*Ecology of Freshwater Fish 2012*
*Printed in Malaysia · All rights reserved*

ECOLOGY OF
FRESHWATER FISH

# Pelagic larval duration of three amphidromous Sicydiinae gobies (Teleostei: Gobioidei) including widespread and endemic species

**Laura Taillebois[1], Ken Maeda[2], Stéphane Vigne[1], Philippe Keith[1]**
[1]Biologie des Organismes Marins et Ecosystèmes (UMR BOREA 7208 CNRS-MNHN), Muséum national d'Histoire naturelle, Département Milieux et Peuplements Aquatiques, CP-026, 43 rue Cuvier, 75231, Paris, France
[2]Marine Genomics Unit, Okinawa Institute of Science and Technology Graduate University, 1919-1 Tancha, Onna-son, Okinawa, 904-0412, Japan.

Accepted for publication April 21, 2012

Abstract – Sicydiinae species have an amphidromous life cycle during which they undergo a pelagic larval phase allowing them to disperse through the ocean and to recruit in distant island rivers. Hypotheses for the differences observed in dispersal abilities between species include the variation in pelagic larval duration (PLD). However, the implication of the PLD as a proxy for explaining the dispersal ability of a species is not clear in the Sicydiinae subfamily. In this study, otolith microstructure of three Sicydiinae species was analysed. One of these species, *Sicyopus zosterophorum*, has a widespread distribution in the West Pacific area, whereas the other two species, *Smilosicyopus chloe* and *Akihito vanuatu*, are endemic to New Caledonia and to Vanuatu, respectively. Deposition of the daily growth increments on the otoliths of *S. zosterophorum* was validated using an alizarin complexone time marking technique. We estimated the PLD for the three species by counting the number of growth increments from the core to the metamorphosis check mark, and it was shorter than the one of previous studies on Sicydiinae species. The PLD of the widespread species, *S. zosterophorum* (54.6 ± 5.6 days), was similar to those of the endemic species, *S. chloe* (53.6 ± 5.7 days) and *A. vanuatu* (55.4 ± 7.5 days). Here, we show that in contrast to the most diverse Sicydiinae genus, *Sicyopterus*, the PLD could not explain endemism, and we must take into account other elements to explain the differences observed in the distribution range.

Key words: dispersal; *Akihito*; *Sicyopus*; *Smilosicyopus*; otolith microstructure; amphidromy; pelagic larval duration

## Introduction

Insular river systems in the tropical and subtropical Indo-Pacific area are mainly colonised by freshwater gobioids. Species from the Sicydiinae subfamily have an amphidromous life cycle, which allows them to disperse through the ocean and to recruit in distant island rivers. This cycle is adapted to the conditions in these distinctive habitats, which are young oligotrophic rivers subject to extreme climatic and hydrological seasonal variation (Keith 2003; McDowall 2007). The adults grow, feed and reproduce in freshwater habitats. Hatched larvae drift downstream towards the sea (Luton et al. 2005; Maeda & Tachihara 2010) where they spend a variable amount of time, ranging from 2 to 6 months (Yamasaki et al. 2007; Iida et al. 2008; Lord et al. 2010). At the end of the pelagic larval phase, the postlarvae recruit to rivers and they undergo a metamorphosis (Keith et al. 2008; Valade et al. 2009; Taillebois et al. 2011) while migrating upstream to settle in the upper reaches.

At certain times of the year, the biomass of gobioid larvae recruiting is so great that they become a major source of food for local human populations in the Indo-Pacific area (e.g., Reunion Island, Vanuatu and French Polynesia) (Bell 1999; Valade et al. 2009; Lord et al. 2010). The adult phase, the larval downstream migration and the recruiting phase are only starting to be understood in detail (Keith et al. 2006;

*Correspondence*: L. Taillebois, Biologie des Organismes Marins et Ecosystèmes (UMR BOREA 7208 CNRS-MNHN), Muséum national d'Histoire naturelle, Département Milieux et Peuplements Aquatiques, CP-026, 43 rue Cuvier, 75231 Paris, France. E-mail: taillebois@mnhn.fr

doi: 10.1111/j.1600-0633.2012.00575.x

Yamasaki & Tachihara 2006; Valade et al. 2009; Lord et al. 2010; Yamasaki et al. 2011). However, the processes undergone during the pelagic larval phase remain poorly known (Radtke & Kinzie 1996; Shen et al. 1998; Radtke et al. 2001) although their understanding would help elucidate how these species disperse and are distributed. Additionally, understanding these processes is a necessity to implement conservation measures to protect Sicydiinae as they contribute most to the diversity of fish communities in the tropical Indo-Pacific insular river systems and have the highest level of endemism (Lord & Keith 2008; Keith & Lord 2011a).

The Sicydiinae subfamily comprises nine genera and nearly 110 species (Keith & Lord 2011b; Keith et al. 2011a). No two genera are similarly distributed, with each having a unique distribution of their own (Keith et al. 2011a), for example *Akihito* is only distributed in the South Pacific Ocean (Keith et al. 2007; Watson et al. 2007), whereas *Sicyopus* is widely distributed from Madagascar in the West Indian Ocean to Fiji in the South Pacific Ocean (Watson 1999; Keith et al. 2011b). In the present study, pelagic larval duration (PLD) was investigated for one widespread and two rare endemic species belonging to different genera of the Sicydiinae subfamily: *Sicyopus zosterophorum* (Bleeker, 1856) is widely distributed from southern Japan to Micronesia and from Indonesia to Fiji (Watson 1999); *Smilosicyopus chloe* (Watson et al. 2001) is endemic to New Caledonia and Vanuatu; and *Akihito vanuatu* Watson, Keith & Marquet 2007 is endemic to Vanuatu (Fig. 1a). All of them inhabit swift, clear, high-gradient streams. The two endemic species are sympatric with the widespread *S. zosterophorum.*

Otoliths are well-known paired calcified structures in the fish's inner ear. They are metabolically inert, grow continuously on a daily basis throughout the individual's life cycle (Campana 1999; Lecomte-Finiger 1999) and do not undergo any mineral resorption (Mugiya & Uchimura 1989). They have therefore long been used for age estimation in many fish species (Victor 1986; Wellington & Victor 1989; Victor & Wellington 2000; Kuroki et al. 2007), including Sicydiinae (Radtke et al. 1988, 2001; Shen & Tzeng 2002, 2008; Yamasaki et al. 2007; Lord et al. 2010). The Sicydiinae metamorphosis is materialised on the otolith by a metamorphosis check mark, reflecting a decrease in the rate of calcareous growth, formed as the postlarvae recruit to the rivers and start to settle the upper reaches (Shen & Tzeng 2002; Keith et al. 2008). The increment count from the core to the metamorphosis check mark is therefore an estimation of the PLD.

The purpose of this study is to validate the formation of daily increments on otoliths of *S. zosterophorum* and to estimate the PLD of *S. zosterophorum*, *S. chloe* and *A. vanuatu* in order to better understand the differences between endemic and widespread species. The PLD was compared between the three species to test the hypothesis that endemic species has shorter PLD than widely distributed species.

## Material and methods

### Studied areas and sample collection for ageing

Specimens used in the present study were collected in Vanuatu, New Caledonia, Indonesia and Japan. In Vanuatu, samples of *S. zosterophorum* and *S. chloe* were caught on Santo and Gaua (July 2005), Ambae, Pentecost, and Malekula Islands (January–February 2010). The endemic species of Vanuatu, *A. vanuatu,* was collected on Ambae and Pentecost Islands (January–February 2010) (Fig. 1e). In New Caledonia, samples of *S. zosterophorum* and *S. chloe* were caught in the north-eastern side of Grande Terre (January and October 2010) (Fig. 1d). The widespread species *S. zosterophorum* was also collected in rivers on Okinawa and Iriomote Islands (December 2010–April 2011) (Fig. 1b) in the Ryukyu Archipelago, Japan, and in Papua Province (Indonesia) (October 2010) (Fig. 1c).

A total of 59 *A. vanuatu* (adults, 22.3–39.9 mm in standard length – SL), 62 *S. zosterophorum* (adults and juveniles, 20.4–45.0 mm SL) and 47 *S. chloe* (adults, 21.2–40.4 mm SL) were caught for the age estimation (Table 1). Specimens were sampled by electro-fishing (Portable Dekka 3000 electric device; Dekka Ltd, Leutkirch, Germany), using a large hand net, or only with the use of hand nets while snorkelling. Fish were put to sleep and killed using an overdose of 10% clove essential oil and were then kept in 95% ethyl alcohol.

### Validation of daily increments

To validate the daily deposition of the growth increments in the otolith of *S. zosterophorum*, we used an alizarin complexone (ALC) time marking technique. Six juveniles were collected from a stream on the northern part of Okinawa Island on 27 and 28 November 2010. These juveniles were brought alive to the laboratory where they were transferred in the evening of the 28th November to a 3-l freshwater tank containing a 50 $\mathrm{mg \cdot l^{-1}}$ solution of ALC and were held there for 24 h. All six juveniles were then kept in two 4-l freshwater tanks (each tank containing three juveniles) for 12 days before a second treatment with the 50 $\mathrm{mg \cdot l^{-1}}$ ALC solution for 24 h. After an additional 8-day rearing in freshwater tanks, all fish were put to sleep and killed using an overdose of

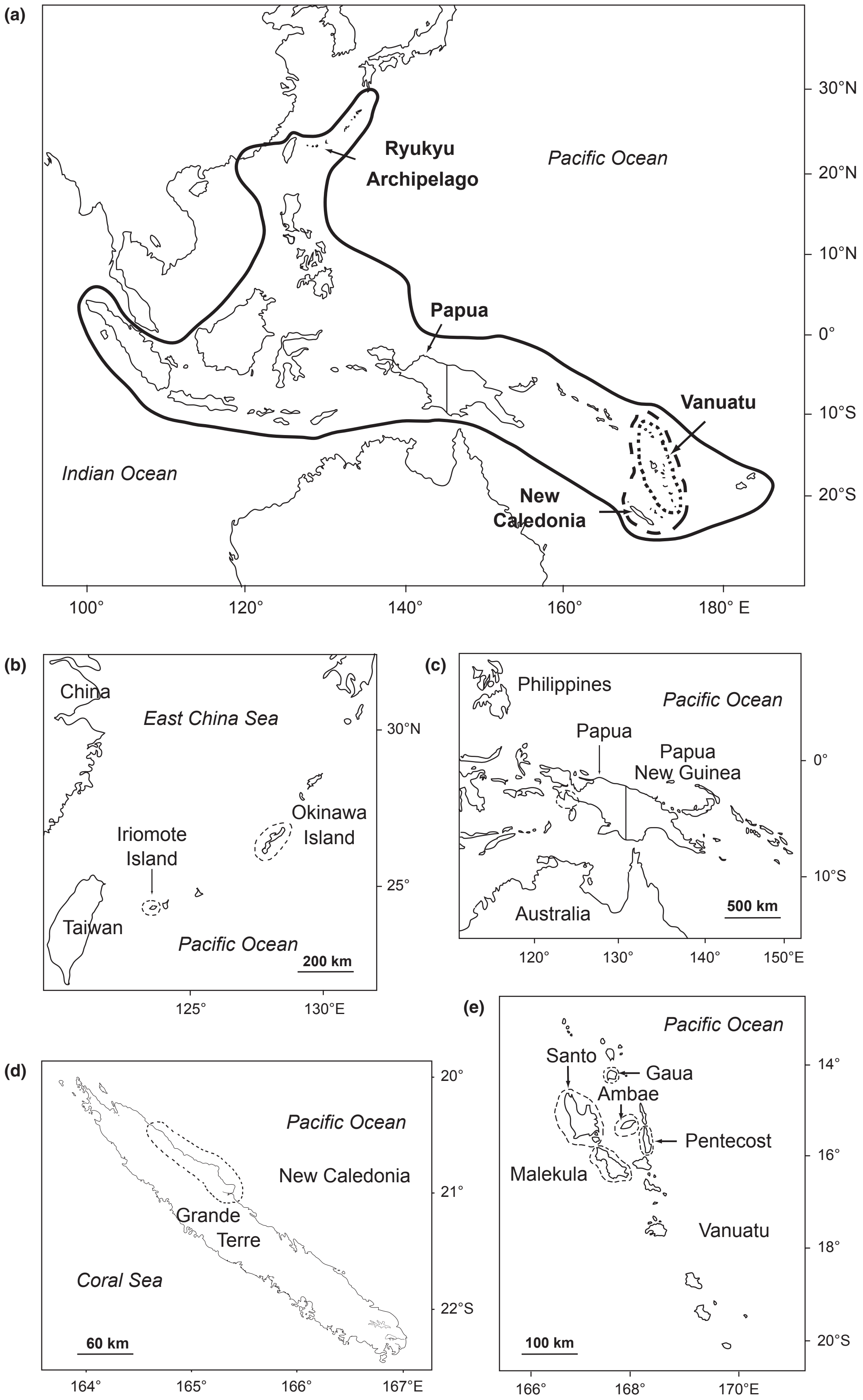

*Fig. 1.* The distribution range of (a) *Sicyopus zosterophorum* (solid line), *Smilosicyopus chloe* (broken line) and *Akihito vanuatu* (dotted line) and various sampling sites (b–e) (dotted line) on the Ryukyu Archipelago, Papua, New Caledonia, and Vanuatu, respectively.

Table 1. Sampling localities and numbers of *Sicyopus zosterophorum*, *Smilosicyopus chloe* and *Akihito vanuatu* specimens.

| | | | | | | |
|---|---|---|---|---|---|---|
| Vanuatu | Santo Island | Malekula Island | Pentecost Island | Ambae Island | Gaua Island | Total |
| Date | Jul. 2005 | Nov. 2008/Feb. 2010 | Jan. 2010 | Nov. 2007/Jan. 2010 | Jul. 2005 | |
| *S. zosterophorum* | *n* = 0 | *n* = 16 | *n* = 0 | *n* = 0 | *n* = 0 | *n* = 16 |
| *S. chloe* | *n* = 4 | *n* = 9 | *n* = 0 | *n* = 0 | *n* = 5 | *n* = 18 |
| *A. vanuatu* | *n* = 0 | *n* = 0 | *n* = 28 | *n* = 31 | *n* = 0 | *n* = 59 |
| New Caledonia | Po Vila | Kokengone | Newe Dena | Wewec | Wan Pwé On | Total |
| Date | Jan. 2010 | Jan. 2010/Oct. 2010 | Jan. 2010 | Oct. 2010 | Jan. 2010 | |
| *S. zosterophorum* | *n* = 11 | *n* = 0 | *n* = 9 | *n* = 4 | *n* = 0 | *n* = 24 |
| *S. chloe* | *n* = 2 | *n* = 17 | *n* = 6 | *n* = 3 | *n* = 1 | *n* = 29 |
| Papua | Bichain Creek | Akuyama | | | | Total |
| Date | Oct. 2010 | Oct. 2010 | | | | |
| *S. zosterophorum* | *n* = 4 | *n* = 4 | | | | *n* = 8 |
| Japan | Okinawa Island | Iriomote Island | | | | Total |
| Date | Mar.-Apr. 2010 | Jul. 2007 | | | | |
| *S. zosterophorum* | *n* = 12 | *n* = 2 | | | | *n* = 14 |

10% clove essential oil and were then kept in 99% ethyl alcohol. Fish were then dissected under a binocular magnifier (40 X; Olympus VMZ, Germany). The otoliths were placed in distilled water to clean them, and we eliminated remaining tissues from the macula and the vestibule using fine tweezers (Secor et al. 1992). Standard lengths of the six juveniles were 18.6–21.0 mm at the end of the experiment. During the treatment, fish were fed on *Artemia salina* nauplii and small pieces of dried krill every day, and the water temperature was 22.5–23.0 °C.

The otoliths were embedded in epoxy resin (Epofix; Struers, Champigny-sur-Marne, France) and ground along a transverse section to expose the edge using sandpaper (400–2000 grains per inch). Otoliths were polished with abrasive powder (grain diameter, 0.5–3.0 μm). The polished otolith sections were observed under an optical microscope (AXIO Imager Z1; Zeiss, Germany) and photographed using a digital camera (AxioCam HRC; Zeiss) under a UV and a normal light sources (1000× magnification with immersion oil). The two alizarin-stained bands were located under a UV light source, and then, numbers of opaque increments between those two bands were counted in the photographs taken under a normal light source.

### Ageing

Left sagittal otoliths were extracted as in previous section. The otoliths extracted from adults and juveniles were embedded in epoxy resin (Araldite 2020; Escil, Chassieu, France). They were then ground in transverse section down to the core of the otolith using first a 1200-grain carbide silicon abrasive disc and then a finer 2400-grain disc (Escil, Chassieu, France). The embedded otoliths were polished with alumina paste of decreasing grain diameter (3–0.1 μm) on a felt-polishing disc. Grinding and polishing were performed on an automatic grinder (TegraPol 35; Struers, Champigny-sur-Marne, France). All observations were made under an Olympus BX51 light microscope equipped with an Olympus DP20 digital camera (200× magnification). Each otolith was photographed (Fig. 2). The first increment after the core is assumed to occur at hatching (Lecomte-Finiger 1999). The number of increments on each otolith was independently counted by two readers, from the core to the metamorphosis check.

### Statistical analysis

The data were statistically processed using XLSTAT2011 software (version 2011.4.02, Addinsoft). First, the normality of the data was systematically verified using Shapiro–Wilk normality test, allowing us to choose between parametric and non-parametric tests. The consistency of the results between the two readers was tested using Wilcoxon's paired test. The difference in the PLD between sampling localities of *S. zosterophorum* was tested by a one-way analysis of variance (ANOVA). The variability of the PLD between sampling localities of *S. chloe*

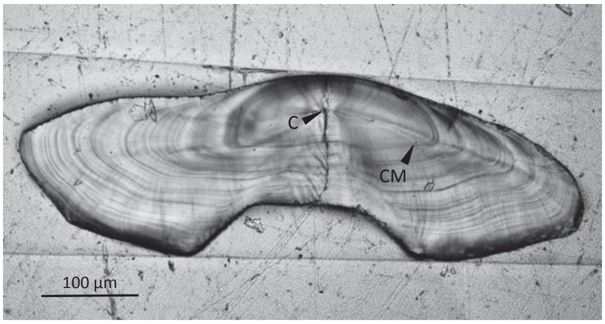

*Fig. 2.* Transversal section of sagittal otolith of a *Sicyopus zosterophorum* adult. (C, core; CM, metamorphosis check mark).

was tested with a Mann–Whitney *U*-test. A Kruskal–Wallis test was conducted to analyse the differences between species.

## Results

### Validation of daily increments

All of the six *S. zosterophorum* juveniles were successfully marked with ALC solution (Fig. 3). The number of increments between the two alizarin-stained bands was 11 for five juveniles and 12 for one juvenile. Here, we validated daily increments deposited in *S. zosterophorum* otoliths, and we assumed that this was the case for the other studied species, *S. chloe* and *A. vanuatu*.

### Ageing

For all otoliths, the daily increments were counted from the core to the metamorphosis check mark by two different readers. There was no significant difference between the two readers (Wilcoxon's test, $P = 0.058$). Consequently, we used the results of the first reader. Results are summarised in Table 2.

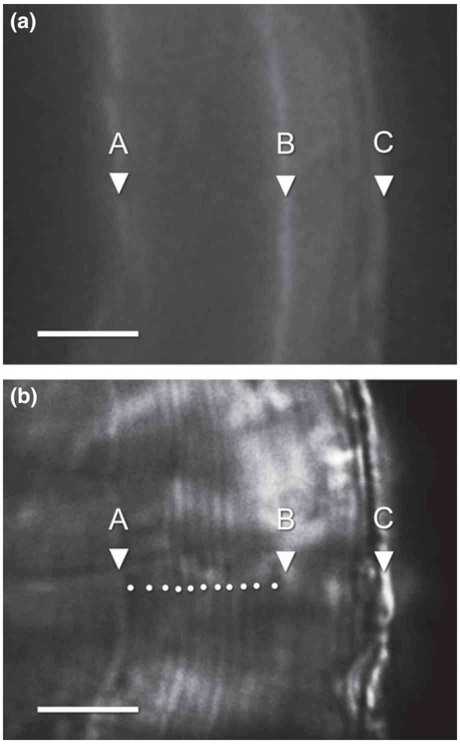

*Fig. 3.* Sagittal otolith of a *Sicyopus zosterophorum* juvenile (19.1 mm in standard length) immersed in alizarin complexone solution twice with a twelve-day interval. Photographs (a) and (b) were taken on same position of the otolith under a UV and a normal light sources, respectively. Triangle A, first alizarin-stained band; triangle B, second alizarin-stained band; triangle C, edge of the otolith; white dots, increments between two alizarin-stained bands; scale bars, 5 μm.

The age at recruitment (mean ± SD) for *S. zosterophorum* is 54.6 ± 5.6 days, for *S. chloe* 53.6 ± 5.7 days and for *A. vanuatu* 55.4 ± 7.5 days. There was no significant difference in the age at recruitment between the species (Kruskal–Wallis test, $P = 0.154$). Within *S. zosterophorum*, there was no significant difference in PLDs between the different sampling localities (ANOVA, $P = 0.269$), as for *S. chloe* (Mann–Whitney *U*-test, $P = 0.478$).

## Discussion

There were 11 daily growth otolith increments between the two alizarin-stained bands in five of the six *S. zosterophorum* individuals examined although we expected to find 12 as there was 12 days between the two ALC treatments. The fact that some individuals are missing increments has been reported in other studies on Sicydiinae species using the ALC time marking technique (Yamasaki et al. 2007; Iida et al. 2010). In our study, it is considered that there is no otolith increment on the first day after the ALC treatment for five individuals because of physiological stress during the experiment as explained by Iida et al. (2010) on *Sicyopterus japonicus*.

No significant differences were found between PLDs for the three studied species (54.6 ± 5.6 days for *S. zosterophorum*, 53.6 ± 5.7 days for *S. chloe*, 55.4 ± 7.5 days for *A. vanuatu*) despite the fact that *S. zosterophorum* is a widespread species unlike the other two. The two endemic species *S. chloe* and *A. vanuatu* have a shorter PLD than some previously studied endemic Sicydiinae such as *Sicyopterus aiensis* (mean ± SD – 79.2 ± 4.6 days) endemic to Vanuatu and *Sicyopterus sarasini* (76.5 ± 3.9 days) endemic to New Caledonia (Lord et al. 2010), *Cotylopus acutipinnis* (99.5 ± 18.5 days) endemic to the Mascarene Islands (Hénaff 2008) or *Lentipes concolor* (86.2 ± 8.5 days) endemic to Hawaii (Radtke et al. 2001). The widespread species *S. zosterophorum* has a shorter PLD than the Indo-Pacific widespread species *Stiphodon percnopterygionus* (99 ± 16 days) from the Ryukyu Archipelago (Japan) to Micronesia (Yamasaki et al. 2007), *Sicyopterus lagocephalus* and the endemic species cited above. Lord et al. (2010) showed that *S. lagocephalus* had a longer PLD (131 ± 3.4 days) than the endemic congeners *S. aiensis* and *S. sarasini* cited above. They suggested in this case a positive relationship between dispersal abilities, geographical distribution and the PLD, that is, a species with a long PLD would disperse further than a species with a shorter PLD. The diadromous species *Kuhlia rupestris* (Percoidei), which is widely distributed in the Indo-Pacific area, has a longer PLD (40.6 ± 6.9 days) than *K. sauvagii* (32.3 ± 3.4 days), endemic to the Indian Ocean

Table 2. Age at recruitment (mean days ± SD) for *Sicyopus zosterophorum*, *Smilosicyopus chloe* and *Akihito vanuatu* in the different localities.

| | Vanuatu | New Caledonia | Papua | Japan | Total |
|---|---|---|---|---|---|
| *S. zosterophorum* | 52.9 ± 4.0<br>(*n* = 16) | 54.1 ± 5.8<br>(*n* = 24) | 56.1 ± 4.1<br>(*n* = 8) | 56.6 ± 7.2<br>(*n* = 14) | 54.6 ± 5.6<br>(*n* = 62) |
| *S. chloe* | 54.2 ± 8.5<br>(*n* = 18) | 53.2 ± 4.0<br>(*n* = 29) | | | 53.6 ± 5.7<br>(*n* = 47) |
| *A. vanuatu* | 55.4 ± 7.5<br>(*n* = 59) | | | | 55.4 ± 7.5<br>(*n* = 59) |

(Feutry et al. 2012). The authors concluded that the PLD is probably one factor controlling the extent of distribution range in *Kuhlia*. However, for *Sicyopterus japonicus,* endemic to the Taiwan–Japan region, Shen & Tzeng (2008) showed that the PLD of this species in Taiwan was 163 ± 12.79, and Iida et al. (2008) showed that the age at recruitment in Wakayama, Japan, was 208 ± 22 days; both results are similar to *S. lagocephalus* PLD, and despite its endemicity, *S. japonicus* has a long PLD. But *S. japonicus* is the only temperate Sicydiinae species, and its long PLD may be linked to the timing of reproduction and recruitment during specific seasons, which are well marked in the temperate zone unlike in the tropical zone (Iida et al. 2008). Finally, Wellington & Victor (1989) and Victor & Wellington (2000) compared the PLD of endemic (28–68 days) and widespread (18–74 days) marine congeners of wrasses and damselfish in the eastern Pacific Ocean, and they concluded that there was no correlation between the PLD and the geographical distribution of these species.

The discrepancy of these results suggests that elements other than the PLD should be considered to explain the differences in the geographical distribution of the studied species. The interaction of biological processes such as reproduction, larval development, larval behaviour and survival, and physical processes such as climate and ocean currents (direction and strength), could affect dispersal, recruitment and distribution of Sicydiinae species (McDowall 2010). Each species might also exhibit different habitat preferences. Parameters such as the nature of the substrate could regulate the survival of juveniles and adults. For example, *S. sarasini* exclusively colonises rivers that run on an ultramafic substrate (nickel rich substrate) in New Caledonia (Lord et al. 2010). The substrate in streams could also regulate recruitment, because the microchemistry of the rivers is suggested to act as a specific signal for post-larval recruitment into the estuary (Lord et al. 2010).

Even though the PLD of *S. zosterophorum*, *S. chloe* and *A. vanuatu* was shorter in comparison with the other Sicydiinae species studied so far, the PLD of all Sicydiinae species is much longer than those found in the typical coastal marine gobies (ca. 30–45 days: Brothers et al. 1983; Beldade et al. 2007; Maeda et al. 2008a). Some amphidromous gobioids, such as *Eleotris* and *Awaous*, also have a longer PLD (Radtke et al. 1988; Maeda et al. 2007). This may reflect sparseness of the habitat of those amphidromous gobioids (insular freshwater streams) compared with coastal fish, as colonisation to the sparsely distributed habitats might require greater dispersal ability with longer PLD (Maeda et al. 2007, 2008b, 2011). The metamorphosis of Sicydiinae post-larvae is a physiological phenomenon involved with the recruitment (Taillebois et al. 2011), which implicates a relatively high plasticity in the recruitment timing. The potential of longer PLD enables a delay in metamorphosis to find suitable habitat (Victor 1986; Keith et al. 2008). However, the lack of variation of PLD observed between and within (SD between 5.6 and 7.5) the three Sicydiinae species in the present study suggests that these three species cannot delay the metamorphosis as much as *Sicyopterus* species for example. Although some Sicydiinae species have generally been considered to have a certain plasticity in timing of the recruitment (Keith et al. 2008), the results of the present study suggest that this concept should be reconsidered for some species.

The current study has improved our knowledge with regard to the PLD of endemic and more widely distributed Sicydiinae species. PLD is not the only factor determining species' distribution and most likely interacts with other variables such as larval behaviour, environment, distribution of the pelagic larvae, currents, substrate preferences of adults and juveniles, etc. These variables and factors should be further studied to understand Sicydiinae dispersal. These new insights into PLD and recruitment plasticity will help implement conservation measures for these species and their habitat.

## Acknowledgements

First, we would like to thank all the partners that have financially supported this work: the New Caledonian Government, the National Museum of Natural History of Paris, the BIONEOCAL ANR, the French Ichtyological Society (SFI) and the UMR BOREA 7208. We also thank the Vanuatu Environment

Unit (D. Kalfatak), the New Caledonian North Province (J-J. Cassan) for allowing us sampling and euthanasia (permit No 60912-2320-2010/JJC), Paul's conservation area (Ambae), Silengwasu Village (Pentecost), the 'Lengguru' field expedition (Papua). This study was possible with the assistance of following colleagues: G. Marquet, P. Feutry, C. Flouhr, P. Gaucher, G. Segura, M. Kondo, H. Saimaru, the New Caledonian 2010 hydrobiology RAP team, Conservation International and Dayu Biik Association. We extend our thanks to Dr C. Lord, native English speaker, for correcting the manuscript and three anonymous reviewers for helpful comments.

## References

Beldade, R., Pedro, T. & Gonçalves, E.J. 2007. Pelagic larval duration of 10 temperate cryptobenthic fishes. Journal of Fish Biology 71: 376–382.

Bell, K.N.I. 1999. An overview of the goby fry fisheries, Naga ICLARM Quarterly 22: 30–36.

Bleeker, P. 1856. Nieuwe bijdrage tot de kennis der ichthyologische fauna van Bali. Natuurkundig tijdschrift voor Nederlandsch Indië 12: 291–302.

Brothers, E.B., Williams, D.M. & Sale, P.F. 1983. Length of larval life in twelve families of fishes at "One Tree Lagoon", Great Barrier Reef, Australia. Marine Biology 76: 319–324.

Campana, S.E. 1999. Chemistry and composition of fish otoliths: pathways, mechanism and applications. Marine Ecology Progress Series 188: 263–297.

Feutry, P., Valade, P., Ovenden, J.R., Lopez, P.J. & Keith, P. 2012. Pelagic larval duration of two diadromous Kuhliidae species (Teleostei: Percoidei) from Indo-Pacific insular systems. Marine and Freshwater Research 63: 397–402.

Hénaff, F. 2008. Etude de l'âge au recrutement et approche des stratégies de reproduction et de dispersion larvaire des cabots bouches-rondes, *Sicyopterus lagocephalus* et *Cotylopus acutipinnis*, poissons amphidromes des rivières de la Réunion. Master 1 thesis, University of Western Britany, pp. 27.

Iida, M., Watanabe, S., Shinoda, A. & Tsukamoto, K. 2008. Recruitment of the amphidromous goby *Sicyopterus japonicus* to the estuary of Ota River, Wakayama, Japan. Environmental Biology of Fishes 83: 331–341.

Iida, M., Watanabe, S. & Tsukamoto, K. 2010. Validation of otolith daily increments in the amphidromous goby *Sicyopterus japonicus*. Coastal Marine Science 34: 39–41.

Keith, P. 2003. Biology and ecology of amphidromous Gobiidae of the Indo-Pacific and Caribbean regions. Journal of Fish Biology 63: 831–847.

Keith, P. & Lord, C. 2011a. Tropical freshwater gobies: Amphidromy as a life cycle. In: Patzner, R.A., Van Tassell, J.L., Kovačić, M. & Kapoor, B.G., eds. The Biology of Gobies. CRC Press: Science Publishers Inc, pp. 243–277.

Keith, P. & Lord, C. 2011b. Systematics of Sicydiinae. In: Patzner, R.A., Van Tassell, J.L., Kovačić, M. & Kapoor, B. G., eds. The Biology of Gobies. CRC Press: Science Publishers Inc, pp. 119–128..

Keith, P., Lord, C. & Vigneux, E. 2006. In vivo observation on post-larval development of freshwater gobies and eleotrids from French Polynesia and New Caledonia. Ichthyological Exploration of Freshwaters 17: 187–191.

Keith, P., Marquet, G. & Watson, R.E. 2007. *Akihito futuna*, a new species of freshwater goby from the South Pacific (Teleostei: Gobioidei: Sicydiinae). Cybium 31: 471–476.

Keith, P., Hoareau, T.B., Lord, C., Ah-Yane, O., Gimonneau, G., Robinet, T. & Valade, P. 2008. Characterisation of postlarval to juvenile stages, metamorphosis and recruitment of an amphidromous goby, *Sicyopterus lagocephalus* (Pallas) (Teleostei: Gobiidae: Sicydinae). Marine and Freshwater Research 59: 876–889.

Keith, P., Lord, C., Lorion, J., Watanabe, S., Tsukamoto, K., Cruaud, C., Couloux, A. & Dettai, A. 2011a. Phylogeny and biogeography of Sicydiinae (Teleostei: Gobioidei) inferred from mitochondrial and nuclear genes. Marine Biology 158: 311–326.

Keith, P., Marquet, G. & Taillebois, L. 2011b. Discovery of the freshwater genus *Sicyopus* (Teleostei: Gobioidei: Sicydiinae) in Madagascar, with a description of a new species and comments on regional dispersal. Journal of Natural History 45: 43–44.

Kuroki, M., Aoyama, J., Wouthuysen, S., Sumardhiharga, K., Miller, M.J. & Tsukamoto, K. 2007. Age and growth of *Anguilla bicolor bicolor* leptocephali in the eastern Indian Ocean. Journal of Fish Biology 70: 538–550.

Lecomte-Finiger, R. 1999. L'otolithe: la "boîte noire" des Téléostéens. Année Biologique 38: 107–122.

Lord, C. & Keith, P. 2008. Threatened fishes of the world: *Sicyopterus sarasini* Weber & Beaufort, 1915 (Gobiidae). Environmental Biology of Fishes 83: 169–170.

Lord, C., Brun, C., Hautecoeur, M. & Keith, P. 2010. Insights on endemism: comparison of the duration of the marine larval phase estimated by otolith microstructural analysis of three amphidromous *Sicyopterus* species (Gobioidei: Sicydiinae) from Vanuatu and New Caledonia. Ecology of Freshwater Fish 19: 26–38.

Luton, C.D., Brasher, A.M.D., Durkin, D.C. & Little, P. 2005. Larval drift of amphidromous shrimp and gobies on the island of Oahu, Hawai'i. Micronesica 38: 1–16.

Maeda, K. & Tachihara, K. 2010. Diel and seasonal occurrence patterns of drifting fish larvae in the Teima Stream, Okinawa Island. Pacific Science 64: 161–176.

Maeda, K., Yamasaki, N. & Tachihara, K. 2007. Size and age at recruitment and spawning season of sleeper, genus *Eleotris* (Teleostei: Eleotridae). Raffles Bulletin of Zoology Supplement 14: 199–207.

Maeda, K., Yamasaki, N., Kondo, M. & Tachihara, K. 2008a. Occurrence and morphology of larvae and juveniles from six *Luciogobius* (Gobiidae) species collected at Aritsu beach on Okinawa Island. Ichthyological Research 55: 162–174.

Maeda, K., Yamasaki, N., Kondo, M. & Tachihara, K. 2008b. Reproductive biology and early development of two species of sleeper, *Eleotris acanthopoma* and *Eleotris fusca* (Teleostei: Eleotridae). Pacific Science 62: 327–340.

Maeda, K., Mukai, T. & Tachihara, K. 2011. Newly collected specimens of the sleeper *Eleotris acanthopoma* (Teleostei: Eleotridae) from French Polynesia indicate a wide and panmictic distribution in the West and South Pacific. Pacific Science 65: 257–264.

McDowall, R.M. 2007. On amphidromy a distinct form of diadromy in aquatic organism. Fish and Fisheries 8: 1–13.

McDowall, R.M. 2010. Why be amphodromous: expatrial dispersal and the place of source and sink population dynamics? Reviews in Fish Biology and Fisheries 20: 87–100.

Mugiya, Y. & Uchimura, T. 1989. Otolith resorption induced by anaerobic stress in the goldfish, *Carassius auratus*. Journal of Fish Biology 35: 813–818.

Radtke, R.L. & Kinzie, R.A. 1996. Evidence of marine larval stage in endemic Hawaiian stream gobies from isolated high-elevation locations. Transaction of the American Fisheries Society 125: 613–621.

Radtke, R.L., Kinzie, R.A. & Folsom, S.D. 1988. Age at recruitment of Hawaiian freshwater gobies. Environmental Biology of Fishes 23: 205–213.

Radtke, R.L., Kinzie, R.A. & Shaffer, D.J. 2001. Temporal and spatial variation in length and size at settlement of Hawaiian amphidromous gobiy *Lentipes concolor*. Journal of Fish Biology 59: 928–938.

Secor, D.H., Dean, J.M. & Campana, S.E.. 1992. Otolith removal and preparation for microstructural examination. In: Stevenson, D.K. & Campana, S.E., eds. Otolith microstructure examination and analysis. Ottawa, Canada: Canadian Special Publication of Fisheries and Aquatic Sciences, 117: 19–57.

Shen, K.N. & Tzeng, W.N. 2002. Formation of metamorphosis check in otoliths of the amphidromous goby *Sicyopterus japonicus*. Marine Ecology Progress Series 228: 205–211.

Shen, K.N. & Tzeng, W.N. 2008. Reproductive strategy and recruitment dynamics of amphidromous goby *Sicyopterus japonicus*. Journal of Fish Biology 73: 2497–2512.

Shen, K.N., Lee, Y.C. & Tzeng, W.N. 1998. Use of otolith microchemistry to investigate the life history pattern of gobies in Taiwanese stream. Zoological Studies 37: 322–329.

Taillebois, L., Keith, P., Valade, P., Torres, P., Baloche, S., Dufour, S. & Rousseau, K. 2011. Involvement of thyroid hormones in the control of larval metamorphosis in *Sicyopterus lagocephalus* (Teleostei: Gobioidei) at the time of river recruitment. General and Comparative Endocrinology 173: 281–288.

Valade, P., Lord, C., Grondin, H., Bosc, P., Taillebois, L., Iida, M., Tsukamoto, K. & Keith, P. 2009. Early life history and description of larval stages of an amphidromous goby, *Sicyopterus lagocephalus* (Gobioidei : Sicydiinae). Cybium 33: 309–319.

Victor, B.C. 1986. Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). Canadian Journal of Fisheries and Aquatic Sciences 43: 1208–1213.

Victor, B.C. & Wellington, G.M. 2000. Endemism and the pelagic larval duration of reef fishes in the eastern Pacific Ocean. Marine Ecology Progress Series 205: 241–248.

Watson, R.E. 1999. Two new subgenera of *Sicyopus*, with a redescription of *Sicyopus zosterophorum* (Teleostei: Gobioidei: Sicydiinae). Aqua Journal of Ichthyology and Aquatic Biology 3: 93–104.

Watson, R.E., Keith, P. & Marquet, G. 2001. *Sicyopus* (*Smilosicyopus*) *chloe*, a new species of freshwater goby from New Caledonia (Sicydiinae). Cybium 25: 41–52.

Watson, R.E., Keith, P. & Marquet, G. 2007. *Akihito vanuatu* a new genus and new species of freshwater goby from the South Pacific (Teleostei: Gobioidei: Sicydiinae). Cybium 31: 341–349.

Wellington, G.M. & Victor, B.C. 1989. Planktonic larval duration of one hundred species of Pacific and Atlantic damselfish (Pomacentridae). Marine Biology 101: 557–567.

Yamasaki, N. & Tachihara, K. 2006. Reproductive biology and morphology of eggs and larvae of *Stiphodon percnopterygionus* (Gobiidae: Sicydiinae) collected from Okinawa Island. Ichthyological Research 53: 12–18.

Yamasaki, N., Maeda, K. & Tachihara, K. 2007. Pelagic larval duration and morphology at recruitment of *Stiphodon percnopterygionus* (Gobiidae: Sicydiinae). Raffles Bulletin of Zoology supplement 14: 209–214.

Yamasaki, N., Kondo, M., Maeda, K. & Tachihara, K. 2011. Reproductive biology of three amphidromous gobies, *Sicyopterus japonicus*, *Awaous melanocephalus*, and *Stenogobius* sp., on Okinawa Island. Cybium 35: 345–359.