Early life history and description of larval stages of an amphidromous goby, *Sicyopterus lagocephalus* (Gobioidae: Sicydiinae)

by

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**ABSTRACT.** - *Sicyopterus lagocephalus* is an amphidromous fish: adults live in rivers, but after hatching larvae are carried to the sea (dispersion stage). After a certain time spent at sea, post-larvae return to rivers to grow and reproduce. *Sicyopterus lagocephalus* post-larvae recruiting to Reunion Island rivers (Mascarene Archipelago), provide an important food source to local populations and this fishing activity has a significant socio-economic impact. A better understanding of the early life traits of this species and the characterisation of larval stages should improve the biological and physiological knowledge needed to understand the processes involved in the dispersion stage and help managers to implement conservation measures. In Reunion Island, we characterised the development of larvae from hatching to migration to the sea. The results show that larvae do not undergo any development in freshwater, and that it is the arrival at sea that triggers the morphological transformations. Our results have also revealed that development is quicker when the temperature is high and that development varies according to water depth during the downstream migration. In natural temperature conditions, the maximum survival rate in freshwater is four days. This suggests that when the downstream migration takes too long because of anthropogenic or hydraulic factors, the free embryos would die before they reach the sea.

**RÉSUMÉ.** - Premiers stades de vie et description des stades larvaires d’un gobie amphidrome, *Sicyopterus lagocephalus* (Gobioidae: Sicydiinae).

*Sicyopterus lagocephalus* est un poisson amphidrome : les adultes vivent et se reproduisent en rivière. À l’éclosion les larves sont transportées en mer par le courant (phase dispersive), puis, après un certain temps, les post-larves retournent aux rivières et s’y installent. Lorsque les post-larves de *Sicyopterus lagocephalus* recrutent dans les rivières de La Réunion (archipel des Mascareignes), elles sont pêchées de façon intensive par la population locale et cette pêche a une grande importance socio-économique. Une meilleure connaissance des stades de vie précoces devraient permettre d’améliorer les connaissances biologiques et physiologiques nécessaires à la compréhension des processus impliqués dans la phase de dispersion de l’espèce, et ainsi aider à la mise en place de mesures de gestion. Nous avons caractérisé à l’île de La Réunion le développement des larves, depuis l’éclosion jusqu’à la migration vers la mer. Les résultats indiquent que celles-ci ne se développent pas en eau douce et que c’est l’arrivée en mer qui déclenche les transformations. Le développement est plus rapide lorsque la température est plus élevée et il varie selon la profondeur de l’eau. En conditions naturelles, le taux maximum de survie en eau douce est de 4 jours. Ceci suggère que si la dévalaison est trop longue, en raison de facteurs anthropiques ou hydrauliques, les embryons libres meurent avant d’atteindre la mer.

Key words. - Gobioidae - *Sicyopterus lagocephalus* - Reunion Island - Amphidromy - Larval stages - Dispersion.

In the tropical Indo-Pacific and the Caribbean regions, insular river systems are mainly colonised by Gobiidae (Sicydiinae). Their life cycle is adapted to the conditions in these distinctive habitats, i.e., oligotrophic rivers that have formed relatively recently, that are subject to extreme seasonal climatic and hydrological variations (Keith, 2003; Keith *et al*., 2005a). These species spawn in freshwater and the free embryos drift downstream to the sea where they undergo a planktonic phase before returning to the rivers to grow and reproduce; they are called amphidromous (McDowall, 1997, 2007). The early life history of these species is poorly known, as are the parameters leading to such extreme evolution (Keith *et al*., 2000; Lord and Keith, 2006), but it is extremely important to understand the processes involved in the dispersion and colonisation of new habitats (Houde, 1989; Keith *et al*., 2005b) along with the internal and external factors governing these processes.

Amphidromous gobies contribute to a significant degree of diversity to the fish communities in the Indo-Pacific and the Caribbean insular systems (Nelson *et al*., 1997; Watson *et al*., 2002; Keith *et al*., 2007; Watson *et al*., 2007). *Sicyopterus lagocephalus* is one of these gobies. At certain times of the year, the biomass of post-larvae migrating upstream is so great that it provides an important source of food for local

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Human populations (Bell, 1999; Watson *et al.*, 2001; Keith *et al.*, 2004, 2006). This is the case in particular in Reunion Island (Mascarene Archipelago, Indian Ocean). However, harvesting of this food resource in estuaries is highly unsustainable, on account of the complexity of the species’ life cycle and the hydrological particularities of these islands (Delacroix, 1987).

Recently, Keith *et al.* (2008) described the different post-larval and juvenile stages of *S. lagocephalus*, in Reunion Island when recruiting back to rivers. They established a reference ontogenetic scale for this species from the post-larval marine stage to the adult freshwater stage. The purpose of this paper is to describe the various larval stages of *S. lagocephalus* (Gobiidae: Sicydiinae), from hatching to arrival at sea, to complete the reference scale. There is an urgent need to improve our knowledge of the early life history of this species. The characterisation of the various stages should improve the biological and physiological knowledge needed to understand the processes involved in the dispersion phase and help managers to implement conservation measures (Lord and Keith, 2008; Keith and Marion, 2002).

**METHODS**

*Sicyopterus lagocephalus* layings were collected under stones and stuck on them in the same sector of the Langevin River (21°38.527 S.; 0.55°64.420 E.) in Reunion Island (Indian Ocean), between December 1999 and April 2000.

**Description of larval development**

We collected seven layings that were placed in individualised tanks [circular, diameter 15 cm, 7 litres, water depth (H): 50 cm (mean river depth in the collected sites)] filled with water from the river. Water parameters were controlled to match the conditions in natural environment: natural photoperiod; conductivity around 80 µS.cm⁻¹; pH ranges from 7.0 to 9.0; $O_2$ = 7-9 mg.l⁻¹; constant temperature although ranging from 20 to 26°C between the various experiments. The five largest layings were divided into three or four equal batches, therefore giving a total of 19 batches (Tab. I). Some batches were kept in freshwater; others were transferred to saltwater, in similar tanks filled with water collected at sea and for which the parameters were also controlled (natural photoperiod and salinity; constant temperature ranging from 20 to 26°C between the various experiments).

<table>
<thead>
<tr>
<th>Hatching date</th>
<th>Layings (n)</th>
<th>Batch (n)</th>
<th>Age of transfer at sea</th>
<th>Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A- 8 Dec. 1999</td>
<td>1</td>
<td>1</td>
<td>-</td>
<td>20°C</td>
</tr>
<tr>
<td>11 Dec. 1999</td>
<td>2</td>
<td>2</td>
<td>-</td>
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</tr>
<tr>
<td>B- 21 Dec. 1999</td>
<td>3</td>
<td>3</td>
<td>-</td>
<td>20°C</td>
</tr>
<tr>
<td>27 Dec. 1999</td>
<td>3</td>
<td>4</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>C- 10 Jan. 2000</td>
<td>4</td>
<td>4</td>
<td>-</td>
<td>20°C</td>
</tr>
<tr>
<td>14 Jan. 2000</td>
<td>4</td>
<td>5</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>D- 24 Jan. 2000</td>
<td>5</td>
<td>6</td>
<td>E56</td>
<td>22°C</td>
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<tr>
<td>2 Feb. 2000</td>
<td>5</td>
<td>7</td>
<td>E56</td>
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</tr>
<tr>
<td>E- 10 Apr. 2000</td>
<td>7</td>
<td>8</td>
<td>E4</td>
<td>26°C</td>
</tr>
<tr>
<td>15 Apr. 2000</td>
<td>7</td>
<td>9</td>
<td>E4</td>
<td></td>
</tr>
</tbody>
</table>

Table I. - Conditions set to the different larval batches for the study of the first larval stages in *Sicyopterus lagocephalus*. The larva age is indicated “Ex”, x being the number of hours after hatching.

Figure 1. - *Sicyopterus lagocephalus* egg just before hatching. Photo: ARDA

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The larva age is written Ex, x being the number of hours after hatching. Different temperature conditions and times of transfer to saltwater have been imposed on the various batches (Tab. I). In order to describe their developmental stage, photographs of larvae were taken every 6 hours, at given times: 2, 8, 14 and 20 h. The specimens were anaesthetised and were photographed using an image capture station composed of a binocular magnifier (Olympus SZ61; Olympus Ltd, Paris) (magnification x8) coupled to a digital camera (Olympus C-5050; optical zoom x3; Olympus Ltd, Paris) linked to a computer. Each larva was then studied and measured to the nearest tenth millimetre, using image processing software (ImageJ, v1.39, rsbweb.nih.gov/ij/). For the duration of the experiment, the larvae had their yolk sac (until its absorption) and were not fed. The larvae were monitored until their death occurring either in freshwater or saltwater.

Survival time of larvae in freshwater

During the experiments undertaken in freshwater, the survival time of larvae, corresponding to the presumed death of the last larvae in the batch, was logged. The determined time corresponds to the maximum survival time for a larva at an imposed temperature and for a water depth (H) of 50 cm.

A series of additional experiments were performed to determine the mortality of larvae according to temperature and water depth. Three columns of 600 ml (water depth H = 9 cm) and one filled with 9 litres [circular, diameter 8 cm, water depth H = 200 cm] were filled with water from the river; the conditions were controlled. One hundred larvae were placed in each column. Dead larvae were counted twice a day at 8 and 16 h and retrieved from the column with a glass pipette.

This experiment was repeated five times, at three different temperatures (20, 23, and 26°C). The larvae mortality was established as a percentage of dead larvae and as a function of their age, the water depth and water temperature. The larvae mortality at a given temperature is defined as the lethal period 50% (PL50), which corresponds to the age of the larvae when 50% of the individuals are dead.

RESULTS

Before hatching, the eggs measure 500 to 700 μm. Figure 1 shows an isolated Sicyopterus lagocephalus egg just before hatching (500 μm in diameter); the larvae can be seen inside the egg. After hatching, the larvae measures 2 mm, it is translucent, and many organs are already visible in outline. Figure 2 shows a larva 4 h after hatching (E4); the otoliths, the yolks sac with the lipidic droplets, the notochord, the chromatophores (three to four according to the different larvae), the caudal fin, and the digestive tract are all visible in the larvae.

Larval development in freshwater

For the batches maintained in freshwater, the larval development was monitored until the individual death. For each of these larval batches, no apparent modification has been noted. The various photos taken for each batch show identical individuals: the yolk sac appears to incur no modification, the mouth is closed, no fin appears, the chromatophores do not extend and the eyes remain translucent.

Figures 3 and 4 show the larvae just before their death, respectively 62 h and 72 h old (20°C, H = 50 cm). Their morphology is identical to that of hatching larvae (Fig. 2). Therefore, larvae do not undergo any development in freshwater, and seem to remain at the free embryo stage.

Larval development in saltwater

The transfer of larvae to saltwater induces morphological changes. In each experiment, the time of the first major modification visible on the larvae was noted. According to water temperature, it was possible to define five larval stages (L1a to L1d and L2) (Figs. 2, 5-8; Tab. II) adapted and modified from Bell (1994), Valade (2001) and Keith et al. (2008). Larvae at hatching (L1a) have no trace of eye, no sign of jaw, are translucent and the yolk sac is at its maximum size. Just after arrival at sea, larvae (L1b) have eyes on the sides of the head and the posterior tip of the mandible is detectable as a bump or a prominence; yolk sac absorption has begun. After 20 h to 40 h in seawater (hSW) and depending on the temperature, larvae (L1c) have lenses with early
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...pigment, the migration of eyes to the antero-lateral position of the head begins, the mouth is formed, but closed, and the pectoral fins appear. After 40 to 65 hSW, larvae (L1d) are lens-pigmented and the eyes are in antero-lateral position of the head; the mouth appears formed, but closed; appearance of pectoral fins; multiplication of chromatophores on the body; marine stage.

Finally, after 65 hSW (2.5 days), larvae (L2) are lens-pigmented, the mouth seems to be well formed, open in terminal position and operating, there is no more yolk sac and all internal organs are in place (Tab. II).

Table III sums up, for each monitored batch and according to the temperature, the age and time spent in saltwater when the larvae reach a new developmental stage, visible throughout these modifications.

In the experiment at 22°C, the larvae were transferred to saltwater at two different ages (E4 and E56), however, they reached the L1b to L2 stages after nearly the same time spent in saltwater. The developmental rate in saltwater therefore seems to be independent of the larvae’s age (i.e., the time spent in freshwater) when they arrive at sea, for a given temperature. The time spent in freshwater therefore has no incidence on the development.
The final experiment was carried out at a much higher temperature than for the latter two experiments (26°C vs 20°C and 22°C). This higher water temperature led to faster development of the larvae: transferred to SW at the same time (E4), they reached the L2 stage after 54 h spent at sea, this period is nearly half that required by the larvae in water at 22°C (88 h). Moreover, in water at 26°C, the larvae died after 126 h spent in saltwater, which is 70 h less than for larvae kept in water at 22°C (196 hSW). Water temperature has an influence on the speed of development: the higher it is, the quicker the development, and the sooner the larvae die.

After the L2 stage, the larval development seems to come to a stop; they can however stay alive for more than 100 h at 22°C and 70 h at 26°C. As the larvae have finished their yolk reserves at this stage, the lack of food leads to their death.

**Survival time in freshwater according to temperature and water depth**

The various experiments carried out in the water columns allowed us to establish mortality trend curves for the larvae according to freshwater temperature and water depth (Fig. 9). For the different temperatures, the first deaths appear between 24 h and 48 h after hatching.

Table IV sums up the PL50 evaluated according to the experimental conditions (temperature and water depth). In shallow depths (9 cm), the larvae show an optimal survival rate in freshwater for temperatures between 20 and 23°C. The PL50 greatly decreases at higher temperatures. The
optimal lethal period 50% for larvae in Reunion freshwater (for a temperature between 20 and 23°C) is close to three days. The first deaths appear from 24 h after hatching. The maximal survival rate is between 3 and 4 days.

The water depth has a significant effect on larvae mortality. For a water temperature of 23°C, the larvae in the 2 m water column show a PL50 of 40 h, whereas those in the 9 cm water column show a PL50 of 80 h, which is twice as much. In addition, the maximum survival rates observed during the monitoring of the larval development for a water depth of 50 cm confirm these results (Tab. V). The water depth in the rivers seems to be an important factor affecting larvae survival.

The maximal survival rates observed decrease as the temperature increases. At 26°C, the effect of the water depth becomes insignificant compared to the effect of the temperature; indeed the maximal survival rate is identical for water depths of 9 and 50 cm.

**DISCUSSION**

Our study characterises the early developmental stages of *Sicyopterus lagocephalus* from hatching to migration to the sea by monitoring changes for eyes, pigmentation, fins, yolk sac size and mouth. We have described 5 stages from L1a to L1d to L2 (Tab. II) for a water temperature of 20-23°C (natural condition in Reunion Island). The L1 stage is the free embryo stage. It is newly hatched [≤ 2 mm total length (TL)], rheoplanktonic, non-feeding, with a yolk sac incompletely absorbed. The yolk-sac absorption only starts at sea. This larval stage comprises four parts (a to d) corresponding to eyes, fins and mouth development. Bell (1994) characterised the different larval growth stages of another freshwater Sicydiinae from Dominica (West Indies) (*Sicydium* spp.) and obtained similar results. He described the larval stages between hatching and migration to sea by observing the development of eye pigmentation and jaw development. He noted that newly hatched larvae of *Sicydium punctatum* were approximately 1.8 mm in TL, and were at stages from eye with lens present and pigment beginning to appear on retina. In his study the mouth is incompletely developed until three days. In Okinawa Island, southern Japan, Yamasaki and Tachihara (2006) have studied newly hatched larvae [1.20-1.32 mm notochord length (NL)] of *Stiphodon percnopterygionus*. They were poorly developed, with large yolk sacs and unopened mouths. Three days after hatching [1.87-2.05 mm NL], eyes were fully pigmented and mouths were open. In *Rhinogobius* sp. (Gobiidae), Hirashima and Tachihara (2000) noted that the yolk sac was completely consumed in three to seven days after hatching. In *Awaous melanocephalus*, Yamasaki and Tachihara (2007) showed, under controlled conditions [larvae reared in 50% sea water (salinity 20 ppt)], that newly hatched larvae [0.93-1.04 mm in total length (TL)] were poorly developed, lacking a mouth and having a large yolk sac and unpigmented eyes. The mouth and anus had not yet formed. One day after hatching, the yolk sac was reduced in size and the pectoral fin bud was apparent. Two days after hatching, larvae had grown to 1.49-1.60 mm TL, the yolk was further reduced and the pigmentation of eyes had begun. Three days after hatching, the mouth and anus were open, the gas bladder appeared and the eyes became fully pigmented (1.88-2.10 mm TL). The yolk sac was completely absorbed 5 days after hatching at a water temperature of 27-28°C, and no larvae survived beyond this stage corresponding to 120 hSW. In our study, no larvae survived after 126 hSW.

During the last larval stage (L2), larvae of *Sicyopterus lagocephalus* acquire the ability to intake and digest exogenous food and the yolk sac is completely absorbed. Com-
pleting the study made by Keith et al. (2008) on post-larvae and juveniles, the present work now provides a nearly complete ontogenic reference scale from hatching to recruitment in freshwater. The morphological transformation of *S. lagocephalus* between hatching and adult phase is composed of two larval stages (L1a to d, L2, this study), three post-larval stages (PL0 to PL2) and two juvenile stages (J1, J2) (Keith et al., 2008). However, the morphological changes between L2 and PL0 must be better studied by catching larvae at sea.

Our work shows that larvae do not undergo any development in freshwater, where they remain at the same stage, holding off any development until their arrival at sea, where the transfer to saltwater triggers the series of larval transformations for *Sicyopterus lagocephalus*, namely the fin development and the opening of the mouth. Some other authors have demonstrated that newly hatched larvae are better adapted physiologically to life in seawater, while prolonged exposure to freshwater postponed development and increased mortality markedly (Lindstrom and Brown, 1994; Valade, 2001; Yokoi and Hosoya, 2005). Bell and Brown (1995) also showed that there is an active salinity choice by the vesiculate larvae of *Sicydium punctatum* in Dominica (West Indies).

In our study, the speed of the larval development in saltwater seems to be independent of the time spent in freshwater before reaching the sea. One of the consequences of this is a limited life time in freshwater for *Sicyopterus lagocephalus*. In *Sicydium* spp. larvae, Bell and Brown (1995) and Bell (2007) thought that mortality in freshwater cannot be due to lack of available food and must be a result of the inability of the larvae to develop beyond an early stage in these environments before becoming inactive. On the other hand, in their saline treatments, Bell and Brown (1995) noted that the yolk exhaustion is coupled with more complete development of larvae suggesting that mortality of larvae may have resulted from starvation. Moriyama et al. (1998) estimated that in normal or low river flow, embryos from the upstream reaches die of starvation before they reach the sea. Since there is practically no food available for drifting larvae, extended downstream migration may enhance the risk of starvation. Iguchi and Mizuno (1999) hypothesized that early starvation of larvae limits reproductive success of fish located far from the sea, which would result in strong selection for fish reproduction in certain regions of rivers within a given distance from the sea. Tamada and Iwata (2005) have studied newly hatched *Rhinogobius* sp. CB (cross-band type). Since larger and older individuals usually inhabit the upper reaches of rivers, larvae from larger females are more likely to suffer higher risks of starvation or predation during their longer migration to the sea. Tamada and Iwata (2005) have measured egg volumes and clutch sizes, as well as larval starvation tolerance. They noted that there was a significant positive correlation between egg size and the 72-hour survival rate of unfed hatchlings. Intra-specific variation of egg volumes and clutch sizes in this species seems to be an adaptation for enhancing offspring survivorship during migration to the sea (McDowall, 2007). Success for *Sicyopterus* life cycle is in part a question of getting as many larvae as possible transported downstream, established, feeding and growing in the marine environment, before their endogenous energy supply (provided by the yolk) becomes exhausted (McDowall, 2009).

In our experimental conditions, the larvae of *S. lagocephalus* have an optimal survival time in freshwater for temperatures held between 20 and 23°C, which corresponds to the mean daily temperatures in the Langevin River during reproduction (upstream: 19°C, downstream: 23°C). The age of the larvae when 50% of the individuals are dead (PL50) greatly decreases for higher temperatures, whatever the depth: the optimal PL50 for larvae in freshwater is three days. At these temperatures (20 to 23°C), the first deaths appear 24 h after hatching, mortality is total after four days in freshwater. Ego (1956) reported that larvae of *Awaous guamensis* placed in seawater (34 ppt) lived up to eight days, while larvae in freshwater lived only four days. *Gymnogobius urotaenia*, with large larvae [5.3 mm TL at hatch], is reported to possess chloride cells soon after hatching, and larvae kept in 50% seawater lived more than 30 days while those in freshwater lived less than seven days (Katsura and Hamada, 1986). Todd (1975) reported that larvae of *Dormitator latifrons* ceased to swim 68 h in nearly fresh (3 ppt) water. Yokoi and Hosoya (2005) have studied the larval salinity tolerance for the endangered amphidromous goby, *Rhinogobius* sp. BI, an amphidromous endemic to the Bonin Islands. They showed that hatching larvae could generally survive for 72 h under any salinity conditions. However, all individuals died after 144 h in 100% artificial seawater, whereas over 60% survived for a longer term in freshwater and 50% artificial seawater. However, larval numbers fell drastically ca. 40 days after hatching in 50% artificial seawater. Such a reduction in number indicates a critical depletion period in the early developmental stages. Finally, Bell and Brown (1995) showed that swimming endurance was mar-
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ginally longer in seawater than in freshwater, and the greatest swimming endurance was in haloclines. The preference shown by larvae in haloclines for low salinities is consistent with their superior swimming endurance compared to larvae in freshwater or seawater treatments and, therefore, suggests an adapted response to the downstream migration.

We showed that the seawater temperature has an influence on the speed of larval development, which is quicker at 26°C than at 22°C. Although the basic sequence of embryonic developmental events was maintained at different temperatures, there was some delay in the timing of the appearance of some structures at lower temperatures; this phenomenon in fish development has been known for some time (Blaxter, 1969). In the Gobiidae Gobius cobitis, the embryonic development was studied at two temperature ranges (12-16°C and 15-18°C), and was faster at higher temperatures (Gil et al., 1997; Borges et al., 2003). For Gobius paganelus, the basic sequence of larval development was similar at different temperatures, being faster at higher temperatures, and the larvae reached a similar size at the completion of development regardless of temperature (Borges et al., 2003). Finally, Fukuhara (1990) showed that for Rhinogobius brunneus consumption of yolk is regulated by metabolism, which varies according to water temperature and other physical factors. The temperature has crucial role in the duration of each phase between L1b and L2. This factor could explain the variability of the pelagic larval duration in Sicyopterus and its seasonality (Lord et al., 2010).

In our study the depth difference, at a given temperature, has an effect on larval mortality. So, in rivers, the water depth could act as an important factor for larval survival. In shallow water, the swimming effort would be far less compared to that made by the larvae to maintain itself in a greater water mass, in which larvae would therefore tire more quickly, thus reducing their survival. Indeed, in previous studies on Sicyopterus, just after hatching, L1a larvae have a characteristic behaviour during their downstream migration. Free embryo of Sicyopterus stimpsoni from Hawaii and of S. lagocephalus from Reunion Island “swim” repeatedly upwards until they contact the water surface, then for a while cease “swimming” and sink and then move towards the surface again (Kinzie, 1993; Keith et al., 1999; Valade, 2001). With such behaviour, a deep river could be more energy consuming. This behaviour facilitates their transport to the sea (Balon and Bruton, 1994). Larvae of Sicydium punctatum remain in the water column by alternately swimming upward and sinking, and are passively carried toward the sea by river currents (Bell, 1994). This passive seaward transport to coastal nursery areas would be promoted by keeping larvae suspended in the river flow (Bell and Brown, 1995). This ‘swim-up/sink-down’ behaviour has also been observed in several related gobies: Awaous guamensis, Dormitator latifrons, and Evorthodus lyricus (Ego, 1956; Todd, 1975; Foster and Fuiman, 1987).

The larvae of S. lagocephalus have completed their development at the L2 marine stage, the organs are in place, and the yolk sac is completely absorbed. They are then capable of feeding. This is the last stage of our experiment. According to Keith et al. (2008), the larva is competent when it is morphologically and physiologically capable of colonising freshwaters; the larva is able to respond to a signal triggering the processes leading to recruitment (i.e., beginning of the morphological transformation and migration towards the coast). From then on, after the L2 stage, they are referred to as post-larvae (PL0) subject to the colonisation signal (Keith et al., 2008). Nevertheless the morphological changes between L2 and PL0 stages (a long period of 4 to 6 months) must be better studied by catching larvae at sea. But where are these L2 and PL0 larvae when at sea? Do they stay near the coast or are they far away from rivers in the open sea? At this stage, nobody really knows and nobody knows how they feed. Sorensen and Hobson (2005) used stable isotope analysis to evaluate the sources of nutrients used by amphidromous gobid fishes (Lentipes concolor, Sicyopterus stimpsoni, Awaous guamensis) caught migrating into and living in Hakalau Stream, Hawaii (United States). Although considerable variation amongst the stable isotope values of stream items was noted across all four years of the study, the relationships between the fishes were relatively constant. Stable isotope values of recruiting gobies were consistently closer to those of both inshore plankton and freshwater adults than those of offshore plankton, suggesting that the larvae of these species derive much of their nutrition from inshore environments influenced by fresh water (Sorensen and Hobson, 2005). Small differences between the stable values of these species further suggested that their larvae come from different inshore locations. However, in their interesting study, Sorensen and Hobson (2005) did not integrate the time necessary to metabolise the nutrients, i.e., how long the larvae have been under the influence of inshore nutrients. They have only worked on specimens caught migrating into and living in the stream and have concluded that the larvae spent their early life near the river mouths. Their study shows that competent larvae are liable to spend a certain amount of time in front of the river mouth in order to wait for appropriate recruiting conditions. How far larvae drift from their natal river cannot be estimated. To date one can only propose various scenarios concerning the marine planktonic stage of larvae: it is unknown if larvae are retained close to shore or are transported out to sea (Murphy and Cowan, 2007). Recent molecular and otolith studies on Sicyopterus japonicus concluded that the larvae are capable of drifting in large oceanic currents in an offshore environment, transporting the larvae from the southern to the northern parts of the species’ range (Watanabe et al., 2006; Iida et al., 2008; Iida et al., 2010). We will learn more about the marine planktonic phase once
we manage to catch larvae at sea.

In conclusion, the results obtained in our work add significant information to the study of fish populations, thereby providing managers with precise knowledge of the developmental state while monitoring gobid populations. Indeed, transformations between hatching and marine migration have been characterised precisely thereby completing the reference scale elaborated by Keith et al. (2008). The morphological transformation of S. lagocephalus between hatching and the adult phase is therefore composed of five larval stages (L1a-d, L2) (this study, and awaiting the description of the pelagic larval stages between L2 and PL0), three post-larval stages (PL0 to PL2) and two juvenile stages (J1, J2) previously defined by Keith et al. (2008). After hatching, the free embryo passively drifts to the sea (Stage L1). The shift to saltwater triggers the first transformations corresponding to the development of the eyes, fins and mouth. When the lens is pigmented, the mouth open and operating, it then becomes an L2 larva. This larval phase ends when all the temporary embryonic and larval organs disappear and are replaced by rudimentary structures that are characteristic of post-larvae subject to the colonisation signal (Keith et al., 2008).

Murphy and Cowan (2007) have shown that the mechanism of larval production, retention, dispersal to sea, and recruitment to freshwater are both governed by biological and physiological processes. Our study has pointed out the role of the duration of the larval downstream migration and of water’s physical parameters (temperature and depth) on the larval development and survival. The life cycle and migration of amphidromous species are critically dependent on the integrity of the mountain-river-ocean corridor. Anthropogenic alterations of the environment may have an impact on the performance of species and on their ability to migrate to the sea: for example, adding obstacles in the watershed (e.g., dams) will increase the duration of the downstream migration after hatching and so the mortality rate of larvae. Some major climatic events, increasing the depth and the velocity of rivers, like heavy rains, or decreasing this depth, like drought, could positively or negatively impact the downstream migration and the survival of larvae. Other anthropogenic impacts on streams, like pollution or deforestation, could also diminish the flow rates and alter downstream larval migration and dispersion, and therefore the recruitment success (Houde, 1989; Brasher, 2003; Lord and Keith, 2008). Derivation channels on the main river flow could also act as significant trap for early life stages.

Growing urbanisation in Reunion Island is driving the need for water supply and electricity. The water basins are subject to extensive change and destruction, but the species’ amphidromous life cycle means it is important to maintain the mountain-ocean corridor, on the one hand, for the larvae’s downstream migration after hatching and, on the other hand, for the post-larval and juvenile upstream colonisation after recruitment in freshwaters (Keith et al., 2008).

Finally, the physiological state of each larval stage of S. lagocephalus can now also be characterised, as can the hormones responsible for triggering downstream migration and morphological transformation. Moreover, it would be beneficial to assess the duration of the L1 (b to d) and L2 stages, by catching larvae at sea, in order to describe the pelagic stages between L2 and PL0, and allowing spatio-temporal modelling of the oceanic dispersal.

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Early life history of Sicyopterus lagocephalus


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