Amphidromous life cycle of *Eleotris fusca* (Gobioidei: Eleotridae), a widespread species from the Indo-Pacific studied by otolith analyses

by

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Abstract. – *Eleotris fusca* is a widespread amphidromous fish found in the Indo-Pacific area. Its life cycle is characterised by a marine pelagic larval phase allowing the species to disperse in the ocean and then to recruit to remote island rivers. In order to examine its migratory history and pelagic larval duration (PLD), otolith microchemical and microstructural analyses were undertaken on 100 specimens collected in the rivers of four areas: Mayotte, Reunion Island (Indian Ocean), Vanuatu and French Polynesia (Pacific Ocean). Variations of Sr:Ca ratios were observed along the otoliths using a femtosecond laser ablation-inductively coupled plasma spectrometer (fs-LA-ICP-MS). The variation of the Sr:Ca ratio allowed us to reconstruct fish migratory movements between sea water (high Sr:Ca) and freshwater (low Sr:Ca), and led us to assume that *Eleotris fusca* is an amphidromous species. Using microstructural analysis, we observed that the PLD depended on the sampling site. In the Pacific Ocean, the PLD is similar in Vanuatu (mean ± SD: 90 ± 19.2 days) and French Polynesia (96.2 ± 17.5 days) whereas a significant difference emerged in the Indian Ocean between Mayotte (63.3 ± 11 days) and Reunion Island (114.8 ± 21.8 days).

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Résumé. – Étude de l'histoire migratoire et de la durée de la phase larvaire d'*Eleotris fusca* (Gobioidei: Eleotridae), une espèce à large répartition dans l'Indo-Pacifique, à travers l'analyse des otolithes.

Eleotris fusca est une espèce de poisson amphidrome colonisant les milieux insulaires de l'Indo-Pacifique. Son cycle de vie est caractérisé par une phase larvaire marine lui permettant de disperser dans l'océan et ensuite de recruter dans les rivières d'îles plus éloignées. Dans le but de comprendre l'histoire migratoire ainsi que la durée de la phase larvaire (DPL), des analyses microchimiques et microstructurales des otolithes ont été réalisées sur 100 spécimens collectés dans les rivières de quatre zones : Mayotte, La Réunion (océan Indien), Vanuatu et Polynésie française (océan Pacifique). Les variations des ratios de Sr:Ca ont été observées le long des otolithes en utilisant un couplage ablation laser femtosecondes-spectromètre de masse à plasma induit (fs-LA-ICP-MS). La variation du ratio Sr:Ca nous a permis de reconstruire les mouvements migratoires des poissons entre l'eau de mer (Sr:Ca élevé) et l'eau douce (Sr:Ca faible), et de valider le cycle amphidrome d'*Eleotris fusca*. Avec l'analyse microstructurale, nous avons observé que les DPL dépendaient du site d'échantillonnage. Dans l'océan Pacifique, la DPL est similaire entre le Vanuatu (moyenne ± écart type: 90 ± 19,2 jours) et la Polynésie française (96.2 ± 17,5 jours) alors que pour l'océan Indien, nous observons une différence significative entre Mayotte (63,3 ± 11 jours) et La Réunion (114,8 ± 21,8 jours).

Key words
Eleotridae
Eleotris fusca
Indo-Pacific
Amphidromy
Pelagic larval duration
Otolith analysis

Insular river systems of the Indo-Pacific area are mostly inhabited by amphidromous species (teleost fish, crustaceans and molluscs). These species are the biggest contributors to the diversity of freshwater communities (Nelson *et al.,* 1997; Keith *et al.,* 2007; Watson *et al.,* 2007; Keith and Lord, 2011). Two fish families are predominant: Gobiidae and Eleotridae (Gobioidei). These gobioids spawn in freshwater. After hatching, free embryos drift downstream to the sea, where the pelagic larval phase takes place. After this marine pelagic phase, which extends nearly from three to nine months (Radtke *et al.,* 1988; Maeda *et al.,* 2007; Yamasaki *et al.,* 2007; Iida *et al.,* 2008; Lord *et al.,* 2010), individuals (post-larvae) return to rivers (recruitment phase) to grow and reproduce. Such a life cycle is called amphidromous. Sometimes, the biomass of larvae migrating upstream is so great that they become a major source of food for local human populations in the Indo-Pacific and Caribbean areas (e.g. Reunion Island and Vanuatu) (Bell, 1999; Keith, 2003). This food resource is probably unsustainable considering the complexity of the gobioid life cycle and the lack of fisheries management.

Eleotris fusca (Bloch & Schneider, 1801) (Eleotridae) is a widespread species found in the Indo-Pacific area, from the Western Indian Ocean to New Caledonia, Vanuatu and French Polynesia (Keith *et al.,* 2006, 2010, 2013). In insular rivers, it is a common carnivorous species distributed

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primarily in freshwater (Maeda and Tachihara, 2004, 2006). This species is euryhaline and is found in brackish waters, but mainly in the lower part of freshwater areas. It prefers to be close to the riverbank where the current is slow, or in the lentic zones (Keith *et al.,* 2010).

The life history of some *Eleotris* (*E. melanosoma* Bleeker, 1853, *E. acanthopoma* Bleeker, 1853, as well as *E. fusca*) in Pacific area has been relatively studied with, for example, reproduction and early development (Maeda *et al.,* 2008), downstream migration (Maeda and Tachihara 2010; Yamasaki *et al.,* 2011), pelagic larval duration (Maeda *et al.,* 2007; Shiao *et al.,* 2015), recruitment (Maeda and Tachihara, 2005; Shiao *et al.,* 2015) and feeding habits (Resh *et al.,* 1999; Maeda and Tachihara, 2004). But generally, these studies were done at a local or regional scale.

In tropical islands, especially in Reunion Island, *E. fusca* undergoes pressures linked to the loss of the hydrological corridor and the habitat degradation. If the threats on this species were not clearly identify at the international scale due to a lack of investigations, the association of the habitat loss and fisheries in the Reunion Island lead the IUCN France to classify *E. fusca* as "Endangered" on the red List of Endangered Species in France (IUCN France *et al.,* 2013). Because of its role in the freshwater ecosystem and the fishing of its post-larvae, it is important to understand the life cycle of this species to implement conservation measures.

Fish otoliths are calcified structures located in the inner ear of the fish. They usually show a series of growth structures formed on a daily basis called increments (Pannella, 1971). The otoliths are acellular, metabolically inert (Campana, 1999) and do not undergo any mineral resorption or alteration (Campana and Thorrold, 2001). Because of these characteristics, otoliths are used to reconstruct many details about the fish physiological and environmental past. Therefore, microstructures are used to accurately estimate fish age and to analyse and date specific events such as recruitment, metamorphosis or reproduction (Lecomte-Finiger, 1999; Radtke *et al.,* 2001; Shen *et al.,* 1998). For amphidromous species, a check mark is formed at recruitment on the otolith when larvae enter the estuaries and start to colonise the riv-

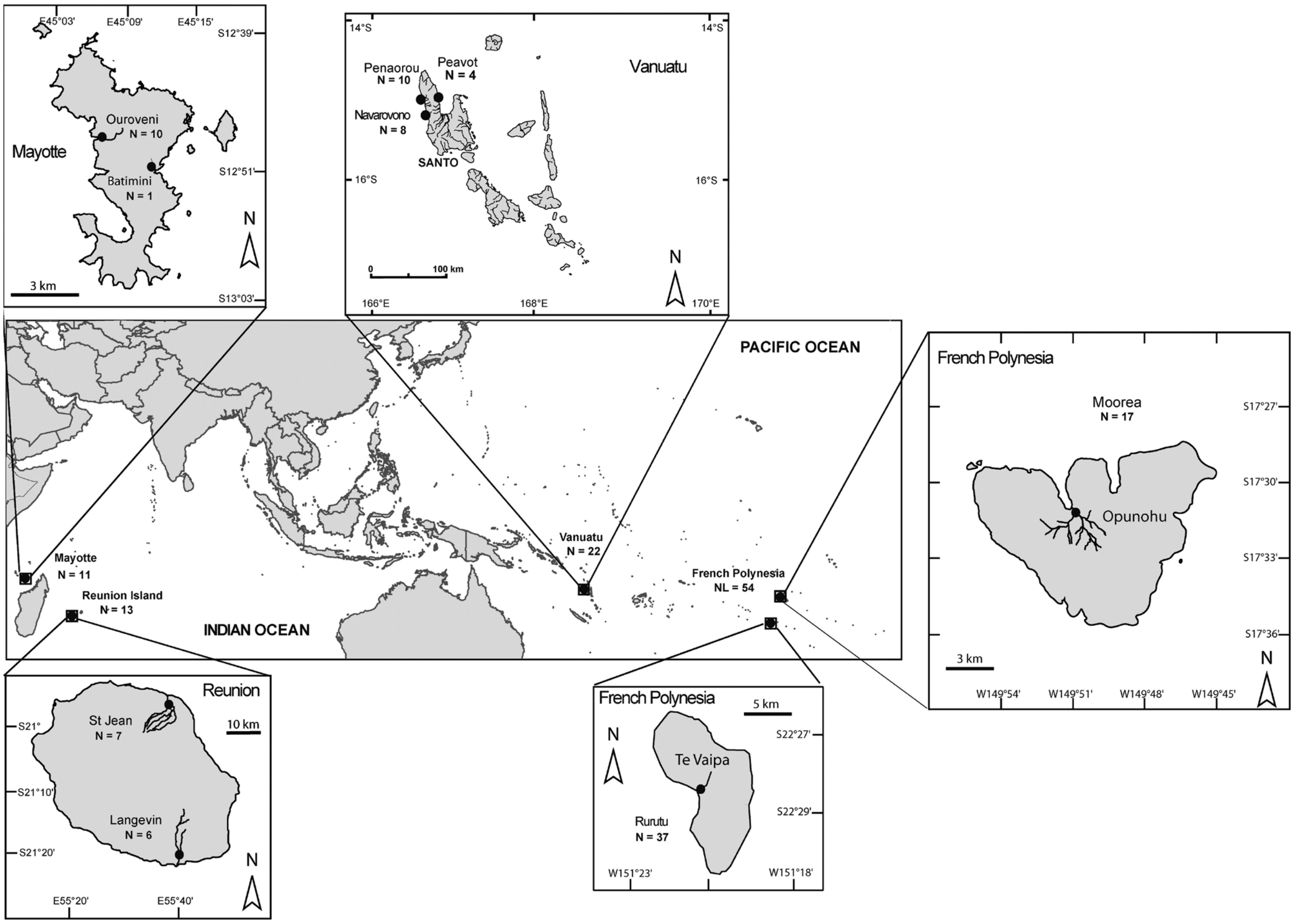

Figure 1. - Sampling locations of *Eleotris fusca* in the rivers (●) of four sites (■) in the Indo-Pacific: Mayotte (N = 11), Reunion Island (N = 13), Vanuatu (N = 22) and French Polynesia (N = 54).

ers (Shen *et al.,* 2002; Keith *et al.,* 2008). This mark allows to easily distinguish the marine larval phase from the juvenile and adult phases in freshwater. Daily increments from the core to the check mark are therefore an estimation of the pelagic larval duration (Yamasaki *et al.,* 2007; Taillebois *et al.,* 2012).

The otolith matrix is also able to trap minor and trace elements coming from the surrounding water and food. The otolith elemental composition is widely used for the reconstruction of the migratory and the environmental history of fish (Daverat *et al.,* 2005; Shiao *et al.,* 2006; Arai *et al.,* 2007; Lord *et al.,* 2011). Indeed, the strontium:calcium ratio (Sr:Ca) is used to reconstruct the migratory movements of diadromous fish between sea water and freshwater (Milton *et al.,* 2008; Tabouret *et al.,* 2010; Feutry *et al.,* 2011, 2012). For amphidromous species, elevated Sr:Ca ratios in fish otoliths are widely accepted as proof of occupation of marine habitats (Howland *et al.,* 2001; Crook *et al.,* 2006) or of a marine larval stage (Closs *et al.,* 2003), as opposed to low Sr:Ca ratio, which reflects occupation of freshwater habitats.

The aim of our study was to investigate, for the first time on a large scale, the life history traits and pelagic larval duration of the widespread species *Eleotris fusca* collected in four areas (Vanuatu and French Polynesia in Pacific Ocean and, Reunion Island and Mayotte in Indian Ocean) through the otolith microstructure and microchemistry. Firstly, we studied the elemental composition of the otolith to investigate the nature of the amphidromous life cycle of the species and secondly, we estimated the pelagic larval duration (PLD) and the larval growth, using the daily increments of the otoliths.

MATERIALS AND METHODS

Sampling and measurement

One hundred specimens were collected in the rivers of four areas distributed in the Pacific Ocean (Vanuatu and French Polynesia) and the Indian Ocean (Mayotte and Reunion Island) (Fig. 1) using a DEKA 3000 electrofishing system (Gerätebau, Marsberg, Germany). Due to the threatened status of the species in the Indian Ocean (Endangered in Reunion Island, IUCN FRANCE *et al.,* 2013), fewer specimens have been collected in this area. All the fish were sampled in the lower part of the freshwater streams, as defined by Keith *et al.* (2013), at 5-50 m depth. Fish were put to sleep and killed using an overdose of clove essential oil (10%), then stored and preserved in 95% alcohol. The standard length (N = 62) was measured using a dial caliper (Mitutoyo) (Tab. I).

Table I. - Sampling locations in the four countries and number (N) of *Eleotris fusca* specimens used for the standard length (N_{SL}), the marine pelagic larval duration estimation (N_{PLD}) and for the microchemistry analysis. SL: Standard length; PLD: Pelagic larval duration; SD: Standard deviation.

Ocean	Location country/island	River	Date	N	N per site	SL in mm (mean ± SD)	N_{SL}	PLD for each country (days) (mean ± SD)	PLD for each ocean (days) (mean ± SD)	N_{PLD}	Otoliths used for microchemistry analysis
Pacific (N = 76)	Vanuatu-Santo	Navarovono	Nov. 2007	8	22	54.4 ± 7.6 range [31.4-69.1]	13	90 ± 19.2 range [57-130.5]	93 ± 18.4	20	11
	Vanuatu-Santo	Penaorou	Nov. 2006	10							
	Vanuatu-Santo	Peavot	Nov. 2006	4							
	French Polynesia-Moorea	Opunohu	Jun. 2007	17	54	61.6 ± 13.3 range [35.7-88.7]	25	96.2 ± 17.5 range [62-131.5]		19	15
	French Polynesia-Rurutu	Te vaipa	Jul. 2007	37							
						Total N_{LS} = 38		Total N_{PLD} = 39			Total N = 26
Indian (N = 24)	Mayotte	Batimimi	Nov. 2003	1	11	61.8 ± 17.4 range [42.7-82.4]	11	63.3 ± 11 range [38-78]	91.4 ± 31.5	10	4
	Mayotte	Ouroveni	Apr. 2009	3							
	Mayotte	Ouroveni	May 2006	7							
	Reunion	Saint Jean	Mar. 2007	7	13	64.5 ± 14.1 range [44.5-83.2]	13	114.8 ± 21.8 range [82.5-141]		12	5
	Reunion	Langevin	Nov.1998	6							
						Total N_{LS} = 24		Total N_{PLD} = 22			Total N = 9

Otolith preparation and estimation of the PLD

Pairs of sagittal otoliths were extracted from fish under a binocular stereomicroscope (Olympus VZ), rinsed in distilled water and dried. Otoliths were individually embedded in epoxy resin (Araldite 2020, Escil, France). For each specimen, one of the otoliths was ground on a transverse section down to the core, using carbide silicon abrasive discs of decreasing grain size (Escil, France). The embedded otolith was polished with alumina paste (Escil, France) and thoroughly rinsed in MilliQ water. Preparations were finally dried and kept in dry clean tubes. Otolith microstructure observations were made under an Olympus BX51 light microscope; each otolith was photographed with an Olympus DP20 digital camera.

According to previous studies that validated the daily accretion growth of fish, especially *Eleotris* (Maeda *et al.*,

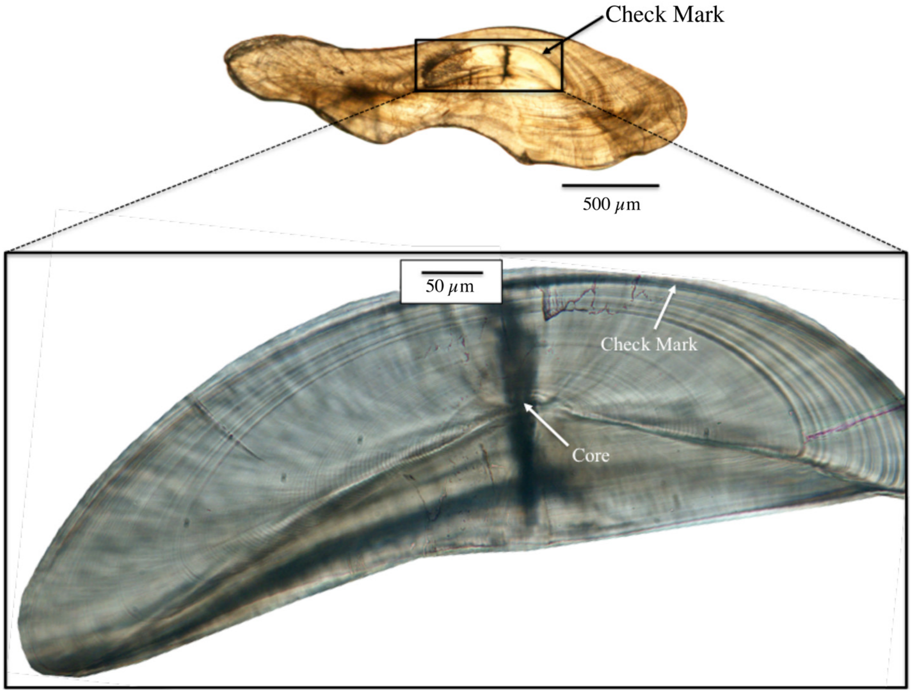

Figure 2. - Transverse section of sagittal otolith of an *Eleotris fusca* from French Polynesia. The detailed area is a magnification of the marine larval phase, *i.e.* the area included between the core and the check mark.

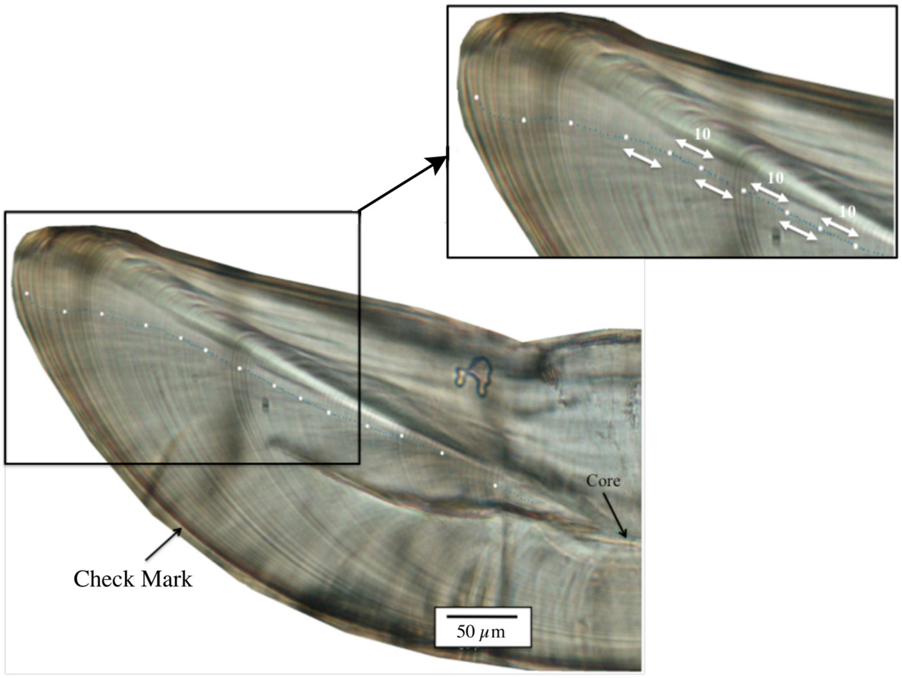

Figure 3. - Growth rate analysis of : *Eleotris fusca* otolith; white dots every 10 daily increments.

2007), or amphidromous gobies (Yamasaki *et al.,* 2007; Iida *et al.,* 2010a; Taillebois *et al.,* 2012), we assumed that the otolith increments of *E. fusca* were formed on a daily basis. The first increment after the core is assumed to occur at hatching (Lecomte-Finiger, 1999). To estimate the PLD, the daily increments were counted from the core to the check mark (Fig. 2). For each otolith, two readers independently counted the number of increments.

Pannela (1971) showed that the growth of the otolith reflects the metabolism of the fish and, therefore, its growth. So, we assumed that the otolith growth rate from the core to the check mark represents the larval growth of the individual. The mean growth rate of the otolith (μm/day) during the marine larval phase was calculated using AnalySIS work 5.0 software (Olympus, Germany) by measuring the distance (μm) every 10 daily increments from the core to the check mark along the longest radius (Fig. 3).

Microchemical analysis

Eleven otoliths from Vanuatu, fifteen otoliths from French Polynesia, five from Reunion Island and four from Mayotte were analyzed with an IR 10130 nm femtosecond laser (Alfamet-Novalase, France) coupled to an Elan DRC II (Perkin Elmer) inductively coupled plasma-mass spectrometer (ICPMS). A linear raster scan ablation 20 μm width was made along the longest radius of the otolith. The ablation started 70 μm before the core and ended at the otolith edge passing through the core and the check mark. The laser beam was applied with a 500 Hz frequency at a speed of 5 $\mu m.s^{-1}$. Ablation conditions were described in previous studies on Gobiidae species (Lord *et al.,* 2011; Tabouret *et al.,* 2011). ^{43}Ca was used as an internal standard for each ablation to check for variation in ablation yield. Quantification of ^{86}Sr concentration was allowed using three certified reference glasses: NIST614, NIST612 and NIST610 (National Institute of Standards and Technology, USA). Analytical accuracy was achieved with the fish certified otolith reference material NIES22 (National Institute for Environmental Studies, Japan). Strontium was standardized to calcium (*i.e.* Sr:Ca) based on the stoichiometry of calcium carbonate (380,000 μg Ca g^{-1} otolith), as this element can substitute for calcium in the otolith matrix (Campana, 1999). The average detection limit based on three standard deviations (SD) of the blank gas was 3.28 $\mu g.g^{-1}$ for ^{86}Sr *i.e.* 0.86×10^{-5}.

Statistical analysis

The data was statistically processed using the free R software (version 3.0; R Development Core Team, 2014). First, the normality of the data was systematically verified using Shapiro-Wilks normality test, allowing us to choose between parametric and non-parametric tests. In order to test whether larval and pelagic phase were different, the Sr:Ca values for each island were compared between the pelagic larval phase and the freshwater phase using a Kruskal-Wallis test and, for each individual, using a pair-sample Wilcoxon or Student test. In order to test the PLD estimated by the two readers, a paired-t test was performed. A one-way ANOVA was used to compare PLDs among the four sampling PLD. With a Student test, we compared PLD between the two oceans, and within each ocean: Indian (Mayotte-Reunion Island) and Pacific (Vanuatu-French Polynesia). The relationship between the standard length and the longest radius of otoliths was tested with a Spearman test. Then, the total growth rate of the otolith in the four areas was tested with a Kruskal-Wallis test. For each test the Bonferonni correlation was applied to avoid any error due to the repetition of analyses.

RESULTS

Considering the reading difficulty of some otoliths, not all otoliths were used for the analyses. Sixty-one were used for the PLD and 35 for the microchemistry (Tab. I).

Otolith Sr:Ca ratios

For all individuals of *Eleotris fusca* used for microchemical analyses ($N = 35$), the Sr:Ca ratios show the same pattern ($p > 0.4$ for each site). The Sr:Ca ratio is high and constant during the marine pelagic larval phase, *i.e.* from the core to the check mark, with mean values of (mean ± SD) $8.55 \pm 0.59 \times 10^{-3}$, $8.75 \pm 0.78 \times 10^{-3}$, $8.89 \pm 0.83 \times 10^{-3}$, $9.57 \pm 0.62 \times 10^{-3}$ for Vanuatu (individual V1 to V11), French Polynesia (individual FP1 to FP15), Reunion Island (individual R1 to R5) and Mayotte (individual M1 to M4) specimens, respectively (Fig. 4). Then, it decreases drastically at the check mark and reaches a lower ratio of $2.94 \pm 1.34 \times 10^{-3}$ for the individuals from Vanuatu, $3.38 \pm 0.55 \times 10^{-3}$ for those from French Polynesia ($N = 26$, $p < 0.001$) and, to $3.37 \pm 0.12 \times 10^{-3}$ for samples from Reunion Island and $4 \pm 0.34 \times 10^{-3}$ for Mayotte ($N = 9$, $p < 0.001$).

PLD Estimation

Since there was no significant difference in the age at recruitment between the two independent readers ($t = -1.5607$, $p = 0.1249$), we used the mean of the two readings to have the best PLD estimation.

PLDs in the four areas were analysed by a one-way ANOVA and it revealed that at least one locality among the four showed a significantly different PLD ($p < 0.001$). Moreover, a Student test indicated that mean PLDs are similar between Pacific (mean ± SD: 93.0 ± 18.4 days) and Indian oceans (91.4 ± 31.5 days) ($t = -0.2171$, $p = 0.8296$). The same result was obtained when we compared Vanuatu (90.0 ± 19.2 days [range of: 57-130.5 days]) and French Polynesia (96.2 ± 17.5 days [62-131.5 days]) ($t = -1.0551$, $p = 0.2982$). However, there is a significant difference between Mayo-

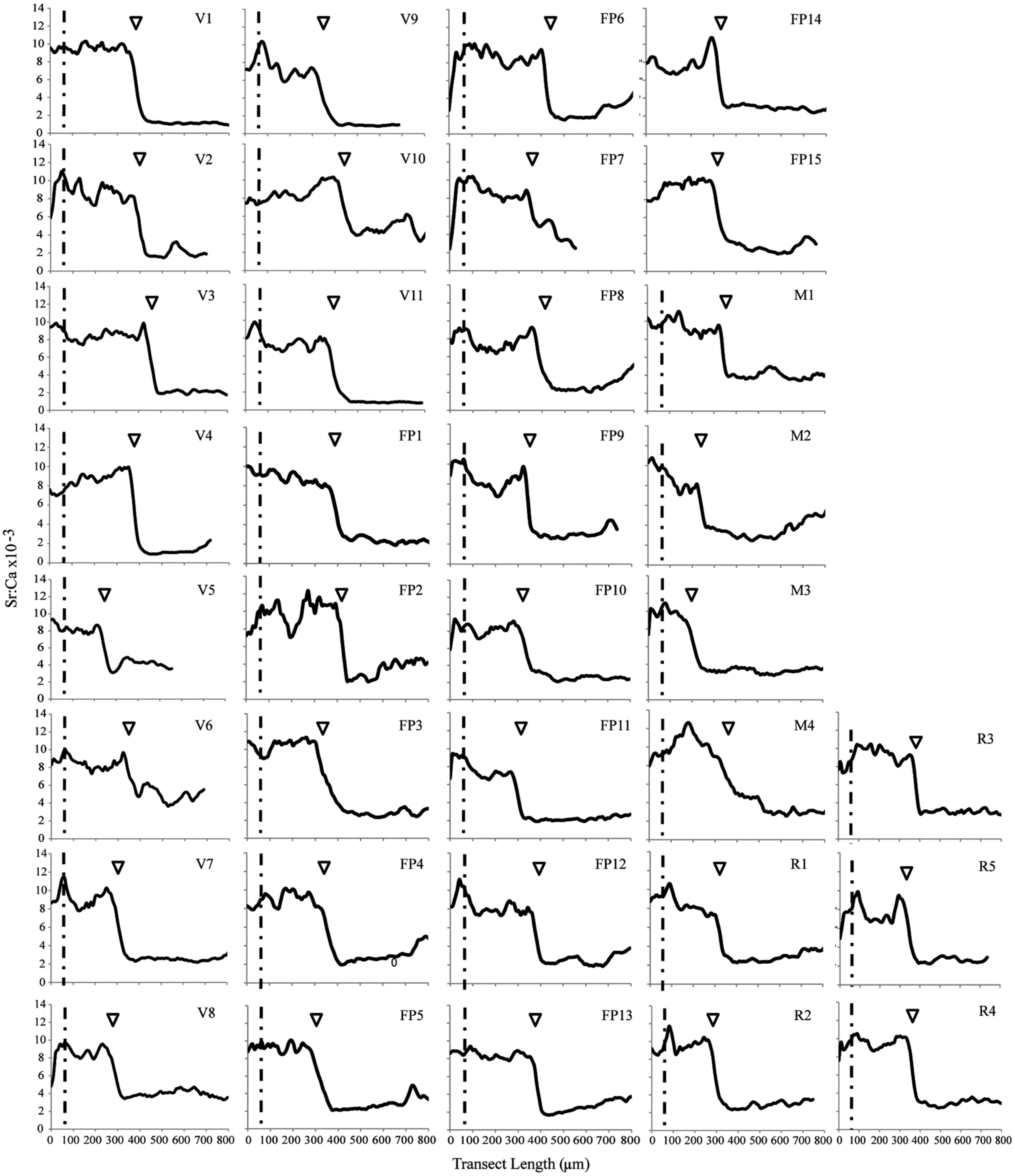

Figure 4. - Sr:Ca profiles (black line) provided by fs-LA-ICP-MS on otoliths of *Eleotris fusca* from Vanuatu (V1 to V11), French Polynesia (FP1 to FP15), Mayotte (M1 to M4) and Reunion Island (R1 to R5). Dotted line: core; White triangle: check mark.

tte (63.4 ± 5.8 days [38-78 days]) and Reunion Island (114.8 ± 21.8 days [82.5-141 days]) specimens in the Indian Ocean ($t = -6.7752$, $p < 0.001$).

In other terms, the pelagic larval duration depends on the sampling site. The Pacific Ocean PLD appears homogenous whereas significant differences emerge in the Indian Ocean between Mayotte and Reunion Island (Tab. I).

Otolith growth

According to the Spearman test, there is a significant relationship between the standard length and the longest radius of otoliths (N = 62, S = 8360, $p < 0.0001$; $r^2 = 0.69$).

For all site, the same pattern occurs (Fig. 5): the otolith growth rate is high during the first 10 days of the larval life (mean ± SD: 6.79 ± 1.57 µm/day for Vanuatu; 6.43 ± 2.11 µm/day for French Polynesia, 8.25 ± 5.17 µm/day for Mayotte and 6.51 ± 1.79 µm/day for Reunion Island), then it decreases drastically (4.26 ± 0.72 µm/day for Vanuatu; 3.38 ± 1.26 µm/day for French Polynesia, 4.97 ± 2.13 µm/day for Mayotte and 2.91 ± 0.6 µm/day for Reunion Island) between the 10th and the 20th day, and more gradually from the 20th day to the recruitment mark (around 2.7 µm/day). A Kruskal-

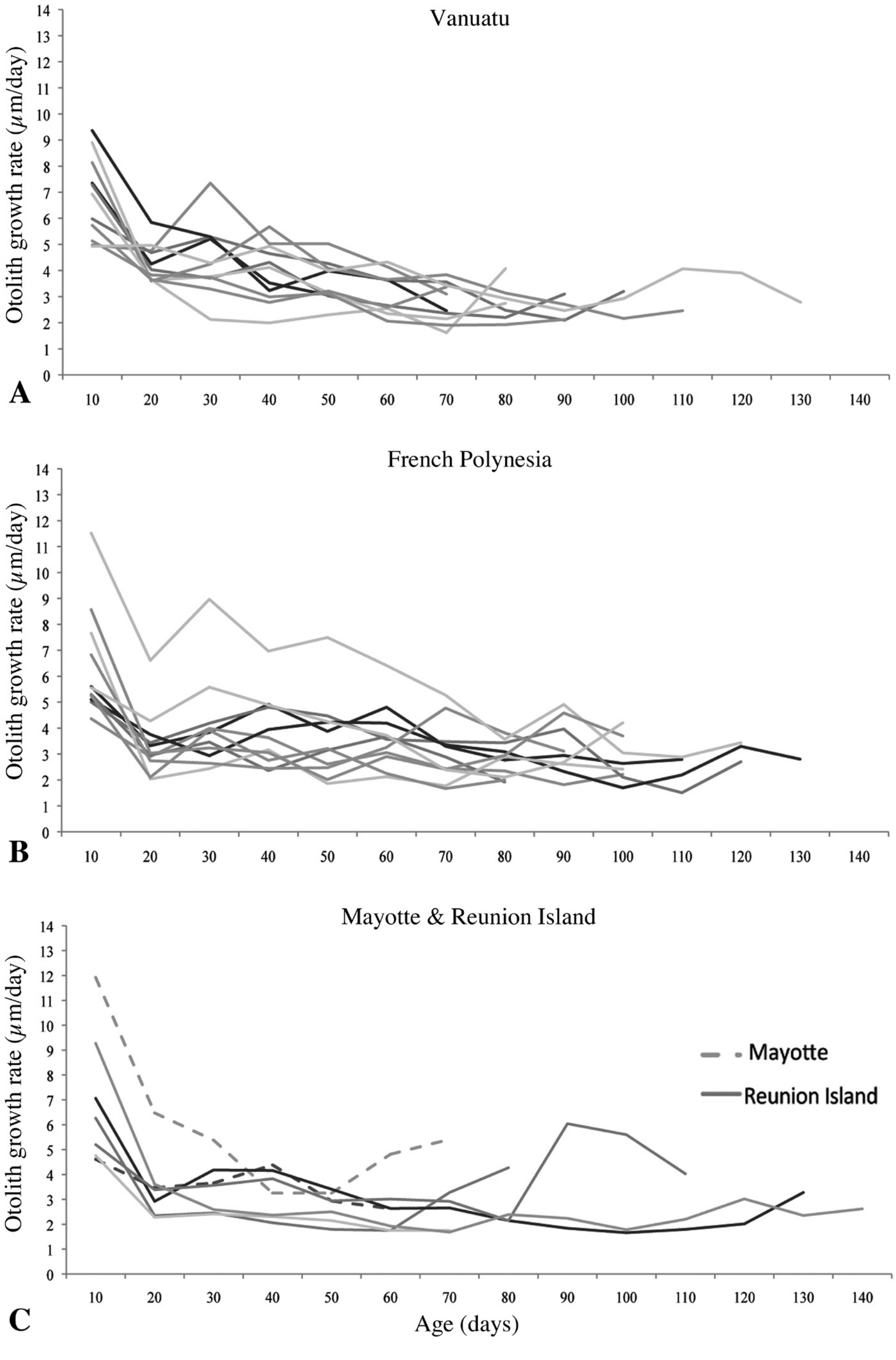

Figure 5. - Otolith growth rate from the core to the check mark as a function of age for the Vanuatu (**A**), French Polynesia (**B**), and Mayotte and Reunion Island (**C**) samples. The age 0 is assumed to correspond to hatching (core) and the older age to the recruitment check mark.

Wallis test showed that the total growth rate from the core to the check mark of the otolith changes with a similar pattern in the four areas (N = 37, $\chi^2 = 12$, p = 0.4457).

DISCUSSION

Otolith Sr:Ca

Whatever the island considered, microchemical analysis of *Eleotris fusca* otoliths revealed high Sr:Ca ratios from the core (hatching) to the check mark and low values after the check mark to the edge of the otolith.

We know that individuals were caught in freshwater, so we used the Sr:Ca values at the otolith edge as a reference to characterise the Sr:Ca in freshwater *i.e.,* values under 2×10^{-3}. Sr:Ca ratios from the check mark to the core of the otolith are higher than those of the edges ($8.55 \pm 0.59 \times 10^{-3}$ to $9.57 \pm 0.62 \times 10^{-3}$), suggesting that these values indicate an area with high salinity (estuary and ocean). Such elevated ratios in fish otoliths are widely accepted as a marine fingerprint (Tzeng, 1996; Tsunagawa and Arai, 2009; Tabouret *et al.,* 2010) and the decrease of Sr:Ca ratio ($2.94 \pm 1.34 \times 10^{-3}$ to $4 \pm 0.34 \times 10^{-3}$) always coincides with the check mark *i.e.* when individuals enter rivers. This pattern and the values observed were usually found for other amphidromous species like *Sicyopterus lagocephalus* (Pallas, 1770) (high Sr:Ca values: $10\text{-}12 \times 10^{-3}$ and low values: $2\text{-}4 \times 10^{-3}$) (Lord *et al.,* 2011), *Sicydium punctatum* Perugia, 1896 ($9.39 \pm 0.50 \times 10^{-3}$ and $2\text{-}4 \times 10^{-3}$) (Tabouret *et al.,* 2011) or other Gobiidae (Radtke and Kinzie, 1996; Chang *et al.,* 2006; Taillebois *et al.,* 2015). *E. fusca* is generally known as amphidromous (Keith *et al.,* 2010, 2013). Maeda and Tachihara (2004, 2005) have demonstrated the amphidromy of this species in Japan. On the other hand, it was considered as an estuarine species by several authors (e.g., Kuo and Shao 1999; Vivier *et al.,* 2010). However, the results of our study on otolith microchemistry support the amphidromy of *E. fusca* on all sites studied.

After the check mark, *i.e.* during freshwater life, the Sr:Ca ratio is relatively stable, except for some profiles such as Vanuatu individual V2, French Polynesian individual FP2 or Mayotte individual M2 (Fig. 4), where we observed a slight increase. Some physiological processes are known to leave a chemical mark on the otolith, such as stressful events and reproductive activity, both in the form of elevated Sr:Ca ratios (Campana, 1999). The ability of some individuals to move from freshwater habitats to brackish, or in some parts of the river, could explain the slight fluctuation of Sr:Ca observed (Lord *et al.,* 2011). Indeed, Maeda and Tachihara, 2004) showed that in the Teima River (Okinawa, Japan) *E. fusca* is distributed from the upper limit under tidal influence area to freshwater area. This distribution might explain why certain profiles present some Sr:Ca variations. Moreover, elemental concentration in tropical rivers or estuaries can be modified by extreme climatic and hydrological seasonal variations or by sediment loads or river flows (Tabouret *et al.,* 2011). But attributing a particular event to a peak or a particular variation of the ratios is difficult without a good knowledge of the event (e.g., Fig. 4. V2).

Duration of the pelagic larval phase (PLD)

Some studies have been conducted on the PLDs of Eleotridae and found similar results. Sirot (2009) found PLD around 75 ± 17.24 days (N = 36) for *Eleotris perniger* (Cope, 1871), a species in Guadeloupe (French West Indies). In Dominica, the age at recruitment of *E. pisonis* (Gmelin, 1789) (N = 21) was about 80 to 160 days (Bell *et al.,* 1995). Maeda *et al.* (2007) found for *E. fusca, E. melanosoma* and *E. acanthopoma* PLDs around two to four months in Okinawa Island, Japan. Moreover, Shiao *et al.* (2015) obtained a PLD of about 84-111 days (N = 12) for *E. fusca* in Taiwan and Corbarieu (2008) found 150 ± 17.24 days (N = 82) in Reunion Island. But all these studies focused on a small geographical scale (one island).

In this present study, we focused on a larger scale (four islands in two oceans). We showed that, depending on the area, the pelagic larval duration of *E. fusca* individuals is not the same and is highly variable. Significant differences were found in the Indian Ocean; PLD varied by means of two between the studied islands, Mayotte (63.4 ± 5.8 days; [38-78 days]) and Reunion Island (114.8 ± 21.8 days; [82.5-141 days]), although ranges of standard length are similar. On the contrary, both PLD and standard length ranges are similar for Vanuatu (90 ± 19.2 days; [57-130.5 days]) and French Polynesia (96.2 ± 17.5 days; [62-131.5 days]) in the Pacific Ocean (Tab. I).

Some studies showed that PLD could vary with the season (McDowall *et al.,* 1994; Bell *et al.,* 1995; Radtke *et al.,* 2001, Maeda *et al.,* 2007, Teichert *et al.,* 2014). These studies revealed that short PLDs and high growth rates were generally observed during the warmer season. This phenomenon may explain the PLD difference in the Indian Ocean. Indeed, in Reunion Island, Corbarieu (2008) showed that there is a significant difference in the age at recruitment for *E. fusca* (*i.e.* in PLDs). When the individuals were born in summer (hot [25-27°C, mean: 26°C] and humid season), between November and April, the PLDs were shorter (110 ± 14 days; [76-128 days]; N = 30) than those born in winter (cool [24-27°C, mean: 25°C] and dry season), between May and October (193 ± 22 days; [152-228 days]; N = 23). On the same island, Teichert *et al.* (2014) showed similar results for *Sicyopterus lagocephalus*: PLDs and size are related to the hatching date, showing that the seasonal effect was the main component of variability for these two parameters. Indeed, the youngest and smallest post-larvae (short PLDs) hatched from November and January (summer) and recruited from

March and May, whereas the oldest and largest (high PLDs) hatched between June and August (winter) and recruited in January-March. There is the same seasonality in Mayotte but the sea surface temperatures (SST), recorded around Mayotte from the NOAA's Coral Reef Watch Program's satellite (http://coralreefwatch.noaa.gov/satellite/index.php) for the two seasons, are higher than around Reunion Island (i.e. 27-29°C in summer, mean: 28°C and 26-29°C in winter, mean: 27°C); this could explain why the PLDs are shorter in Mayotte, whatever the season, compared to Reunion Island.

The pluviometry, which varied according to the season, can also effect the pelagic larval duration. Indeed, the heavy rain in summer seems to be associated with two important life stages: the drift to the sea of the newly hatched larvae and the recruitment of marine post-larvae in freshwater. The increase of freshwater flows in the season may help newly hatched larvae to drift downstream to sea sooner, and these flows seem to trigger the post-larvae migration inland (Keith, 2003).

The seasons seem to have a major impact on the PLD with the difference of SST and the variability of the freshwater flow. But according to Grant and Bowen (1998), the larval dispersal could be subject to numerous physical barriers such as the depth, the salinity, the gyres and the current patterns (Borkin, 1991; Hare and Cowen, 1996; Murphy and Cowan, 2007). And larvae could also actively swim in the sea as described in gobiids (Balon and Bruton, 1994; Leis and McCormick, 2002; Iida *et al.,* 2010b). All of these may have an impact on the PLD.

The distance and the difficulty to reach some islands may lead to longer PLDs and increase the probability of a suitable stream for recruitment (Radtke and Kinzie, 1996; Keith, 2003). In the widespread amphidromous species *S. lagocephalus,* as it is the case for *E. fusca*, PLDs in Pacific islands are shorter (130 ± 3.4 days; Lord *et al.,* 2010) than those of Reunion Island (201 ± 40 days, Hoareau, 2005; 170.4 ± 43.7 days, Teichert, 2014). Thus, it seems that Reunion Island is submitted to special current conditions. Indeed, the island appears to be isolated by the anticyclonic subtropical gyre in the South-Western Indian Ocean (Wyrtki, 1973). Larvae emitted from Reunion Island or from Maurice Island may stay in the sea for a longer period of time, which would explain increased PLDs. Moreover, the percentage of auto- and allo-recruitment is unknown but we know that there is gene flow between Indian islands (Mennesson, unpubl. data).

Nevertheless, more studies are needed to explain these results. A phylogeographic study on the populations of *E. fusca* would bring insights into the dispersal of the species.

Otolith growth

For all the samples, during growth, pattern is observed for all fish during the larval phase. Indeed, no significant difference in the otolith growth rate (µm/day) was detected between the four sites and between both oceans (Fig. 5). The otolith growth reflects the fish growth and evolves according to three phases. During the first phase (first 10 days), the growth is rapid (e.g. Vanuatu individuals: 6.79 ± 1.57 µm/day); then in the second phase, it drops 10 days after (4.26 ± 0.72 µm/day) and decreases gradually (3.93 to 2.5 µm/day) in the third phase (from the 30th day), until it reaches a plateau. These phases might be related to the morphological and physiological modifications of larvae during the marine phase (Valade, 2001; Keith *et al.,* 2008). However, the timing of the first deposition is not yet known for *Eleotris fusca* and it may also have several days lag. But it is generally known for a lot of fish species that the first increment is deposited during their first feeding when the larva has completed yolk absorption (Brothers *et al.,* 1976; Laroche *et al.,* 1982; Tzeng and Yu, 1988) but it needs to be studied for *E. fusca*. Maeda *et al*. (2008) studied the reproductive biology and the early development of *E. fusca*. This study showed that embryos spend more than 24 hours in their egg and that the yolk sac decreases the first day after hatching and disappears the fourth day under rearing condition. The mouth and the pectoral fins begin to form the second day. On the third day the mouth is opened. Thus, the mouth is functional before the yolk sac is completely absorbed. In the sea, larvae are supposed to be planktonic and feeding on zooplankton, which is less energetic than the yolk sac; that could induce a decrease of growth rate after the first 10 days (Lord *et al.,* 2010; Teichert *et al.,* 2014).

It is important to specify that there is an individual variability in the otolith growth rate in amphidromous fish (Lord *et al.,* 2010; this study). Some aspects and events might affect it, such as genetic or environmental variability like the food resources (Jones, 1986; Cushing, 1990) or water temperatures (McCormick and Molony, 1995; Shafer, 2000; Radtke *et al.,* 2001), depending themselves on the seasons.

CONCLUSION

This study shows that *Eleotris fusca* is an amphidromous species with a high variability in the PLD according to the sampling localities. This variability illustrates the fact that *E. fusca* has a high plasticity in its pelagic larval duration and thus reveals an important adaptation capacity, according to the environmental conditions encountered. Nevertheless, amphidromous species are distributed along the river from the estuary to higher reaches according to their ecology. And it is important to allow species to move freely (no barriers) between downstream and upstream in the river and between the river and the sea. The success of such a life cycle depends highly on the management and the conservation of their habitats.

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