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Involvement of thyroid hormones in the control of larval metamorphosis in *Sicyopterus lagocephalus* (Teleostei: Gobioidei) at the time of river recruitment

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ABSTRACT

After oceanic migration, post-larvae of the amphidromous *Sicyopterus lagocephalus* recruit to rivers in Reunion Island. As they enter the river mouth, post-larvae undergo many morphological, physiological and behavioural changes. These drastic changes, which allow them to change feeding regime and to colonise the juvenile and adult freshwater habitat, are defined as metamorphosis. The endocrine control of these changes has never been investigated in Gobioid fish. Here, we investigated whether thyroid hormones (TH) influence metamorphosis in recruiting *S. lagocephalus*. An analytical study was first performed on a cohort of 2400 fish caught at post-larval stage 1 and maintained for 37 days after capture in a flume tank (fluvarium), which replicates as closely as possible the natural conditions. Biometrical parameters (total and standard lengths, corner of mouth angle, body mass and condition factor) and whole-body thyroxine (T_4) and triiodothyronine (T_3) contents were measured on fish, sampled at regular intervals during these 37 days (192 fish). TH levels, measured by radioimmunoassays, were highest when morphological changes, such as the change in the position of the mouth, were most important. An experimental approach was then used to test the effect of the hormonal treatment (T_4 or thiourea, TU, a TH inhibitor) on biometrical parameters of 576 post-larvae. The change in the position of the mouth was significantly accelerated in the T_4-treated post-larvae, while it was significantly delayed in the TU-treated post-larvae, compared to controls. Our study suggests that *S. lagocephalus* post-larva undergoes a true metamorphic event under the control of thyroid hormones at the time of its recruitment into the river.
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1. Introduction

In the Indo-Pacific areas, river systems are colonised by freshwater gobies (Teleostei: Gobioidei) with a life cycle adapted to the conditions in these distinctive habitats, which are, particularly in islands, young oligotrophic rivers subject to extreme climatic and hydrological seasonal variation. These species spawn in freshwater, the free embryos drift downstream to the sea where the larvae undergo a planktonic phase, before returning to rivers to grow and reproduce [13], hence they are called amphidromous. Amphidromy is a strategy involving migration of post-larvae from the sea to fresh water, which is the main feeding, growing and reproductive biome [22]. *Sicyopterus lagocephalus* (Pallas, 1770) is one of the most common amphidromous species inhabiting island freshwaters from the Indian Ocean to the Pacific. Its larvae hatch in freshwater and are rapidly carried by river currents to the sea where they begin a planktonic life phase [40]. After 130–300 days spent in the ocean for their larval growth [19], they return to the river mouth as post-larvae; this is the recruitment phase. Soon after entering fresh water, they undergo several morphological changes in body, mouth position, fin shape and colour, related to the planktonic to benthic environment switch and the feeding mode modification [16,40]. According to Keith et al. [16], they undergo a metamorphosis. Then, juveniles migrate upstream using their sucker, resulting from the fusion of the pelvic fins, in order to colonise the juvenile and adult habitat [15,19].

Metamorphosis in teleosts occurs when species experience an abrupt transition from larval form to juvenile form, consisting of morphological, physiological and behavioural modifications associated with the colonisation of a new habitat (for review, see [44]). In pleuronectiforms such as flounders or halibuts, a symmetrical pelagic larva metamorphosises into an asymmetrical benthic juvenile, with among other changes, a spectacular eye migration [29,33]. In elopomorphs such as congers, tarpons or eels, oceanic leptocephalus larvae migrate from the ocean and metamorphose into glass eels off the continental shelf [31]. During this

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metamorphosis, the pelagic leptocephalus larva, which is translucent and leaf-shaped transforms into a benthic cylindrical glass eel. These metamorphoses are called true, first or larval metamorphosis: changes in morphology and non-reproductive structures between the larva and the juvenile are observed, and the larva occupies an ecological niche different from the adult [44].

Larval metamorphosis has been fully documented in amphibians and shown to be regulated by thyroid hormones (TH: thyroxine, T_4 and triiodothyronine, T_3) [5,36]. In teleosts, such as pleuronectiforms (*Verasper variegatus*: [37]; *Paralichthys dentatus*: [33]; *P. olivaceus*: [3,26,27]; *Scophtalmus maximus* [21]) and elopomorphs (*Conger myriaster*: [42]; *Anguilla japonica*: [43]; *Megalops cyprinoides*: [34]), analytical and experimental studies indicated that larval metamorphosis is under the control of thyroid hormones as in amphibians. A recent paper in Florida amphioxus (*Branchiostoma floridae*) [28] demonstrated that TH via thyroid receptor (TR) regulated cephalochordate metamorphosis, suggesting an ancestral feature of all chordates.

In elopomorphs, larval metamorphosis is thought to start at the oceanic leptocephalus larval stage and to end at the post-larval glass eel stage in the estuary [18,31]. Once the glass eel stage is reached, more metamorphic changes are observed during ongoing post-larval development. Some of these changes, such as the progression of pigmentation, were shown to be regulated by thyroid hormones [12]. In the case of *S. lagocephalus*, as described by Keith et al. [16], metamorphic changes start at sea during the transition from larvae to post-larvae but can not be studied due to the impossibility, at present, to collect larvae in the marine environment. As fish recruit to the estuary, more metamorphic changes are observed as fish change through several post-larval stages which allow them to colonise the river. In both cases, these larval and post-larval transformation events are a continuum, constituting the entire larval metamorphosis.

For the moment, as for eel leptocephalus larvae, the first metamorphic changes occurring in the ocean are unknown for *S. lagocephalus*. There are similarities between glass eel post-larvae and *S. lagocephalus* post-larvae as that they both correspond to estuarine stages and to the last stages of larval metamorphosis. In addition, as for glass eels when they enter fresh water, recruiting *S. lagocephalus* post-larvae migrating upstream represent an important source of food for local populations and have been targeted for many decades. They are of high economical and patrimonial values [1,14]. But these fisheries targeting post-larvae are highly unsustainable on account of the complexity and the fragility of the species life cycle. Moreover, very little is known about *S. lagocephalus* metamorphosis but increased knowledge of this event would help develop management and conservation policies.

The purpose of this paper is to investigate the hormonal control of *S. lagocephalus* larval metamorphosis at late stages and especially to study the influence of thyroid hormones in the metamorphic changes. First, an analytical approach was used to measure the variations in whole-body T_3 and T_4 concentrations during the larval morphological changes. Then, an experimental study was used to assess whether the morphological changes observed in recruiting *S. lagocephalus* were under the control of thyroid hormones.

2. Material and methods

2.1. Fish

Sicyopterus lagocephalus post-larvae were caught at St. Etienne River mouth in Reunion Island (21°18′S; 55°24′E) in January 2009. They were collected as they entered fresh water in the estuary, at the limit of the influence of the sea, using a traditional trapnet with the help of local fishermen. Post-larvae were transferred to the ARDA (Association Réunionaise pour le Développement de l'Aquaculture) station of Etang Salé Les Bains.

2.2. Fluvarium

The 2400 post-larvae collected on January 22, 2009, between 12 and 2 pm, at St. Etienne River mouth (21°18′S; 55°24′E) were randomly distributed into the two ramps (1200 individuals in each ramp) of the flume tank which replicated as closely as possible the natural conditions in the river. The entire structure is called fluvarium. Each ramp was a 2000 L outdoor fluvarium filled with river water. Each one had a closed-loop system, reproducing natural river conditions such as temperature (26–30 °C), water current and natural photoperiod. The bottoms of the tanks were laid with pebbles and river stones collected on the riverbed, covered in periphyton, which constitutes fish food.

Fish were maintained 37 days in the fluvarium. Sixteen specimens from the fluvarium (eight for each ramp) were collected every day until day 15, every 3 day until day 33 and every 2 day until day 37. The fish collected were anesthetised, biometrically monitored then frozen and stored at −20 °C until extraction and hormonal assays.

2.3. Hormonal treatment in tanks

Seven hundred and fifty post-larvae from the January 2009 catch were placed in six 50 L experimental tanks each containing 125 individuals; 10% (5 L) of the water was renewed daily. During 10 days, post-larvae were immersed in water containing either T_4 (two tanks) or thiourea (TU, a thyroid inhibitor) (two tanks), to respectively increase and decrease TH levels. The two remaining tanks constituted the control group. Pebbles enriched in periphyton were placed on the bottom of the tanks. Based on previous studies on glass eel [7], we applied the same concentrations of T_4 (0.5 mg T_4 L^{-1}) and TU (500 mg TU L^{-1}). T_4 (Sigma Aldrich Corp., Saint Louis, MO) stock solution was dissolved in 0.1 N NaOH (1.25 mg mL^{-1}) and kept at 4 °C, and TU (Sigma) was directly dissolved in the tanks. Both TU-treated and control groups received the same dilution of NaOH (T_4 solvent). Fish were treated for 10-days with T_4, TU or solvent. Concentration of TU, T_4 and NaOH was maintained constant throughout the experiment by adding drugs daily to the 5 L renewed water.

Fish were sampled during 37 days. Eight specimens from each experimental group (four for each tank) were collected every day until day 15, every 3 day until day 33 and every 2 day until day 37. The fish collected were anesthetised, biometrically monitored then frozen and stored at −20 °C until extraction and hormonal assays.

2.4. Biometrical analysis

Biometrical criteria were chosen according to prior studies on *S. lagocephalus* post-larvae [16]. After being anesthetised with clove oil (1%), fish from the fluvarium and tanks were measured. Total length (TL) and standard length (SL) were measured from the snout to the extremity of the caudal fin (TL) or the base of the caudal fin (SL) to the nearest tenth of millimetre (mm) using a digital dial calliper. Fish were then photographed alive using a binocular magnifier (Olympus SZ61) coupled to a digital camera (Olympus C-5050, optical zoom 3×) linked to a computer. At the end, fish were placed into individual plastic pockets after removing water surplus by absorption and frozen (−20 °C). Corner of mouth angle was measured on standardised photographs and adapted from Keith et al. [16]. The spike of the opercula and the centre of the orbit were used to measure this angle so that a line could be

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