INTRODUCTION

Tropical island streams are colonised by amphidromous gobies belonging to the Sicydiinae sub-family and they are the major contributors to fish biodiversity. There are eight known genera: Akihito Watson, Keith & Marquet, 2007; Lentipes Günther, 1861; Cotylopus Guichenot, 1864; Sicyopterus Gill, 1860; Sicyopus Gill, 1863; Smilosicyopus Gill, 1863; Stiphodon Weber, 1895 and Sicydium Valenciennes, 1837, totalling nearly 110 species distributed in the Indo-Pacific, West Africa, Central American and Caribbean areas (Keith & Lord 2011a, Taillebois et al. 2014). These gobies are especially adapted to life on small volcanic islands; they colonise steep rapid streams in altitude by clinging to rock surfaces and climbing over waterfalls using their pelvic sucker (modified pelvic fins), pectoral fins and mouth (Schoenfuss & Blob 2003, Keith & Lord 2011b). Sicyopterus and Stiphodon are the most diverse genera with about 25-30 valid species each. Most Stiphodon species are in the western and southern Pacific Ocean and also colonise the Indo-Pacific barrier islands, with possibly a species in Sri Lanka (Watson et al. 2000, Keith & Lord 2011a). Most Sicydiinae species are endemic to archipelagos or even one island (Radtke & Kinzie 1996, Lord et al. 2012). Only a few species are able to colonise entire oceans or even both the Indian and Pacific oceans like Sicyopterus lagocephalus (Lord et al. 2012).

Sicydiinae life cycle is adapted to the distinctive conditions in these habitats, i.e. subjected to important hydrological and seasonal variations and poor in nutrients. The adults live and reproduce in freshwater. As soon as they hatch, larvae drift downstream to the ocean where they undergo larval development while having a planktopelagic lifestyle (Ellien et al. 2011, Keith & Lord 2011b, Iida et al. 2013). After a usually long marine phase, post-larvae return to rivers, and as soon as they enter freshwater, they undergo an important metamorphosis (Keith et al. 2008, Taillebois et al. 2011) allowing them to migrate upstream and colonise the adult habitat. It has been suggested that the marine stage is likely to be a key element to the dispersal and to the distribution of these species (McDowall 2003, 2007, Keith et al. 2008, Keith & Lord 2011b, Lord et al. 2012). Freshwater species with a diadromous life cycle and marine species with a pelagic larval stage exhibit a higher dispersal ability and lower interpopula-
tion structure than strictly freshwater species or marine species lacking a pelagic larval stage (Allibone & Wal lis 1993, Doherty et al. 1995). The pelagic larval duration (PLD) can thus be considered in many cases as a proxy to the dispersal ability of larvae, which should be closely linked to the population structure of these species (Vict or & Wellington 2000, Bernardi et al. 2003, Lord et al. 2012). There is an increasing effort made towards the understanding of the biology and ecology of Sicydiinae gobies as they show interesting features: they show high levels of endemism (Lord et al. 2012) with high species richness (Keith et al. 2011).

A few recent studies have worked on identifying the pelagic larval duration of Sicydiinae species and in some cases the PLD results have been coupled to population structure analyses. If we look at all the PLD studies, we can conclude that the PLD of amphidromous Sicydiinae roughly ranges from 60 to 160 days (Radkte et al. 2001, Yamasaki et al. 2007, Shen & Tzeng 2008, Lord et al. 2010, Taillebois et al. 2012), meaning that even for species restricted to one island the PLD is long, greater than that generally found for reef fish (maximum PLD of about 30 days) (Victor & Wellington 2000). The genetic stud- ies done on Sicydiinae showed that species endemic to a small geographic region show no population structure, as the stream jewel goby. 

Watson & Chen, 1998, otherwise known as the Asian part of its distribution using the partial mitochondrial marker, cytochrome oxydase I (COI) and thus to infer larval dispersal, especially in the zone of the Kuroshio current, which could potentially act as a barrier to dispersal between the western and eastern parts of the distribution.

MATERIALS & METHODS

Sampling and molecular analyses: A total of 88 specimens were collected in the Ryukyu Islands (Amami, Ishigaki, Iri mome and Okinawa), on Ogasawara Island and in Taiwan (Table 1, Fig. 1).

The specimens were preserved in 95 % ethanol. Total DNA was extracted from a fin clip using the DNeasy Tissue Kit (Qiagen ©) following the manufacturer’s instructions. A fragment of the Cytochrome oxydase I (COI) mitochondrial gene was amplified using primers FishF1-5’TCAACCAACCAACAAAGACATTGGCAC3’ and FishR1-5’ACTTCAAGGTGACCGAAGAATCAGAA3’ (Ward et al. 2005).

All PCRs were performed on Biometra thermocyclers in a 25 µl volume of 5 % of DMSO, 5 µg of bovine serum albumin, 300 µM of each dNTP, 0.3 µM of Taq DNA polymerase from Qiagen, 2.5 µl of the corresponding buffer, and 1.7 pM of each of the two primers. After a 2-minute denaturation at 94°C, the PCR ran 50 cycles of 25 seconds at 94 °C, 25 seconds at 52 °C and 1 minute at 72 °C, with a 3-minute terminal elongation.

The PCR products were used as the template DNA for cycle sequencing reactions performed using Dye Terminator Cycle Sequencing FS Ready Reaction Kits (Applied Biosystems) and were run on an ABI 377 DNA Sequencer (Applied Biosystems). The forward primer FishF1 and the reverse primer FishR1 were used for the direct cycle sequencing reaction. All sequences were obtained in both directions and checked manually against

<table>
<thead>
<tr>
<th>Locality</th>
<th>n</th>
<th>Nh</th>
<th>h</th>
<th>S</th>
<th>k</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amami</td>
<td>8</td>
<td>3</td>
<td>0.464 ± 0.200</td>
<td>0.0015 ± 0.0014</td>
<td>3</td>
</tr>
<tr>
<td>Iriomote</td>
<td>8</td>
<td>4</td>
<td>0.643 ± 0.184</td>
<td>0.0015 ± 0.0014</td>
<td>3</td>
</tr>
<tr>
<td>Ishigaki</td>
<td>16</td>
<td>8</td>
<td>0.700 ± 0.127</td>
<td>0.0027 ± 0.0020</td>
<td>10</td>
</tr>
<tr>
<td>Ogasawara</td>
<td>7</td>
<td>4</td>
<td>0.714 ± 0.181</td>
<td>0.0031 ± 0.0024</td>
<td>4</td>
</tr>
<tr>
<td>Okinawa</td>
<td>28</td>
<td>10</td>
<td>0.696 ± 0.088</td>
<td>0.0023 ± 0.0017</td>
<td>11</td>
</tr>
<tr>
<td>Taiwan</td>
<td>21</td>
<td>12</td>
<td>0.860 ± 0.071</td>
<td>0.0036 ± 0.0024</td>
<td>10</td>
</tr>
<tr>
<td>Total</td>
<td>88</td>
<td>28</td>
<td>0.709 ± 0.054</td>
<td>0.05 ± 0.035</td>
<td>26</td>
</tr>
</tbody>
</table>

Table I. – Diversity indices for each sampling location and for all localities for Stiphodon percnopetrogygious: number of samples (n); number of haplotypes (Nh); haplotype diversity (h); nucleotide diversity (π); segregating sites (S); number of pairwise differences (k).
their chromatogram using Sequencher (Gene Codes Corporation). They were aligned by hand using Bioedit (Hall 1999) with the criteria listed by Barriel (1994).

**Molecular diversity:** For each location, diversity indices such as the number of haplotypes, the number of variable positions, the haplotype diversity (h) and the nucleotide diversity (π) were estimated with Arlequin 3 software (Excoffier et al. 2005). The relationship among all observed haplotypes was inferred by median joining haplotype networks, drawn from the haplotype data using Network v.4.5.02 (Bandelt et al. 1999; fluxus-engineering.com). We used default parameters implemented in Network.

Levels of genetic structure between different locations were estimated by FST statistics (Weir & Cokerham 1984), using the estimator implemented in Arlequin; it integrates both the haplotype frequencies and the pairwise nucleotide differences. Distributions of the FST statistic under the null hypothesis of genetic homogeneity through localities were obtained from 10,000 random permutations of specimens among localities and used to test the significance of values calculated from real data.

**Population demographics:** Neutrality (equilibrium) was assessed by calculating Fu’s Fs (Fu & Li 1993) as Fu’s Fs is more robust regarding small samples. Fu’s Fs gives an estimate of the population demographics; a negative value indicates an overabundance of low frequency haplotypes, a possible signature of recent demographic expansion or of directional selection. Significance was tested using 10,000 coalescent simulated from the observed number of haplotypes in Arlequin. The distribution of the number of pairwise differences between haplotypes based on computed inter-haplotypeic distances (mismatch distributions) were also calculated (Avise 2004).

Mismatch distribution was calculated under Arlequin which provides an estimate of the mutational parameters ($\theta = 2\mu N$, $\theta_0$, $\theta_1$ and $\tau$) which are values that respectively represent the effective population size at the time of the most common ancestor, the current effective population size and the time needed to go from $\theta_0$ to $\theta_1$ (age of expansion) (Rogers & Harpending 1992, Schneider & Excoffier 1999). This distribution is usually multimodal in samples drawn from populations at demographic equilibrium, but is usually unimodal in populations having passed through recent demographic expansion (Slatkin & Hudson 1991, Rogers & Harpending 1992). The validity of this stepwise expansion model is tested using a parametric bootstrap approach. 1000 simulations (number of random samples) under a coalescent algorithm modified from Hudson (1990) were done using the calculated parameters, to define the parameters’ 99 % confidence intervals and the sum of squared derivations of these parameters, SSD_{obs}. The same calculation is done on simulated

Fig. 1. – Sampling locations and number of specimens collected at each location.
parameters, SSD_{obs}. The p-value of the test is then approximated by:

\[ p\text{-value} = \frac{\text{SSD}_{\text{obs}} \text{ larger or equal to SSD}_{\text{obs}}}{\text{Number of random samples}} \]

Non-significant values for SSD mean that the observed data do not deviate from that expected under an expansion model. The raggedness index is also calculated (Harpending 1994), similarly to the SSD. The raggedness index takes larger values for multimodal distributions found in a stationary population than for unimodal and smoother distributions typical of expanding populations. Non-significant raggedness index also indicate population expansion.

Observed mismatch distributions were plotted along with two demographic models, one being at the mutation-drift equilibrium (constant population size) using the nucleotidic diversity as an estimation of \( \theta \) (Rozas & Rozas 1995) and the other under a demographic expansion model in DnaSP v.5 (Librado et al. 2009).

**RESULTS**

**Genetic diversity and population structure**

A total of 496 base pairs of the COI mitochondrial gene were sequenced for the 88 individuals of *S. percnopterygionus*. There were a total of 26 variable sites (5.24% of 496 bp). According to these variable sites, a total of 28 haplotypes were found for these 88 individuals. Both the overall haplotype diversity and the nucleotide diversity

![Fig. 2. – Median joining network. Each circle represents a haplotype; circle size indicates the proportion of individuals. The scale bar gives the number of mutational steps. Each color represents a locality.](image)

**Table II. – AMOVA results for *Stichodon percnopterygionus*. FST values are under diagonal, p-values are above diagonal.**

<table>
<thead>
<tr>
<th>FST</th>
<th>Amami</th>
<th>Iriomote</th>
<th>Ishigaki</th>
<th>Ogasawara</th>
<th>Okinawa</th>
<th>Taiwan</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amami</td>
<td>-0.04348</td>
<td>-0.03814</td>
<td>0.02745</td>
<td>-0.01003</td>
<td>0.00124</td>
<td>0.02313</td>
</tr>
<tr>
<td>Iriomote</td>
<td>0.99 ± 0.003</td>
<td>0.96 ± 0.014</td>
<td>0.02745</td>
<td>-0.01003</td>
<td>0.00124</td>
<td>0.02313</td>
</tr>
<tr>
<td>Ishigaki</td>
<td>-0.02388</td>
<td>-0.03814</td>
<td>0.02707</td>
<td>0.01520</td>
<td>0.02924</td>
<td>-0.05439</td>
</tr>
<tr>
<td>Ogasawara</td>
<td>0.02745</td>
<td>0.02745</td>
<td>0.25 ± 0.038</td>
<td>0.05 ± 0.014</td>
<td>0.58 ± 0.049</td>
<td>0.41 ± 0.059</td>
</tr>
<tr>
<td>Okinawa</td>
<td>-0.01003</td>
<td>-0.01003</td>
<td>0.05 ± 0.014</td>
<td>0.12 ± 0.031</td>
<td>0.05 ± 0.049</td>
<td>0.58 ± 0.049</td>
</tr>
<tr>
<td>Taiwan</td>
<td>0.00124</td>
<td>0.01477</td>
<td>0.05368</td>
<td>0.05 ± 0.014</td>
<td>0.02924</td>
<td>0.05 ± 0.049</td>
</tr>
</tbody>
</table>
are high ($h = 0.709 \pm 0.003; \pi = 0.05 \pm 0.035$) (Table I). The values for the haplotype diversity for each site varied from 0.46 to 0.86. The median joining haplotype network showed that there are shared haplotypes in all 6 localities suggesting no evidence of genetic structure within these localities (Fig. 2). This median joining network is supported by the fact that pairwise $F_{ST}$ values were very low and insignificant among all localities (Table II), once again showing no evidence of a genetic structure between the sampled $S. \text{percnopterygionus}$ in its distribution area.

**Population demographics**

Fu’s $F_s$ values are all negative and significant except for Amami and Ogasawara (both small samples, respectively $n = 8$ and $n = 7$) (Table III).

As no structure was detected between all the locations sampled, it is only pertinent to discuss these statistical simulations on the total number of samples, and the overall Fu’s $F_s$ is both negative and significant.

The difference between the observed mismatch distribution and the simulated mismatch under a demographic expansion model is insignificant for all the samples (SSD $p$-value $= 0.69$). The observed mismatch distribution for the total sample is unimodal (peak at 2 mutational steps). The observed mismatch distribution is very close to the distribution for a demographic expansion model (Fig. 3). Population expansion is also supported by the raggedness index for which the overall value is low (0.037), which is typical of a unimodal distribution, and insignificant ($p$-value $= 0.84$), indicative of a good fit of the data to a model of population expansion. Furthermore, this is supported by the haplotype network, as a star like pattern is generally associated to a colonization scenario followed by a recent expansion.

**DISCUSSION**

Freshwater species with a diadromous life cycle and marine species with a pelagic larval stage exhibit higher dispersal ability and lower interpopulation structure than strictly freshwater species or marine species lacking a pelagic larval stage (Allibone & Wallis 1993, Doherty et al. 1995). Sicydiinae gobies, via their amphidromous life cycle, have the ability to disperse over long distances as larvae, one of the reasons being their long larval duration. The pelagic larval duration (PLD) can thus be considered in many cases as a proxy to dispersal ability and it should be closely linked to the population structure of these species.

<table>
<thead>
<tr>
<th>Tau</th>
<th>$T_{theta\ 0}$</th>
<th>$T_{theta\ 1}$</th>
<th>$r_g$</th>
<th>$r_g\ p$-value</th>
<th>SSD</th>
<th>SSD $p$-value</th>
<th>Fu’s $F_s$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amami</td>
<td>2.210</td>
<td>0</td>
<td>0.95</td>
<td>0.130</td>
<td>0.75</td>
<td>0.0100</td>
<td>0.65</td>
</tr>
<tr>
<td>Iriomote</td>
<td>0.960</td>
<td>0</td>
<td>$\infty$</td>
<td>0.220</td>
<td>0.45</td>
<td>0.0340</td>
<td>0.25</td>
</tr>
<tr>
<td>Ishigaki</td>
<td>1.330</td>
<td>0.360</td>
<td>4.03</td>
<td>0.025</td>
<td>1.00</td>
<td>0.0010</td>
<td>1.00</td>
</tr>
<tr>
<td>Ogasawara</td>
<td>2.580</td>
<td>0.004</td>
<td>3.21</td>
<td>0.045</td>
<td>1.00</td>
<td>0.0110</td>
<td>0.70</td>
</tr>
<tr>
<td>Okinawa</td>
<td>1.110</td>
<td>0.021</td>
<td>$\infty$</td>
<td>0.710</td>
<td>0.50</td>
<td>0.0030</td>
<td>0.75</td>
</tr>
<tr>
<td>Taiwan</td>
<td>1.840</td>
<td>0</td>
<td>$\infty$</td>
<td>0.060</td>
<td>0.25</td>
<td>0.0040</td>
<td>0.40</td>
</tr>
<tr>
<td>Total sample</td>
<td>1.068</td>
<td>0.238</td>
<td>$\infty$</td>
<td>0.037</td>
<td>0.84</td>
<td>0.0017</td>
<td>0.69</td>
</tr>
</tbody>
</table>

Fig. 3. – Overall mismatch distribution analysis for $S. \text{percnopterygionus}$ population sampled in all locations.

Table III. – Estimated demographic parameters for $S. \text{percnopterygionus}$ population at each sampling location and for the total sample. Raggedness index ($r_g$); sum of squared derivations (SSD); * corresponds to a $p$-value $\leq 0.05$; ** corresponds to a $p$-value $\leq 0.01$. 

*Vie Milieu*, 2015, 65 (2)
cies (Victor & Wellington 2000, Bernardi et al. 2003, Lord et al. 2012). The molecular approach is an effective method for studying connectivity between populations. There are few molecular studies on amphidromous gobies, involving species more or less widely distributed in their geographic range to uncover the degree of connectivity within each species’ distribution area.

The present work showed that *Stiphodon percnopterygionus* has a relatively high haplotype diversity ($h = 0.709 \pm 0.003$). High haplotype diversity is commonly found for Sicydiinae gobies; Watanabe et al. (2006) found 74 haplotypes for 77 *Sicyopterus japonicus* specimens. Other authors found the same results for amphidromous species from Hawaii (Fitzimons et al. 1990, Zink et al. 1996, Chubb et al. 1998). For *Sicyopterus sarasini* and *Sicyopterus aiensis*, respectively endemic to New Caledonia and Vanuatu, for *Sicyopus zosterophorum* and *Smiloscyopus fehlmanni* both widely distributed across the Central West Pacific, haplotype diversities ranged from 0.9 to 0.99 (Lord et al. 2012, Taillebois et al. 2013). Grant & Bowen (1998) suggested that high levels of both haplotype and nucleotide diversities are indicative of either a long stable evolutionary history or secondary contact among differentiated lineages.

The median joining haplotype network for *Stiphodon percnopterygionus* had a star shaped structure with one predominant haplotype shared in all sampled locations. The presence of shared haplotypes at distant locations suggests that there is gene flow. This may indicate that gene flow between distant populations has occurred on a relatively recent evolutionary time scale (Horne et al. 2008). This is consistent with phylogenetic results show-

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Fig. 4. – Major ocean currents in the northwest Pacific Ocean. The Kuroshio Current emerges from the north of the Philippines and flows along the east coast of Taiwan, in the Ryukyu archipelago and along the east coast of the Japanese mainland (modified from Barkley 1970).
ing that Sicydiinae species have recently evolved and that the number of species has remarkably increased only 2.5-5.8 Myrs ago (Keith et al. 2011). Many haplotypes, differing by one or two mutational steps, radiate from this central one and this star-like pattern is concordant with a recent expansion (Grant & Bowen 1998, Chabarra et al. 2014). The demographic analysis is congruent with previous facts. Mean Fu’s Fs are negative and statistically significant, indicating expanding populations. The mismatch distribution is unimodal and fits the expected frequencies under an expanding population model (supported by both SSD and raggedness index). The dispersal pattern for this species, as for other Sicydiinae species, seems to enable S. percnopterygionus to disperse all around potential habitats that may be suitable in its distribution area from Japanese islands to Taiwan, Guam and Palau.

*Stiphodon percnopterygionus* is not the only Sicydiinae goby inhabiting this Asian area. Other species co-occur such as *Sicyopterus japonicus*. *Sicyopterus japonicus* is the only tropical and temperate Sicydiinae goby; its distribution ranges from Taiwan to central eastern coast of Japan. In their study of the mitochondrial control region (Dloop), Watanabe et al. (2006) found no evidence of genetic structure throughout the species distribution range, as we found on *S. percnopterygionus*. The distribution range of *Sicyopterus japonicus* and *Stiphodon percnopterygionus* partly overlap. *S. percnopterygionus* is abundant in the Ryukyu Archipelago and Taiwan, but rather rare in other regions. Recently, this species was recorded from the northern range, *i.e.* Shikoku and Honshu, but the occurrences are local and populations are very small (Shibuya & Takahashi 1998, Kitahara 2012, Nakao & Hirashima 2012). Northernmost record is from a stream in the Izu Peninsula of Honshu, Shizuoka Prefecture, central Japan, where the water temperature keeps around 20 degrees during the winter due to the existence of a hot spring (Kitahara 2012). It is also very rare (only 1 or 2 individuals were discovered) in Guangdong, China (Nip 2010). The distribution of these Sicydiinae gobies in this area may be related to the long larval period allowing long distance dispersal and to the presence of the north-flowing Kuroshio Current on the West side of the north Pacific Ocean (Barkley 1970). This northward current emerges from the south of the Philippines and flows along the east coast of Taiwan, in the Ryukyu archipelago and along the east coast of the Japanese mainland (Fig. 4). This current probably transports larvae of amphidromous fish and facilitates the colonisation of streams on the islands along the current (Watanabe et al. 2006, Iida et al. 2010, Maeda et al. 2011). The Kuroshio Current allows occasional migrants from islands in the south at its origin, such as *Stiphodon alcedo* recently discovered in the Ryukyu Archipelago but in low abundance (Maeda et al. 2011). The low abundance for this species in this area is probably due to competition with congeners such as *Stiphodon percnopterygionus*.

The rarity of *S. percnopterygionus* in Guan and Palau is probably due to the same type of mechanism; this species is abundant in Taiwan and the Japanese Islands, along the path of the Kuroshio current, and it can sporadically migrate further than its main distribution area, especially since this species also has a long pelagic larval duration of 99 ± 16 days (Yamasaki et al. 2007). Indeed with such a long PLD, it is possible that some of the larvae may be caught in currents other than the main Kuroshio Current via different gyres, and carried to the south towards Guam (Fig. 4). The north equatorial current breaks south into the Mindanao current, which can carry larvae towards Palau. These dispersal routes are probably not frequent, explaining the very low abundance of *S. percnopterygionus* in Guam and Palau. Alternatively, *S. percnopterygionus* may also be present in unexplored areas further south, explaining the sporadic dispersal to Palau and Guam.

The main advantage in being amphidromous is the colonisation of new favourable habitats (McDowall 2010). Indeed, island streams are unstable and represent an environmental extreme, due to seasonal hydrological and climatic variations, but also, at deeper time scales, islands have continuously appeared and disappeared due to volcanic activity, glacial periods impacting sea level and also due to erosion and subsidence of islands. Sicydiinae gobies have the ability to stay at sea for long periods during their larval stage, enabling them to find suitable habitats to colonise. The success in the colonisation of tropical island streams is linked to the long larval marine phase, but the processes leading to many endemic species, to the co-occurrence of several congeneric species in the same streams and the processes shaping the current distribution of Sicydiinae species remain unknown. The lack of population structure commonly found for Sicydiinae species, as we found for *S. percnopterygionus*, denotes their strong potential to find and colonise suitable habitats, but each species is differently confronted to limitations in their capacity to colonise habitats always further. The strength and direction of marine currents, the duration of the marine phase, habitat preferences, interspecific competition or even the biogeographic history represent some factors that could influence the dispersal ability, the species distribution area and the evolution of the group. These factors, shaping species boundaries are not yet fully understood, and need to be studied for conservation purposes. In future studies, areas at the boundaries of the species distribution, such as Guam and Palau, need to be thoroughly sampled to see whether there are barriers to the dispersal of *S. percnopterygionus* explaining it’s low abundance in these areas. Conservation and management plans will only be pertinent when the population connectivity is known for the entire distribution range.

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POPULATION STRUCTURE OF STIPHODON PERCNOPTERYGIONUS


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