**Abstract—**Dottybacks (family Pseudochromidae) are small, colorful, important predators on juvenile fishes on Indo-Pacific coral reefs. Most aspects of their larval ontogeny are little studied. Reared larvae of the orchid dottyback (*Pseudochromis fridmani*) of 4 to 12 mm body length (BL) were used to document both morphological and swimming ontogeny in 3 cohorts. Development is direct. Larvae are slender, lightly pigmented, lack obvious specializations to pelagic existence, and settle at about 12 mm BL. This morphology is similar to that of several families of tropical waters including silliganids, scarids, some labrids, and plesiopids. Critical swimming speed (Ucrit) was measured in 85 larvae, which swam at 0.2 to 19 cm/s. In an unplanned comparison, larvae reached greater Ucrit values at 28°C than at 26°C. Only larvae of ≥9 mm BL could swim fast enough to reach an inertial hydrodynamic environment, wherein swimming is likely to be sustainable enough to influence dispersal. However, 60% of larvae of ≥9 mm were unable to do so, and half of these swam in a viscous environment dominated by frictional drag. Results from this study will allow *Pseudochromis* larvae from field sampling to be identified, may assist studies of pseudochromid relationships, and will help determine the extent to which horizontal swimming of *Pseudochromis* larvae may influence dispersal and population connectivity and be influenced by temperature.

# Morphological and swimming ontogeny in larvae of a small predator on coral reefs: the orchid dottyback (*Pseudochromis fridmani*) (Teleostei, Pseudochromidae)

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## Introduction

The Pseudochromidae, commonly called dottybacks, are small, although important, reef-based predators of the Indo-Pacific. For example, *Pseudochromis fuscus* is one of "4 predator species known to be responsible for a majority of predation on juvenile reef fish on shallow lagoonal reefs throughout the Indo-Pacific" (Holmes and McCormick, 2010). The family has more than 152 species, and the genus *Pseudochromis* has at least 71 described species (Gill, 2004; Nelson et al., 2016), with more being discovered annually. Yet little is known of the early life history of any pseudochromid species in the wild, even though they are very popular aquarium fishes and several species are reared commercially for that trade. All reported species spawn a demersal egg ball, with eggs of about 1–2 mm diameter, which hatch in about 4–5 days into eyed larvae about 2.5–4.5 mm long (Brons, 1996; Olivotto et al., 2006; Mies et al., 2014; Araújo et al., 2016; Madhu et al., 2016). All existing descriptions of larval development in *Pseudochromis* species are from aquarium aquaculture literature (citations above). These descriptions are based on days after hatching rather than size and are brief, generalized, and, if illustrated, use photographs of varying quality that do not show details necessary for identification. Four larvae of an unidentified pseudochromid from plankton tows are illustrated in a regional identification guide (Gill et al., 2000). Aspects of the developmental osteology of the Red Sea endemic orchid dottyback (*Pseudochromis fridmani*) are described (Wittenrich and Turingan, 2011). Here, we describe the development of orchid dottybacks from reared larvae of 4.4 to 12.8 mm in body length (BL). A popular aquarium fish, the orchid dottyback is widely cultured by both commercial aquaculturists and hobbyists, who report that larvae are about 3.7 mm in total length (TL) at hatching and 12 mm in TL at settlement (Brons, 1996).

The behavior of larval fishes can influence their dispersal (Leis, 2006; Faillettaz et al., 2018), and swimming ability and its ontogeny are particularly important in this respect (Nanninga and Manica, 2018; Burgess et al., 2022). There is a report of the critical swimming speed (Ucrit) of a total of 14 larvae of 3 unidentified pseudochromid species from the Great Barrier Reef, but they were all settlement-stage individuals of about 17–18-mm

TL (about 13.5–14.5-mm BL—i.e., excluding the caudal fin) captured in light traps: species Ucrit means were 23–30 cm/s (Fisher et al., 2005). In the present study, we measured the ontogeny of swimming ability, in the form of Ucrit, of orchid dottyback larvae of 4.4–12.8-mm BL. Ucrit is readily measured in a laboratory flume by increasing the water flow in a stepwise manner until the larvae can no longer maintain position (Brett, 1964).

Herein, we provide the first detailed description of the development of morphology and swimming in larvae of any pseudochromid species. This will allow *Pseudochromis* larvae to be identified in plankton samples, may assist future studies of the relationships of the family, and will assist in determining the extent to which the behavior of *Pseudochromis* larvae may influence dispersal and population connectivity by horizontal swimming. Unexpectedly, swimming performance differed substantially between the 2 times when we measured it. This coincided with a 2°C difference in water temperature between times. We therefore undertook an unplanned comparison of the differences in Ucrit between times to attempt to estimate if the difference was likely to have been due to this small temperature difference and to examine the implications.

Geoff Moser's research career provides an inspiration to anyone studying the early life-history stages of marine fishes. Geoff was interested in every aspect of larval-fish biology as shown by his seminal chapter (Moser, 1981) in the book edited by Ruben Lasker (Lasker, 1981) that provides an overview of the hotbed of larval-fish research that was the NOAA Southwest Fisheries Science Center during and following the tenure of E. H. Ahlstrom. By example, Geoff demonstrated that budding larval fish biologists need not have a career restrained to a narrow pathway but that there are a wide range of fascinating and important questions that can be approached through the perspective of early life-history studies. Thanks, Geoff, for that inspiration.

## Materials and methods

The source of larvae and the methods used in the present study were exactly the same as those used in the study of Leis et al (2012a) on the fairy basslet (*Gramma loreto*) with the exception that only 2 cohorts of the latter were available for study. Larvae were reared from captive brood stock at Lautan Production, Meze, France, an aquarium-trade aquaculture company (which has since gone out of business), where swimming was measured in temperature-controlled facilities in October 2010. Adults spawned naturally, and newly hatched larvae were moved from spawning tank to rearing tanks with constant illumination and "green water." Until 5 days after hatch (DAH), rotifers were supplied, and from 6 DAH, larvae were fed brine shrimp (*Artemia* sp.) nauplii. We used larvae of 3 cohorts that were hatched in September 2010: 1 (hatched ca. 12th), 2 (ca. 19th), and 3 (ca. 29th). Ucrit was measured in cohorts 1 and 2 on 3 October (water temperature 28°C) and in cohorts 2 and 3 on 10 October (26°C). Cohort 1 had settled by 10 October.

### Morphological development

The larvae used in this study are lodged at the Australian Museum, Sydney (AMS): collection numbers I.45584-001 to 046 (cohort 1), I.45585-001 to 045 (cohort 2), and I.45586-001 to 022 (cohort 3). Three to 4 months after initial fixation and a change of alcohol, the larvae had shrunk an average of 7.4% BL from the size measured within 24 hours of fixation. The sizes reported for swimming tests are the pre-shrinkage BL values because these are closest to the size of the larvae when swimming speed was measured. Sizes reported in the descriptions of morphological development are post-shrinkage values because they were the sizes of the larvae when measured for descriptive purposes. A total of 85 larvae provided Ucrit data: 4 preflexion (4.6–5.8 mm), 4 flexion (5.9–6.4 mm), and 77 postflexion (5.2–12.8 mm). Description of morphological development is based on 34 larvae tested in the swimming chamber, plus 3 untested larvae included to fill size gaps: 5 preflexion (4.4–5.1 mm), 5 flexion (5.3–6.3 mm), and 24 postflexion (6.4–11.4 mm). These 37 larvae were also used to assess shrinkage. The description of morphological development is based on at least 5 larvae within each 1-mm-BL size increment, but in some size increments, insufficient larvae were available to achieve this.

Measurements and abbreviations follow Leis and Carson-Ewart (2000), with 2 additions: dorsal peduncle length measured from the base of the last dorsal-fin ray to the tip of the notochord until flexion is complete and then to the edge of the hypural plate; and maxilla length measured along the axis of the maxilla from its anterior tip to the posterior end. Lengths are BL. Note that in postflexion larvae BL is equivalent to standard length. Percentages are of BL unless otherwise noted. Pigment refers to melanophores in preserved specimens. Larvae were examined using a dissecting microscope (Wild Stereo Microscopes, now manufactured by Leica Microsystems Inc., Buffalo Grove, IL) and measured using an ocular micrometer. Illustrations were prepared with the aid of a camera lucida.

### Critical swimming speed development

A swimming chamber, or flume, made of clear Perspex with 6 laneways, each 30 mm wide, 50 mm high, and 180 mm long (Stobutzki and Bellwood, 1994), was used to measure the swimming abilities of the larvae.

A black line across the chamber lid provided the larvae with a point of reference while swimming. The chamber was identical to that of Stobutzki and Bellwood (1994, 1997), except that plankton mesh was used at the laneway ends to retain the small, slender larvae. The same chamber was used by previous Australian Museum-based studies (Fisher et al., 2022), making results directly comparable. Even flow distribution was achieved by a T-piece diffuser placed in the header portion of the chamber. Turbulence in the chamber was minimized by a 40-mm-long section of flow straighteners at the start of each laneway. This also minimized possible boundary layers. Previous measurements showed that water speed in the 5 mm closest to the wall of the chambers of this design was not significantly different from that in the center of the chamber (Stobutzki and Bellwood, 1997; Fisher et al., 2000). Water flow speed was controlled by a calibrated valve. Flow rates were calibrated by recording the time taken for water flowing over the chamber's outlet weir to fill a container of known volume, divided by the cross-sectional area of the chamber. The average of 3 to 5 calibrations was used at the flow speed for a given valve angle. Ucrit, which quantifies maximum swimming speed over periods of minutes, was determined. Ucrit is a measure of prolonged, rather than sustained speed (Fisher and Leis, 2010). Starting at 1.8 to 2.0 cm/s, speed was increased by a target increment of 3.3 cm/s every 2 minutes until a larva was unable to swim against the flow. The time elapsed at the point when each larva drifted onto the downstream mesh ($t$ in the equation below) was recorded. Ucrit was calculated using the following equation (Brett, 1964):

$$Ucrit = U_p + (t/t_i \times U_i), \quad (1)$$

where $U_p$ = penultimate speed (in centimeters per second);
$U_i$ = speed increment (3.3 cm/s);
$t$ = time (in seconds) larva had swum in the final speed increment; and
$t_i$ = 120 s, the time interval for each velocity increment.

It was possible to measure swimming ability at the rearing facility only twice, and in the interim, larvae of cohort 1 had settled and cohort 3 had been spawned. We had no influence over rearing conditions at Lautan; we simply purchased larvae from Lautan and measured Ucrit in a corner of the Lautan aquarium facilities where the larvae had been reared. Nor did we anticipate—based on experience measuring the ontogeny of Ucrit in another species at a nearby aquaculture company (Leis et al., 2012b)—that temperatures might differ by 2°C between dates. When the Ucrit measurements were found to differ substantially between 3 and 10 October, we suspected that the 2°C difference between dates might have influenced the results. An unplanned, retrospective comparison of the Ucrit results was then undertaken in an attempt to determine if the 2°C difference could have had a role in causing these unexpected results.

This retrospective comparison included calculation of the Reynolds numbers (Re) of the various combinations of temperature, size, and Ucrit for the larvae on the 2 dates to determine the hydrodynamic environment in which the larvae were swimming. Fish swim more efficiently in an inertial rather than in a viscous hydrodynamic environment (Webb and Weihs, 1986). At a given water viscosity, the larger and the faster a larva is, the more likely it is to be swimming in an inertial environment. A hydrodynamic measure called the Reynolds number is used to indicate in which hydrodynamic environment swimming is taking place.

$$Re = U \times L/k, \quad (2)$$

where $U$ = speed, in this case, Ucrit;
$L$ = TL; and
$k$ = the kinematic viscosity of sea water (Webb and Weihs, 1986).

A Re of <300 indicates a viscous hydrodynamic environment, and a Re of >1000 an inertial hydrodynamic environment, with intermediate values indicating that both viscous and inertial forces are important.

Larvae were provided by Lautan staff on the day swimming was measured and kept in the same water in which they were reared. Using a small beaker, they were gently placed into a swim chamber lane and allowed to acclimate for 2 minutes. Following swimming in the chamber, larvae were removed using the small beaker, euthanized, and fixed in 70% ethanol. Within 24 hours of fixation, the larvae were examined under a dissecting microscope and BL was recorded. The Ucrit values are reported as both absolute speed (in centimeters per second) and relative speed (in BL per second). Full Ucrit data from this study are contained in a recent data publication (Fisher et al., 2022). Regression statistics were calculated using Microsoft Excel 2010 (Microsoft Corp., Redmond, WA).

This research was carried out under permits issued by Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE), in Perpignan, France, to conduct research experiments in the field and laboratory (under the "Hygiène et Sécurité" section).

## Results

### Morphological development

Orchid dottyback adults have 10+16=26 vertebrae and fin ray counts of D III, 24–27; A III, 13–16; P1 15–17;

**Table 1**

Morphometric and meristic information collected from larval orchid dottyback (*Pseudochromis fridmani*) reared at an aquarium facility in France in October 2010 and measured in February 2011. Larvae were categorized into 3 stages of notochord flexion (Flex) development: preflexion (pre), flexion (flex), and postflexion (post). The measurements collected (in millimeters) are as follows: notochord flexion (Flex), body length (BL), pre-anus length (PreAL), pre-dorsal-fin length (PreDL), head length (HL), orbit diameter (OD), snout length (SnL), body depth at base of pectoral fin (BD(P)), body depth at anus (BD(A)), length of caudal peduncle dorsally (PedL), and length of maxilla (MaxL). Meristic data collected were dorsal fin (D Fin), anal fin (A Fin), pectoral fin (P1 Fin), pelvic fin (P2 Fin), and preopercular spines on inner (PreOS inner) or outer (PreOS outer) preopercular border. The values in square brackets indicate forming fin elements. d=damaged; f=forming, but incomplete nostril; bud=a small membrane lacking fin rays.

| Flex | BL | PreAL | PreDL | HL | OD | SnL | BD(P) | BD(A) | PedL | MaxL | Nostrils | D Fin | A Fin | P1 Fin | P2 Fin | PreOS inner | PreOS outer |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| pre | 4.40 | 2.25 | 1.70 | 1.10 | 0.34 | 0.34 | 0.67 | 0.55 | | 0.43 | no | | | | | | |
| pre | 4.40 | 2.02 | 1.43 | 1.24 | 0.42 | 0.37 | 0.60 | 0.56 | | 0.51 | no | | | | | | |
| pre | 4.48 | 2.47 | 1.02 | 1.14 | 0.38 | 0.38 | 0.64 | 0.51 | | 0.44 | no | | | | | | |
| pre | 4.60 | 2.58 | 1.88 | 1.17 | 0.40 | 0.35 | 0.61 | 0.58 | | 0.44 | no | | | | | | |
| pre | 5.11 | 2.89 | 2.00 | 1.25 | 0.38 | 0.40 | 0.79 | 0.63 | | 0.52 | no | | | | | | |
| flex | 5.25 | 3.10 | 1.73 | 1.43 | 0.48 | 0.40 | 1.00 | 0.75 | | 0.49 | no | | | | | | 1 |
| flex | 5.45 | 2.88 | 2.47 | 1.40 | 0.44 | 0.44 | 0.90 | 0.70 | | 0.57 | no | | | [6] | | | |
| flex | 5.70 | 3.16 | 2.30 | 1.42 | 0.45 | 0.50 | 0.97 | 0.77 | | 0.60 | no | | | | | 1 | 1 |
| flex | 5.97 | 3.34 | 2.81 | 1.45 | 0.49 | 0.53 | 1.12 | 0.96 | | 0.63 | no | | | [3] | | 1 | 2 |
| flex | 6.25 | 3.50 | 2.56 | 1.58 | 0.50 | 0.60 | 1.04 | 0.94 | | 0.66 | no | | | [4] | | 1 | 2 |
| post | 6.44 | 3.88 | 1.95 | 1.83 | 0.55 | 0.65 | 1.20 | 1.05 | 1.12 | 0.65 | no | [11] | [11] | [6] | | 1 | 2 |
| post | 6.50 | 3.78 | 2.34 | 1.70 | 0.52 | 0.60 | 1.10 | 1.00 | 1.06 | 0.50 | no | [10] | [11] | [7] | | 1 | 2 |
| post | 6.88 | 4.30 | 2.60 | 2.05 | 0.58 | 0.68 | 1.30 | 1.20 | 1.03 | 0.60 | no | [5]15 | [I],14 | [6] | | 1 | 1 |
| post | 7.25 | 4.18 | 3.13 | 1.96 | 0.64 | 0.54 | 1.32 | 1.20 | 0.86 | 0.84 | no | [5]21 | [I],19 | [8]3 | | 1 | 1 |
| post | 7.33 | 4.48 | 3.36 | 2.25 | 0.62 | 0.72 | 1.40 | 1.30 | 1.20 | 0.82 | no | [10]15 | [I],15 | [11] | | 2 | 2 |
| post | 7.44 | 4.05 | 2.54 | 2.48 | 0.84 | 0.58 | 1.84 | 1.75 | 1.17 | 0.94 | no | [5]21 | II,16 | [1]14 | | 2 | 2 |
| post | 7.68 | 4.20 | 2.64 | 2.21 | 0.68 | 0.68 | 1.56 | 1.40 | 0.84 | 0.94 | no | [16]13 | [I]II,17 | 8[6] | bud | 2 | 2 |
| post | 7.68 | 4.70 | 2.76 | 2.36 | 0.66 | 0.66 | 1.55 | 1.50 | 0.93 | 1.05 | no | [II],[5]20 | I,18 | [2]8 | bud | 2 | 2 |
| post | 7.88 | 4.43 | 2.59 | 2.22 | 0.67 | 0.52 | 1.48 | 1.30 | 1.00 | 0.90 | no | [6]19 | I,19 | [3]8 | bud | 2 | 2 |
| post | 8.16 | 4.81 | 3.00 | 2.42 | 0.75 | 0.56 | 1.72 | 1.59 | 1.03 | 1.02 | no | [I],[3]22 | [I],18 | [2]18 | bud | 1 | 2 |
| post | 8.32 | 5.30 | 3.36 | 2.56 | 0.81 | 0.63 | 1.81 | 1.81 | 1.03 | 1.06 | no | [I],25 | [I]I,18 | [1]15 | [I],5 | 1 | 1 |
| post | 8.40 | 5.00 | 2.88 | 2.63 | 0.75 | 0.68 | 1.70 | 1.63 | 1.00 | 1.00 | no | III,25 | III,18 | [2]13 | [I],3 | 1 | 1 |
| post | 8.56 | 4.60 | 3.56 | 2.66 | 0.81 | 0.66 | 1.78 | 1.59 | 1.28 | 0.94 | f | [II],22 | II,16 | [2]14 | [I],2 | 2 | 2 |
| post | 8.88 | 5.05 | 3.13 | 2.53 | 0.95 | 0.63 | 1.75 | 1.83 | 1.33 | 1.05 | f | III,25 | III,16 | 16 | [I],[4] | 2 | 2 |
| post | 9.04 | 5.05 | 3.20 | 2.80 | 1.00 | 0.72 | 2.04 | 1.84 | 1.44 | 1.08 | f | III,25 | II,15 | 16 | I,[4] | 1 | 2 |
| post | 9.20 | 4.95 | 3.30 | 2.68 | d | d | 2.12 | 2.00 | 1.32 | 1.12 | yes | [I]II,25 | II,16 | 16 | I,5 | 1 | 2 |
| post | 9.50 | 5.50 | 3.06 | 3.20 | 0.97 | 0.79 | 2.03 | 1.88 | 1.44 | 1.08 | yes | III,24 | III,14 | 15 | I,5 | 0 | 3 |
| post | 9.70 | 5.25 | 3.36 | 3.16 | 0.91 | 0.72 | 2.16 | 2.06 | 1.38 | 1.22 | yes | II,26 | II,16 | 16 | I,5 | 1 | 2 |
| post | 9.92 | 5.63 | 3.48 | 2.81 | 1.02 | 0.78 | 2.12 | 2.12 | 1.52 | 0.97 | yes | II,25 | II,14 | 15 | I,5 | 0 | 3 |
| post | 10.30 | 5.63 | 3.75 | 3.31 | 0.95 | 0.91 | 2.47 | 2.41 | 1.59 | 1.16 | yes | III,25 | III,15 | 16 | I,5 | 0 | 2 |
| post | 10.40 | 6.00 | 3.56 | 3.44 | 1.03 | 0.97 | 2.53 | 2.31 | 1.66 | 1.09 | yes | III,25 | III,14 | 16 | I,5 | 0 | 2 |
| post | 10.50 | 6.19 | 3.78 | 3.40 | 1.18 | 0.82 | 2.64 | 2.60 | 1.56 | 1.32 | yes | III,25 | III,14 | 16 | I,5 | 0 | 2 |
| post | 10.80 | 6.13 | 3.93 | 3.66 | 1.12 | 0.96 | 2.76 | 2.48 | 1.56 | 1.20 | yes | III,25 | III,14 | 16 | I,5 | 0 | 1 |
| post | 10.90 | 6.19 | 3.72 | 3.50 | 1.09 | 0.69 | 2.63 | 2.44 | 1.69 | 1.34 | yes | III,25 | III,14 | 16 | I,5 | 0 | 3 |
| post | 11.40 | 6.31 | 3.95 | 3.80 | 1.10 | 1.00 | 2.88 | 2.64 | 1.72 | 1.28 | yes | III,25 | III,14 | 15 | I,5 | 0 | 1 |
| post | 11.50 | 6.44 | 4.00 | 3.64 | 0.96 | 1.04 | 2.60 | 2.48 | 1.64 | 1.24 | yes | III,25 | III,14 | 15 | I,5 | 0 | 2 |
| post | 11.50 | 6.90 | 4.08 | 3.60 | 1.22 | 1.03 | 3.00 | 3.00 | 1.60 | 1.38 | yes | III,25 | III,14 | 16 | I,5 | 0 | 0 |

P2 I, 5; and C 9+8 (Randall, 1983; Gill, 2004). The description is based on larvae 4.4 to 11.5 mm BL (post shrinkage): see Table 1 and Figs. 1 and 2 for details.

Larvae are relatively non-descript and elongate (body depth [BD] 13–19% BL) until about 7 mm, after which BD is up to 26% BL. Notochord flexion takes place between 5.3 and 6.3 mm. Myomeres are 26: either 10+16 or 11+15. The anus is close to mid body, with snout-to-anus length increasing slightly from the mean of 54% BL to 58% BL following flexion. The gut has a partial coil in the smallest larvae, and this gradually transforms to a full coil in early postflexion larvae. The small gas bladder is located just posterior to the P1 base initially and at the upper portion of the P1 base from about 7.5 mm. The head is of moderate size (22–25% BL) throughout. The moderately oblique mouth extends to the anterior

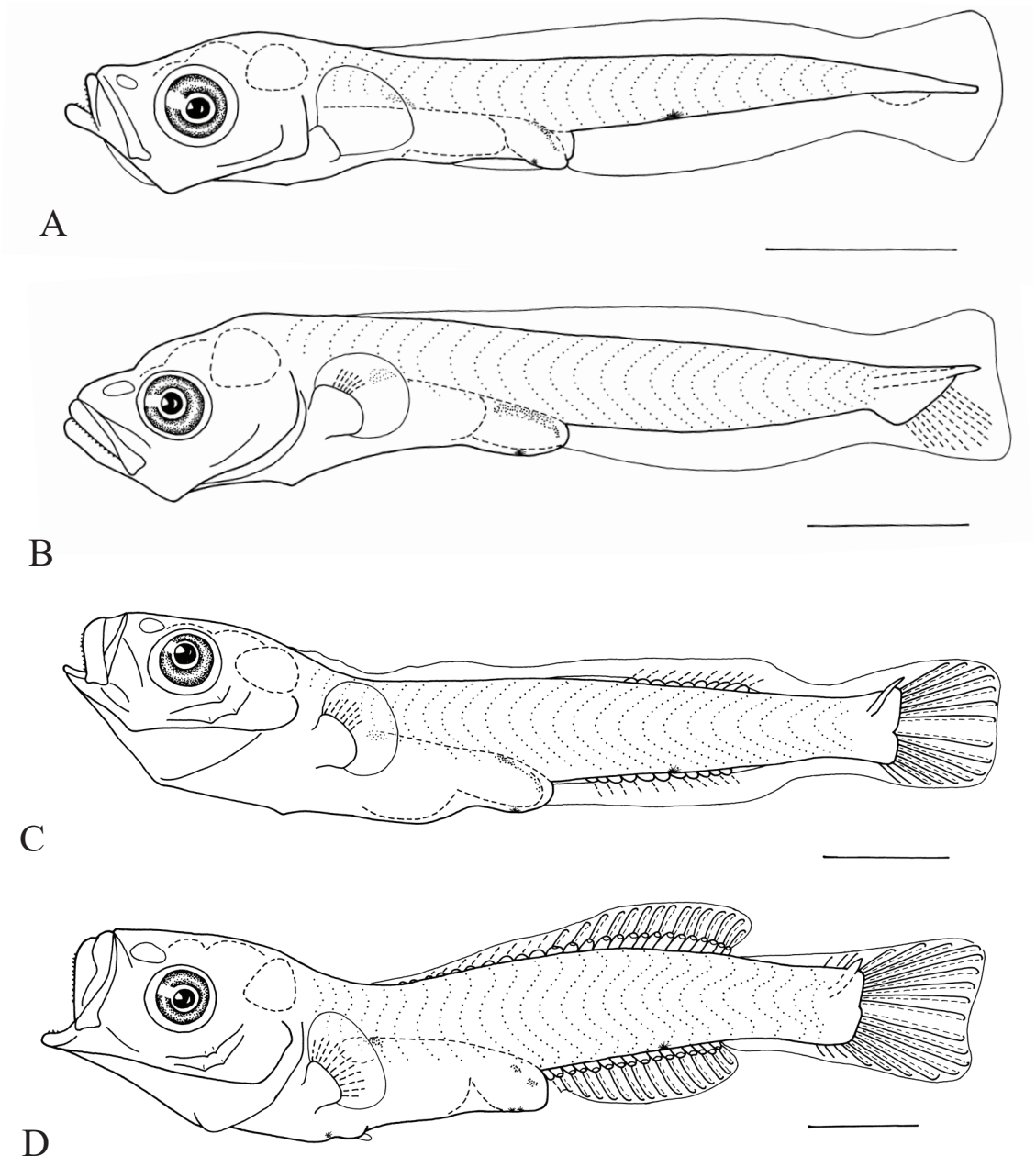


**Figure 1**

Illustrations of 4 developmental stages of larval orchid dottyback (*Pseudochromis fridmani*) reared at an aquarium facility in France in 2010: (**A**) 4.6 mm body length (BL) (Australian Museum, Sydney [AMS] I.45585-001); (**B**) 5.5 mm BL (AMS I.45585.002); (**C**) 6.5 mm BL (AMS I.45585.003); (**D**) 7.3 mm BL (AMS I.45584.002). Larvae A, B, and C are from cohort 2, and D is from cohort 1; all were preserved on 3 October. Neither neuromast cupolae nor scales are present in the larvae of these sizes. Size and pigment of the swim bladder are usually obscured by the overlying pectoral fin. Scale bar=1 mm.

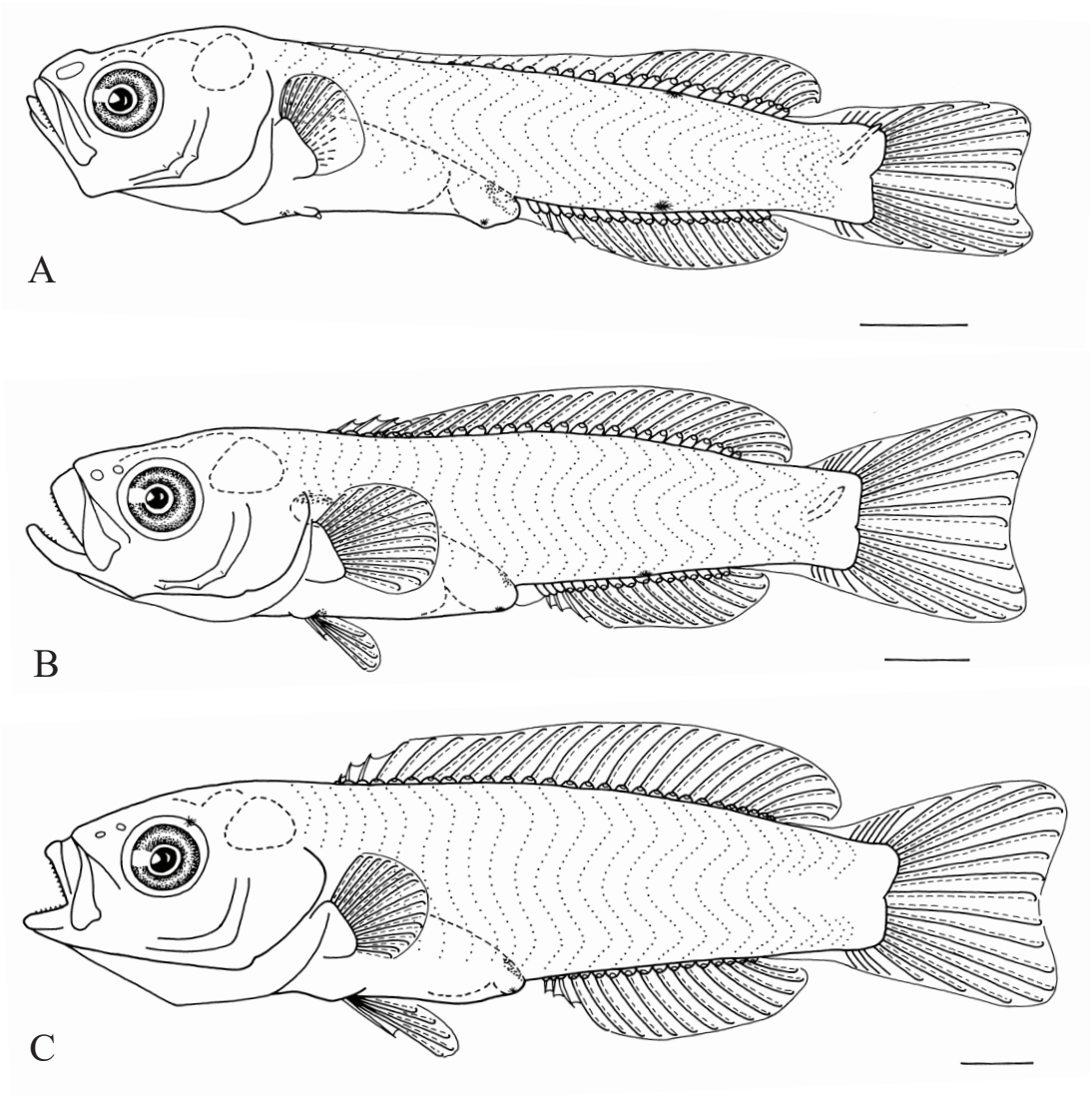


**Figure 2**

Illustrations of 3 developmental stages of larval orchid dottyback (*Pseudochromis fridmani*) reared at an aquarium facility in France in 2010. (**A**) 7.7 mm body length (BL) (Australian Museum, Sydney [AMS] I.45586.002). Larva is from cohort 3 and was preserved on 10 October. (**B**) 9.5 mm BL (AMS I.45584.00). The lateral-line neuromast cupolae are present but not shown, whereas no scales are present. (**C**) 11.3 mm BL (AMS I.45584.003). Scales cover most of the body, and neuromast cupolae are extensive, but neither is shown. The larvae from B and C are from cohort 1 and were preserved on 3 October. Scale bar=1 mm.

portion of the eye and is armed with small teeth. Head spination is limited to very small spines on the preopercle borders. These first appear at 5.3 mm. The inner border has 1–2 spines, usually 1, that disappear by 9.5 mm. The outer border may have up to 3 spines, usually 2, which persist until the settlement stage. The nasal pit begins to roof over at 8.5 mm, with 2 nostrils present from 9.2 mm.

Fin anlagen first appear in the D and A fins at 5.3 mm, and in the caudal fin at 4.3 mm. Rays in both D and A fins form from posterior to anterior, with a full ray compliment by 8.4 mm. The posterior 16 D rays form from typical soft-ray bases, whereas the anterior soft rays form from much smaller bases. These smaller anterior bases are similar to the base of the posterior-most D spine in many perciform fishes, which initially forms as a soft, often segmented, ray before becoming a spine (Leis and Carson-Ewart, 2000). The 3 spines are

the last elements to form in the D fin. Soft A rays form in the typical manner, and the spines are the last elements to form. Incipient rays are present in the P1 fin from 6 mm, and a full complement of 15–16 rays is present at about 9 mm. The P2 bud is present from 7.7 mm, with the first rays forming by 8.3 mm and a full complement by 9.2 mm. No fin rays are particularly elongated, and D and A spines are much shorter than rays.

Lateral-line neuromast cupolae along the midline are visible from about 8 mm: one on each of the posterior 16 myomeres. By 9.5 mm, neuromast cupolae are present along the base of most of the dorsal fin. Scales first appear at 10.3 as tiny scales on much of the tail. By 11.5 mm, cycloid scales cover most of the trunk, lateral-line scales cover the neuromasts, and neuromast cupolae also extend the full length of the soft dorsal fin base and onto the caudal fin, parallel and ventral to rays 5 and 8. A settlement-stage larva of 11.5 mm is fully scaled and lacks preopercular spines (Fig. 2G).

Melanistic pigment is extremely limited. Most larvae, regardless of size, have an internal pigment cap over the swim bladder and pigment over the posterior-most hindgut. In postflexion larvae, a third melanophore is often present over the gut between the other 2 but may be difficult to observe through the overlying musculature. Ventrally, an external melanophore is present just anterior to the anus, and a single melanophore is present at about the sixth postanal myomere. From 7 to 8 mm, a ventral midline melanophore is present just anterior to the P2 base. A deeply embedded melanophore over the hindbrain is sometimes visible, and some larvae larger than 10 mm have a melanophore on the posterior edge of the orbit. A single 7.7-mm larva has a dorsal melanophore opposite the ventral one on the tail. Only the internal pigment dorsally on the gut and hindbrain consists of anything more than a single, very small melanophore.

## Swimming speed development

Ucrit ranged from 0.2 to 19.0 cm/s, with an overall mean of 7.1 cm/s, but speeds were higher on 3 October when the water temperature was 28°C than on 10 October when the water temperature was 26°C. The highest speed on 3 October was 19.0 cm/s, whereas on 10 October, it was 11.8 cm/s, and the mean speeds were 8.5 and 7.1 cm/s, respectively.

The relationship between Ucrit and size varied among cohorts and measurement dates (Table 1). On 3 October, both cohorts 1 (ca. 21 DAH larvae of 7.5–12.5 mm) and 2 (ca. 14 DAH larvae of 4.6–7.6 mm) had reasonably strong, significant, positive linear relationships between Ucrit and size, with Ucrit increasing by 2.5–3.2 cm/s for each 1 mm increase in BL (Fig. 3A, Table 2). These relationships explained 23% and 48% of the variation, respectively. When the cohorts 1 and 2 were combined, a significant, positive relationship was returned, but the increase in speed was lower at 1.4 cm/s for each 1 mm increase in BL, and only 30% of the variation was explained (Table 2).

In contrast, on 10 October, neither cohort 2 (ca. 21 DAH larvae of 8.2–12.8 mm) nor 3 (ca. 11 DAH larvae of 5.2–9.3 mm) had a significant relationship between speed and size (Fig. 3B, Table 2). The same was true when cohorts 2 and 3 were combined.

When cohort 2 data from both 3 and 10 October were combined, a non-significant result was obtained, but when cohort 2 and 3 data from 10 October were combined, a marginally significant negative linear relationship that explained about 10% of the variation was found (Table 2). Finally, when all 3 cohorts from both dates were combined, a significant, but weak, positive relationship with an increase in Ucrit of 0.7 cm/s for each 1 mm increase in BL that explained only 7% of the variation was found (Table 2).

When expressed as relative Ucrit (Rel Ucrit, in BL per second), a swimming speed difference was again found between 3 and 10 October. There was no significant relationship between size and Rel Ucrit on 3 October, and overall mean Rel Ucrit was 9.1 BL/s (Standard Error [SE]=0.9) ($n$=41). In contrast, on 10 October, there was a highly significant ($P$<0.001), negative linear relationship between size and Rel Ucrit ($Rel\ Ucrit$=–1.63$BL$+21.8, coefficient of determination [$r^2$]=0.33, $n$=44). Given there was no significant relationship between BL and Ucrit on 10 October, it is to be expected that Rel Ucrit would decrease with size. However, it is noteworthy that only a third of the larvae measured on 10 October had Rel Ucrit greater than the 3 October mean value and that 34% of 41 larvae on 3 October swam at 14 BL/s or more compared to only 1 of 44 larva on 10 October.

At the size of settlement of about 12 mm, Ucrit varied from 7 to 20 cm/s in cohort 1 (3 October, Fig. 3A) and 1 to 12 cm/s in cohort 2 (10 October, Fig. 3B). In both cases, the settlement-stage larvae were ca. 21 days posthatch.

## Hydrodynamics of swimming

Because orchid dottyback larvae were on average swimming slower on 10 October (26°C) than on 3 October (28°C), the Re show a clear decrease in the proportion of larvae that were swimming in an inertial hydrodynamic environment (Fig. 4). Furthermore, although the smallest larvae that were able to swim in an inertial hydrodynamic environment were of similar size on both dates, the proportion larger than the minimum size that did so was about 4 times greater on 3 October than on 10 October. At 28°C (3 October), only larvae 10 mm or larger swam in an inertial hydrodynamic environment (Re >1000), and those that did so constituted 76% of larvae

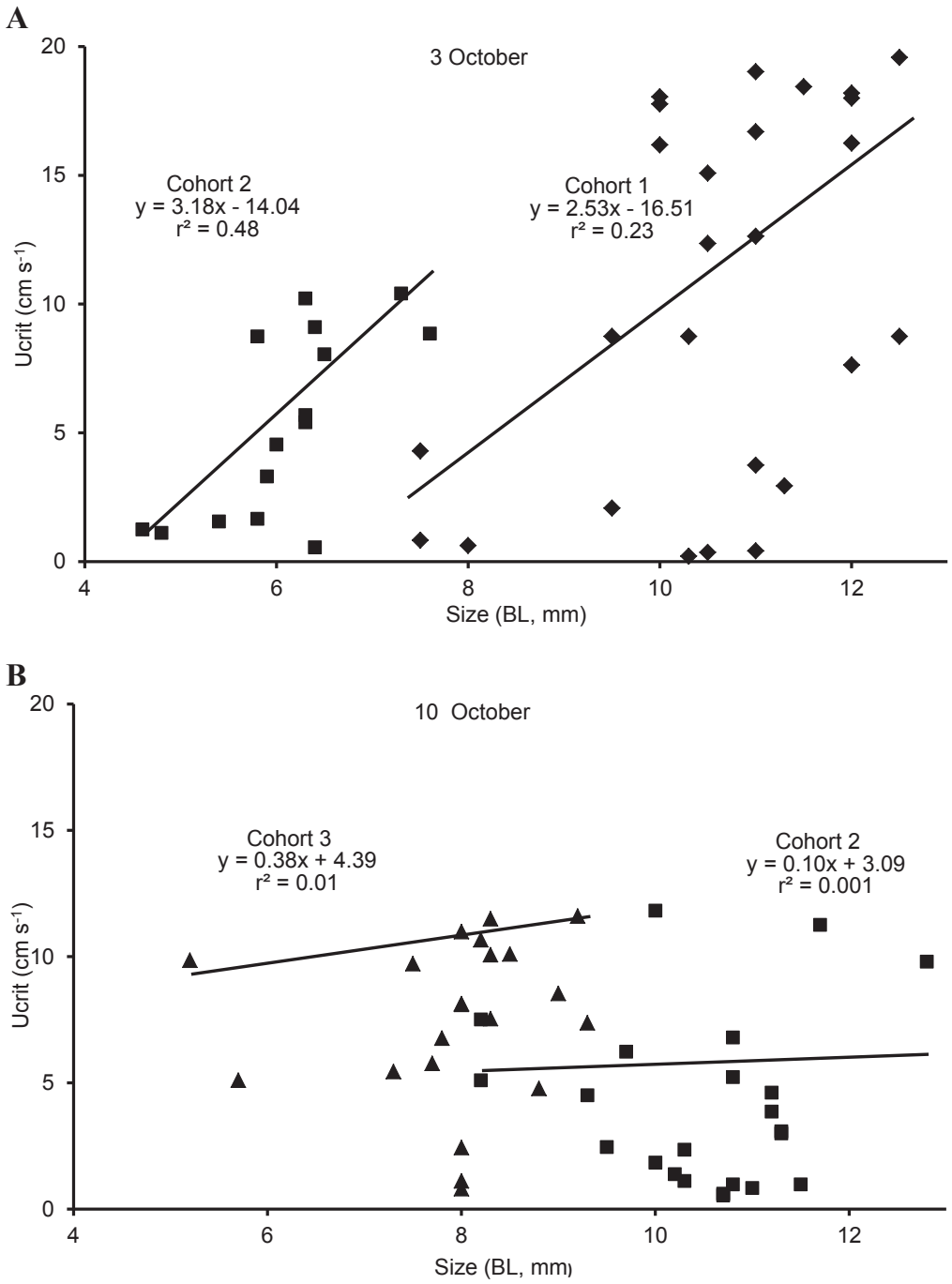


**Figure 3**

Comparison of the linear relationships between critical swimming speed (Ucrit) and size (as body length [BL]) for 3 reared cohorts of larval orchid dottyback (*Pseudochromis fridmani*) during laboratory experiments conducted at an aquarium facility in France. (**A**) Comparison of cohorts 1 (diamonds) and 2 (squares) as measured on 3 October 2010. On 3 October, the slope of the linear relationship between size and speed was positive and significantly different from zero in both cohorts. (**B**) Comparison of cohorts 2 (squares) and 3 (triangles) as measured on 10 October 2010. On 10 October, neither cohort had a significant relationship between size and speed. For each cohort, trend lines, linear regression equations, and coefficients of multiple determination ($r^2$) are shown. See Table 2 for data on the relationships in this figure. Some symbols overlap.

**Table 2**

Relationship between critical swimming speed (Ucrit) and body length (BL) for reared orchid dottyback (*Pseudochromis fridmani*) larvae during laboratory experiments conducted at an aquarium facility in France in October 2010. The approximate hatch dates for cohorts 1, 2, and 3 were 12 September 2010, 19 September 2010, and 29 September 2010, respectively. Regression statistics are for linear relationships. *n*=sample size; $r^2$=coefficient of determination.

| Cohort | Date measured | *n* | BL range (mm) | Mean Ucrit (cm/s) | Ucrit (cm/s) | $r^2$ | *P* |
|---|---|---|---|---|---|---|---|
| 1 | 3 Oct | 26 | 7.5–12.5 | 10.29 | = 2.53BL - 16.51 | 0.23 | 0.01 |
| 2 | 3 Oct | 15 | 4.6–7.6 | 5.36 | = 3.18BL - 14.04 | 0.48 | <0.01 |
| 1 + 2 | 3 Oct | 41 | 4.6–12.5 | 8.49 | = 1.45BL - 4.44 | 0.30 | <0.001 |
| 2 | 10 Oct | 23 | 8.2–12.8 | 4.17 | = 0.10BL + 3.09 | <0.01 | 0.88 |
| 3 | 10 Oct | 21 | 5.2–9.3 | 7.96 | = 0.04BL + 7.70 | 0.01 | 0.62 |
| 2 + 3 | 10 Oct | 44 | 5.2–12.5 | 5.74 | = -0.71BL + 12.30 | 0.10 | 0.04 |
| 2 | 3 & 10 Oct | 38 | 4.6–12.8 | 4.64 | = -0.08BL + 5.35 | <0.01 | 0.74 |
| 1 + 2 + 3 | 3 & 10 Oct | 85 | 4.6–12.8 | 7.06 | = 0.70BL + 0.69 | 0.07 | 0.01 |

in this size range (16 of 21, Fig. 4A). Between 5.8 and 9.5 mm, 69% (11 of 16) swam in an intermediate hydrodynamic environment (Re: 300–1000, Fig. 4A). The 3 larvae smaller than 5.8 mm swam in a viscous hydrodynamic environment (Re <300) but so did 9 other larvae, ranging in size up to 11 mm (Fig. 4A). In contrast, on 10 October, when there were fewer small larvae and the water was 26°C, most larvae regardless of size swam in an intermediate hydrodynamic environment. On 10 October, the only larvae to swim in an inertial hydrodynamic environment were 8.3 mm or larger, but this constituted only 17% (5 of 29) of larvae in this size range (Fig. 4B). Also, among larvae 8.3 mm or larger, 10 and 14 larvae swam in a viscous or intermediate hydrodynamic environment, respectively. Among the 14 larvae smaller than 8.3 mm, 79% swam in an intermediate hydrodynamic environment (including the 3 smallest larvae), and 21% swam in a viscous hydrodynamic environment (Fig. 4B). The apparent difference between 3 (28°C) and 10 October (26°C) in the smallest larva swimming in an inertial hydrodynamic environment (10.3 mm and 8.3 mm on 3 and 10 October, respectively) is not meaningful because on 3 October, no Ucrit measurements were made on larvae between 8 and 9.5 mm BL.

## Discussion

### Morphology

Larvae of the orchid dottyback have few distinguishing features. This is consistent with what is known of the development of other pseudochromine pseudochomids (Gill et al., 2000). Larvae of the orchid dottyback lack the gut rugosities reported in some pseudochromines (Gill et al., 2000). The orchid dottyback is one of the least pigmented larval pseudochromines illustrated to date.

Thus, larvae of the orchid dottyback are likely to be confused with the larvae of a number of other families, particularly silliginids, labrids, scarids, and plesiopids of similar body shape and little or no pigmentation. Gill et al. (2000) detail how to distinguish larval pseudochromine pseudochromids from other pseudochromid subfamilies and from other similar Indo-Pacific families.

Dottyback larvae are not common in plankton samples from coral reef waters, and the large number of species with similar meristic values makes identification challenging. Melanistic pigmentation in the orchid dottyback is minimal and varies among individuals. Gill et al. (2000) characterized the larvae of some pseudochromid species as "nearly devoid of pigment," a description that applies to the orchid dottyback. Still, other pseudochromid species, such as the unidentified species from the Great Barrier Reef illustrated by Gill et al. (2000), have relatively extensive pigment series along the dorsal and ventral midlines of the tail and ventrally on the trunk. Clearly, larval descriptions of more pseudochromid species are required to understand which morphological characteristics can be useful in identifying field-captured larvae to the species level. Genetic barcoding will probably be necessary to establish the identities of larvae.

### Swimming

The swimming speeds of larvae as measured by Ucrit on 10 October were not as great as those on 3 October. Cohort 2 larvae on 10 October had a mean speed of about 40% of those of cohort 1 larvae on 3 October, in spite of the fact that they were of similar size and age. Further, neither the older cohort 2 nor the younger cohort 3 had the expected positive relationship between speed and size

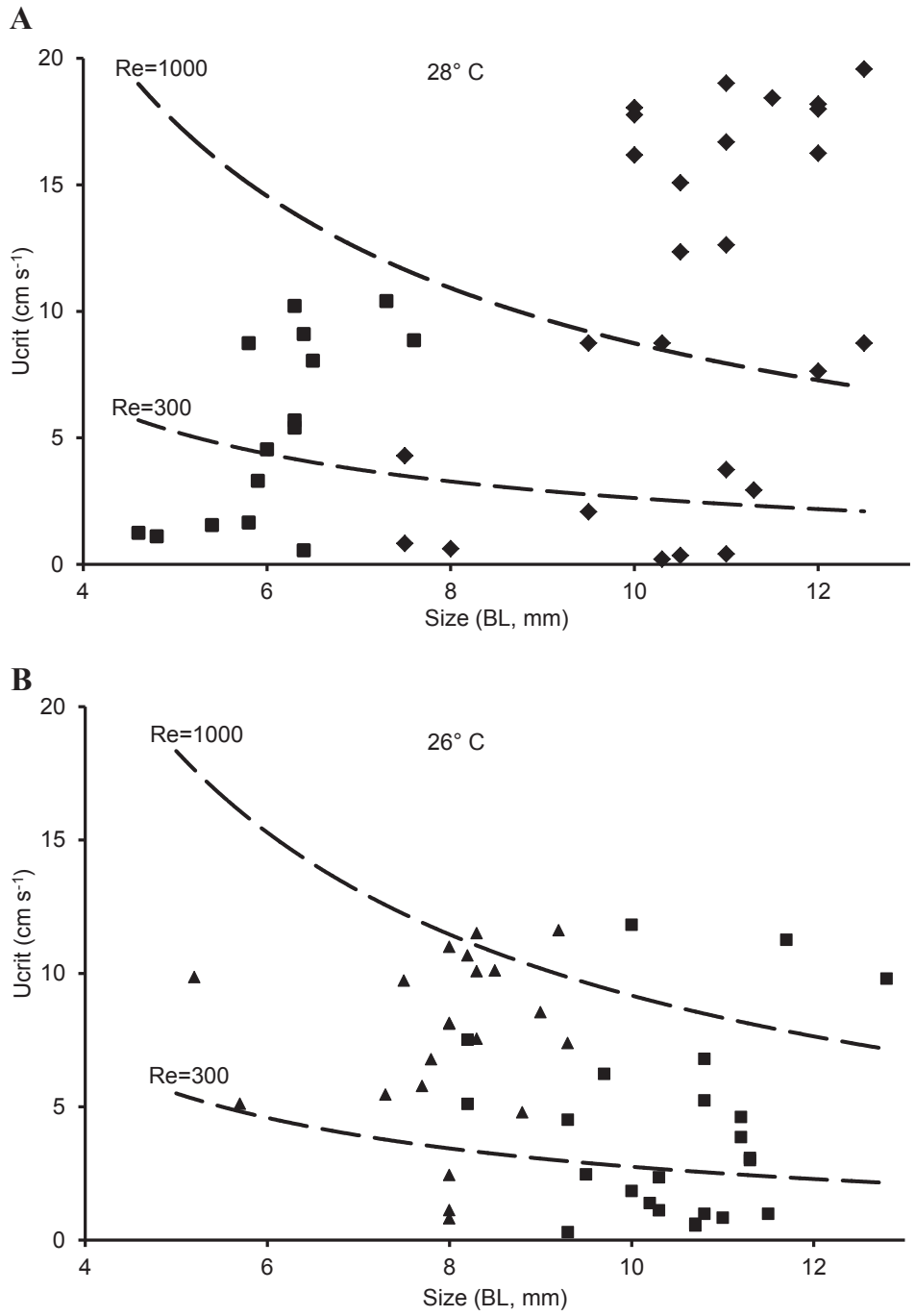


**Figure 4**

The hydrodynamic environment occupied by reared larval orchid dottyback (*Pseudochromis fridmani*) of 3 cohorts as determined by their size (body size [BL]) and critical swimming speed (Ucrit) and identified by Reynolds number (Re) on 3 October (28°C) and 10 October (26°C) in experiments conducted in a laboratory swimming chamber at an aquarium facility in France. (**A**) Cohorts 1 (diamonds) and 2 (squares) as measured on 3 October 2010 at 28°C. (**B**) Cohorts 2 (squares) and 3 (triangles) as measured on 10 October 2010 at 26°C. The hydrodynamic environments on both dates are defined by the Reynolds number (Re, curved lines): Re <300 (below the lower curve) indicates a viscous environment dominated by frictional drag, Re >1000 (above the upper curve) indicates an inertial environment where swimming is more sustainable, and 300<Re<1000 (between the 2 curves) indicates an intermediate environment. Some symbols overlap.

(Leis, 2010) on 10 October, whereas both the older cohort 1 and the younger cohort 2 did on 3 October.

Similar results were obtained with the fairy basslet (*Gramma loreto*), a species with similar larval morphology, that was also tested for Ucrit at Lautan on 3 and 10 October 2010 (Leis et al., 2012a). The cohorts of the fairy basslet tested on 3 October (28°C) had significant, positive, linear relationships between Ucrit and size, whereas the cohorts tested on 10 October (26°C) did not. As with the orchid dottyback, the ontogenetic increase in Ucrit in the fairy basslet was about 2.7 cm/s for each 1 mm increase in BL on 3 October with a significant but weaker increase of 1.6 cm/s for each 1 mm increase in BL for the combined 3 and 10 October measurements.

There are no data on swimming speed of pseudochromid larvae in the ocean (in situ speed). Based on measurements of other taxa, in situ speeds of pseudochromid larvae are likely to be 30% to 90% of Ucrit (Leis, 2010). The Re (Fig. 4) show that only larvae larger than about 9 mm BL (about the size when all fins are fully formed) are capable of reaching an inertial hydrodynamic environment where swimming is more efficient and are therefore likely to be able to substantially influence their dispersal by horizontal swimming. However, there are no data on endurance swimming of pseudochromid larvae, and endurance is not readily predictable from Ucrit data. So, it is not clear how long orchid dottyback larvae might be able to maintain swimming speeds that are likely to be able to influence dispersal outcomes.

Although the reasons for the difference in swimming performance on the different dates are unclear, it is clear that, compared to many other tropical reef fishes (Leis, 2010), orchid dottyback larvae are relatively slow swimmers, with a slow rate of increase in speed with increasing size. This can probably be attributed to their slender morphology, with low lateral area at any size, plus the fact that they settle at a small size of 12 mm BL. This is supported by comparisons of body size and shape with swimming performance (Fisher and Hogan, 2007; Downie et al., 2021). Other pseudochromid larvae have similar morphology, and it seems that they also settle at a small size. For example, Gill (2004) examined museum collections of 57 *Pseudochromis* species and found settled specimens smaller than 18 mm BL in 19 species, with some as small as 10 mm. Furthermore, the largest reported pelagic pseudochromid larva is 14.5 mm in BL (Fisher et al., 2005). So, other pseudochromids can be expected to have swimming performance similar to that of the orchid dottyback. This expectation is supported because other taxa with larval morphology similar to that of the orchid dottyback have similar swimming performance: a grammatid (Leis et al., 2012a) and a settlement-stage sillaginid and several labrids (Jenkins and Welsford, 2002; Leis et al., 2011). However, the mean Ucrit of 3 species of wild pseudochromid settlement-stage larvae was 27 cm/s or 15.5 BL/s (Fisher et al., 2005). This is greater than the 11.6 cm/s (10.7 BL/s) of reared settlement-stage orchid dottybacks, which are somewhat smaller at settlement. Comparisons between the 2 studies are problematic due to differences in water temperature, species, and size of larvae.

We can only speculate on the reasons for the different swimming results on 3 and 10 October, but a likely factor is that the water temperature was 2°C warmer on 3 October (28°C versus 26°C). A study that measured Ucrit in larvae of a pomacentrid species that were both reared and swam at either 25°C or 28°C found average speeds 13% to 36% faster at 28°C (Green and Fisher, 2004). Importantly, Green and Fisher concluded that relative to size, Ucrit was less in larvae reared at 25°C than at 28°C—a result similar to ours. The Green and Fisher study was not specifically about the ontogeny of swimming, so the results are not directly applicable to our results. This is particularly the case as we know only what the temperature was at the times we measured Ucrit in orchid dottybacks, not what it might have been at other times during rearing. Nevertheless, the Green and Fisher results do indicate how temperature might influence Ucrit.

Temperature can influence swimming speed in larval fishes in 2 ways: by altering water viscosity and by influencing muscle physiological processes (Hunt von Herbing, 2002). Small larvae, swimming at slow speeds, swim in a viscous hydrodynamic environment (Re <300) dominated by frictional drag, but with growth and increased swimming ability, larvae eventually swim in an inertial hydrodynamic environment (Re >1000). Swimming in an inertial hydrodynamic environment is more sustainable, and thus, swimming becomes increasingly relevant to dispersal. Reynolds numbers between 300 and 1000 represent an intermediate hydrodynamic environment where both viscous and inertial forces are important. However, the difference in Re between 26°C and 28°C for a given combination of speed and size is small—about 4%.

In ectothermic vertebrates, the relationship between physiological rates and temperature is typically dome-shaped (Hochachka and Somero, 2002). So, it would be expected that swimming performance would increase as temperature increases, at least initially. Both the orchid dottyback and the fairy basslet are tropical species that occur in areas where summer ocean temperatures of 28°C or greater are common. Thus, a difference in temperature from 26°C to 28°C would be expected to decrease water viscosity and increase muscle activity, both of which would tend to increase swimming speed (Hunt von Herbing, 2002), as was found here.

No differences in orchid dottyback growth rate or percent body depth at pectoral-fin base versus BL (a

proxy for condition) were apparent between 3 and 10 October. Although a change in temperature of 2°C might be expected to result in a difference in swimming speed, the typical increase in speed with increase in size of the larvae found in previous studies of both temperate and tropical species (Guan et al., 2008; Leis, 2010; Moyano et al., 2016) occurred in the present study at 28°C (3 October) but not at 26°C (10 October). This was not expected. The cooler temperature on 10 October might have reduced swimming speed without influencing growth or condition, but as rearing conditions during the week between 3 and 10 October, including temperature, are unknown, we cannot be sure to what extent the differences in Ucrit between the 2 dates were due to temperature.

If the results from 10 October were not an artifact of rearing conditions other than temperature, at least some orchid dottyback larvae of about 9 mm BL or larger would be capable of swimming in an inertial hydrodynamic environment at both 26°C and 28°C. Although at 28°C, a much greater percentage (ca. 74% versus 17%) of larvae larger than 9 mm would be able to do so than at 26°C and might therefore be able to influence dispersal to some degree by horizontal swimming.

Studies of the ontogeny of swimming in larval fishes that have considered temperature found inconsistent temperature influences (Moyano et al., 2016). However, a nearly universal result is that, at any temperature, swimming performance increases with size of the larvae, and it is commonly found that mean speed increases with temperature, at least to a point. In our unplanned comparison of Ucrit in the orchid dottyback, at the lower temperature of 26°C an increase in Ucrit with size was not found in either cohort 2 or cohort 3. In contrast, at 28°C the expected ontogenetic increase in Ucrit with size was found in both cohorts 1 and 2. At 26°C, average Ucrit was 6.6 BL/s, and at 28°C, mean Ucrit was 9.1 BL/s, an expected result. Interpretation of these results is difficult, and it is not clear why a difference in temperature of 2 degrees could result in the lack of an ontogenetic increase in swimming speed. However, this indicates that future studies of swimming ontogeny should consider the influence of temperature from the start.

## Conclusions

The orchid dottyback has direct morphological development with few specializations for pelagic existence and settles at a relatively small size of about 12 mm BL. The larvae are slender and are nearly devoid of melanophores. The development of swimming as measured by Ucrit differed between the 2 times, a week apart, when it was measured in larvae of 4.6 to 12.8 mm BL. On 3 October, Ucrit increased linearly at 2.5–3.2 cm/s for each 1 mm increase in BL to a maximum of 20.0 cm/s at settlement size. In contrast, on 10 October, no significant relationship between Ucrit and BL was found. This difference may have been due to a 2°C difference in temperature between dates. Some larvae of at least 9–10 mm BL swam fast enough to reach an inertial hydrodynamic environment (Re >1000) on both dates, but the proportion of larvae that did was about 4 times greater on 3 October (28°C) than that on 10 October (26°C). It is likely that orchid dottyback larvae will have minimal influence on their dispersal via horizontal swimming until shortly before settlement.

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