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Larval traits of the Caribbean amphidromous goby *Sicydium punctatum* (Gobioidei: Sicydiinae) in Guadeloupe

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Abstract – Amphidromous fish are the biggest contributor to the diversity of fish communities in river systems of Caribbean islands. Among them, *Sicydium punctatum* Perugia, 1896, which is endemic to the West Indies, represents the vast majority of fish in these rivers. The otolith microstructure and the biometry of *S. punctatum* postlarvae from Guadeloupe were investigated to explore the dispersal modalities of this species through an appreciation of the growth pattern, the pelagic larval duration (PLD) and the size-at-recruitment. The study was made on one cohort of 83 recruited postlarvae, fished at the Capesterre River's mouth on 2 November 2011. The mean (±SD) size-at-recruitment of the postlarvae was 24.6 ± 1.3 mm (range of 20.5–28.1 mm, $n = 83$). We found a mean (±SD) PLD of 72.2 ± 10.5 days (range of 54–101.5 days, $n = 67$). The growth rate estimated from the otolith increments showed a globally decreasing pattern during the marine larval phase. Growth rates at the beginning of the larval stage were significantly different between hatching periods, suggesting a relation between the hatching period and the growth rate in *S. punctatum*. This study adds on to the general understanding of the life cycle of *S. punctatum* in Guadeloupe that will help implement strategies to manage amphidromous fish populations in the Caribbean region.

Key words: amphidromy; otolith; larval dispersal; Sicydiinae; Lesser Antilles

Introduction

Gobioidei, and especially species of the Sicydiinae subfamily, are the largest contributors to the diversity of fish communities in tropical insular systems and have the highest level of endemism in these particular habitats (Radtke & Kinzie 1996; Keith & Lord 2011). All the known species of this subfamily exhibit an amphidromous life cycle (Keith et al. 2011). The adults grow, feed and spawn in freshwater. The newly hatched larvae drift downstream and quickly reach the marine environment where they spend 2–6 months while undergoing their larval development (Iida et al. 2008; Lord et al. 2010; Taillebois et al. 2012). At the end of this marine larval phase, the postlarvae move back to the river mouth while they come across a metamorphosis (Taillebois et al. 2011). Soon after entering the river, the juveniles swim upstream and settle in the upper reaches.

Despite the great contribution of amphidromous species to the diversity of fish communities on tropical islands, the details of their biological cycle remain poorly known (Lord & Keith 2006). Tropical island ecosystems are naturally unstable and ephemeral and have become even more so in recent years as result of human alteration (Smith et al. 2003). Moreover, recruiting postlarvae is a declining fishery resource in many areas, as Caribbean region (Bell 1999).

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Designing appropriate biodiversity management plans for species which are distributed on remote islands relies on a better understanding of their life cycle.

Otoliths are paired calcified structures in the inner ear of the fish that work as mechanoreceptor and are involved in equilibrium and locomotion. They are metabolically inert and grow continuously on a regular time period basis (Pannella 1971; Lecomte-Finiger 1999) during the entire fish's life and do not undergo any mineral resorption (Mugiya & Uchimura 1989). They are made of successive discrete layers of aragonite crystalline microstructure growth increments that are deposited on a protein matrix (Campana 1999). The daily periodicity of these increments was validated at larval stage on several fish species (Pannella 1971), including Sicydiinae (Yamasaki et al. 2007; Taillebois et al. 2012). In the case of amphidromous species, metamorphosis is materialised by a checkmark, appearing when the postlarvae recruit to the rivers (Shen & Tzeng 2002). The increment count from the core to the metamorphosis checkmark is therefore an estimation of the marine pelagic larval duration (PLD). Investigations on PLD are of particular interest because they provide insights on the distribution ranges and the dispersal processes that occur in Sicydiinae as illustrated by recent studies (Lord et al. 2010; Taillebois et al. 2012).

The relationship between the otolith growth rate and the individual growth rate in some amphidromous species has been used to study the relative growth rates during the larval stage (Shen & Tzeng 2008; Lord et al. 2010). Because the individual growth depends on intrinsic factors such as the age and the size of the fish and on external components such as food supply, water salinity and temperature (Boeuf & Payan 2001), studying the growth patterns can provide information on the environmental conditions which occurred in the life stages of the fish.

This study focuses on the species *Sicydium punctatum* Perugia, 1896, distributed in the Caribbean freshwaters, living in sympatry with *Sicydium plumieri* (Bloch, 1786). Within the *Sicydium* genus, species are distributed in West Africa from Congo to Gabon and on both sides of the Panama isthmus (Keith et al. 2011). Juveniles of the genus *Sicydium* are harvested in the estuaries of Caribbean rivers when they recruit and constitute fry fisheries in this region (Fièvet & Le Guennec 1998; Bell 1999). Recruitment is panseasonal in this species and age- and size-at-recruitment vary seasonally (Bell et al. 1995). The amphidromous species are dominant in fauna biomass in Caribbean hydrosystems (Covich & McDowell 1996) and recruited postlarvae provide an important source of food for many fish species in estuaries (Hostache 1992). Despite its ecological, economical and cultural values, only few conservation measures have been developed to protect *Sicydium punctatum* at local and global scales. The lack of management measures is probably due to the lack of knowledge of *S. punctatum* life history traits. Although few studies have explored larval recruitment of *S. punctatum* in Dominica (Bell & Brown 1995; Bell et al. 1995; Bell 2009) and confirmed the amphidromy of the species (Tabouret et al. 2011), it is the first time larval traits are explored in individuals from Guadeloupe. We aim to provide a better understanding of the characteristics of the marine dispersal phase as well as the recruitment of *S. punctatum*. To achieve this aim, we estimated the PLD and examined the size-at-recruitment and the growth rate patterns during the marine phase of one cohort of recruiting postlarvae in Guadeloupe, using the otolith microstructure.

Material and methods

Sampling and biometry

The postlarvae were sampled with traditional woven funnel traps at the mouth of the Capesterre River on Basse-Terre Island in Guadeloupe on 2 November 2011 (Fig. 1). Fish were kept in 95% ethanol. Among these fish, 96 individuals were randomly sampled for the study. Eighty-three individuals were used after barcoding (see details in the result section). The standard length (SL) and total length (TL) of each postlarva were measured using a digital Mitutoyo dial calliper (Mitutoyo, Aurora, Illinois, USA) with 0.01 mm accuracy. According to the Spearman's test, the TL and SL were positively significantly correlated ($\rho = 0.882$; $P < 0.001$, $n = 83$); therefore, we used the TL as an indicator of the size-at-recruitment for the statistical analyses.

Barcoding

Sicydium punctatum is the most common fish species in Guadeloupe rivers. However, postlarvae belonging to other species such as *S. plumieri* may have recruited at the same time. Because the morphologic differences between close species at the postlarval stage are not easily picked up, we performed genetic barcoding analyses to definitely identify our samples. Total genomic DNA was extracted from fin clips with the robot Eppendorf epMotion 5075 and the NucleoSpin®96 Tissue kit (Macherey-Nagel) following the manufacturer's instructions. A 680 length fragment of the mitochondrial DNA cytochrome oxydase I (COI) gene was amplified for each of the individuals according to the method described in Taillebois et al. (2014), using the primers *Fish*F1 (5′–TCAACCAACCACAAAGACATTGG–3′) and

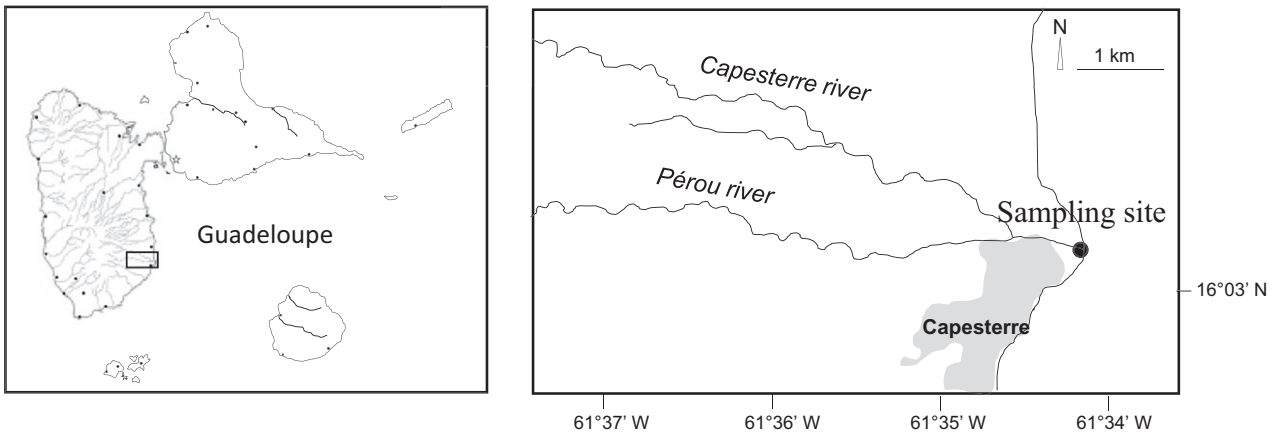

Fig. 1. Sampling site on Guadeloupe Island (West Indies) (modified from Tabouret et al. 2011).

*Fish*R1 (5′–ACTTCAGGGTGACCGAAGAATCA–3′) (Ward et al. 2005).

PCR products were purified using exonuclease I and phosphatase and sequenced using BigDye Terminator v3.1 kit (Applied Biosystems) and the ABI 3730XL sequencer at Genoscope (http://www.genoscope.cns.fr/) using the same primers. All gene fragments were sequenced in both directions. Chromatograms were edited manually using Sequencher v4.8 (Gene Codes Corporation) and aligned by hand using Bioedit (Hall 1999).

We used mismatch distributions implemented in Arlequin (Excoffier et al. 2005) and performed a phenetic tree with Mega software (Tamura et al. 2007) using the *neighbour-joining* method (Saitou & Nei 1987) and the model of *Kimura 2-Parameter* (Kimura 1980). In this model, the substitution rate does not change with the position of the nucleotide in the sequence but if it is a transversion or a transition. We compared the COI sequences with COI sequences of other species available in our database. Eleotridae sequences constituted the outgroup.

Otolith extraction and preparation

Right and left sagittal otoliths were extracted from the fish under a binocular stereoscopic microscope Olympus VMZ (Olympus, Tokyo, Japan). Each otolith was cleaned with ultra pure water and dried. Otoliths were individually embedded in an epoxy resin (Araldite 2020A®, Escil, Chassieu, France) and ground in transverse section to the core using grinding discs of decreasing grades (800, 1200 and 2400) in order to highlight and count all the increments. The otoliths were polished with a felt disc covered with alumina powder (Escil, Chassieu, France). Grinding and polishing were performed manually and on an automatic MetaServ®3000 grinder (Buehler, Dardilly, France). Finally, each otolith was pictured at ×100 and ×200 magnifications with an optical microscope equipped with an Olympus DP20 camera (Olympus, Tokyo, Japan).

Ageing and back calculation of hatching date

As the Sicydiinae embryos cannot spend more than 3 days in the freshwater after hatching (Valade et al. 2009; Ellien et al. 2011), we assumed that the PLD is equivalent to the age-at-recruitment of the postlarvae, as assumed in previous studies (Lord et al. 2011). In this study, we also assumed that the accretionary growth of the otolith occurs on a daily basis (Pannella 1971) as it is the most likely in the case of fish postlarvae under nonstressful conditions (Jones 1992), and it has been previously proved in Sicydiinae (Yamasaki et al. 2007; Iida et al. 2010; Taillebois et al. 2012).

Two persons independently counted the daily growth increments, from the nucleus to the edge on each panorama photocomposed using Photoshop 10.0.1 (Adobe, Photoshop CS3). As the PLDs estimated by the two readers were not significantly different (Wilcoxon's test for paired series: $W = 1044.5$; $P > 0.1$) the mean of the two readers was used to calculate the PLD. The hatching date of the postlarvae was back-calculated for all the postlarvae for which we estimated the PLD.

Otoliths growth rate

We measured the distance between points located on a straight line each five daily increments using Photoshop 10.0.1 (Fig. 2). The otolith average daily growth rate ($\mu m \cdot day^{-1}$) on this 5-days time interval was then calculated. The value was normalised to the longest radius length in order to avoid the bias due to sample preparation and to enable comparisons between otoliths.

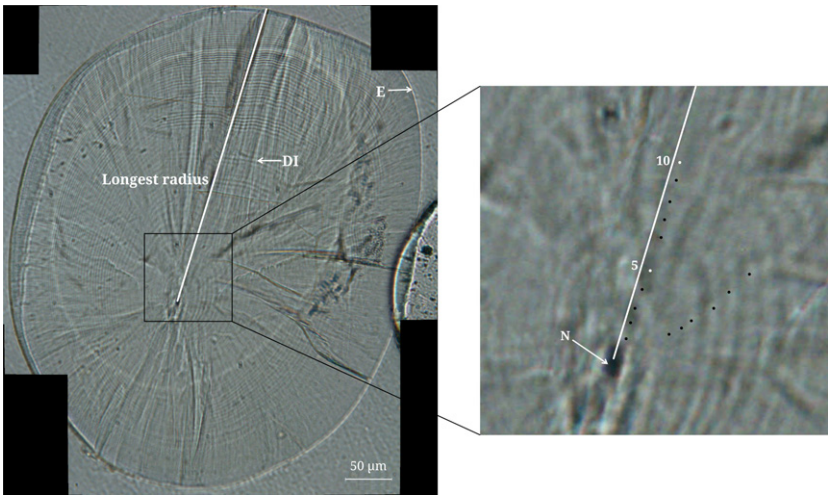

Fig. 2. Otolith of *Sicydium punctatum*. For otolith growth analysis, the distance between each 5 daily increment is measured along the otolith's longest radius (*N*, nucleus; DI, daily increment; and E, edge of the sagitta).

Statistical analysis

The data were statistically processed using R v2.8 (R Development Core Team, 2008, http://www.r-project.org/). The normality of the data was systematically checked using Shapiro's test. We used the Wilcoxon's test for paired series to test whether the PLD estimated by the two counters were significantly different. A Spearman's test was used to test the relationship between the PLD and the size-at-recruitment, as the size-at-recruitment was not normally distributed (Shapiro–Wilk's test, TL: $W = 0.959$, $P = 0.027$, $n = 67$). The correlation between the size-at-recruitment and the length of the longest radius was tested by a Spearman's test too. A Pearson's test as well as a linear regression were used for testing the correlation between the PLD and the otolith average growth rate, as both variables were normally distributed (growth rate: $W = 0.981$, $P > 0.1$ $n = 60$; PLD: $W = 0.971$, $P > 0.1$, $n = 60$). To test the relationship between hatching period and growth rate, we used a Mann–Whitney U-test with a false discovery rate control. For every 5-days step, we tested the difference in the mean otolith growth rates between individuals born in two different hatching periods: August and September.

Results

Species identification

Of the 96 samples, 90 were successfully sequenced for the COI gene and 667-bp length fragments were obtained for each of the 90 individuals. No evidence for pseudo-gene amplification was found (no ambiguous alignment, low sequence quality, double peaks or stop codons). The distribution of pairwise genetic distances showed three nonoverlapping modes. The first one grouped p-distances between 0% and 2%. The second one grouped p-distances between 8.2% and 10.9%. The third one grouped p-distances between 2.8% and 3.7%, which corresponded to the distance between one sequence and the others. This sequence was excluded from further analysis, as we suspected it was an artefact. The two other groups corresponded to intraspecific and interspecific p-distances.

The phenetic tree highlighted two major groups supported by bootstrap's values of 93% and 100%. These groups were identified thanks to reference sequences as the species *S. punctatum* and *S. plumieri*. The whole data set was thus composed of 83 postlarvae *S. punctatum.*

Pelagic larval duration

No obvious checkmark was found in the otoliths, as the postlarvae were newly recruited, but a decrease in the increment width was observed at the otolith edge, indicating a change in the environmental conditions and/or the physiological condition of the fish. We assumed it was the evidence of the transition between salt and fresh waters.

We were able to count the growth increments on 67 otoliths of *S. punctatum*, as the others were too damaged. The average (±SD) PLD of *S. punctatum* postlarvae was 72.1 ± 10.4 days with a range of 54–101.5 days. The coefficient of variation (cv) was 0.15. Considering the sampling date (2 November 2011), when postlarvae arrived at the river's mouth and the PLD, we back-calculated the hatching period. Hatching of these individuals occurred from 23 July 2011 to 9 September 2011. One individual was born in July (<1%), 50 were born in August (75%) and 16 in September (24%).

Size-at-recruitment

All the 83 postlarve of *S. punctatum* were measured. The average (±SD) size-at-recruitment of postlarvae

was 24.5 ± 1.3 mm, with a range of 20.5–28.1 mm. The coefficient of variation was 0.05. PLD and size-at-recruitment were not significantly correlated (Spearman's correlation test: $\rho = -0.116$, $P > 0.1$).

Otolith growth rate

The otolith growth rate was performed on 60 individuals of *S. punctatum* for which the PLD and size-at-recruitment were estimated and measured, as the pictures of seven individuals' otolith did not allow to estimate the growth rate. To know whether the otolith growth is a good proxy of the postlarvae growth, we tested the correlation between the size-at-recruitment of postlarvae and the length of the longest radius using the nonparametric Spearman's test. The test showed a significant positive correlation ($\rho = 0.642$, $P < 0.001$, $n = 60$). Therefore, we assumed that the otolith growth rate from the nucleus to the edge could be a good proxy of the larval growth for *S. punctatum* individuals.

The results of the linear regression (Fig. 3, $R^2 = 0.7536$, $P < 0.001$) and the Pearson's test ($t = -13.173$; $P < 0.001$) showed that there was a strong negative relationship between the PLD and the daily growth rate of the otoliths. The oldest individuals at recruitment had a low average daily growth rate. Indeed, the postlarvae born in September had an average growth rate significantly higher than those born in August (Wilcoxon's test: $W = 599$; $P < 0.001$).

The growth rate changes during larval stage had the same pattern in both the individuals born in September and in August (Fig. 4). Four stages can be distinguished on the growth rate curves: a fast growth rate stage during the first days of the marine larval phase was followed with a decreased growth rate between the fifth and the tenth days. Then, the growth rate rose between the tenth and the twentieth days. Finally, the growth rate progressively decreased during the remaining of the marine larval phase to reach around 2 μm·day^{-1}. The growth rate was higher for individuals born in September during the first 5 days, from the 20th to 25th day and from the 45th to 50th day (Fig. 4). No significant difference in the growth rate between August and September was observed during the other periods of the marine larval phase.

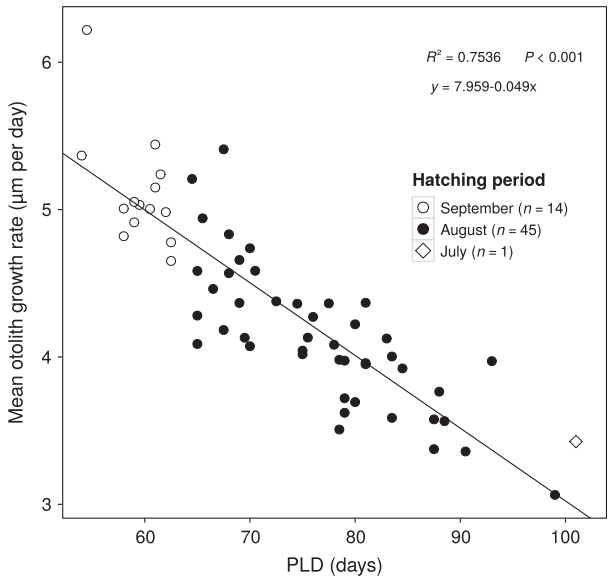

Fig. 3. Mean otolith growth rate (μm·day) of *Sicydium punctatum* postlarvae depending on their PLD. The curve is fitted by: $y = -0.04936x + 7.95894$. $R^2 = 0.7536$, $P < 0.001$. $N = 60$.

Discussion

Pelagic larval duration

The average PLD found for *S. punctatum* from Guadeloupe (average ± SD: 72.16 ± 10.5 days, with a range of 54–101.5 days) was slightly lower than what was reported by Bell et al. (1995) in Dominica (average ± SE: 83.4 ± 1.3 days, with a range of 54–132 days). Although it seems average PLDs are slightly different in these two localities, there are large variations of the PLD of *S. punctatum* in Dominica (54–132 days), partly due to the periodic seasonal variability (Bell et al. 1995). Looking more closely to the data, Bell et al. (1995) found PLDs of around 75 days for recruits of October, which is consistent with the timing of our sampling and with the PLD we found in the present study. The PLD of *S. punctatum* bracketed within the range observed in endemic closely related amphidromous gobies (Lord et al. 2010). In Sicydiinae, PLD is not a good proxy to explain the distribution range of species (Taillebois et al. 2012) even if it may play a role in the ability to colonise rivers at the individual scale. In the Caribbean region, only short distances separate the potential habitats of Sicydiinae. Given this short distance and the length of the larval phase in *S. punctatum*, individuals should be able to reach a suitable habitat. Other parameters of a physiological, ecological and physical nature may influence the dispersal ability and thus the recruitment of postlarvae (Bradbury & Snelgrove 2001; Radtke et al. 2001).

Larval growth rate

Variation of the larval growth rate during the larval development

Just after hatching, the larvae of Sicydiinae species have only few days to reach the sea (Bell & Brown 1995; Valade et al. 2009) where they undergo all the transformations allowing them to survive in salt water. The arrival in salt water triggers these morphological

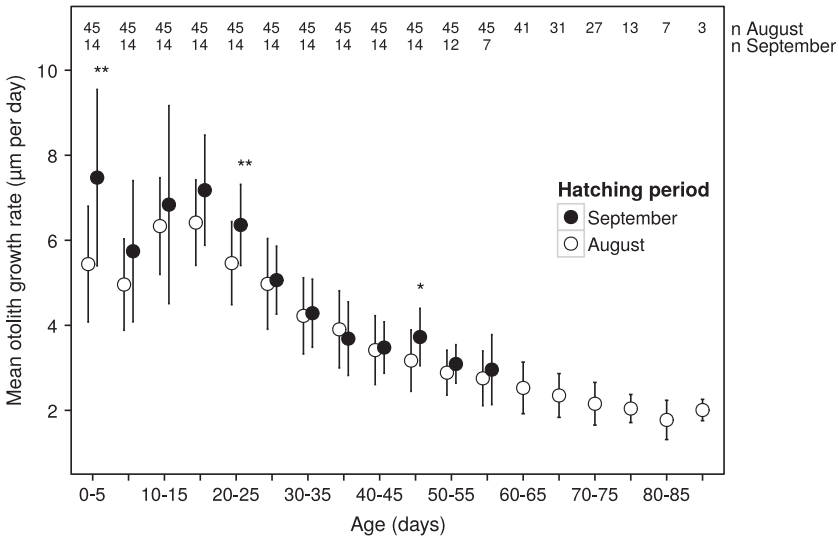

Fig. 4. Mean otolith growth rate ± standard deviation (µm·day^{-1}) of *Sicydium punctatum* during the pelagic larval phase for two hatching periods, August (white filled dots) and September (black filled dots), in relation with the age. Asterisks indicate a significant difference (Mann–Whitney U-test with false discovery rate control) between the growth rate of individuals hatched in August and September (**: alpha-level = 0.05, *: alpha-level = 0.10). Numbers above are the sample sizes for each time interval and each hatching period (*n* August and *n* September).

transformations (Lindstrom & Brown 1994; Lindstrom 1998), and within 48 h, the yolk sac is absorbed and the mouth opens (Ellien et al. 2011). The yolk supplies are totally consumed after an average of 4 days after hatching in Sicydiinae (Valade et al. 2009; Ellien et al. 2011). This would explain why the growth rate is high (5.9 µm·day^{-1} for the otoliths) during the early life stages of the larvae while they are still able to feed off the yolk sac. After that period, the daily growth rate decreases of up to 2.6 µm·day^{-1} as major physiological and morphological transformations occur (Depeche & Billard 1994). When these transformations that require a great amount of energy happen, the larvae allegedly feed off plankton, which may not be as energetic as the yolk sac reserves. This would explain the global decrease in the larvae's growth rate. Similar patterns of globally decreasing growth rates during the marine larval phase have been described in other Sicydiinae species (Lord et al. 2010; Teichert 2013). This trend lasted until the larvae reached the river mouth. Based on stable isotope analyses, Sorensen & Hobson (2005) suggested that larvae of amphidromous species in Hawaii derived much of their nutrition from inshore environment influenced by freshwater. One would expect an increase in the growth rate at the end of the marine larval stage due to rich inshore feeding ground. However, it coincides with the beginning of the morphological transformations occurring during their metamorphosis. This would explain why the daily growth rate does not increase close to shore despite the large amount of nutrients available in this environment.

Variation of the larval growth pattern in relation to the hatching period

The hatching period of the sampled individuals occurred from mid-July to the beginning of September, with individuals born in September growing significantly faster than those born in August at the beginning of the larval phase. Studies showed that reproduction and recruitment in amphidromous gobies in the tropical regions generally occur all year round (Bell et al. 1995; Keith 2003). Our sampling was limited in time, and all year round sampling should give us more details on the spawning–hatching periods. Bell et al. (1995) showed that *S. punctatum* growth rates exhibit seasonal variations with a peak of highest growth rates for larvae hatched in midsummer (month of July) and of lowest growth rates for larvae hatched in late December. Seasonal variations were also found in *Sicyopterus japonicus* in Taiwan (Shen & Tzeng 2008). These two studies suggest that growth rates may be related to hatching periods as found in our study. The pelagic larval environment (e.g., water temperature, food availability and oceanographic features) was shown to influence the rates of larval growth (Otterlei et al. 1999; Keller & Klein-MacPhee 2000) in a variety of marine fish. More recently, Teichert (2013) has brought a correlation between sea surface temperature and pelagic larval traits to light. Food availability does not seem to explain the growth disparities we found, as there is no clear difference between the chlorophyll concentration near the coast in West Indies in August and September 2011 (NASA Earth observations, http://neo.sci.gsfc.nasa.gov/). Variations observed could also be due to individual differences, as found in amphidromous gobies in Japan (Iguchi & Mizuno 1990).

Modalities of recruitment

Nonsignificant correlation between age and size-at-recruitment of *S. punctatum* was also found in other amphidromous gobies (Hoareau et al. 2007; Shen &

Tzeng 2008; Lord et al. 2010). The coefficient of variation of the size-at-recruitment (0.05) is more than twice lower than the coefficient of variation of the PLD (0.15), suggesting that the recruitment is more likely to be size dependent rather than age dependent. Similar results have already been observed in other Sicydiinae species (Radtke et al. 2001; Shen & Tzeng 2008). In other groups of fish, the variation in size-at-recruitment might have important consequences for postsettlement survival (see the study on the reef fish by Vigliola & Meekan (2002)).

The PLD data of this study (mean ± SD: 72.2 ± 10.5 days) and Tabouret (2010) (mean ± SD: 62.6 ± 10.4 days) for *S. punctatum* from Guadeloupe highlight a high variability among individuals. Some of them experience larval durations twice as long as the observed minimum. Because postlarvae recruitment is likely to be size dependent, the variations of growth rate between the individuals would explain the variations of PLDs between the same individuals. A longer PLD would allow an individual with a lower larval growth rate to reach the required size for recruitment. The large range of PLDs observed has been shown to be due to the postlarvae waiting near shore for a signal of recruitment in coral reef fish (Cowen & Sponaugle 1997).

Optimal conditions for recruitment can be predictable (seasonal for instance) or random. In Sicydiinae species, lunar phases and seasons seem to affect the timing of recruitment (Bell et al. 1995; Iida et al. 2008; Bell 2009; Teichert et al. 2012). In amphidromous gobies where dispersal occurs through pelagic larvae, a greater variability of PLDs increases the likelihood of finding streams (Maeda et al. 2007). It has been shown in reef fish that potential of a longer larval life enables a delay in metamorphosis (Victor 1986; Wellington & Victor 1989, 1992). Theoretically, individuals able to adjust their development in adequacy with the conditions (a larva having a low growth rate tends to stay in the ocean longer than the faster growing ones) have more successful recruitment than others. Many invertebrates are able to extend their larval life after reaching a competent size in the absence of recruitment cues and suitable settlement conditions (Jackson & Strathmann 1981). In Teleost, such abilities have been suggested in reef fish species (Victor 1986; McCormick 1999; Searcy & Sponaugle 2000).

Conclusion

Our study of the larval life of *Sicydium punctatum* is consistent with our general understanding of amphidromous larval traits. The larval growth rate of the studied species was described for the first time and revealed variations between individuals that may be in relation with the environment of the larvae. These observed variations in the pelagic larval traits such as the variation in growth rates in relation to hatching date, the variation in the pelagic larval duration (PLD) and size-at-recruitment might reflect life history variation among larvae. Even if *S. punctatum* is recognised to be an amphidromous species based on otolith microchemistry analyses (Tabouret et al. 2011), whether the larvae stay near shore or disperse further offshore still remains unknown and would potentially affect the populations' connectivity and persistence. A near shore habitat would promote the colonisation of the rivers of birth, limiting dispersal and gene flow and would support the 'passive dispersal' hypothesis whereas an offshore habitat would ensure more dispersal and gene flow and support the 'nonpassive dispersal' hypothesis (Hogan et al. 2014; Huey et al. 2014). The link between the differences in larval traits and larvae habitats (*i.e.,* near shore or offshore) must be tested using genetic tools (to explore the connectivity between populations of different catchments) and otolith microchemistry (to find elemental and isotopic signatures of habitats) and might offer a path forward in our understanding of amphidromous larval life. Because *S. punctatum* postlarvae are a fishery resource in the Caribbean region and a key species for the Caribbean hydrosystems, information on the larval life will be essential to set up relevant and efficient tools for the management of their populations.

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