PRIMARY RESEARCH PAPER



Variation in reproductive strategies of two amphidromous gobies of the West Indies: *Sicydium plumieri* and *Sicydium punctatum*

Marion Labeille[®] · Alain Devaux · Estelle Lefrançois · Khédidja Abbaci · Raphaël Santos · Aurélien Besnard · Sylvie Bony · Jean-Jacques Lareyre · Nils Teichert

Received: 20 November 2023 / Revised: 7 May 2024 / Accepted: 5 June 2024 © The Author(s), under exclusive licence to Springer Nature Switzerland AG 2024

Abstract The trade-off between current and future reproduction remains a central issue for understanding the diversity of fish life-histories along a slow-fast continuum. Fish living in rivers of tropical oceanic islands generally have a fast type life-history, but variations in key reproductive traits can occur in response to spatial changes in selection pressures. Here, we investigated the reproductive strategies of two

Handling editor: Louise Chavarie

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-024-05609-z.

M. Labeille (⊠) Sentinelle Lab, 97125 Bouillante, France e-mail: marionlabeille@yahoo.fr

A. Devaux · S. Bony Univ Lyon, Université Claude Bernard Lyon 1, ENTPE, CNRS, INRAE, USC 1369, UMR 5023 LEHNA, 69518 Vaulx-en-Velin, France

E. Lefrançois Eco-in-Eau, 34980 Montferrier Sur Lez, France

K. Abbaci Laboratoire d'écotoxicologie, INRAE, UR RiverLy, 69616 Villeurbanne, France

R. Santos Univ Lyon, Université Claude Bernard Lyon 1, ENTPE, CNRS, UMR 5023 LEHNA, 69518 Vaulx-en-Velin, France sympatric amphidromous gobies widely distributed in Caribbean streams, *Sicydium plumieri* (n=308) and *Sicydium punctatum* (n=383), along a river gradient of Guadeloupe Island. Beyond the new insights provided on the reproductive traits (ovarian organization, gonadal development, length at maturity, and spawning season), the histological observations of testes and ovaries revealed variation in reproductive strategies. *Sicydium punctatum* showed a time-minimizing strategy, featuring early reproduction, a high spawning frequency, an extended reproductive period, and a broad spawning area along the river course. *Sicydium plumieri* displayed a size-maximizing strategy,

A. Besnard CEFE, Université Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France

J.-J. Lareyre INRAE, LPGP UR1037, Fish Physiology and Genomics, Biosit, Biogenouest, Campus de Beaulieu, 35042 Rennes Cedex, France

N. Teichert UMR 7208 BOREA, MNHN, CNRS, IRD, SU, UCN, UA, Laboratoire de Biologie Des Organismes Et Ecosystèmes Aquatiques, Paris, France

N. Teichert MNHN, Station Marine de Dinard, CRESCO, Dinard, France featuring a delayed maturity, lower spawning frequency, and a shorter reproductive period restricted to the upper reaches of rivers. We discuss the advantages provided by these two strategies in response to the spatial changes in predation and disturbance levels along the upstream–downstream continuum, which probably affects the survival rate and mortality risk before the first reproduction.

Keywords Spawning period · Ovarian development · Length at maturity · Histology · Sicydiinae

Introduction

Understanding variation in life-history traits and how they combine into life-history strategies remains a core concept in evolutionary ecology (Stearns, 1992; Healy et al., 2019) and a main issue for sustainable resource management (Winemiller & Rose, 1992; Bjørkvoll et al., 2012). The diversity of life-history strategies is mostly described along a slow-fast continuum (Healy et al., 2019), ranging from highly reproductive species with an early age at maturity and a relatively short life span to slow life-history with long life expectancy and late reproduction (MacArthur & Wilson, 1967). Selective pressures, including environmental stochasticity or density-dependent processes, are often involved in shaping life-history traits by maximizing fitness through differing rates of survival, development, and reproduction (Stearns, 1992; Wright et al., 2019). Stable environmental conditions, characterized by high adult survival rates, favor slow life-history species with a long generation time. Fast life-history strategists, on the other hand, are advantaged in frequent and highly disturbed environments or in those with a high level of competition and/or predation (Kindsvater et al., 2016) where adult mortality is high. Following this concept, reproductive traits are key components of species life strategy as they define the species' capacity to cope with selection pressures and environmental hazards.

Aquatic organisms living in rivers of tropical and subtropical oceanic islands generally have a fast type life-history and migratory behaviors between freshwater and sea (McDowall, 1997). Most fish, crustaceans and gastropod mollusks of these areas experience an amphidromous life cycle (Keith, 2003; McDowall, 2007): adults reproduce in freshwater and then larvae quickly drift to brackish or marine waters where they grow for several months before returning to rivers as young juveniles that grow and become adults (Myers, 1949). This life cycle is particularly adapted to cope with the stochastic conditions encountered by individuals in short and fast-flowing insular streams (McDowall, 2007). Oceanic islands are recurrently subject to extreme hydrological variations and natural disturbances caused by extreme climatic events, such as tropical storms or cyclonic floods (McDowall, 2010; Smith and Kwak, 2015; Teichert et al., 2016). Amphidromous fishes are mostly small bodied and highly fecund species, with an early maturity, probably in response to selection from environmental stochasticity and resource availability (McDowall, 2007, 2010). Their high fecundity also, in part, compensates for the high mortality rate suffered by larvae during their drift toward the sea (Bell 2009; Teichert et al., 2014; Lagarde et al., 2018). When reaching the marine environment, early hatched larvae take advantage of the high food availability, while lotic rivers appear poorly suitable for pelagic larval life (Closs et al., 2013; Ramírez-Álvarez et al., 2022). After their marine phase, juveniles and adults endure intensive competition and predation pressures in insular rivers, especially in lower reaches where species diversity is maximal (Gillet, 1983; Fièvet et al., 2001; Lagarde et al., 2021b). Some goby species with distinct morphology can nonetheless climb upstream to reduce predation pressure as most of the predators are unable to cross waterfalls and fast-flowing reaches (Fitzsimons et al., 2002; Blob et al., 2010; Diamond et al., 2019, 2021). In such conditions, the metabolic cost of upstream migration can be compensated by an enhanced survival in upper reaches (Bonte et al., 2012), which offer more stable and safer conditions with regard to predation, but also disturbances induced by cyclonic floods.

Among amphidromous species, Sicydiinae are widely distributed across oceanic islands, from the mid-Pacific to the western Indian Ocean and in the Caribbean (McDowall, 2010). They are generally gonochoric iteroparous species, which can reproduce over prolonged spawning season when environmental conditions are favorable (Bell, 1994; Ha & Kinzie, 1996; Smith, 2012; Teichert et al., 2014, 2016). For example, *Sicyopterus lagocephalus* in Réunion Island can reproduce throughout the year in downstream

reaches where the water temperature remains high, whereas the spawning period is shortened upstream (Teichert et al., 2016). In Puerto Rico Island, Sicvdium spp. reproduce from late spring through early fall, with a peak between May and September (Smith, 2012). Sicydiinae are usually nest spawners (Keith, 2003). Females lay tens of thousands of eggs per spawning event in a nest built by male under stones (Bell 1994; Teichert et al., 2013b, a). Larvae drift downstream to the sea a few hours after hatching (Teichert et al., 2021) and then pelagic larvae develop and grow in estuaries or sea (Bell 1994; Ellien et al., 2020). In Caribbean islands, *Sicydium* spp. larvae spend from 59 to 87 days in the marine environment and measure on average 20-25 mm when recruiting in rivers (Erdman, 1961; Bell et al., 1995; Lejeune et al., 2016; Engman et al., 2017).

Sicydiinae generally become sexually mature after a few months once back in rivers, with a size ranging between 30 and 45 mm (Manacop, 1953; Yamasaki et al., 2011; Smith, 2012; Teichert et al., 2014). However, variations in key reproductive traits have been highlighted within and between species (Yamasaki et al., 2011; Watanabe et al., 2014). For example, Lagarde et al. (2020) demonstrated that age at maturity was influenced by the duration of the pelagic larval stage at sea and the season of return in freshwater, with substantial differences between two goby species of Réunion Island (9 and 7 months for S. lagocephalus and Cotylopus acutipinnis, respectively). Such interspecific difference can reveal distinct strategies and sensitivities to anthropogenic disturbances and should be considered in management and conservation practices. Indeed, anthropic activities in tropical islands, such as in-stream barriers and river flow disturbances, channelization, or alteration of water quality, can jeopardize the achievement of amphidromous life cycle and alter reproductive success (Neal et al., 2009; Kwak et al., 2016).

In this study, our aim is to comprehend the reproductive strategies of two Sicydiinae gobies, namely *Sicydium plumieri* (Bloch, 1786) and *Sicydium punctatum* Perugia, *1896*, across the river gradient on Guadeloupe Island. These two species dominate the freshwater fish assemblages and are widely distributed along the longitudinal gradient of rivers, thanks to high climbing capacities. Our primary objective is to investigate potential variations in ovarian organization, size at maturity, and spawning season among these species. Although the two gobies are sympatric throughout the river length, they are not subjected to hybridization, which implies that mechanisms of reproductive isolation and niche partitioning occur (Engman et al., 2019). Previous studies demonstrated distinctiveness in trophic behavior and food resources of both species (Monti et al., 2018; Frotte, 2019), which are also associated with morphological differences: S. plumieri being much larger than other Sicydium of the Caribbean area (Watson, 2000; Engman et al., 2019). The two species can be distinguished on the field based on external criteria as synthetized in Robert et al. (2015). Here, we hypothesize that the two species may also have distinct reproductive strategies along the slow-fast life-history continuum, related to their size difference and their spatial distribution along the watercourse.

Materials and methods

Study area and fish sampling

Sicydium plumieri and S. punctatum were sampled in two sites located in the Grande Rivière de Vieux-Habitants (19 km long), Guadeloupe Island, French West Indies (Fig. 1). It was a typical tropical little island river with a torrential hydrological regime with rapids, riffles, and pools alternance and a rocky substrate dominance (depth: 5–100 cm—width: 4–25 m). The downstream and upstream sites were positioned 2.7 and 7.1 km from the river mouth, respectively. Water temperature was recorded continuously during the study in the two sites using a data logger (HOBO data logger U22 Water Temp Pro V2±0.2 °C). However, the probe deteriorated in the downstream site, resulting in a temporal gap between September 2019 and August 2020.

Fish were collected monthly between January and December 2019 and then quarterly (February, May, August and November) in 2020, using a 500-V crenulated current (60 Hz, 20% duty cycle) backpack electrofishing device (LR-24, Smith-RootTM). A minimum of 30 sampling points were randomly distributed in the station to take into account the available habitat diversity. For each point, the anode was dipped during 30 s in water, while operators collect the fish using dip nets. For each survey, 15 *S. plumieri* and 15 *S. punctatum* were collected using a



Fig. 1 Localization maps of Guadeloupe island in the Caribbean (A) and geographical positions of the two sampling sites (i.e., downstream and upstream) in the Grande Rivière de Vieux-Habitants River of Guadeloupe (B), West Indies, Caribbean region

size-stratified sampling procedure with about 5 individuals collected and categorized into 3 body length classes 45–55 mm, 56–65 mm, and > 65 mm. These size thresholds allowed to provide a balanced overview of the size classes and maturity stages occurring in the population (immature vs. mature), while avoiding an overestimation of the dominant size classes at the sampling time. In addition, smaller fish < 45 mm were collected because there was no previous knowledge about the size at first reproduction for these two species. Sampling was adapted to ensure the representativeness of each species and each size class. Although a blue-green iridescence can occur in S. punctatum male during the reproductive period (Lim et al., 2002; Bell 2009), there is no obvious morphological criteria to distinguish males from females of Sicydium sp. (Bell 1994). Accordingly, the sex was not known during the field surveys and was inferred a posteriori based on histological observations of the gonads.

After being capture in the morning (9–11 a.m.), fish were brought back to the laboratory, where they were anaesthetized with an eugenol oil solution before being euthanized by decapitation with a scalpel blade in the afternoon. For each fish, the total length (TL±1 mm) and wet weight (BW±0.01 g) were measured, as well as the wet gonadal weight (GW±0.001 g). Finally, the gonado-somatic index (GSI, %) was calculated as the ratio of gonads weight to the body weight, following the formula: GSI=GW/ BW*100.

Histological preparation and development stages of gametes

For all collected fish, the gonads were fixed in Finefix® (Milestone) and then embedded in paraffin and sectioned to 7 μ m thickness. The histological sections were stained with Groat Hematoxylin and Eosin according to standard histological procedures. The sections were observed under a light transmitted microscope and then photographed at different positions and magnifications depending on the size of the gonads (i.e., $\times 40$, $\times 100$, and $\times 200$). The histological observations were then used to assign the sex and the phase of sexual maturation of each fish.

For females, four stages of oocytes development were observed in ovaries according to Brown-Peterson et al. (2011) and Teichert et al. (2014). The first stage corresponds to the primary growth oocytes (PG), which is featured by a small cell size and a large nucleus (Fig. 2). The three following stages



00 um

Fig. 2 Histological observations of gonads depending on the reproductive phases of females (A immature, B developing, C spawning capable, D post-spawning, E regression, F regeneration) and males (G immature, H active, I non-active) of *Sicy-dium* sp. *PG* primary growth oocyte, *CA* cortical alveoli, *EVO* early vitellogenic oocyte, *VO* vitellogenic oocyte, *POF* post-

100 µm

ovulatory follicle, *ATS* attretic oocyte, *Sg* spermatogonia, *Sc* spermatocytes, *St* spermatids, *Sz* spermatozoa, *Lu* lumen of the seminiferous lobules. Histological observations were provided separately for *Sicydium punctatum* and *Sicydium plumieri* as supplementary material (Figs. S1, S2)

100 µm

correspond to secondary growth oocytes, including the cortical alveoli oocytes (CA) featured by cortical alveoli in the periphery of nucleus and cytoplasm, the early vitellogenic oocytes (EVO) with small granules of yolk occurring around either the periphery of the oocyte or of the nucleus, and the vitellogenic oocytes (VO) with numerous large yolk globules that fill the cytoplasm and oil droplets starting to surround the nucleus. In addition, other ovarian components were recorded in histological sections, such as hydrated oocytes (indicating final oocytes maturation before ovulation), post-ovulatory follicles, and atretic oocytes (Fig. 2).

For males, four spermatogenic development stages were reported in testicular sections that depend on the presence and abundance of different differentiating germ cell types and development of the tubular lumen (Grier and Uribe-Aranzábal, 2009; Pecio, 2019): spermatogonia (Sg), spermatocytes (Sc), spermatids (St), and spermatozoa (Sz). The different germ cell types were differentiated according to their size, cell and nucleus shapes, nucleus-to-cytoplasm ratio, and compaction of the chromatin within the nucleus (Fig. 2). In addition, the increased number of germ cells was accompanied by an enlargement of the tubular lumen with testicular fluid accumulation.

Female reproductive phases

Females were assigned to six reproductive phases depending on the morphological aspect of gonads and the preponderant stage of maturity of oocytes, as well as other histological observations, e.g., presence of post-ovulatory follicles, hydrated oocytes, or atresia (Brown-Peterson et al., 2007; Teichert et al., 2014, 2016). The immature phase (1) includes juveniles that had never reproduced before. Their gonads are thin, almost transparent with no visible blood vessel. Only PG oocytes are present. The ovary structure is well organized with little connective tissue between follicles and little space between oocytes (Fig. 2A). The ovarian wall is thin. There is no trace of previous ovulation, such as atresia, muscle fibers, or post-ovulatory follicles. The developing phase (2) corresponds to the growing phase of the gonads before the reproductive period. Individuals initiating this phase for the first time are becoming mature but are not yet ready to spawn. Gonads develop and blood vessels become visible. The eggs are macroscopically visible, and the gonads turn yellow. The cortical alveoli oocytes are generally dominant in histological sections (Fig. 2B). Oocytes in PG and/or early vitellogenic stage can also be observed. During this phase, no post-ovulatory follicles are present. The spawning capable phase (3) reflects the period in which individuals are potentially able to spawn during this ovarian cycle. Gonads are yellow and voluminous. Eggs are macroscopically visible and blood vessels are visible. Most oocytes are at the latest vitellogenic stage (Fig. 2C). The post-spawning phase (4) corresponds to a recent reproduction. The gonads are flaccid, rather wide and translucent. Post-ovulatory follicles and some late hydrated oocytes are observed (Fig. 2D). Oocytes in the PG, AC, and EVO stages may be present. The regression phase (5) reflects the end of the reproductive cycle when there is no more sign of ovarian maturation. The gonads are flaccid and yellowish and characterized by the widespread prevalence of atresia (Fig. 2E), and some post-ovulatory follicles and residual oocytes in vitellogenesis can be observed. The regeneration phase (6) corresponds to the resting period of sexually mature individuals. The gonads are thin to medium thin and translucent, and blood vessels can be observed. Histological sections are very similar to the immature phase with only the presence of oocytes in primary growth. The last two phases were distinguished based on the thickness of the ovarian wall, the presence of more space, interstitial tissue, and capillaries around primary growth oocytes in regenerating individuals, as well as the presence of old atresia stages and muscle bundles (Fig. 2F).

Male reproductive phases

Males were assigned to three reproductive phases depending on morphological aspect of the gonads, the most differentiated germ cell populations, and the occurrence of lumen in the seminiferous tubules reflecting the secretion of testicular fluid (Brown-Peterson et al., 2007). The *immature phase* (1) is featured by only primary spermatogonia in the germinal epithelium and no lumen is observed in the testicular lobules (Fig. 2G). Gonads are very thin and almost invisible. The *active reproductive phase* (2) is characterized by an active spermatogenic activity with the presence of spermatocysts containing many mitotic, meiotic (Sc), or spermiogenic (St) cells. In addition, a large number of spermatozoa is accumulated in the

lumen of the lobule (Fig. 2H). Gonads are filiform and speckled with white. The *non-active reproductive phase* (3) (Fig. 2I) includes individuals with testes in development (i.e., few cysts containing Sc, St, and Sz along the lobules), in regression (residual Sz in the tubular lumen and sporadic cysts containing Sc, St, and Sz), or in regeneration (absence of cyst and proliferation of Sg; and unlike immature phase: lumen with a small surface and sometimes residual Sz). In these animals, the gonads are filiform and not clearly visible. Individuals in these phases were combined due to the low number of fish sampled in these reproductive phases (see results).

Ovarian organization

The ovarian organization was examined to provide insights on the oocyte development (i.e., asynchronous, synchronous, or group-synchronous). In this purpose, 55 S. punctatum and 41 S. plumieri mature females were randomly selected to cover the whole range of gonadal maturation and to investigate their oocyte size frequencies depending on the GSI (Teichert et al., 2014, 2016). For each individual, at least 30 oocyte diameters were measured on quadrats (0.1 mm^2) randomly placed on photographs of histological sections, using the ImageJ 1.53e software (Rueden et al., 2017). When quadrat was initiated, all oocytes with a visible nucleus were measured to determine the relative occurrence of oocyte size in ovaries. The developmental stage of oocytes was also recorded (PG, AC, EVO, and VO) to determine size variation across stages.

Length at maturity

The Length at maturity (L₅₀) was defined as the body size for which 50% of the population has reached sexual maturity (Lowerre-Barbieri et al., 2009). This parameter has been estimated for both sexes, based on individuals for which a reproductive phase has been attributed, using a logistic Generalized Linear Model (GLM with Binomial distribution and *logit* link). The values were fitted to a logistic curve, according to the formula: $logit(\mu_i) = \beta_O + \beta_{TL}X_{TL} + \varepsilon_i$, where μ_i is the maturation status of the fish, X_{TL} is the total length, β_O and β_{TL} are the regression coefficients, and ε_i is the residual error. Males were considered mature when they were assigned to the reproductive and non-reproductive phases, while females were mature when they were assigned to the developing, spawning capable, post-spawning regression, or regeneration phases (Teichert et al., 2016, 2014). This distinction allows to identify individuals who have already started a maturation cycle (mature status) from individuals who have not yet entered the reproductive population (immature status).

Statistical analyses

All statistical analyses were performed in the R environment v. 4.0.5 (R Core Team, 2018) using the 'stats' package for standard analysis. For each species, the proportions of immature individuals were compared between downstream and upstream sites using chi-square proportion tests. Analysis of variance models (ANOVAs) were conducted to compare fish length between species and site, as well to test for differences in GSI between sampling dates and the river sites, separately for males and females of each species. Finally, the influence of temperature and photoperiod on the reproductive activity was investigated using generalized linear models (GLMs) between GSI and environmental parameters. The significances of parameters were assessed with deviance reduction tests using a Chi-squared-based estimate.

Results

A total of 383 S. punctatum and 308 S. plumieri were collected during the surveys (Table 1). For the two species, the proportion of immature individuals was significantly higher in the downstream area in comparison to the upper site (respectively, 2 and 10% for S. punctatum, n=383, $\chi^2=8.36$, P=0.003 and 2 and 53% for S. plumieri, n=308, $\chi^2=79.5$, P<0.001), probably because of the proximity of the river mouth where juveniles come from. However, contrasts between sizes in immature proportions were greater for S. plumieri, for which more than half of individuals were found to be immature in the downstream site, whereas most of the fish were adults in the upper site (Table 1). Overall, the adults of S. plumieri were larger than S. punctatum (n = 568, F = 545.0, P < 0.001), and the mean body length of both species was lower downstream than upstream (Table 1;



Fig. 3 Oocyte size frequencies in ovaries of a *Sicydium punc*tatum (n=55) and b *Sicydium plumieri* (n=41) depending on the gonado-somatic index (GSI %) used as proxy for ovarian development. The size distributions of the different oocyte

development stages are presented in the graphs below. *PG* primary growth, *CA* cortical alveoli; *EVO* early vitellogenic, *VO* vitellogenic

 Table 1
 Number of Sicydium punctatum and Sicydium plumieri fish collected, between January 2019 and November 2020, in the two sampling sites of Grande Rivière de Vieux-Habitants, Guadeloupe—French West Indies

Site	Sampling number			Total length (mm)	
	Female (im)	Male (im)	Total (%im)	Female	Male
S. punctatum					
Upstream	161 (3)	133 (4)	294 (2%)	64.8 (40–114)	65.1 (45–156)
Downstream	75 (7)	14 (2)	89 (10%)	50.7 (33-72)	49.5 (33–71)
Total	236 (10)	147 (6)	383 (4%)	60.3 (33–114)	63.6 (33-156)
S. plumieri					
Upstream	57 (2)	53 (0)	110 (2%)	104.3 (49–148)	118.0 (78–160)
Downstream	158 (88)	40 (17)	198 (53%)	71.0 (43–122)	78.8 (47–116)
Total	215 (90)	93 (17)	308 (35%)	79.8 (53–148)	101.1 (47–160)

The mean total length and size range of fish are also detailed. The number and proportion of immature fish (im) were provided in brackets

n=201, F=128.6, P<0.001 for *S. plumieri* and n=367, F=58.4, P<0.001 for *S. punctatum*).

Analysis of ovarian development

For S. punctatum (n = 55, Fig. 3), oocytes' diameters varied from 10 to 76 µm for PG (n = 1264),

Springer

from 32 to 97 μ m for CA (n = 195), from 71 to 167 μ m for EVO (n = 100), and from 104 to 273 μ m for VO (n = 382). The size-frequency distribution according to the GSI revealed two cohorts of oocytes that progressively segregated during the ovarian development. At the initiation of the ovarian cycle, a batch of oocytes was recruited. Then,

the size of yolked oocytes increased during vitellogenesis, while smaller batch of oocytes (i.e., PG and CA) temporally remained below 100 μ m. The beginning of the ovarian spawning cycle was associated with a GSI higher than 2, with the presence of EVO and VO oocytes in histological sections. The two batches remained clearly segregated, which reflects a group-synchronous ovarian follicle development.

For *S. plumieri* (n=41), oocytes diameters varied from 10 to 75 µm for PG (n=1219), from 34 to 89 µm for CA (n=111), from 65 to 156 µm for EVO (n=72), and from 100 to 324 µm for VO (n=107, Fig. 3). Although, GSI values were not evenly distributed for *S. plumieri* (i.e., lack of values between 5.7 and 13.9%), and the ovarian development appeared similar to *S. punctatum*. Indeed, two cohorts of oocytes were clearly differentiated for the single *S. plumieri* with the most advanced stage of maturation (IGS = 13.9%).

Length at maturity

For *S. punctatum*, the minimum size at maturity observed for both females and males was 33 mm. Although, the probability of being mature significantly increased with length for males (n=147; F=8.92; P=0.002) and females (n=236; F=10.40; P=0.002), the L_{50} could not be properly estimated due to the low number of small fish (i.e., < 33 mm) in the sample.

For *S. plumieri*, the minimum size at maturity observed from the whole sampling was 49 mm for males and 59 mm for females. The probability of being mature significantly increased with the length of females (n=215; F=230.09; P<0.001) and males (n=93; F=52.52; P<0.001). The L_{50} was significantly lower for males (Fig. 4, $L_{50}=63.3\pm6.3$ mm) than for females ($L_{50}=74.5\pm1.5$ mm; P<0.001).



Fig. 4 Length at maturity of *Sicydium punctatum* (female: n=236 and male: n=147) and *Sicydium plumieri* (female: n=215 and male: n=94) in the Grande Rivière de Vieux-Habitants, Guadeloupe Island

Spatio-temporal fluctuation in reproductive activity

Immature fish were excluded from the following analyses to highlight seasonal patterns in reproductive activity, which thus focused on adults, i.e., 367 *S. punctatum* and 201 *S. plumieri* (Table 1).

Sicydium punctatum

GSI of S. punctatum females varied significantly depending on the sampling dates (Fig. 5) and between the downstream and upstream sites, but the interaction between date and sites remained non-significant (Table 2). These results suggest a greater investment of energy by the fishes in reproduction in the upstream site (higher GSI values in average), but without any difference in female seasonal reproduction dynamic between sites. Overall, GSI values were higher between May and December, which also corresponded to the period with the larger proportion of females assigned to the spawning capable phase (Fig. 5). No sign of ovarian development was observed in January and February for the two sites. After this resting period, the ovarian maturation appeared to begin in March and April with the occurrence of females assigned to the developing phase.



	df	Sum Sq	Mean Sq	F value	P value			
S. punctatum—female								
Date	15	655.66	43.71	3.51	< 0.001			
Site	1	71.19	71.19	5.71	0.017			
Date x site	14	152.47	10.89	0.87	0.587			
S. punctatum—male								
Date	14	1.54	0.11	2.35	0.006			
Site	1	0.06	0.06	1.26	0.263			
Date x site	6	0.04	0.01	0.15	0.988			
S. plumieri—female								
Date	15	47.61	3.17	1.92	0.031			
Site	1	26.44	26.44	16.00	< 0.001			
Date x site	13	43.32	3.33	2.02	0.027			
S. plumieri—male								
Date	14	0.05	0.00	3.49	< 0.001			
Site	1	0.01	0.01	9.92	0.002			
Date x site	11	0.01	0.00	0.88	0.568			

Significant P values are highlighted in bold



Two females (one in August and one in October) caught in the upstream site presented post-ovulatory follicles, which indicates a recent spawning event.

somatic index (GSI %) are also represented by the black-

Fig. 5 Monthly fluctuation in the reproductive phases of adult a females and b males of *Sicydium punctatum* in the upstream and downstream sites of the Grande Rivière de Vieux-Hab-

a)

Proportion of mature females

1.00

0.75

0.50

0.25

0.00

1.00

0.75

0.50

0.25

0.00

200

2

Developing

Considerably lower than the GSI values of females, the GSI values of *S. punctatum* males varied monthly but did not differ between sites (Table 2), probably due to the reduced number of adult males caught in the downstream site. In the upstream site, the highest GSI values were recorded between April and August (Fig. 5). Overall, 94% of males had testes whose lumen was enlarged and filled with spermatozoa indicating they were able to reproduce although no spermating male was detected. A blue-green coloration was observed for 77 individuals before dissection and the histological observations revealed that 94% of them were males in the active reproductive phase.

Sicydium plumieri

The GSI of *S. plumieri* females varied significantly across the months and between the two sites, in particular depending on the sampling date (Table 2). These results denote a greater reproductive investment of energy by the fishes in the upstream site, associated with differences in the temporal dynamic of reproduction between sites (Fig. 6). Indeed, the GSI values remained very low in the downstream site and adult females presented ovaries in the regeneration phase, which corresponds to the resting period. In contrast, the GSI values of females caught in the upper site increased between April and June (Fig. 6). In this site, between April and September, females were classified into the developing or spawning capable phases. A female with ovaries in regression was observed in October, which reflects the end of the reproductive period. No female was caught and observed in the post-spawning phase for this species.

For males, GSI values remained very low in the two sites, with a maximum of 0.17% observed in June. GSI varied with the sampling dates and between sites, but the interaction between date and site was not significant (Table 2). These results suggest a lower investment in male reproduction in the downstream site, as only 40% of adult males were assigned to the reproductive phase (Fig. 6). In the upstream site, 65% of males were in reproductive phase, essentially from January to October, and GSI values were higher between January and September. No spermating male was captured.



Fig. 6 Monthly fluctuation in the reproductive phases of adult a females and b males of *Sicydium plumieri* in the upstream and downstream sites of the Grande Rivière de Vieux-Hab-

itants, Guadeloupe Island. The mean variations in gonadosomatic index (GSI %) are also represented by the blackdashed lines Fig. 7 Monthly fluctuation of water temperatures (°C) and photoperiod (daylength, h) in the upstream and downstream sites of the Grande Rivière de Vieux-Habitants, Guadeloupe Island. The colored bands represent the extreme temperature ranges (minimal and maximal hourly values)



Environmental drivers of reproductive activity

During the study period, the monthly temperature of the downstream site varied from 21.5 °C in January 2019 to 26.8 °C in September 2019, with extreme hourly temperatures reaching 36.5 in August (Fig. 7). In upstream, the water temperature was slightly cooler, ranging between 20.1 and 23.7 °C, with a maximum value of 26.8 °C recorded in September 2019. The study covered a complete annual cycle of photoperiod, with a daylength extending from 11.2 h in January to 13.1 h in July.

GSI values were used as a proxy of reproductive activity to examine the influence of environmental factors, i.e., temperature and photoperiod, on Sicydium sp. reproduction. For S. punctatum females,

Table 3 Summary of reduction deviance tests Image: State of the stat	Parameter	df	Residual deviance	Explained deviance	P value		
conducted on GLMs investigating the influence of temperature and photoperiod on the gonado- somatic index of <i>Sicydium</i> <i>punctatum</i> and <i>Sicydium</i> <i>plumieri</i>	S. punctatum—female						
	Null model	226	2907.200	_	_		
	Temperature	225	2831.900	75.350	0.017		
	Photoperiod	224	2563.500	268.420	< 0.001		
	S. punctatum—male						
	Null model	141	10.617	_	_		
	Temperature	140	10.611	0.006	0.781		
	Photoperiod	139	10.118	0.493	0.011		
	S. plumieri—female						
	Null model	125	263.120	_	_		
	Temperature	124	259.890	3.231	0.228		
	Photoperiod	123	216.030	43.864	< 0.001		
	S. plumieri—male						
	Null model	76	0.123	_	_		
	Temperature	75	0.123	0.001	0.483		
Significant P values are	Photoperiod	74	0.106	0.017	0.001		

highlighted in bold

GSI was positively related to the photoperiod and the water temperature (Table 3). For *S. plumieri* females, GSI was positively associated to the photoperiod, but was not related to the monthly river temperature. Overall, the explained deviance was higher for the photoperiod than for the water temperature in both species (Table 3). For males, the GSI significantly increased with photoperiod for *S. punctatum* and for *S. plumieri*, but GSI was not significantly affected by temperature (Table 3).

Discussion

Amphidromous gobies generally have a multiple spawning strategy, associated with early age at maturity and high fecundity. This is expected to increase the likelihood of larvae encountering suitable environmental conditions and such a strategy compensates for the high mortality rate due to environmental unpredictability (McDowall, 2007; Artzrouni et al., 2014). Although the number of mature fish sampled each month remained relatively low due to the difficulty in discriminating immature individuals from the adults and the different sex during sampling, our results clearly highlight the main reproductive traits of S. punctatum and S. plumieri along a river gradient of Guadeloupe Island. In particular, our findings reveal differences in the reproductive traits of the two species, both in development and maturation of the gonads but also in the spatio-temporal fluctuations of the reproductive activity.

Ovarian development and spawning frequency

The investigation of oocyte size frequencies revealed that both studied species were multiple spawners with a group-synchronous ovarian development. Indeed, at least two populations of oocytes were simultaneously observed in ovaries: (i) a clutch of vitellogenic oocytes released during the current spawning cycle and (ii) another population of smaller oocytes at earlier stages to be released later (Murua and Saborido-Rey, 2003). This pattern of development has been previously observed in other Sicydiinae, such as *Sicyopterus lagocephalus* (Manacop, 1953; Teichert et al., 2014), *Cotylopus acutipinnis* (Teichert et al., 2016) in tropical areas, and *Sicyopterus japonicus* (Iida et al., 2011) in temperate areas. For the two studied species, no vittelogenic or large cohort of hydrated oocytes were observed in post-spawning ovaries, indicating that females probably laid their eggs in a single spawning event. In aquaria, Bell (2009) reported that S. punctatum females collected in Dominica Island could repeat spawning at intervals of about 14 days. This observation indicated that fecundity is indeterminate for this species, so that females can grow successive batches of oocytes throughout the reproductive season and thus have multiple spawning occasions (Murua and Saborido-Rey, 2003). In Réunion Island, Teichert et al. (2014, 2016) estimated that the spawning interval ranged from one to two months for S. lagocephalus and C. acutipinnis, respectively. Although it remains difficult to accurately estimate the spawning rate based on our data, the larger proportions of S. punctatum females in spawning capable and post-spawning phases during the main reproductive season suggests a faster spawning frequency for this species than for S. plumieri.

Length at maturity

The time allocated to somatic growth before the first reproduction is a key life-history trait, which can fluctuate within and between species in response to the trade-off between survival rate and egg production (Winemiller & Rose, 1992; Bjørkvoll et al., 2012). Indeed, favoring growth contributes to increasing the reproductive fitness of females, as their fecundity increases exponentially with length, but individuals can be exposed to mortality risk before reproduction. In contrast, early spawning can provide a competitive advantage by minimizing the risk of mortality in unpredictable environmental conditions (Winemiller & Rose, 1992; Teichert et al., 2017). For example, in two amphidromous gobies, Lagarde et al. (2020) demonstrated that fish exhibiting a long pelagic larval stage at sea matured faster once in freshwater, which may minimize the risk of predation or extirpation due to catastrophic events before reproduction. As expected in amphidromous species, immature Sicydium spp. were mostly concentrated in the downstream site, whereas adults dominated in the upstream site. While the size at recruitment (i.e., when postlarvae return to the river) is very similar between S. punctatum (20-25 mm, Bell et al., 1995; Lejeune et al., 2016) and S. plumieri (21-23 mm, (Bell et al., 1995)), the length at maturity was much lower for S. punctatum than for S. plumieri. For S. punctatum, the smallest size at maturity of males and females observed by histological analysis (~33 mm) was close to the one observed by Bell (2009) based on the color change in males (~ 30 mm) which corresponds to individuals under 12 months of age spawning in aquaria (Bell et al., 1995). For S. plumieri, the smallest sizes at maturity and the L50 inferred from histological sections were much larger than in S. punctatum and a sexual dimorphism was emphasized between male $(L_{50} = 63.3 \pm 6.3 \text{ mm})$ and female $(74.5 \pm 1.5 \text{ mm})$. Such sexual disparity in size at maturity is common in teleost fish, for which the production of female gametes is more costly, requiring longer time to acquire enough energetic reserves to initiate a reproductive cycle (Wootton & Smith, 2014). This pattern was not reported for S. punctatum, suggesting that male and female reproduce as soon as possible after arriving in freshwater. Our data indicate that S. plumieri allocate more energy in somatic growth and spend more time in freshwater before reproduction in comparison to S. punctatum. Despite that gamete production in males was not limited by fish length, the size at maturity of S. plumieri males was larger in comparison to S. punctatum, suggesting a sexual selection of female based on male body size, as has been highlighted for S. lagocephalus in Réunion Island (Teichert et al., 2013a). Larger males can have a competitive advantage to access spawning areas, to build and defend a nest, and finally to mate with a female (Fitzsimons, 1993; Teichert et al., 2013a).

Spatio-temporal fluctuation in reproductive activity

In most of the teleost fish species, reproductive activity depends on environmental factors, such as temperature and photoperiod (Billard and Breton, 1981; Brown-Peterson et al., 2011). In tropical and subtropical regions, Sicydiinae can reproduce throughout the year (Manacop, 1953; Bell et al., 1995; Teichert et al., 2014, 2016) or over six months (Kinzie, 1993; Yamasaki & Tachihara, 2006). For several species, including *S. japonicus* and *S. lagocephalus*, the temperature was identified as the predominant factor affecting spawning cycles, leading to distinct reproductive periods that depend on the geographical latitude (Iida et al., 2011; Yamasaki et al., 2011; Iida et al., 2013) or on the downstream–upstream position within watersheds

(Teichert et al., 2016). Nevertheless, the photoperiod is also expected to greatly influence fish reproduction in tropical areas where seasonal fluctuations in water temperature are low (Bapary and Takemura 2010). According to our results, the reproductive period of Sicydium spp. was essentially shaped by change in photoperiod, which probably played a decisive role in stimulating ovarian and testis development, especially at the beginning of the reproductive season. In contrast, the water temperature was only slightly related to gonadal maturation of S. punctatum females. Similar findings have been reported for Gobiomorus dormitor in Guadeloupe Island, for which the development of gonads was more affected by photoperiod lengthening than modifications in temperature or food resources (Gillet, 1983). Variation in river flow could also be a regulation factor affecting reproductive activity; however, discharge values were not available in the studied river. Nevertheless, a previous study did not highlight clear relationship between river flow and reproductive activity of an amphidromous goby of La Réunion island (Teichert et al., 2016).

Despite the lack of variation in photoperiod, male and female GSI were contrasted between the upstream and downstream sites, revealing intra- and inter-species variations in the reproductive activity. Despite that the water temperature remained lower in the upstream site, the reproductive investment appeared greater in this area for females of the two Sicydium species and S. plumieri males. In the downstream site, adult females of S. plumieri remained in the regeneration phase without sign of gonad maturation and the proportion of males was reduced in comparison to the upper site. Because the climatic factors did not appear to be involved in these spatial variations, we assume that S. plumieri selected the upper reach of the catchment as spawning areas. In contrast, S. punctatum seems more opportunistic in its spawning location as the reproduction occurred in both upstream and downstream sites. For both species, the beginning of female reproductive season occurred in March-April, followed by a peak in reproduction between May and December for S. punctatum and between April and June for S. plumieri in the upstream site. Thus, it seems that S. plumieri females have a longer resting period than S. punctatum females. In contrast, males remained in reproductive phase almost all year round, with a noticeable increase in GSI between April and August for *S. punctatum* and between June and July for *S. plumieri*. These reproductive periods are quite similar to those observed in Puerto Rico by Erdman (1961) who reported females of *S. plumieri* presenting large yellow ovaries from April to July and by Engman (2017) who estimated the *Sicydium* spp. reproduction period between May and November. In Dominica Island, Bell (1994) observed that *S. punctatum* larvae drift throughout the year principally in downstream areas, suggesting that spawning is panseasonal except for the upstream locations.

Variation in reproductive strategies in *Sicydium* gobies

While periodic or equilibrium reproductive strategies characterized by a high fecundity but late maturation are expected in stable environments, opportunistic strategies are widespread among amphidromous tropical fish living in a scholastic environment (Winemiller & Rose, 1992; Teichert et al., 2016). Overall, *S. punctatum* and *S. plumieri* showed an opportunistic reproductive strategy, featured by an early maturation, frequent reproduction, rapid larval growth, and population turnover rates, when compared to other teleost fish. However, our findings also bring evidences distinctiveness in reproductive traits of the two conspecific *Sicydium* species of the West Indies, stressing that variation occurs within this category.

Among the two species studied, Sicydium punctatum displayed a time-minimizing strategy, featured by an early reproduction in freshwater, a high spawning frequency, an extended reproductive period, and also a broad spawning area along the river course. This fast type strategy with a great investment in reproduction can contribute to overcoming the unexpected risks encountered by juveniles and adults in freshwater, as well as those experienced by drifting larvae. Indeed, tropical and subtropical river flow is seasonal and subject to extreme cyclonic flood, which can directly affect fish survival in freshwater (Smith and Kwak, 2015) and impair the reproductive success (Teichert et al., 2016). Early maturity can thus limit the risks of drifting downstream due to cyclonic floods, before the first spawning (McDowall, 2010; Lagarde et al., 2020). Furthermore, interspecific competition and predation pressures are expected to be higher in downstream reaches (Diamond et al., 2019, 2021), contributing to increase in the risk of mortality (Blob et al., 2010). In these areas, early maturity associated with repeated spawning along the year may maximize reproduction opportunities and increase the likelihood of larvae encountering suitable marine conditions (Teichert et al., 2016). Moreover, spawning downstream also reduces the larvae drifting time after hatching, thus decreasing the associated risks of mortality (Bell 2009; McDowall, 2009; Lagarde et al., 2018; Teichert et al., 2021).

In contrast, S. plumieri displayed a size-maximizing strategy featured by a delayed maturity (i.e., larger size at maturity), lower spawning frequency, and a shorter reproductive period restricted to the upper reaches. This strategy based on the maximization of fish length, and thus absolute fecundity, could provide a competitive advantage in upstream areas where environmental conditions are more stable. However, the reproductive success can be impaired by the strong mortality rates suffered by larvae during their drift toward the sea. The interspecific competition and predatory pressures remain limited in upper reaches, as only a few predators are adapted to climb over tropical waterfalls (Diamond et al., 2021; Lagarde and Ponton, 2022). Furthermore, disturbances induced by cyclonic floods are expected to be lower. In this context, the enhanced survival in upper reaches compared to downstream areas could compensate for the metabolic cost of upstream migration (Bonte et al., 2012) and favor a strategy based on the energy investment in somatic growth (Winemiller & Rose, 1992). Beyond the size-selective advantage against predation and competition, the higher fecundity associated to larger size might also compensate for the high mortality during larval drift from the far upstream spawning areas.

Overall, while providing new knowledge on the reproductive biology of *Sicydium* sp., our findings also emphasized distinct life-history strategies that should be used to improve management and conservation of these species in the West Indies. Such interspecific variations in key life-history traits, along with a spatial partitioning of spawning areas, could imply disparities between species in their sensitivity to anthropogenic threats (Kindsvater et al., 2016). Because of its larger size at maturity and its shorter reproductive period restricted to upstream areas, *S. plumieri* is expected to be less resilient and more vulnerable to anthropogenic pressures, including disturbance of continuity along the land-sea continuum

(Franklin and Gee, 2019). However, disturbances of habitats, water quality and continuity remain majors concerns for the preservation of all Sicydiinae and more broadly of amphidromous species, which are closely dependent on both freshwater and marine areas for the success of their life cycles. In this context, the preservation and/or restoration of ecological continuity is of crucial importance to safeguard headwater accessibility for juveniles during the colonization process (Lagarde et al., 2021a) but also to ensure the drift success of larvae from the upper spawning areas (Jarvis and Closs, 2019).

Acknowledgements This study was conducted with the financial support of the Office Français pour la Biodiversité and Office de l'eau Guadeloupe and Martinique. We are grateful to the two anonymous referees for their comments and suggestions that have contributed to improve the relevance and quality of the manuscript. We are also thankful to colleagues who assisted us during the field surveys, especially Jean-Michel Olivier, Jules Villeneuve, Alexandra Le Moal, Erwan Lefol, Sarah Tolla, Thérèse Bastide, and Patrice Noury, as well as Delphine Jacquemet, Mathilde Benoit, Margaux Bissieres, and Margot Courtial who performed the histological preparations and Laura Goddard for her relevant comments on the manuscript.

Funding Funding was provided by Office Français de la Biodiversité (2017-28 ENTPE) and Office de l'Eau Martinique et Guadeloupe (033-10-2017).

Data availability Data will be made available on request.

Declarations

Conflict of interest The authors declare that they have no competing interests that might be perceived to influence the results and/or discussion reported in this paper.

Ethical approval Fieldworks were conducted under the responsibility of Marion Labeille who are permitted to practice electric fishing. The study and all the manipulation were approved by the local authorities and conducted under the permit of the Direction de l'Environnement de l'Aménagement et du Logement de Guadeloupe (No. 971-2019-05-06-004) and of the Parc National de la Guadeloupe (No. 19/14).

References

- Artzrouni, M., N. Teichert, & T. Mara, 2014. A Leslie matrix model for Sicyopterus lagocephalus in La Réunion: Sensitivity, uncertainty and research prioritization. Mathematical Biosciences 256.
- Bapary, M. A. J., & A. Takemura, 2010. Effect of temperature and photoperiod on the reproductive condition and

performance of a tropical damselfish Chrysiptera cyanea during different phases of the reproductive season. Fisheries Science 76: 769–776.

- Bell, K. N. I., 1994. Life cycle, early life history, fisheries and recruitment dynamics of diadromous gobies of Dominica, WI, emphasising Sicydium punctatum Perugia. Memorial University of Newfoundland, Biology Dept., St. John's, NL, CA.
- Bell, K. N. I., 2009. What comes down must go up: the migration cycle of juvenile-return anadromous taxa. American Fisheries Society Symposium. pp 321–341.
- Bell, K. N. I., J. A. Brown, & P. Pepin, 1995. Seasonal, inverse cycling of length-and age-at-recruitment in the diadromous gobies Sicydium punctatum and Sicydium antillarum in Dominica, West Indies. Canadian Journal of Fisheries and Aquatic Sciences, Canada 52: 1535–1545.
- Billard, R. & B. Breton, 1981. Le cycle reproducteur chez les poissons téléostéens. Cahiers Du Laboratoire D'hydrobiologie De Montereau 12: 43–46.
- Bjørkvoll, E., V. Grøtan, S. Aanes, B. E. Sæther, S. Engen & R. Aanes, 2012. Stochastic population dynamics and life-history variation in marine fish species. American Naturalist 180: 372–387.
- Blob, R. W., S. M. Kawano, K. N. Moody, W. C. Bridges, T. Maie, M. B. Ptacek, M. L. Julius & H. L. Schoenfuss, 2010. Morphological selection and the evaluation of potential tradeoffs between escape from predators and the climbing of waterfalls in the hawaiian stream goby *sicyopterus stimpsoni*. Integrative and Comparative Biology 50: 1185–1199.
- Bonte, D., H. Van Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck, E. Matthysen, K. Mustin & M. Saastamoinen, 2012. Costs of dispersal. Biological Reviews 87: 290–312.
- Brown-Peterson, N., S. Lowerre-Barbieri, B. J. Macewicz, F. Saborido-Rey, J. Tomkiewicz, & D. M. Wyanski, 2007. An improved and simplified terminology for reproductive classification in fishes. http://hdl.handle.net/10261/ 11844.
- Brown-Peterson, N. J., D. M. Wyanski, F. Saborido-Rey, B. J. Macewicz & S. K. Lowerre-Barbieri, 2011. A standardized terminology for describing reproductive development in fishes. Marine and Coastal Fisheries 3: 52–70.
- Closs, G. P., A. S. Hicks & P. G. Jellyman, 2013. Life histories of closely related amphidromous and non-migratory fish species: a trade-off between egg size and fecundity. Freshwater Biology 58: 1162–1177.
- Diamond, K. M., R. Lagarde, H. L. Schoenfuss, J. A. Walker, D. Ponton & R. W. Blob, 2019. Relationship of escape performance with predator regime and ontogeny in fishes. Biological Journal of the Linnean Society 127: 324–336.
- Diamond, K. M., R. Lagarde, J. G. Griner, D. Ponton, K. E. Powder, H. L. Schoenfuss, J. A. Walker & R. W. Blob, 2021. Interactions among multiple selective pressures on the form-function relationship in insular stream fishes. Biological Journal of the Linnean Society 134: 557–567.
- Ellien, C., R. Causse, U. Werner, N. Teichert & K. Rousseau, 2020. Looking for environmental and endocrine factors inducing the transformation of *Sicyopterus lagocephalus* (Pallas 1770) (Teleostei: Gobiidae: Sicydiinae)

freshwater prolarvae into marine larvae. Aquatic Ecology 54: 163–180.

- Engman, A. C., T. J. Kwak & J. R. Fischer, 2017. Recruitment phenology and pelagic larval duration in Caribbean amphidromous fishes. Freshwater Science 36: 851–865.
- Engman, A. C., G. M. Hogue, W. C. Starnes, M. E. Raley & T. J. Kwak, 2019. Puerto Rico Sicydium goby diversity: species-specific insights on population structures and distributions. Neotropical Biodiversity 5: 22–29.
- Erdman, D. S., 1961. Notes on the biology of the gobiid fish *Sicydium plumieri* in Puerto Rico. Bulletin of Marine Science 11: 448–456.
- Fièvet, E., S. Dolédec & P. Lim, 2001. Distribution of migratory fishes and shrimps along multivariate gradients in tropical island streams. Journal of Fish Biology 59: 390–402.
- Fitzsimons, J. M., 1993. Courtship and territorial behavior in the native Hawaiian stream goby, *Sicyopterus stimpsoni*. Ichthyological Exploration of Freshwaters 4: 1–10.
- Fitzsimons, J., J. E. Parham & R. T. Nishimoto, 2002. Similarities in behavioral ecology among amphidromous and catadromous fishes on the oceanic islands of Hawai'i and Guam. Environmental Biology of Fishes 65: 123–129.
- Franklin, P. & E. Gee, 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.
- Frotte, L., 2019. Réponses trophique et démographique aux perturbations de continuité écologique chez les espèces amphiromes de Guadeloupe. Doctoral dissertation, Antilles.
- Gillet, C., 1983. Les peuplements de poissons et de crevettes des rivières de la Guadeloupe: quelques données sur la biologie, la reproduction, la répartition des espèces. Revue D'hydrobiologie Tropicale 16(4): 327–340.
- Grier, H. J. & M. C. Uribe-Aranzábal, 2009. The testis and spermatogenesis in teleosts. Reproductive biology and phylogeny of fishes (agnathans and bony fishes) Science Publishers Enfield. New Hampshire 8: 119–142.
- Ha, P. Y. & R. A. Kinzie, 1996. Reproductive biology of *Awaous guamensis*, an amphidromous Hawaiian goby. Environmental Biology of Fishes 45: 383–396.
- Healy, K., T. H. G. Ezard, O. R. Jones, R. Salguero-Gómez & Y. M. Buckley, 2019. Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. Nature Ecology and Evolution 3: 1217–1224.
- Iida, M., S. Watanabe & K. Tsukamoto, 2011. Reproductive biology of an amphidromous goby *Sicyopterus japonicus* (Gobiidae: Sicydiinae). Cybium 35: 329–336.
- Iida, M., S. Watanabe & K. Tsukamoto, 2013. Riverine life history of the amphidromous goby *Sicyopterus japonicus* (Gobiidae: Sicydiinae) in the Ota River, Wakayama, Japan. Environmental Biology of Fishes 96: 645–660.
- Jarvis, M. G. & G. P. Closs, 2019. Water infrastructure and the migrations of amphidromous species: impacts and research requirements. Journal of Ecohydraulics 4: 4–13.
- Keith, P., 2003. Biology and ecology of amphidromous Gobiidae of the Indo-Pacific and the Caribbean regions. Journal of Fish Biology 63: 831–847.

- Kindsvater, H. K., M. Mangel, J. D. Reynolds & N. K. Dulvy, 2016. Ten principles from evolutionary ecology essential for effective marine conservation. Ecology and Evolution 6: 2125–2138.
- Kinzie, R. A., 1993. Reproductive biology of an endemic, amphidromous goby *Lentipes concolor* in Hawaiian streams. Environmental Biology of Fishes 37: 257–268.
- Kwak, T. J., A. C. Engman, J. R. Fischer, & C. G. Lilyestrom, 2016. Drivers of Caribbean freshwater ecosystems and fisheries. Freshwater, fish and the future: proceedings of the global cross-sectoral conference. Food and Agriculture Organization of the United Nations, Rome, Italy. 219–232.
- Lagarde, R. & D. Ponton, 2022. Predation pressure in amphidromous gobies: how their morphology is selected by predator species. Journal of Zoology 319: 32–41.
- Lagarde, R., N. Teichert, L. Faivre, H. Grondin, H. Magalon, A. Pirog, P. Valade & D. Ponton, 2018. Artificial daily fluctuations of river discharge affect the larval drift and survival of a tropical amphidromous goby. Ecology of Freshwater Fish 27(3): 646–659.
- Lagarde, R., N. Teichert, H. Grondin, T. Hue, P. Gaudin & D. Ponton, 2020. Influence of larval and juvenile life history on age at first maturity in two tropical amphidromous fish species. Ecology of Freshwater Fish 29: 63–73.
- Lagarde, R., D. Courret, H. Grondin, L. Faivre & D. Ponton, 2021a. Climbing for dummies: recommendation for multispecific fishways for the conservation of tropical eels and gobies. Animal Conservation 24: 970–981.
- Lagarde, R., N. Teichert, P. Valade & D. Ponton, 2021b. Structure of small tropical island freshwater fish and crustacean communities: a niche-or dispersal-based process? Biotropica 53: 243–254.
- Lejeune, L., H. Tabouret, L. Taillebois, D. Monti & P. Keith, 2016. Larval traits of the Caribbean amphidromous goby *Sicydium punctatum* (Gobioidei: Sicydiinae) in Guadeloupe. Ecology of Freshwater Fish 25: 272–280.
- Lim, P., F. J. Meunier, P. Keith, & P. Y. Noël, 2002. Atlas des poissons et des crustacés d'eau douce de la Martinique. Collection patrimoines naturels MNHN.
- Lowerre-Barbieri, S. K., N. Henderson, J. Llopiz, S. Walters, J. Bickford & R. Muller, 2009. Defining a spawning population (spotted seatrout *Cynoscion nebulosus*) over temporal, spatial, and demographic scales. Marine Ecology Progress Series 394: 231–245.
- MacArthur, R. H. & E. O. Wilson, 1967. The Theory of Island Biogeography, Princeton University Press:
- Manacop, P. R., 1953. The life history and habits of the goby, *Sicyopterus extraneus* Herre (anga) Gobiidae with an account of the goby-fry fishery of Cagayan River, Oriental Masamis. Philippine Journal of Fisheries 2: 1–57.
- McDowall, R. M., 1997. The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. Reviews in Fish Biology and Fisheries 7: 443–462.
- McDowall, R. M., 2007. On amphidromy, a distinct form of diadromy in aquatic organisms. Fish and Fisheries 8: 1-13.
- McDowall, R. M., 2009. Early hatch: a strategy for safe downstream larval transport in amphidromous gobies. Reviews in Fish Biology and Fisheries 19: 1.

- McDowall, R. M., 2010. Why be amphidromous: expatrial dispersal and the place of source and sink population dynamics? Reviews in Fish Biology and Fisheries 20: 87–100.
- Monti, D., E. Lefrançois, C. Lord, J.-M. Mortillaro, P. J. Lopez & P. Keith, 2018. Selectivity on epilithic diatom consumption for two tropical sympatric gobies: *Sicydium punctatum* Perugia, 1986 and *Sicydium plumieri* (Bloch, 1786). Cybium 3: 1–9.
- Murua, H. & F. Saborido-Rey, 2003. Female reproductive strategies of marine fish species of the North Atlantic. Journal of Northwest Atlantic Fishery Science 33: 23–31.
- Myers, G. S., 1949. Usage of anadromous, catadromous and allied terms for migratory fishes. Copeia JSTOR 1949: 89–97.
- Neal, J. W., C. G. Lilyestrom & T. J. Kwak, 2009. Factors influencing tropical island freshwater fishes: species, status, and management implications in Puerto Rico. Fisheries 34: 546–554.
- Pecio, A., 2019. Testis Structure, Spermatogenesis, and Spermatozoa in Teleost Fishes The histology of fishes. CRC Press: 177–206.
- R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
- Ramírez-Álvarez, R., S. Contreras, A. Vivancos, M. Reid, R. López-Rodríguez & K. Górski, 2022. Unpacking the complexity of longitudinal movement and recruitment patterns of facultative amphidromous fish. Scientific Reports 12: 1–12.
- Robert M., S. Di-Mauro, A. Leblond & J.P. Pointier, 2015. Faune d'eau douce des Antilles. PLB Edition.
- Rueden, C. T., J. Schindelin, M. C. Hiner, B. E. DeZonia, A. E. Walter, E. T. Arena & K. W. Eliceiri, 2017. Image J2: ImageJ for the next generation of scientific image data. BMC Bioinformatics 18: 1–26.
- Smith, W. E., 2012. Reproductive ecology of Caribbean amphidromous fishes. North Carolina State University.
- Smith, W. E. & T. J. Kwak, 2015. Tropical insular fish assemblages are resilient to flood disturbance. Ecosphere 6: 1–16.
- Stearns, S. C., 1992. The evolution of life histories, Oxford University Press, Oxford:
- Teichert, N., P. Keith, P. Valade, M. Richarson, M. Metzger & P. Gaudin, 2013a. Breeding pattern and nest guarding in *Sicyopterus lagocephalus*, a widespread amphidromous Gobiidae. Journal of Ethology 31: 239–247.
- Teichert, N., P. Valade, P. Bosc, M. Richarson & P. Gaudin, 2013b. Spawning-habitat selection of an Indo-Pacific amphidromous gobiid fish, *Sicyopterus lagocephalus* (Pallas). Marine and Freshwater Research 64: 1058–1067.
- Teichert, N., P. Valade, A. Fostier, R. Lagarde & P. Gaudin, 2014. Reproductive biology of an amphidromous goby, *Sicyopterus lagocephalus*, in La Réunion Island. Hydrobiologia 726: 123–141.

- Teichert, N., P. Valade, A. Fostier, H. Grondin & P. Gaudin, 2016. Reproductive biology of an endemic amphidromous goby, *Cotylopus acutipinnis*, from la Réunion Island. Marine and Freshwater Research 67: 526–536.
- Teichert, N., S. Pasquaud, A. Borja, G. Chust, A. Uriarte & M. Lepage, 2017. Living under stressful conditions: Fish life history strategies across environmental gradients in estuaries. Estuarine, Coastal and Shelf Science 188: 18–26.
- Teichert, N., R. Lagarde, N. Occelli, D. Ponton & P. Gaudin, 2021. Water temperature influences larval survival of the amphidromous goby *Sicyopterus lagocephalus*. Ecology of Freshwater Fish 30: 531–540.
- Watanabe, S., M. Iida, C. Lord, P. Keith & K. Tsukamoto, 2014. Tropical and temperate freshwater amphidromy: a comparison between life history characteristics of Sicydiinae, ayu, sculpins and galaxiids. Reviews in Fish Biology and Fisheries 24: 1–14.
- Watson, R. E., 2000. *Sicydium* from the Dominican Republic with description of a new species (Teleostei: Gobiidae): with 4 tables. Staatliches Museum für Naturkunde.
- Winemiller, K. O. & K. A. Rose, 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. Canadian Journal of Fisheries and Aquatic Sciences 49: 2196–2218.
- Wootton, R. J. & C. Smith, 2014. Reproductive biology of teleost fishes, John Wiley & Sons:
- Wright, J., G. H. Bolstad, Y. G. Araya-Ajoy & N. J. Dingemanse, 2019. Life-history evolution under fluctuating density-dependent selection and the adaptive alignment of pace-of-life syndromes. Biological Reviews 94: 230–247.
- Yamasaki, N. & K. Tachihara, 2006. Reproductive biology and morphology of eggs and larvae of *Stiphodon percnopterygionus* (Gobiidae: Sicydiinae) collected from Okinawa Island. Ichthyological Research 53: 13–18.
- Yamasaki, N., M. Kondo, K. Maeda & K. Tachihara, 2011. Reproductive biology of three amphidromous gobies, *Sicyopterus japonicus*, *Awaous melanocephalus*, and *Stenogobius* sp., on Okinawa Island. Cybium 35: 345–359.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.