatment” groups by capturing the fish with a deep
11 net and distributing two fish in each treatment group and one in the control group in turn. The
12 number of individuals in each treatment group was approximately twice the number in the control
13 group. Fish from the control group were placed in a 50 L aquaria without predators until the end of
14 the experiment (Fig. 1c). Fish from the treatment groups were immediately placed in the aquaria
15 where the selected predator was present, predators and prey being separated from each other by an
16 opaque foam fence (Fig. 1a). Fish from the treatment groups were acclimated in these aquaria
17 overnight. The next morning the foam fence was removed and the experiment was launched (Fig.
18 1b). The number of prey which survived the predation was visually estimated every 5 min during the
19 first hour after the experiment was launched and every 1 h to 3 h afterward. Experiments were run
20 until the predators consumed approximately 50% of the prey. This percentage was chosen to observe
21 a significant predation pressure on the treatment group while keeping more than 25 prey not eaten
22 by the predator for morphological measurements. The predators consumed 50% of the prey in one
23 to 20 hours depending of the predator and prey species. At this point, the remaining prey individuals
24 in the treatment groups were removed from the aquaria, and placed in aerated buckets.



1

2

3

4

5

6

7

8

9

10

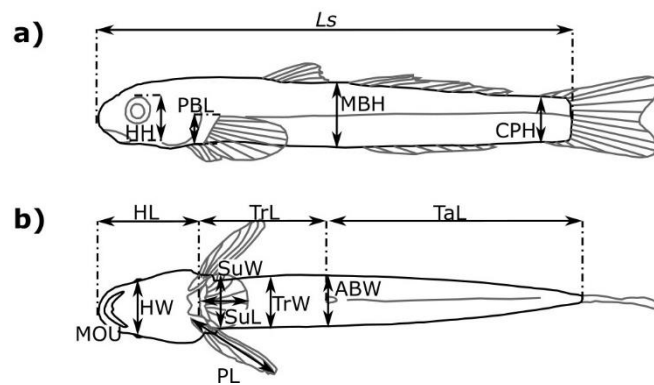
11

Figure 1: Schematic representation of the experimental design for the three predatory species, *E. klunzingerii* (1a-b), *K. rupestris* (2a-b) and *A. marmorata* (1a-b), and the control group (c). During the acclimatization period (a), prey (left of the aquarium) and predators (right of the aquarium) were separated by an opaque foam fence. This fence was removed at the beginning of the experiment (b).

Morphological measurements

Morphological measurements began when all prey from the three treatment groups were removed from the predators' aquaria. The protocol was the same as in Lagarde *et al.* (2018a). In short, fish were euthanized with an overdose of eugenol, then lateral and ventral pictures of each individual immersed in water were taken using an Epson perfection V750 PRO scanner. The delay before each

1 individual is scanned can affect its general condition, and thus its morphology. Individuals in each
 2 group (three treatment groups and one control group) were thus processed in groups of five until
 3 pictures of all individuals were obtained. Each individual was weighed (fresh weight, Fw) before
 4 scanning to estimate its Fulton condition factor (Fulton factor = $100 \cdot Fw \cdot Ls^{-3}$, Fulton, 1902) which
 5 provides a general estimation of a fish's physiological state (Mozsár *et al.*, 2015). Fifteen
 6 morphological variables (Fig. 2) were measured on the lateral and ventral pictures using IMAGE
 7 J v1.47 (Rasband, 2015).



8
 9 Figure 2: Lateral (a) and ventral (b) views illustrating the linear measurements performed on the two
 10 sicydiine species. (a) Ls, standard length; HH, head height, PBL, basal length of the pectoral fin, MBH,
 11 height at mid body, CPH, height of the caudal peduncle. (b) HL, head length, TrL, trunk length, TaL,
 12 tail length, SuL, sucker length, PL, length of the margin of the pectoral fin, HW, head width, SuW,
 13 sucker width, TrW, trunk width, ABW, width of the body at the location of the anal pore, MOU,
 14 perimeter of the inner margin of the mouth lip.

15

16 Statistical analyses

17 Several of the morphological variables studied were correlated to each other with a Pearson
 18 coefficient of correlation >0.8 for at least one of the two prey species. Collinearity between variables
 19 can strongly affect the statistical analyses used (Freckleton, 2011; Laws & Jamieson, 2011). The
 20 following variables were thus removed from the analyses: a) the body width at the location of the

1 anal pore (ABW) correlated to the trunk width (TrW) and the height at mid body (MBH), b) MBH
2 correlated to the Fulton condition factor, and c) the tail length (TaL) correlated to the standard
3 length (Ls) which is known to greatly influence swimming performance.

4 Our fish capture permit specified that the predators could not be sacrificed and needed to be
5 returned to their collection site. This obligation prevented us from comparing morphologies between
6 prey individuals that were eaten and those that survived. Instead, we compared surviving individuals
7 to those which were not exposed to predators (control). This approach is similar to methods
8 presented in Pearce and Boyce (2006) in which the control group was considered as “pseudo-
9 absence” of predation avoidance. The analysis of the selection pressure due to predation on prey
10 morphological variables was performed using logistic generalized linear mixed-effect models
11 (GLMM). Escape from predation was considered as a binary variable (1 for individuals that escaped
12 predation and 0 for the control group). As two experiments were conducted for each predator-prey
13 couple (except for *C. acutipinnis* and *A. marmorata*), an experiment was considered as a pseudo-
14 replicate and the experience ID was integrated as a random factor. The 12 remaining morphological
15 variables and the Fulton condition factor were included as explanatory variables. Variables for which
16 the effect of the selection pressure of predation was the most important were highlighted using a
17 model averaging procedure following the recommendation of Grueber *et al.* (2011). First, all of the
18 possible models were generated and their respective Akaike Information Criteria (AIC) were
19 calculated. Then, the best models were selected as those for which the difference between their AIC
20 and the lowest AIC was less or equal to two. The model averaging procedure was applied to the best
21 models and the significance of each retained variable was assessed using the Wald Z test. Finally, a
22 model performance was assessed via the area under the receiver operating characteristic (ROC)
23 curve. The ROC score ranges from 0 to 1 with a value ≤ 0.5 indicating that predictions are random or
24 worse than random. The closer the ROC score is to 1, the better the model can discriminate between
25 prey that avoid predation and those from the control group.

1 All statistical analyses were conducted using the open-source R software version 3.5.1 (R Core Team
 2 2018) using the lme4 (Bates *et al.*, 2015) and MuMin (Barton, 2020) packages for model averaging
 3 and pROC (Robin *et al.*, 2011) package for estimating the ROC scores.

4 **Results**

5 The predation rate ranged from 47% of *C. acutipinnis* eaten by *A. marmorata* to 60% of *S.*
 6 *lagocephalus* eaten by *A. marmorata* (Table 1). The morphological variables were measured on 347
 7 *C. acutipinnis* and 238 *S. lagocephalus* (Table 1). Note that the same individuals were used as controls
 8 in each of the pseudo-replicates for the three predatory species as the predation experiments were
 9 run simultaneously (Table S1).

10 Table 1: Number of individuals used in the predation experiments for *C. acutipinnis* and *S.*
 11 *lagocephalus*. N control, N before and N after correspond to the number of individuals in the control
 12 group, the number of individual introduced in the aquarium before the experiment and the number of
 13 individuals which survived the predation, respectively. Predation rate correspond to $100 \cdot (1 - N_{\text{after}} / N_{\text{before}})$. N pseudo replicates is the number of experiments performed for each prey-predator couple.
 14 Note that the same individuals were considered as control for the two or three predatory species for
 15 each pseudo replicate.
 16

	<i>C. acutipinnis</i>			<i>S. lagocephalus</i>		
	<i>E. klunzingerii</i>	<i>K. rupestris</i>	<i>A. marmorata</i>	<i>E. klunzingerii</i>	<i>K. rupestris</i>	<i>A. marmorata</i>
<i>N control</i>	97			60		
<i>N before</i>	209	209	105	128	127	126
<i>N after</i>	102	92	56	66	62	50
<i>Predation rate (%)</i>	51.2	56.0	46.7	48.6	51.2	60.3
<i>N pseudo replicates</i>	2	2	1	2	2	2

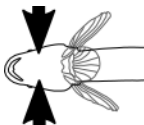
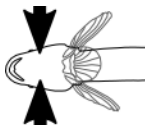
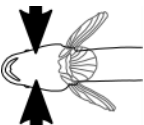

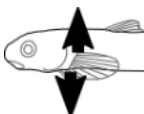
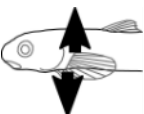
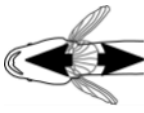
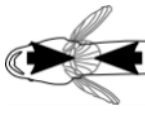



17
 18 The models selected from the model averaging procedure performed differently. For *C. acutipinnis*,
 19 the model that explained the selection pressure of predation by *A. marmorata* performed well (ROC
 20 score = 0.89). However, this result needs to be interpreted with caution as no pseudo-replicate was

1 included in the model. The models that explained the selection pressure of predation by *E.*
2 *klunzingerri* and *K. rupestris* performed moderately (ROC score = 0.73). For *S. lagocephalus*, the
3 models that explained the selection pressure of predation performed moderately for *E. klunzingerri*
4 (ROC score = 0.82) and *A. marmorata* (ROC score = 0.83) and poorly for *K. rupestris* (ROC score =
5 0.67).

6 *Cotylopus acutipinnis* and *S. lagocephalus* individuals that survived the predation of *E. klunzingerri*
7 and *A. marmorata* had a narrower head (Table 2, 3; Supplementary figure S2, S3; Wald Z test $p \leq$
8 0.001) and pectoral fins with a longer base ($p \leq 0.03$) or longer pectoral fins ($p < 0.001$) than those of
9 the control group. *Cotylopus acutipinnis* individuals that survived the predation of *E. klunzingerri* also
10 had and a longer sucker ($p = 0.03$) than those of the control group whereas *S. lagocephalus*
11 individuals that survived predation of *E. klunzingerri* had a longer and a narrower caudal peduncle (p
12 = 0.02). Finally, *C. acutipinnis* individuals that survived the predation of *A. marmorata* also had a
13 narrower sucker ($p = 0.02$) whereas *S. lagocephalus* individuals that survived the predation of *A.*
14 *marmorata* had a narrower head ($p = 0.01$), a longer sucker ($p = 0.01$), and a lower Fulton condition
15 factor ($p = 0.04$).

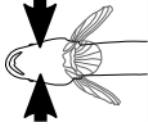
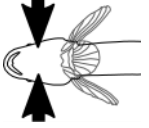
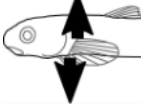

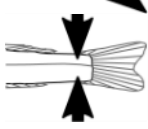




16

1 Table 2: Comparisons of selections imposed by predation on morphological variables based on model
 2 averaging procedure for *C. acutipinnis*. The results are presented for each predator species. The black
 3 arrows in “Dir.” indicates the direction of variation of the morphological variable of individuals which
 4 survived predation compared to control individuals. “ns” indicates a non-significant difference for the
 5 morphological variable. “-” morphological variable not selected by the model averaging procedure.

Morphological variable	<i>C. acutipinnis</i>					
	<i>E. klunzingerii</i>		<i>K. rupestris</i>		<i>A. marmorata</i>	
	Dir.	P	Dir.	P	Dir.	P
Head width (HW)		<0.001		0.03		<0.001
Trunk width (TrW)	-	-		0.01	ns	0.86
Basal length of the pectoral fin (PBL)		0.004	-	-		0.03
Length of the margin of the pectoral fin (PL)	-	-	ns	0.85	ns	0.71
Height of the caudal peduncle (CPH)	ns	0.77	ns	0.82	ns	0.88
Sucker length (SuL)		0.03		0.03	=	0.84
Sucker width (SuW)	-	-	ns	0.85		0.02
Standard length (Ls)	-	-		0.04	ns	0.47
Fulton condition factor (Fulton factor)	-	-		0.005	-	-
Head length (HL)	ns	0.17	-	-	ns	0.06
Head height (HH)	ns	0.55	ns	0.65	ns	0.88
Trunk length (TrL)	-	-	ns	0.70	ns	0.92
Perimeter of the inner margin of the mouth lip (MOU)	-	-	ns	0.91	-	-

1 Table 3: Comparisons of selections imposed by predation on morphological variables based on model
 2 averaging procedure for *S. lagocephalus*. The results are presented for each predator species. The
 3 black arrows in "Dir." indicates the direction of variation of the morphological variable of individuals
 4 which survived predation compared to control individuals. "ns" indicates a non-significant difference
 5 for the morphological variable. "-" morphological variable not selected by the model averaging
 6 procedure.

7

Morphological variable	<i>S. lagocephalus</i>					
	<i>E. klunzingerii</i>		<i>K. rupestris</i>		<i>A. marmorata</i>	
	Dir.	P	Dir.	P	Dir.	P
Head width (HW)		<0.001	ns	0.90		0.01
Trunk width (TrW)	ns	0.68	ns	0.87	ns	0.95
Basal length of the pectoral fin (PBL)	ns	0.36	ns	0.85		0.01
Length of the margin of the pectoral fin (PL)		<0.001	ns	0.91	ns	0.54
Height of the caudal peduncle (CPH)		0.02	ns	0.77	-	-
Sucker length (SuL)	-	-		0.01		0.01
Sucker width (SuW)	ns	0.36		0.01	ns	0.81
Standard length (Ls)	ns	0.88	ns	0.79	ns	0.52
Fulton condition factor (Fulton factor)	ns	0.34	ns	0.59		0.04
Head length (HL)	-	-	ns	0.72	ns	0.87
Head height (HH)	ns	0.85	-	-	-	-
Trunk length (TrL)	ns	0.34	ns	0.81	ns	0.84
Perimeter of the inner margin of the mouth lip (MOU)	ns	0.16	-	-	-	-

1 *Cotylopus acutipinnis* individuals that survived the predation of *K. rupestris* had a narrower head
2 width ($p = 0.03$) and trunk width ($p = 0.01$), a shorter sucker ($p = 0.03$), a longer standard length ($p =$
3 0.04) and a higher Fulton condition factor ($p = 0.005$) than those of the control group. *Sicyopterus*
4 *lagocephalus* individuals that survived the predation of *K. rupestris* had a longer ($p = 0.01$) and
5 narrower pelvic sucker ($p = 0.01$).

6 **Discussion**

7 Four morphological variables selected by the predation pressure were identical for the
8 juveniles of the two sicydiine species studied. This observation is consistent with the identical escape
9 behavior for these two species (Diamond *et al.*, 2019, 2021). Specifically, *C. acutipinnis* juveniles that
10 survived predation by the three predators and *S. lagocephalus* juveniles that survived predation by *E.*
11 *kluzingerri* and *A. marmorata*, each presented a narrower head and/or body than the control
12 individuals. These variables could be associated with a streamlined body that may reduce drag
13 (Webb, 1984) and may enhance the fast-start speed and acceleration in order to avoid predator
14 strikes as observed in other sicydiines (Blob *et al.*, 2010) or in bluegill (*Lepomis macrochirus*, Gerry *et*
15 *al.*, 2012). The opposite pattern was also observed in numerous other fish species for which deeper
16 body was associated with higher fast-start performances (Webb, 1978; Royle, Metcalfe & Lindström,
17 2006; Langerhans & Reznick, 2010). The larger and longer pelvic fins observed in individuals that
18 survived predation by *E. kluzingerri* and *A. marmorata* probably enabled them to generate more
19 thrust and/or to present a better maneuverability during the fast-start escape (Domenici & Blake,
20 1997; Blake, 2004). The influence of the pelvic sucker size on predation escape performance is less
21 clear. Larger pelvic suckers might increase drag and decrease fast-start performance if fish cannot
22 flatten or fold this structure. Under this hypothesis, smaller pelvic suckers observed for *C. acutipinnis*
23 that survived predation by *K. rupestris* and *A. marmorata*, and partially for *S. lagocephalus* that
24 survived predation by *K. rupestris*, could be associated with a higher fast-start escape performance
25 and thus, may have been selected by predation pressure. Alternatively, pelvic suckers are used by

1 sicydiines to attach to the substratum while climbing, especially during rest periods (Lagarde *et al.*,
2 2018a, 2020; Blob *et al.*, 2019). A specific predation escape behavior was observed in approximately
3 10-15 sicydiine juveniles per pseudo replicate during this study. This behavior consisted of jumping
4 out of the water to attach to the aquarium wall using their pelvic sucker. In this context, larger pelvic
5 suckers may increase the likelihood that sicydiines will successfully escape predation by enhancing
6 their ability to attach to emerged substrates.

7 Predator species also had an effect on the morphological variables of the two sicydiines
8 selected by predation pressure. For *S. lagocephalus*, the models selected by the model averaging
9 procedure performed worse for *K. rupestris* compared to *E. kluzingerii* and *A. marmorata*. One
10 hypothesis that could explain this difference is that *K. rupestris* actively chases its prey (personal
11 observation). When avoiding predation from *K. rupestris*, *S. lagocephalus* juveniles had to swim for
12 several seconds (burst swimming defined as the maximum swimming performance maintained up to
13 20 s; Beamish, 1978). The difference in burst swimming performance between the predator and its
14 prey is probably very important. In this context, even *S. lagocephalus* individuals with the best burst
15 swimming performance would have a low probability of escaping predation. In contrast,
16 *S. lagocephalus* can jump out of the water and attach to the walls of the aquarium. Thus, they could
17 increase their likelihood of survival even if *K. rupestris* can also leap out of the water to capture these
18 individuals (personal observation). This probably explains why the pelvic sucker dimension is mainly
19 associated with the likelihood that *S. lagocephalus* survives predation by *K. rupestris*. *Cotylopus*
20 *acutipinnis* individuals that were more likely to escape predation by *K. rupestris* had a narrower body,
21 were longer, had a higher Fulton condition factor and had a shorter pelvic sucker. This observation is
22 interesting as burst swimming performance strongly increases with size (Domenici, 2001). Generally,
23 fish with a higher Fulton condition factor are expected to have faster swimming performance as
24 observed in cod (*Gadus morhua*, Martínez *et al.*, 2004). This hypothesis is consistent with the positive
25 relationship between Fulton condition factor and predation escape from *K. rupestris* in *C. acutipinnis*.
26 Oppositely, *S. lagocephalus* which survived predation from *A. marmorata* had a lower Fulton

1 condition factor than the control group. One hypothesis which could explain this result is that the
2 Fulton condition factor can also be indicative of fish “roundness” (Garenc *et al.*, 1999). In this case, a
3 lower Fulton condition factor may be representative of individuals with a more streamlined body
4 which may increase their predation escape performance as explained above.

5 The morphologies associated with elevated predator escape performance in *C. acutipinnis*
6 and *S. lagocephalus* were different from those associated with higher climbing performance
7 described for the same species in previous studies (Lagarde *et al.*, 2018a, 2020). These studies
8 demonstrated that the selective pressure of climbing waterfalls favors juveniles *S. lagocephalus* with
9 a larger head and oral sucker and a flatter body, compared to the control group (“non-climbers”),
10 and juveniles *C. acutipinnis* with a larger and longer pelvic sucker. In the present study, most
11 individuals from the two species that survived predation had a narrower head and deeper or longer
12 pectoral fins compared to the control group. Consequently, after their arrival in rivers, some juvenile
13 sicydiines could have a body form which favors predation escape, and not necessarily climbing. These
14 morphological traits might make them more likely to grow and reproduce in the downstream reaches
15 (Teichert *et al.*, 2013, 2014b). In these reaches, sicydiines can reproduce almost year-round (Teichert
16 *et al.*, 2014a, 2016a) and, after hatching, larvae have a short drifting time in the river before reaching
17 the sea and thus their risk of mortality in freshwater could be limited (Bell, 2009; Closs, Hicks &
18 Jellyman, 2013). In contrast, individuals with a body form associated with a better climbing
19 performance may climb the first waterfall and reach areas where the predation pressure is reduced
20 (McRae, McRae & Fitzsimons, 2013; Kwak *et al.*, 2016; Lagarde *et al.*, 2021b) which may increase
21 their life expectancy. However, the reproduction season in upstream reach is limited to the warmer
22 months (Teichert *et al.*, 2014a, 2016a) and the risk of mortality of larvae increase with the distance
23 between their hatching site and the sea (Bell, 2009; Closs *et al.*, 2013). At a large regional scale, the
24 co-occurrence of both strategies may increase the fitness of the species. Each strategy may improve
25 individual survival and reproduction success according to local drivers such as the density and type of
26 predators present downstream or the height of the first waterfall. Describing how different drivers

1 affect individual survival and reproduction with respect to its migratory strategy is a challenging but
2 an important task that needs to be addressed in order to better understand sicydiine population
3 dynamics. Additionally, some emerging anthropogenic drivers may also affect sicydiine population
4 dynamics. For example, exotic predators, such as the rainbow trout (*Oncorhynchus mykiss*), were
5 introduced in several upstream reaches on tropical islands (Englund & Polhemus, 2001; Couteyen,
6 2006). These predators probably represent a threat for sicydiine individuals which escape the risk of
7 predation in downstream waters (via climbing) to colonize upstream reaches.

8 The present study demonstrates that body forms associated with high predator escape
9 performance in sicydiines depends on predator species. Future studies must address the relationship
10 between body forms and predation escape, as well as tradeoffs with climbing ability, in the field. For
11 example, a careful description of the predator community would help to understand which
12 predator(s) sicydiine juveniles need to escape in downstream reaches and how this particular
13 predation pressure can select body forms. Ultimately, understanding the relationship between body
14 forms, performance and fitness for the two key sicydiine functional behaviors, which are predator
15 avoidance and waterfall climbing, could provide insights into their population dynamics and may help
16 to highlight conservation needs (Schoenfuss & Blob, 2007).

17

1 Acknowledgments

2 This study was conducted with financial support from the Agence Française pour la Biodiversité
3 (square Félix Nadar, 94300 Vincennes, France). We thank Hydro Réunion for hosting the experiments
4 in their facilities and all of the people who assisted us during the study and especially Guillaume
5 Borie. We also thank Jeanine Almany for her corrections and suggestions concerning the English
6 language of the paper. We are also grateful to Journal of Zoology's associate editor and another
7 anonymous referee for their useful comments on previous versions of this paper.

8 **Authors contributions statement:** Conceptualization, Project administration, Funding acquisition,
9 Data curation, Methodology, Formal analysis, Writing—original draft: RL & DP.

10 References

- 11 Artzrouni, M., Teichert, N. & Mara, T. (2014). A Leslie matrix model for *Sicyopterus lagocephalus* in La
12 Réunion: sensitivity, uncertainty and research prioritization. *Math. Biosci.* **256**, 18–27.
- 13 Barton, K. (2020). MuMIn: Multi-Model Inference. *R package version 1.43.17*.
- 14 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using
15 lme4. *J. Stat. Softw.* **67**, 1–48.
- 16 Beamish, F.W.H. (1978). Swimming capacity. In *Fish physiology*: 101–187.
- 17 Bell, K.N.I. (2009). What comes down must go up: the migration cycle of juvenile-return anadromous
18 taxa. *Am. Fish. Soc. Symp.* **69**, 321–341.
- 19 Berrebi, P., Cattaneo-Berrebi, G., Valade, P., Ricou, J.-F. & Hoareau, T. (2005). Genetic homogeneity
20 in eight freshwater populations of *Sicyopterus lagocephalus*, an amphidromous gobiid of La
21 Réunion Island. *Mar. Biol.* **148**, 179–188.
- 22 Blake, R.W. (2004). Fish functional design and swimming performance. *J. Fish Biol.* **65**, 1193–1222.
- 23 Blob, R.W., Bridges, W.C., Ptacek, M.B., Maie, T., Cediél, R.A., Bertolas, M.M., Julius, M.L. &
24 Schoenfuss, H.L. (2008). Morphological selection in an extreme flow environment: body
25 shape and waterfall-climbing success in the Hawaiian stream fish *Sicyopterus stimpsoni*.
26 *Integr. Comp. Biol.* **48**, 734–749.
- 27 Blob, R.W., Kawano, S.M., Moody, K.N., Bridges, W.C., Maie, T., Ptacek, M.B., Julius, M.L. &
28 Schoenfuss, H.L. (2010). Morphological selection and the evaluation of potential tradeoffs
29 between escape from predators and the climbing of waterfalls in the Hawaiian stream goby
30 *Sicyopterus stimpsoni*. *Integr. Comp. Biol.* **50**, 1185–1199.

- 1 Blob, R.W., Lagarde, R., Diamond, K.M., Keeffe, R.M., Bertram, R.S., Ponton, D. & Schoenfuss, H.L.
2 (2019). Functional diversity of evolutionary novelties: Insights from waterfall-climbing
3 kinematics and performance of juvenile gobiid fishes. *Integr. Org. Biol.* **1**, 1–8.
- 4 Blob, R.W., Wright, K.M., Becker, M., Maie, T., Iverson, T.J., Julius, M.L. & Schoenfuss, H.L. (2007).
5 Ontogenetic change in novel functions: waterfall climbing in adult Hawaiian gobiid fishes. *J.*
6 *Zool.* **273**, 200–209.
- 7 Brown, J.S. (1999). Vigilance, patch use and habitat selection: Foraging under predation risk. *Evol.*
8 *Ecol. Res.* **1**, 49–71.
- 9 Closs, G.P., Hicks, A.S. & Jellyman, P.G. (2013). Life histories of closely related amphidromous and
10 non-migratory fish species: a trade-off between egg size and fecundity. *Freshw. Biol.* **58**,
11 1162–1177.
- 12 Couteyen, S. (2006). Effets de l'introduction de la truite arc-en-ciel (*Oncorhynchus mykiss* Walbaum,
13 1792) sur les populations larvaires de deux espèces de Zygoptères de l'île de la Réunion.
14 *Martinia* **22**, 55–63.
- 15 Diamond, K.M., Lagarde, R., Griner, J.G., Ponton, D., Powder, K.E., Schoenfuss, H.L., Walker, J.A. &
16 Blob, R.W. (2021). Interactions among multiple selective pressures on the form–function
17 relationship in insular stream fishes. *Biol. J. Linn. Soc.* **134**, 557–567.
- 18 Diamond, K.M., Lagarde, R., Schoenfuss, H.L., Walker, J.A., Ponton, D. & Blob, R.W. (2019).
19 Relationship of escape performance with predator regime and ontogeny in fishes. *Biol. J.*
20 *Linn. Soc.* **127**, 324–336.
- 21 Domenici, P. (2001). The scaling of locomotor performance in predator–prey encounters: from fish to
22 killer whales. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **131**, 169–182.
- 23 Domenici, P. (2010). Context-dependent variability in the components of fish escape response:
24 integrating locomotor performance and behavior. *J. Exp. Zool. A Ecol. Genet. Physiol.* **313A**,
25 59–79.
- 26 Domenici, P. & Blake, R. (1997). The kinematics and performance of fish fast-start swimming. *J. Exp.*
27 *Biol.* **200**, 1165–1178.
- 28 Domenici, P., Turesson, H., Brodersen, J. & Brönmark, C. (2008). Predator-induced morphology
29 enhances escape locomotion in crucian carp. *Proc. R. Soc. B: Biol. Sci.* **275**, 195–201.
- 30 Donnelly, W.A. & Whoriskey, F.G. (1991). Background-color acclimation of brook trout for crypsis
31 reduces risk of predation by hooded mergansers *Lophodytes cucullatus*. *N. Am. J. Fish.*
32 *Manag.* **11**, 206–211.
- 33 Englund, R.A. & Polhemus, D.A. (2001). Evaluating the effects of introduced rainbow trout
34 (*Oncorhynchus mykiss*) on native stream insects on Kauai Island, Hawaii. *J. Insect Conserv.* **5**,
35 265–281.
- 36 Freckleton, R.P. (2011). Dealing with collinearity in behavioural and ecological data: model averaging
37 and the problems of measurement error. *Behav. Ecol. Sociobiol.* **65**, 91–101.
- 38 Fulton, T.W. (1902). The rate growth of fishes. *20th annual report of the fishery board of Scotland* **3**,
39 326–346.

- 1 Garenc, C., Couture, P., Laflamme, M.-A. & Guderley, H. (1999). Metabolic correlates of burst
2 swimming capacity of juvenile and adult threespine stickleback (*Gasterosteus aculeatus*). *J.*
3 *Comp. Physiol. B* **169**, 113–122.
- 4 Gerry, S.P., Robbins, A. & Ellerby, D.J. (2012). Variation in fast-start performance within a population
5 of polyphenic bluegill (*Lepomis macrochirus*). *Physiol. Biochem. Zool.* **85**, 694–703.
- 6 Grueber, C.E., Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011). Multimodel inference in ecology and
7 evolution: challenges and solutions. *J. Evol. Biol.* **24**, 699–711.
- 8 Hoarau, P.E., Courtecuisse, E., Treilhes, C.R., Lagarde, R., Teichert, N. & Valade, P.B. (2019).
9 Reproductive biology of a small amphidromous shrimp *Atyoida serrata* on Reunion Island,
10 south-west Indian Ocean. *Limnologica* **76**, 41–47.
- 11 Hoareau, T.B., Bosc, P., Valade, P. & Berrebi, P. (2007). Gene flow and genetic structure of
12 *Sicyopterus lagocephalus* in the south-western Indian Ocean, assessed by intron-length
13 polymorphism. *J. Exp. Mar. Biol. Ecol.* **349**, 223–234.
- 14 Januszkiewicz, A.J. & Robinson, B.W. (2007). Divergent walleye (*Sander vitreus*)-mediated inducible
15 defenses in the centrarchid pumpkinseed sunfish (*Lepomis gibbosus*). *Biol. J. Linn. Soc.* **90**,
16 25–36.
- 17 Johansson, J., Turesson, H. & Persson, A. (2004). Active selection for large guppies, *Poecilia reticulata*,
18 by the pike cichlid, *Crenicichla saxatilis*. *Oikos* **105**, 595–605.
- 19 Kawano, S.M., Bridges, W.C., Schoenfuss, H.L., Maie, T. & Blob, R.W. (2013). Differences in locomotor
20 behavior correspond to different patterns of morphological selection in two species of
21 waterfall-climbing gobiid fishes. *Evol. Ecol.* **27**, 949–969.
- 22 Keith, P., Hoareau, T.B., Lord, C., Ah-Yane, O., Gimonneau, G., Robinet, T. & Valade, P. (2008).
23 Characterisation of post-larval to juvenile stages, metamorphosis and recruitment of an
24 amphidromous goby, *Sicyopterus lagocephalus* (Pallas) (Teleostei : Gobiidae : Sicydiinae).
25 *Mar. Freshw. Res.* **59**, 876–889.
- 26 Kotrschal, A., Deacon, A.E., Magurran, A.E. & Kolm, N. (2017). Predation pressure shapes brain
27 anatomy in the wild. *Evol. Ecol.* **31**, 619–633.
- 28 Kwak, T.J., Engman, A.C., Fischer, J.R. & Lilyestrom, C.G. (2016). Drivers of Caribbean freshwater
29 ecosystems and fisheries. In *Freshwater, fish and the future: proceedings of the global cross-*
30 *sectoral conference.*: 219–232. Rome: Welcomme.
- 31 Lagarde, R., Borie, G., Blob, R.W., Schoenfuss, H.L. & Ponton, D. (2018a). Intra- and inter-specific
32 morphological diversity of amphidromous gobies influences waterfall-climbing performance.
33 *J. Zool.* **306**, 243–251.
- 34 Lagarde, R., Borie, G. & Ponton, D. (2020). Dams select individual morphology but do not modify
35 upstream migration speed of tropical amphidromous gobies. *River Res. Applic.* **36**, 57–67.
- 36 Lagarde, R., Courret, D., Grondin, H., Faivre, L. & Ponton, D. (2021a). Climbing for dummies:
37 recommendation for multi-specific fishways for the conservation of tropical eels and gobies.
38 *Anim. Conserv.* **24**, 970–981.

- 1 Lagarde, R., Teichert, N., Faivre, L., Grondin, H., Magalon, H., Pirog, A., Valade, P. & Ponton, D.
2 (2018b). Artificial daily fluctuations of river discharge affect the larval drift and survival of a
3 tropical amphidromous goby. *Ecol. Freshw. Fish* **27**, 646–659.
- 4 Lagarde, R., Teichert, N., Grondin, H., Magalon, H., Pirog, A. & Ponton, D. (2017). Temporal variability
5 of larval drift of tropical amphidromous gobies along a watershed in Réunion Island. *Can. J.*
6 *Fish. Aquat. Sci.* **74**, 948–957.
- 7 Lagarde, R., Teichert, N., Valade, P. & Ponton, D. (2021b). Structure of small tropical island
8 freshwater fish and crustacean communities: A niche-or dispersal-based process? *Biotropica*
9 **53**, 243–254.
- 10 Langerhans, R.B. & Reznick, D.N. (2010). Ecology and evolution of swimming performance in fishes:
11 predicting evolution with biomechanics. In *Fish Locomotion*. CRC Press.
- 12 Laws, R.J. & Jamieson, I.G. (2011). Is lack of evidence of inbreeding depression in a threatened New
13 Zealand robin indicative of reduced genetic load? *Anim. Conserv.* **14**, 47–55.
- 14 Maie, T., Furtek, S., Schoenfuss, H.L. & Blob, R.W. (2014). Feeding performance of the Hawaiian
15 sleeper, *Eleotris sandwicensis* (Gobioidei: Eleotridae): correlations between predatory
16 functional modulation and selection pressures on prey. *Biol. J. Linn. Soc.* **111**, 359–374.
- 17 Martínez, M., Bédard, M., Dutil, J.-D. & Guderley, H. (2004). Does condition of Atlantic cod (*Gadus*
18 *morhua*) have a greater impact upon swimming performance at Ucrit or sprint speeds? *J.*
19 *Exp. Biol.* **207**, 2979–2990.
- 20 McDowall, R.M. (1988). Diadromy in fishes: migration between freshwater and marine environments.
21 Croom Helm. London: Springer.
- 22 McRae, M.G., McRae, L.B. & Fitzsimons, J.M. (2013). Microhabitat use in an assemblage of native and
23 introduced fishes in a Hawaiian stream. *Pac. Sci.* **67**, 205–217.
- 24 Moody, K.N., Hunter, S.N., Childress, M.J., Blob, R.W., Schoenfuss, H.L., Blum, M.J. & Ptacek, M.B.
25 (2015). Local adaptation despite high gene flow in the waterfall-climbing Hawaiian goby,
26 *Sicyopterus stimpsoni*. *Mol. Ecol.* **24**, 545–563.
- 27 Moody, K.N., Kawano, S.M., Bridges, W.C., Blob, R.W., Schoenfuss, H.L. & Ptacek, M.B. (2017).
28 Contrasting post-settlement selection results in many-to-one mapping of high performance
29 phenotypes in the Hawaiian waterfall-climbing goby *Sicyopterus stimpsoni*. *Evol. Ecol.* **31**,
30 489–516.
- 31 Mozsár, A., Boros, G., Sály, P., Antal, L. & Nagy, S.A. (2015). Relationship between Fulton’s condition
32 factor and proximate body composition in three freshwater fish species. *J. Appl. Ichthyol.* **31**,
33 315–320.
- 34 Pearce, J.L. & Boyce, M.S. (2006). Modelling distribution and abundance with presence-only data.
35 *Journal of Applied Ecology* **43**, 405–412.
- 36 Rasband, W.S. (2015). ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA.
- 37 Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C. & Müller, M. (2011). pROC: an
38 open-source package for R and S+ to analyze and compare ROC curves. *BMC Bioinformatics*
39 **12**, 77.

- 1 Royle, N.J., Metcalfe, N.B. & Lindström, J. (2006). Sexual selection, growth compensation and fast-
2 start swimming performance in Green Swordtails, *Xiphophorus helleri*. *Funct. Ecol.* **20**, 662–
3 669.
- 4 Scharnweber, K., Watanabe, K., Syväranta, J., Wanke, T., Monaghan, M.T. & Mehner, T. (2013).
5 Effects of predation pressure and resource use on morphological divergence in omnivorous
6 prey fish. *BMC Evol. Biol.* **13**, 132.
- 7 Schoenfuss, H.L. & Blob, R.W. (2003). Kinematics of waterfall climbing in Hawaiian freshwater fishes
8 (Gobiidae): vertical propulsion at the aquatic-terrestrial interface. *J. Zool.* **261**, 191–205.
- 9 Schoenfuss, H.L. & Blob, R.W. (2007). The importance of functional morphology for fishery
10 conservation and management: applications to Hawaiian amphidromous fishes. *Bishop Mus.*
11 *Bull. Cult. Environ. Stud.* **3**, 125–141.
- 12 Teichert, N., Richarson, M., Valade, P. & Gaudin, P. (2012). Reproduction and marine life history of an
13 endemic amphidromous gobiid fish of Reunion Island. *Aquat. Biol.* **15**, 225–236.
- 14 Teichert, N., Tabouret, H., Lagarde, R., Grondin, H., Ponton, D., Pécheyran, C. & Bareille, G. (2018).
15 Site fidelity and movements of an amphidromous goby revealed by otolith multi-elemental
16 signatures along a tropical watershed. *Ecol. Freshw. Fish* **27**, 834–846.
- 17 Teichert, N., Valade, P., Bosc, P., Richarson, M. & Gaudin, P. (2013). Spawning-habitat selection of an
18 Indo-Pacific amphidromous gobiid fish, *Sicyopterus lagocephalus* (Pallas). *Mar. Freshwater*
19 *Res.* **64**, 1058–1067.
- 20 Teichert, N., Valade, P., Fostier, A., Grondin, H. & Gaudin, P. (2016a). Reproductive biology of an
21 endemic amphidromous goby, *Cotylopus acutipinnis*, from La Réunion Island. *Mar.*
22 *Freshwater Res.* **67**, 526–536.
- 23 Teichert, N., Valade, P., Fostier, A., Lagarde, R. & Gaudin, P. (2014a). Reproductive biology of an
24 amphidromous goby, *Sicyopterus lagocephalus*, in La Réunion Island. *Hydrobiologia* **726**,
25 123–141.
- 26 Teichert, N., Valade, P., Grondin, H., Trichet, E., Sardenne, F. & Gaudin, P. (2016b). Pelagic larval traits
27 of the amphidromous goby *Sicyopterus lagocephalus* display seasonal variations related to
28 temperature in La Réunion Island. *Ecol. Freshw. Fish* **25**, 234–247.
- 29 Teichert, N., Valade, P., Lim, P., Dauba, F., Labonne, J., Richarson, M., Bosc, P. & Gaudin, P. (2014b).
30 Habitat selection in amphidromous Gobiidae of Reunion Island: *Sicyopterus lagocephalus*
31 (Pallas, 1770) and *Cotylopus acutipinnis* (Guichenot, 1863). *Environ. Biol. Fishes* **97**, 255–266.
- 32 Webb, P.W. (1984). Body form, locomotion and foraging in aquatic vertebrates. *Amer. Zool.* **24**, 107–
33 120.
- 34 Webb, P.W. (1978). Fast-start performance and body form in seven species of teleost fish. *J. Exp. Biol.*
35 **74**, 211–226.
- 36