

Pelagic larval duration of two diadromous species of Kuhlidae (Teleostei: Percoidei) from Indo-Pacific insular systems

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Abstract. Diadromous fish species in the family Kuhlidae are able to colonise freshwater systems in Indo-Pacific islands, but their life cycle and the mechanisms involved in the colonisation of such ecosystems are poorly documented. After validating the daily rate of increment deposition in otoliths of *Kuhlia rupestris*, we estimated the pelagic larval duration (PLD) of *K. rupestris*, widely distributed in the Indo-Pacific area, and *K. sauvagii*, endemic to the Indian Ocean. Median PLD of *K. rupestris* was significantly longer than that of *K. sauvagii* (40.6 ± 6.9 and 32.3 ± 3.4 days (\pm s.d.), respectively), implying that the PLD is probably one factor controlling the extent of distribution range in *Kuhlia*. Within *K. rupestris*, individuals from New Caledonia had longer PLDs than those from Réunion Island (44.3 ± 6.7 and 37.3 ± 4.7 days (\pm s.d.) respectively). Further research on larval migration is needed to determine whether this was due to different environmental conditions or is population-specific. Interestingly, the PLD of these *Kuhlia* species is shorter than the PLD of other tropical diadromous fishes. These results improve our understanding of the dispersal strategies of freshwater fauna, to colonise and persist in tropical islands.

Additional keywords: diadromy, endemism, fish, larval dispersion, otolith increment counts.

Received 4 November 2011, accepted 16 January 2012, published online 4 May 2012

Introduction

Freshwater habitats on volcanic islands in the Indian and Pacific Oceans are geologically recent environments. Because of their isolation from other freshwater habitats, only marine species entering via estuaries or diadromous species have been able to colonise these rivers. Consequently, diadromous species represent the major part of the native ichthyofauna (Keith 2003); there are few (if any) fully freshwater species. On these islands, freshwater diadromous populations use long marine larval dispersal to ensure their persistence within and among islands. Exogenous recruits could ensure their persistence if local reproduction fails (MacArthur and Wilson 1963).

In small volcanic island streams in the tropics, teleostean fish are mostly represented by the Gobiidae, Eleotridae, Anguillidae, Syngnathidae and Kuhlidae families. Gobiidae, Eleotridae and Syngnathidae species are amphidromous (Keith *et al.* 2006b). The adults grow, feed and reproduce in rivers. After hatching, the larvae drift downstream towards the sea where they spend a variable amount of time (Keith *et al.* 2006a). Post-larvae then

return to freshwater to grow, mature and spawn (Keith 2003). Anguillidae are catadromous; larvae hatch at sea and move to fresh water as small juveniles for most feeding and growth. Adults then migrate back to sea (Myers 1949). The freshwater Kuhlidae species are known to be diadromous (Feutry *et al.*, in press *b*) but the reproduction, recruiting phases and the processes experienced during the marine larval phase are unknown. Nevertheless, the larval stage is one of the most important phases to understand how these species disperse and are distributed in Indo-Pacific islands as the size of the distribution range may depend on the PLD (Lord *et al.* 2010).

With 12 species described in a single genus (*Kuhlia*), the Kuhlidae family has a tropical Indo-Pacific distribution (Randall and Randall 2001; Loiselle and Stiassny 2007). Six species are marine, five are diadromous and *K. munda* is partially diadromous because it spends its early life at sea and then colonises estuaries (Feutry *et al.*, in press *b*). *K. rupestris* and *K. sauvagii* are both diadromous species (Hogan and Nicholson 1987; Loiselle and Stiassny 2007; Feutry *et al.*,

in press *b*). *K. rupestris* is widespread in the Indo-Pacific region, extending from the east coast of Africa to Samoa and from north-eastern Australia to the Ryukyu Islands in Japan (Randall and Randall 2001). *K. sauvagii* is restricted to the western Indian Ocean where it occurs in sympatry with *K. rupestris* (Feutry *et al.*, in press *a*).

Because of habitat destruction and overfishing, Kuhlidae representatives have become rare in many streams, particularly in Australia (Lewis and Hogan 1987). Harvesting this resource needs careful management to be sustainable, on account of the complexity of the species' life cycles, which are not yet fully understood. Knowledge on their life history is essential for their protection and management (Merrick and Schmida 1984; Keith *et al.* 2006*b*) and understanding population connectivity is of major importance to implement spatial management measures (Roberts 1997). The PLD is one of the fundamental components to examine in the study of population connectivity (Cowen and Sponaugle 2009).

Since the observation of the daily increments in cross-sections of fish otoliths, studies involving otolith microstructure have provided information on growth rate, hatch date or PLD (Begg *et al.* 2005; Campana 2005). Ring counts and check marks have often been used to estimate the PLD in tropical diadromous species. These PLD estimations were possible because recruitment into freshwater is indicated on the otolith by a check mark (Keith *et al.* 2008). A check mark corresponds to a detectable change in the structure of the otolith, and can be observed either by light or electronic microscopy. Check marks indicating freshwater recruitment have been reported in *K. rupestris* and *K. sauvagii* (Feutry *et al.*, in press *b*). Among the Kuhlidae species, the daily otolith increment deposition has been validated only for *K. xenura* by Benson and Fitzsimons (2002) and additional examples are needed.

Here, we first confirm the deposition of daily otolith increments for *K. rupestris*, and then estimate the PLD of *K. rupestris* and *K. sauvagii* by counting the increments on the otoliths from the core to the check mark. The PLD was compared between the two species, to test the hypothesis that the endemic species *K. sauvagii* has a shorter PLD than the widely distributed species *K. rupestris*. Our study provides basic knowledge for the management of these species, and has increased our understanding of freshwater biodiversity in tropical islands.

Materials and methods

Specimen collection

In total, 45 *K. rupestris* samples were collected in New Caledonia (Pacific Ocean) and Réunion Island (Indian Ocean) and 33 *K. sauvagii* samples were collected in Madagascar (Table 1) by electrofishing with a DEKA 3000 (EFKO, Leutkirch, Germany), 350 V, 4–6 A. All fish were anaesthetised with eugenol and fixed in three successive 90% ethanol baths before otolith extraction. Another 15 *K. rupestris* juveniles were captured in Réunion Island and kept alive for the otolith growth-rate experiment.

Staining experiment

The staining experiment to validate daily growth of otolith rings of *K. rupestris* took place in April 2010 in Réunion Island. The

Table 1. Number (*N*), standard length (SL) in millimetres and sampling dates of the *Kuhlia rupestris* and *K. sauvagii* caught in New Caledonia, Réunion Island and Madagascar

Species	Site	Date	<i>N</i>	SL
<i>K. rupestris</i>	New Caledonia	January 2010	21	17–24
	Réunion Island	August 2008	13	20–26
		January 2009	3	23–25
		March 2009	4	25–26
<i>K. sauvagii</i>	Madagascar	May 2010	33	35–87

fish were exposed for 16 h to a 100–100 mg L⁻¹ solution of alizarin red S (ArS) (Sigma, Seelze, Germany), an aragonite dye useful for staining otoliths in juvenile fish (Blom *et al.* 1994; Lagardère *et al.* 2000), and then transferred to a 1500-L tank of clear freshwater for 20 days. During the experiment, the fish were held outside (ambient temperature ~22–28°C) under natural light/dark conditions and fed twice (at Day 7 and Day 14) with *Oreochromis* spp. larvae. At the end of this 20-day period of growth in unstained water, the fish were exposed to a second treatment with a 200-mg L⁻¹ ArS solution for 16 h. The second ArS bath was conducted in case the first staining had failed because ArS concentration was too low. To the contrary, 200-mg L⁻¹ ArS was too concentrated and all fish died during the second bath. They were numbered from 1 to 15 and their standard length was measured to the nearest millimetre before otoliths were extracted.

Right sagittal otoliths were extracted and organic tissues were removed using an ultrasonic cleaner for 3–5 min. Otoliths were embedded in Araldite 2020 Epoxy resin (Escil, Chassieu, France) and sectioned with a diamond saw as close to the core region as possible along a frontal plane. The sections were mounted on glass slides with thermoplastic adhesive (Crystalbond, SPI Supplies, West Chester, PA, USA) and polished on both sides with grit wet-dry sandpaper of 15.3–10 µm (G1200 and G2400, Escil) until the section was ~40–60 µm thick.

Images were obtained using a Leica DM-IRB microscope coupled to a Z-stage piezo-controller (Sutter Instrument Co., Novato, CA, USA). The objective used was either a ×100 (numerical aperture (NA) 1.4) oil-immersion plan or a ×10 (NA 0.4), and illumination used was a 100-W mercury lamp. The set of filters used to visualise the fluorescence of ArS was 550/20 nm excitation and 620/40 nm emission. The ArS marks and the counting of daily increments were performed by manual inspection from a z-stack of images (total depth of the scan = 20 µm). Images were analysed using Metamorph software 7.7 (Molecular Devices, Sunnyvale, CA, USA). The micro-increments were counted from the edge of the stained section to the edge of the otolith (Fig. 1).

Unstained otolith preparation and increment counts

After otolith sagittae were removed from the 78 fish caught for the examination of PLD, they were cleaned as described above and embedded in a droplet of Araldite 2020 epoxy resin (Escil) on glass slides. They were polished along their sagittal plane with grit wet-dry sandpaper of 15.3 µm and then 10 µm (G1200 and G2400, Escil) until the core was exposed. Once polished and etched with 5% EDTA solution for 2–3 min (etching increased

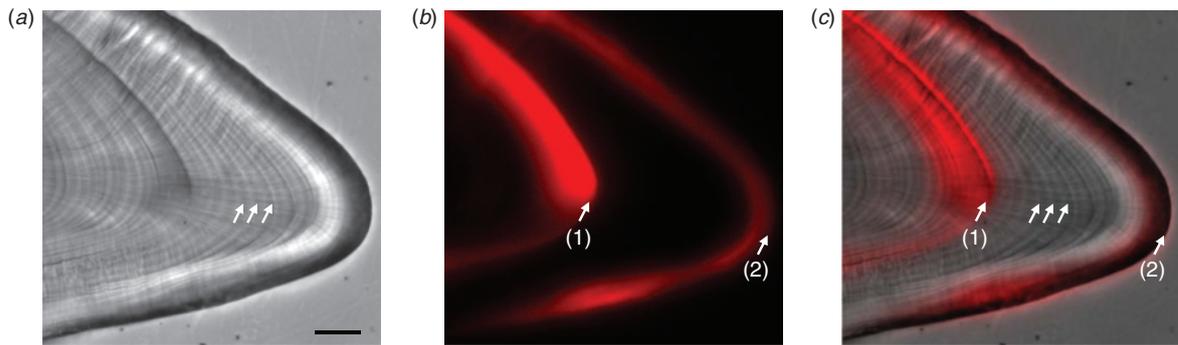


Fig. 1. Otolith section of a *Kuhlia rupestris* after staining. The daily increments and the two stained rings correspond to the first alizarin red S (ArS) bath (1) and the second ArS bath on the edge of the otolith (2) are indicated by arrows. Images correspond to (a) Nomarski, (b) ArS fluorescence and (c) overlay. Scale bar = 50 μm .

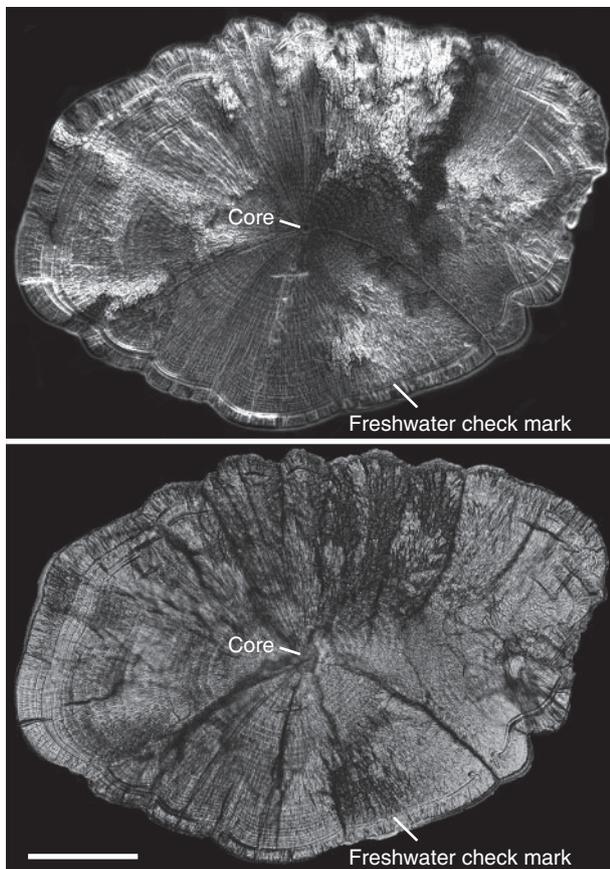


Fig. 2. An otolith of *Kuhlia rupestris* under scanning electron (above) and light (below) microscope after EDTA etching. Scale bar = 200 μm .

the readability of otolith increments, Feutry *et al.*, in press *b*), the otolith was observed under both scanning electron (Tescan, VEGA II LSU, Brno, Czech Republic) and light (Olympus BX51, equipped with an Olympus DP20 digital camera, Olympus, Rungis, France) microscopes. As observations were very similar between microscopes (Fig. 2), only light microscopy was used for the rest of the samples. Each otolith was photographed.

The core was observed as a deep hole in the centre of the etched otolith, and the first increment (surrounding the core) was assumed to occur at hatching (Réveillac *et al.* 2008). The number of daily increments on each otolith was counted from the core to the freshwater check mark (for subadults and juveniles that had completed the transition from marine to freshwater habitats) (Fig. 2) and from the core to the edge of the otolith for new recruits (where a decrease of increment widths is observed but the check is not yet visible because the transition to freshwater had not been completed).

Statistical analyses of the data

We compared the mean PLD between *K. rupestris* and *K. sauvagii* species and between *K. rupestris* individuals from New Caledonia and those from Réunion Island, using the XLSTAT (Addinsoft, Paris, France) add-in for Microsoft Excel. First, the normality of the *K. rupestris* and the *K. sauvagii* data was verified using Shapiro's test. As sample size was small in each location for *K. rupestris* and because normality was rejected for the *K. sauvagii* sample, the variability of the PLD in samples of *K. rupestris* from Réunion Island and New Caledonia and the difference between these two *K. rupestris* samples and *K. sauvagii* were tested by non-parametric Mann–Whitney *U*-tests. We also examined the maximum PLD value found at each sampling site because this measure may be a good estimate of dispersal abilities (Weersing and Toonen 2009).

Results

Experimental validation of the daily increment formation

Otolith sections of all specimens presented a red stain ring at $\sim 60 \mu\text{m}$ from the edge (corresponding to the first ArS bath) and 13 out of the 15 otoliths presented another stain ring on their edge that corresponded to the second ArS bath (Fig. 1, Table 2). As would be expected if the rings were deposited daily, the counts between the first stain and the otolith edge ranged from 19 to 21 and the mean was $20.3 (\pm 0.6 \text{ s.d.})$ for the 15 specimens.

Estimation of the age at recruitment

On the basis of the validation of the daily increment formation on *K. rupestris*, we assumed that the otolith rings in *K. sauvagii* were also deposited daily. Therefore, we defined the PLD of

both species as the number of increments between the core and freshwater check mark or, for new recruits, between the core and the edge of the otolith. The median PLD for pooled data of *K. rupestris* was significantly longer than for *K. sauvagii* ($U=742.5$, $P<0.0001$, Table 3). The median PLD of the *K. rupestris* individuals from New Caledonia exceeded those from Réunion Island ($U=91$, $P<0.0001$, Table 3). The maximum PLD found among the *K. rupestris* individuals from New Caledonia was higher than PLD among individuals from Réunion Island, which was higher than the value found for *K. sauvagii* (Table 3).

Discussion

Daily increment

Otolith increments were deposited daily in *K. rupestris* under the experimental conditions of the present study. Many other studies have also validated the daily accretionary growth in otoliths (Begg et al. 2005; Campana 2005), in particular in diadromous species (Radtke et al. 1988; McDowall et al. 1994; Hoareau et al. 2007; Iida et al. 2010). The need to validate the daily otolith growth rate for every single fish species has been questioned even if increment deposition rate may be affected by environmental conditions (Begg et al. 2005). In the Kuhliidae, the daily growth of otoliths has been validated for *K. xenura* (Benson and Fitzsimons 2002) and *K. rupestris* (the present study). Little doubt remains now that the other Kuhliidae species also exhibit daily growth rings, at least as juveniles.

Table 2. Standard length (SL), increment counts (IC) and presence/absence of a second stain ring (2nd SR) for each *Kuhlia rupestris* included in the staining experiment

Specimen	SL (mm)	IC	2nd SR
1	38	21	Present
2	40	20	Present
3	37	20	Present
4	31	20	Present
5	31	20	Present
6	31	21	Present
7	35	20	Present
8	39	21	Present
9	31	21	Present
10	30	19	Absent
11	33	21	Present
12	43	20	Absent
13	40	20	Present
14	35	21	Present
15	35	20	Present

Interestingly, the second stain observed on the otolith edges of nearly all specimens indicates that the ArS was incorporated almost immediately in otoliths during this experiment. The edge of the otolith was not stained for 2 of 15 fish, probably because they died soon after the beginning of the second ArS treatment.

Age at recruitment

In our study, both the median and maximum PLDs were longer for the widespread species *K. rupestris* than for the species *K. sauvagii* endemic to the western Indian Ocean (Table 3). The observed differences in PLD could explain the different extents of distribution of the two species, as proposed by Lord et al. (2010) for amphidromous gobies of genus *Sicyopterus*. They showed that the PLD was significantly shorter in two endemic *Sicyopterus* species than in a more cosmopolitan one (Table 4). An exception was the endemic species *S. japonicus* for which the PLD was estimated to be as long as 163.7 ± 12.8 days (Shen and Tzeng 2008), or even 208 ± 22 days (Iida et al. 2008). However, this species' distribution is probably driven by temperate temperatures and currents (Watanabe et al. 2006; Iida et al. 2008).

In tropical *Sicyopterus*, the mean PLD of the endemic species studied was ~ 50 days shorter than that for the widespread species, whereas the difference was less than 10 days between *K. sauvagii* and *K. rupestris*. Other factors such as spawning output, larval behaviour, survival under predation, availability of settlement habitat and post-settlement survival may contribute to dispersal (Cowen and Sponaugle 2009), and also could explain the observed differences in the extent of distribution.

The significant differences observed between the sampling locations (New Caledonia, Réunion Island) for *K. rupestris* may be due to phenotypic plasticity or genetic differences between populations. The PLD is known to change seasonally and is affected by water temperature (Maeda et al. 2007). In addition to more thorough investigations of PLD including seasonal and regional variations, knowledge about aspects of the migratory routes of larvae (e.g. depth and temperature) plus molecular analyses of populations are required to be able to distinguish between these two hypotheses.

Surprisingly, the PLDs found in the present study for *Kuhlia* species were much lower than those found in other diadromous fish inhabiting tropical islands (Table 4). The long PLD observed in other diadromous organisms is thought to be an adaptation to their life in unstable habitats in tropical insular streams (Lord et al. 2010), especially to delay metamorphosis and to locate and colonise freshwater habitats (Radtke et al. 2001; Murphy and Cowan 2007). *Kuhlia* species seems not to rely on such strategy to succeed in tropical islands, and our study brings new perspectives for the understanding of the ecology of freshwater fauna in these systems.

Table 3. Mean and range of age at recruitment (in days, \pm s.d.) per sampling location for *Kuhlia rupestris* and *K. sauvagii*

Species	Location sampling size	New Caledonia, $n=21$	Réunion Island, $n=24$	Pooled data, $n=45$	Madagascar, $n=33$
<i>K. rupestris</i>	Mean range	44.3 ± 6.7 (27–58)	37.3 ± 4.7 (29–45)	39.2 ± 6.9 (27–58)	–
<i>K. sauvagii</i>	Mean range	–	–	–	32.3 ± 3.6 (27–40)

Table 4. Pelagic larval durations for various tropical diadromous species, either endemic or more widespread species

Species	Migratory status	Geographical range	Mean pelagic larval duration (days \pm s.d.)	Reference
<i>Stiphodon percopterygionus</i>	Amphidromous	Endemic, Ryukyu Islands and Taiwan	99 \pm 16	Yamasaki <i>et al.</i> 2007
<i>Lentipes concolor</i>	Amphidromous	Endemic, Hawaii	86.2 \pm 8.5	Radtke <i>et al.</i> 2001
<i>Cotylopus acutipinnis</i>	Amphidromous	Endemic, Mascarene	101 \pm 14	Hoareau <i>et al.</i> 2007
<i>Stenogobius hawaiiensis</i>	Amphidromous	Endemic, Hawaii	135 \pm 9.2	Radtke <i>et al.</i> 1988
<i>Awaous guamensis</i>	Amphidromous	Widespread, West Pacific to Hawaii	161 \pm 5.7	Radtke <i>et al.</i> 1988
<i>Sicyopterus lagocephalus</i>	Amphidromous	Widespread, Indo-Pacific	131 \pm 3.4	Lord <i>et al.</i> 2010
<i>Sicyopterus sarasini</i>	Amphidromous	Endemic, New Caledonia	76.5 \pm 3.9	Lord <i>et al.</i> 2010
<i>Sicyopterus aiensis</i>	Amphidromous	Endemic, Vanuatu	79.2 \pm 4.6	Lord <i>et al.</i> 2010
<i>Eleotris fusca</i>	Amphidromous	Widespread Indo-Pacific	84–111	Maeda <i>et al.</i> 2007
Tropical <i>Anguilla</i> spp.	Catadromous	Endemic or widespread	90–150	Arai <i>et al.</i> 2001

Conclusions

In the present study, we validated the daily rate of otolith increment deposition and we demonstrated that the PLD is probably one of the factors explaining the different distribution ranges in *Kuhlia* species. The PLD of *K. sauvagii*, which is restricted to the western Indian Ocean, was significantly shorter than the PLD of the Indo-Pacific species *K. rupestris*. Future studies should focus on larval behaviour, spawning output or salinity tolerance of juveniles and adults, to understand how the *Kuhlia* species are able to ensure their survival in tropical islands with such short PLD, especially during long-term disturbances of their habitats. However, the short PLDs found here in *Kuhlia* species suggest reduced dispersal abilities compared with other diadromous species inhabiting tropical islands. This information is of major importance for the conservation of *Kuhlia* species and we recommend that each population should be managed locally (i.e. for each isolated island or archipelago) because exogenous recruitment may be limited.

Acknowledgements

Field work in New Caledonia was partly financed by the BIONEAL ANR, whereas the sampling in Madagascar was part of the program DIA-MSOI funded by the 'Institut Français de la Biodiversité'. We thank the New Caledonian North and South Provinces (J.-J. Cassan, C. Flouhr, J. Manauté and C. Méresse) for allowing sampling (Permit No 1224-08/PS). We are grateful to Joe Aride from Madagascar National Parks and the Manager of Masoala National Park. We also thank the 'Association Réunionnaise de Développement de l'Aquaculture' (ARDA) and especially H. Grondin, T. Robinet and G. Marquet for their help in field experiments in Réunion Is and Madagascar. Sampling permits in Réunion Is were Nos 38/AM/08 and 117/AM/09. This work was also supported by the ATM 'Formes possibles – Formes réalisées' from the MNHN. Last, we are grateful to Dr A. Boulton and two anonymous referees for their constructive comments on the manuscript.

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