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

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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 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, 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.

Key-words:

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 and 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 and 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, 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 and 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, *Sicydium* 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), 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 synthesized 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 (Figure 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 to 100 cm – width: 4 to 25m). 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 $\pm 0.2^{\circ}\text{C}$). 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, 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-Root™). 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 seconds in water, while operators collect the fish using dip nets. For each survey, 15 *S. plumieri* et 15 *S. punctatum* were collected using a 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 a.m. – 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 ($TL \pm 1\text{mm}$) and wet weight ($BW \pm 0.01\text{g}$) were measured, as well as the wet gonadal weight ($GW \pm 0.001\text{g}$). 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), then embedded in paraffin and sectioned to $7\mu\text{m}$ 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., x40, x100 and x200). 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 (Figure 2). The three following stages 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 (Figure 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-Aranzabal 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 (Figure 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 (Figure 2-A). 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 (Figure 2-B). 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 (Figure 2-C). 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 (Figure 2-D). 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 (Figure 2-E), 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 (Figure 2-F).

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 (Figure 2-G). 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 (Figure 2-H). Gonads are filiform and speckled with white. The *non-active reproductive phase 3*) (Figure 2-I) 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 (L_{50}) 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: $\text{logit}(\mu_i) = \beta_0 + \beta_{TL}X_{TL} + \varepsilon_i$, where μ_i is the maturation status of the fish, X_{TL} is the total length, β_0 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 Chisquared-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 size 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; $n = 201$, $F = 128.6$, $p < 0.001$ for *S. plumieri* and $n = 367$, $F = 58.4$, $p < 0.001$ for *S. punctatum*).

Analysis of ovarian development

For *S. punctatum* ($n = 55$, Figure 3), oocytes' diameters varied from 10 to 76 μm for PG ($n=1264$), from 32 to 97 μm for CA ($n=195$), from 71 to 167 μm for EVO ($n=100$), and from 104 to 273 μm 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 μm . 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 ($n=107$, Figure 3). Although, GSI values were not evenly distributed for *S. plumieri* (*i.e.*, lack of values between 5.7 and 13.9%), 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 (Figure 4, $L_{50} = 63,3 \pm 6,3$ mm) than for females ($L_{50} = 74,5 \pm 1,5$ mm; $p < 0,001$).

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

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 (Figure 5). Overall, 94% of males had testes whose lumen was enlarged and filled with spermatozoa indicating they were able to reproduce although no spermiating 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 (Figure 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 (Figure 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 (Figure 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 spermiating male was captured.

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 (Figure 7). In upstream, the water temperature was slightly cooler, ranging between 20.1°C 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 11.2h 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, 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 vitellogenic 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 and 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 and 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 post-larvae 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 L_{50} inferred from histological sections were much larger than in *S. punctatum* and a sexual dimorphism was emphasized between male ($L_{50} = 63,3 \pm 6,3$ mm) and female ($74,5 \pm 1,5$ 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 and 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, 2013; Yamasaki et al., 2011) 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 pan-seasonal 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 and 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 major 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).

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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 (N°971-2019-05-06-004) and of the Parc National de la Guadeloupe (N°19/14).

Conflict of interest statement

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

Data availability statement

Data will be made available on request.

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

Site	Sampling number			Total length (mm)	
	Female (im)	Male (im)	Total (%im)	Female	Male
<i>S. punctatum</i>					
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)
<i>S. plumieri</i>					
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)
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Table 2: Summary of ANOVAs investigating the influence of the sampling date and the river site on the gonado-somatic index of *Sicydium punctatum* and *Sicydium plumieri*. Significant p-values are highlighted in bold.

<i>S. punctatum</i> - female	df	Sum Sq	Mean Sq	F-value	P-value
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
<i>S. punctatum</i> - 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
<i>S. plumieri</i> - 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
<i>S. plumieri</i> - 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

Table 3: Summary of reduction deviance tests conducted on GLMs investigating the influence of temperature and photoperiod on the gonado-somatic index of *Sicydium punctatum* and *Sicydium plumieri*. Significant p-values are highlighted in bold.

Parameter	df	Residual deviance	Explained deviance	P-value
<i>S. punctatum</i> - female				
Null model	226	2907.200	-	-
Temperature	225	2831.900	75.350	0.017
Photoperiod	224	2563.500	268.420	< 0.001
<i>S. punctatum</i> - male				
Null model	141	10.617	-	-
Temperature	140	10.611	0.006	0.781
Photoperiod	139	10.118	0.493	0.011
<i>S. plumieri</i> - female				
Null model	125	263.120	-	-
Temperature	124	259.890	3.231	0.228
Photoperiod	123	216.030	43.864	< 0.001
<i>S. plumieri</i> - male				
Null model	76	0.123	-	-
Temperature	75	0.123	0.001	0.483
Photoperiod	74	0.106	0.017	0.001

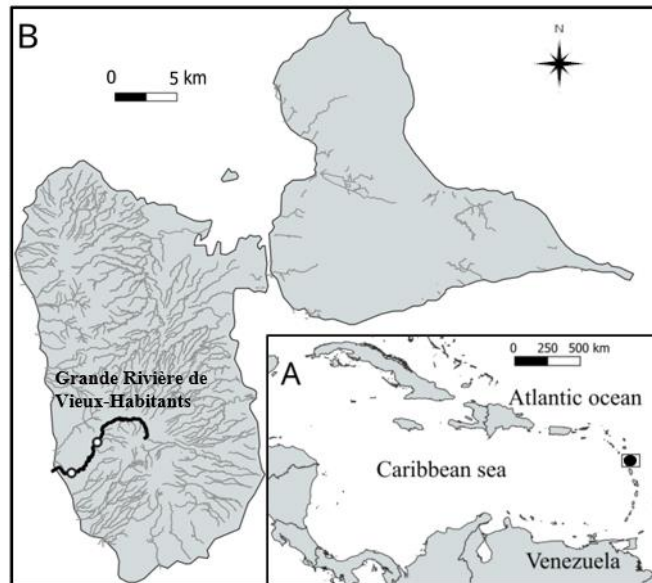


Figure 1: Localization maps of Guadeloupe island in the Caribbean (A) and geographical positions of the two sampling sites (i.e. downstream and upstream) in the Grande Rivière de Vieux-Habitants River of Guadeloupe (B), West Indies, Caribbean region.

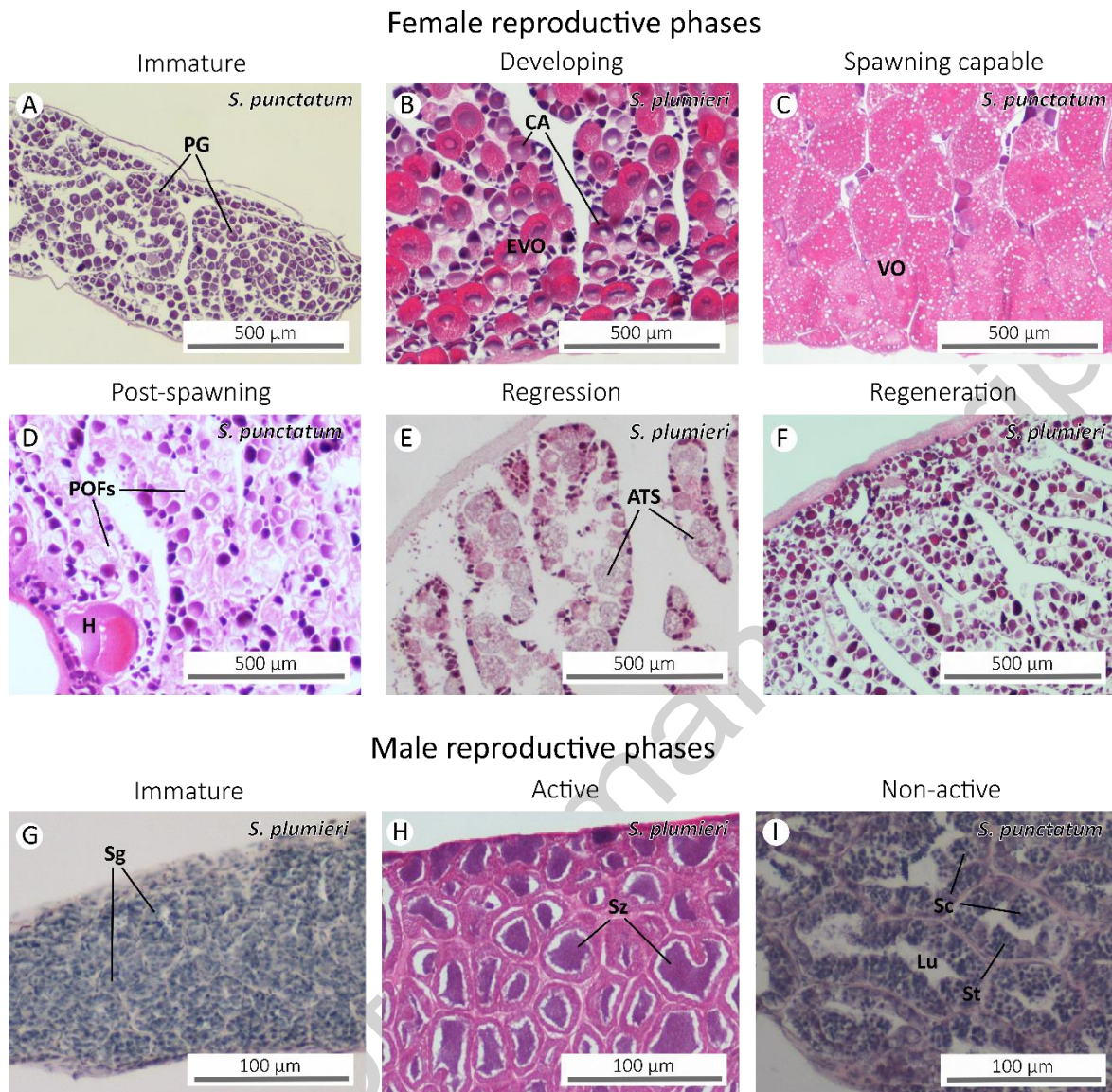


Figure 2: Histological observations of gonads depending on the reproductive phases of females (A – immature, B – developing C – spawning capable, D – post-spawning, E – regression, F – regeneration) and males (G – immature, H – active, I – non-active) of *Sicydium* sp. PG: primary growth oocyte, CA: cortical alveoli; EVO: early vitellogenic oocyte, VO: vitellogenic oocyte, POF: postovulatory follicle, ATS: atretic 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 (Figure S1 and Figure S2).

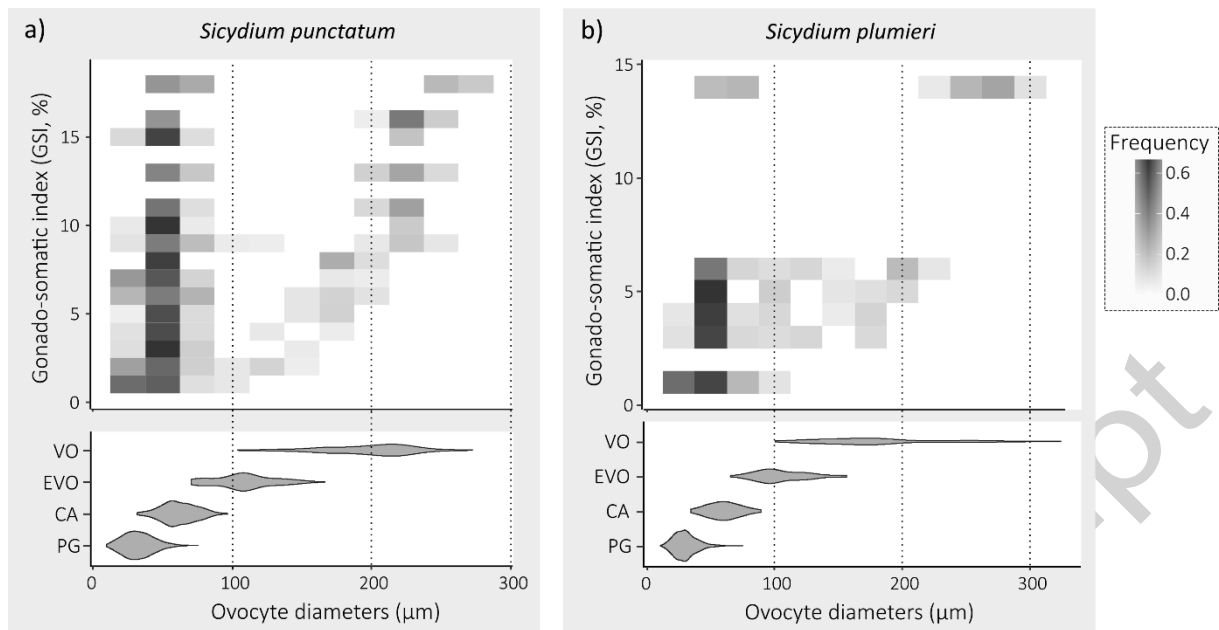


Figure 3: Oocyte size frequencies in ovaries of a) *Sicydium punctatum* (n = 55) and b) *Sicydium plumieri* (n = 41) depending on the gonado-somatic index (GSI %) used as proxy for ovarian development. The size distributions of the different oocyte development stages are presented in the graphs below. PG: primary growth, CA: cortical alveoli; EVO: early vitellogenic, VO: vitellogenic.

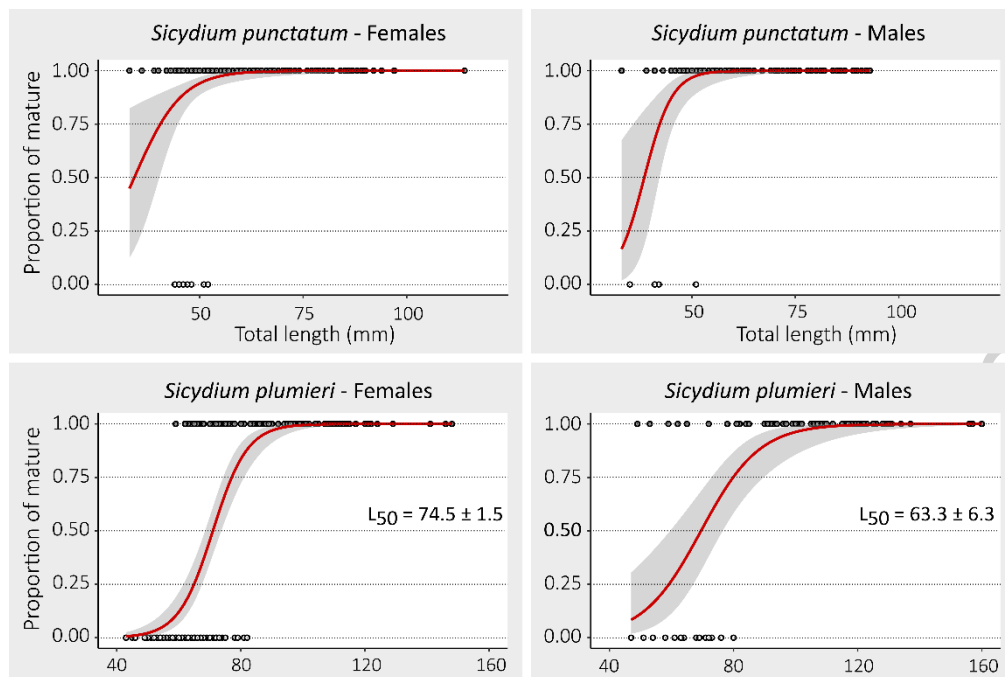


Figure 1: Length-at-maturity of *Sicydium punctatum* (female : n = 236 et male : n = 147) and *Sicydium plumieri* (female: n = 215 et male: n = 94) in the Grande Rivière de Vieux-Habitants, Guadeloupe Island.

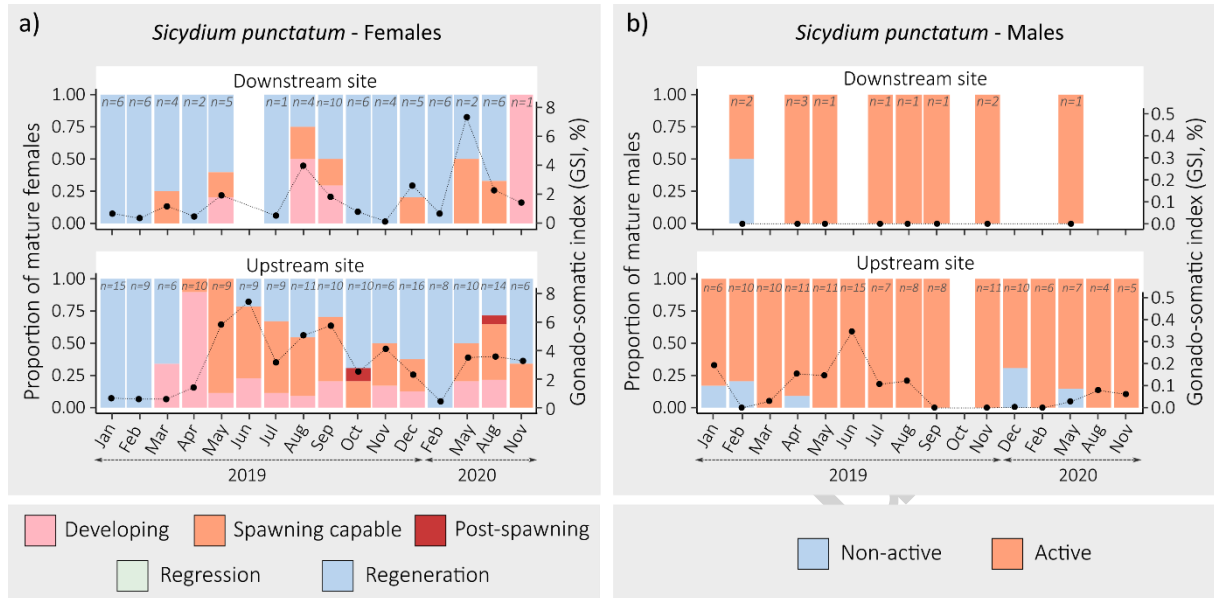


Figure 5: Monthly fluctuation in the reproductive phases of adult a) females and b) males of *Sicydium punctatum* in the upstream and downstream sites of the Grande Rivière de Vieux-Habitants, Guadeloupe Island. The mean variations in gonado-somatic index (GSI %) are also represented by the black dashed lines.

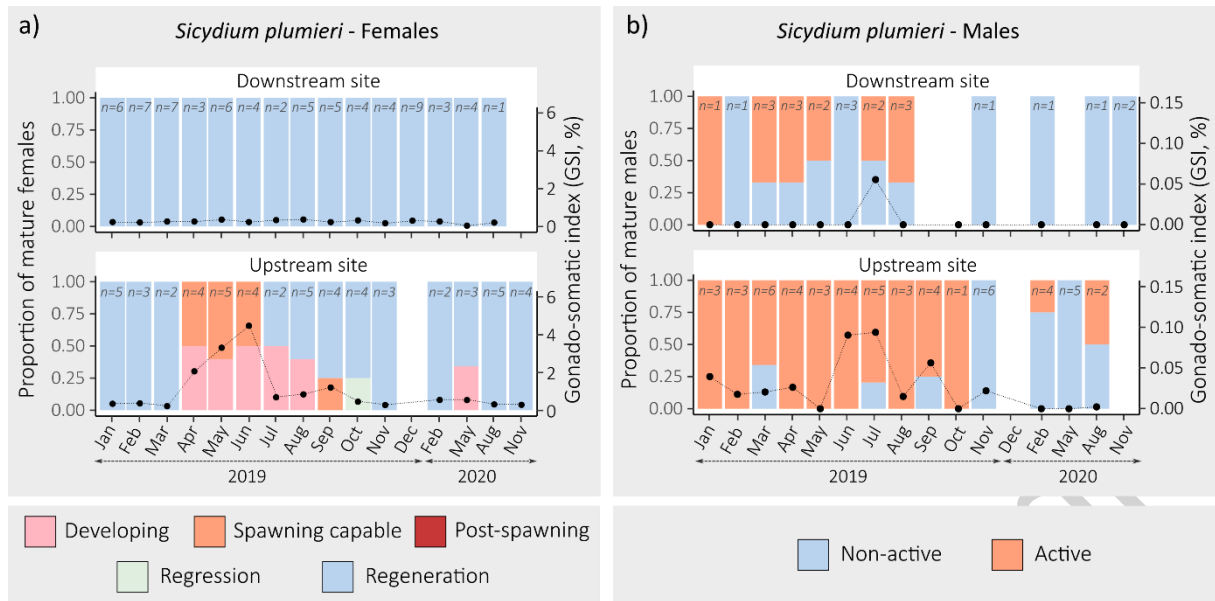


Figure 6: Monthly fluctuation in the reproductive phases of adult a) females and b) males of *Sicydium plumieri* in the upstream and downstream sites of the Grande Rivière de Vieux-Habitants, Guadeloupe Island. The mean variations in gonado-somatic index (GSI %) are also represented by the black dashed lines.

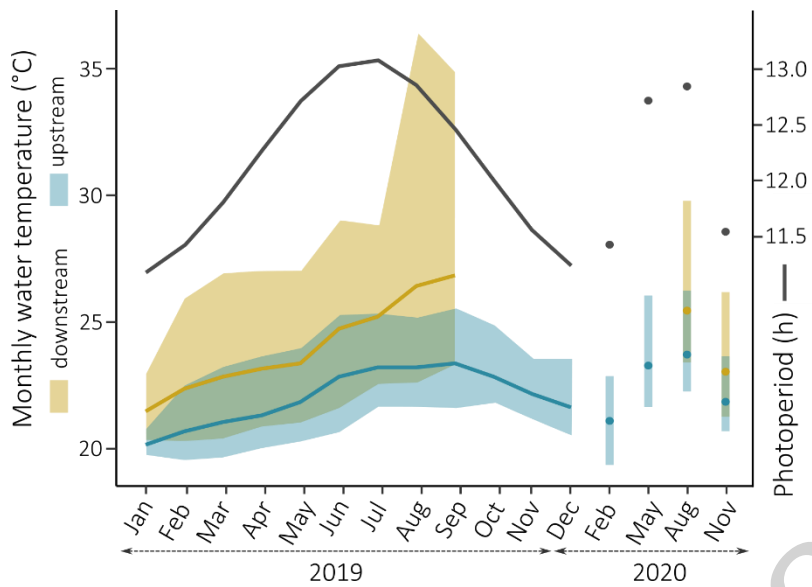


Figure 7: Monthly fluctuation of water temperatures (°C) and photoperiod (daylength, h) in the upstream and downstream sites of the Grande Rivière de Vieux-Habitants, Guadeloupe Island. The colored bands represent the extreme temperature ranges (minimal and maximal hourly values).