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# Sudden degeneration of eyes just before settlement in the larva of *Odontamblyopus lacepedii*, the endemic goby to Ariake Bay, Japan

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**Abstract:** The eel goby, *Odontamblyopus lacepedii*, with vestigial eyes, is endemic to Ariake Bay, Japan and is associated with shallow, muddy bottoms of estuaries. Larval distributions related to the metamorphosis of the species were examined around the upper estuary of the bay, which consists of a heavily turbid, vertically mixed, and strong tidal current. In the present study, we identified the larvae immediately after hatching. Their eyes were still enlarged with growth during the pelagic period but suddenly started to degenerate and became vestigial just before settlement during a 2-mm increment in body length. During this period, the larvae were vertically distributed from the surface and middle layer to the near-bottom and bottom layers with relatively high turbidity, and their pelvic fins rapidly developed; it is assumed that they changed their mode of life to be similar to that of adults. From these results, it is elucidated that the transition from a pelagic to a benthic lifestyle in this species synchronize with the eyes degenerate and buried under the skin, i.e., morphological and ecological changes occur in synchronization.

***Keywords :*** *Odontamblyopus lacepedii*, Metamorphosis, Distribution, Ariake Bay

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## Introduction

The eel goby, *Odontamblyopus lacepedii* (Amblyopinae), is endemic to Ariake Bay, Japan (Takita, 2000). This species is classified in the family Oxudercidae (Nelson *et al*., 2016). Also, *O. lacepedii* is found in western and southwestern Korea, China, Hong Kong, and Taiwan (Murdy and Shibukawa, 2001). The species is unique within the Amblyopinae in having free and silk-like pectoral fin rays and in undergoing metamorphosis represented by eye degeneration during ontogenetic development (Dotsu, 1957).

Ariake Bay is characterized by having brackish, highly turbid water with strong tidal currents (INOUE, 1980). TANAKA (2007) speculated that as the Japan Archipelago separated from the Asian continent, only Ariake Bay retained such an environment, consequently supporting fishes, including *O. lacepedii*, as continental relicts.

Little is known about the early life history of the species, although there is some knowledge about its distribution (DOTSU, 1957; TAKITA, 1980; TAKITA *et al*., 2003) and early development (DOTSU and TAKITA, 1967). Recently, AOYAMA *et al*., (2007) and YAGI *et al*., (2011) observed that *O. lacepedii* juveniles settled mainly around the upper estuary of the bay, indicating its importance as an essential nursery habitat. However, metamorphosing larvae have rarely been found, and information on the relationship between metamorphosis and the corresponding ecological changes in the species is very fragmented. The elucidation of eye degeneration in *O. lacepedii* reveals the importance of morphological and ecological changes during the early life history of the fish and the adaptation of the endemic fish to the unique environment of Ariake Bay.

In this study, we provide a detailed description of *O. lacepedii* larval development and describe its early migration in relation to its metamorphosis to better understand the early life history of the species.

## Materials and methods

*Odontamblyopus lacepedii* larvae and juveniles were collected from the Rokkaku estuary (Stn.) located in the inner part of Ariake Bay (Fig. 1) On 20 July 2016, which was a spring tide. The pelagic larvae and juveniles were collected using oblique tows and a larval net with a mouth diameter of 1.3 m. The mesh aperture of the nets was 0.5 mm. To collect demersal larvae and juveniles, beam trawls (width, 1.5 m; height, 0.3 m; 2 mm mesh aperture) were used according to a method described by KUIPERS (1975) with modifications.

To examine the differences in the size and vertical distribution of species relative to the tidal phase, discrete-depth horizontal tows in the surface and middle layers were conducted with a larva net (1.3 m mouth-diameter, 0.5 mm mesh-aperture) and near-bottom layers were conducted with a specialized beam trawl (width, 1.5 m; height, 0.25 m; 2.0 mm mesh-aperture) and a beam trawl on the bottom from flood to ebb tides at Stn., located outside the river mouth. The specialized beam trawl was modified by KUIPERS (1975), and it was designed to keep the lower beam of the mouth 5 cm above the bottom to collect pelagic larvae distributed near the bottom (EBRAHIM *et al*., 2006).

The towing distances (m) of the larval net were measured using a flowmeter (2030R, General Oceanics), and the towing depths (m) were measured using a depth recorder (DEFI-D10, JFE Advantech) attached to the nets. The towing distances (m) of the beam trawl and seine nets were monitored using a GPS (Colorado300, Garmin).

The number of individuals ($n$) was converted to density ($N$: n × 1000 $m^{-3}$) using the following equation:

$$N_{LN} = (n \times 1000) / (A \times D), \quad (1)$$

where $A$ is the area ($m^2$) of the larval net and $D$ is the towing distance (m).

$$N_{BT} = (n \times 100) / (w \times D), \quad (2)$$

where $w$ is the width (m) of the beam trawl and $D$ is the towing distance (m) for the beam trawl.

All samples were fixed in 10% formalin, and fish larvae and juveniles were sorted and transferred to 80% ethanol. Subsequently, the *O. lacepedii* specimens were measured for size. The developmental stages of larvae and juveniles were assessed as described by KENDALL *et al.* (1984).

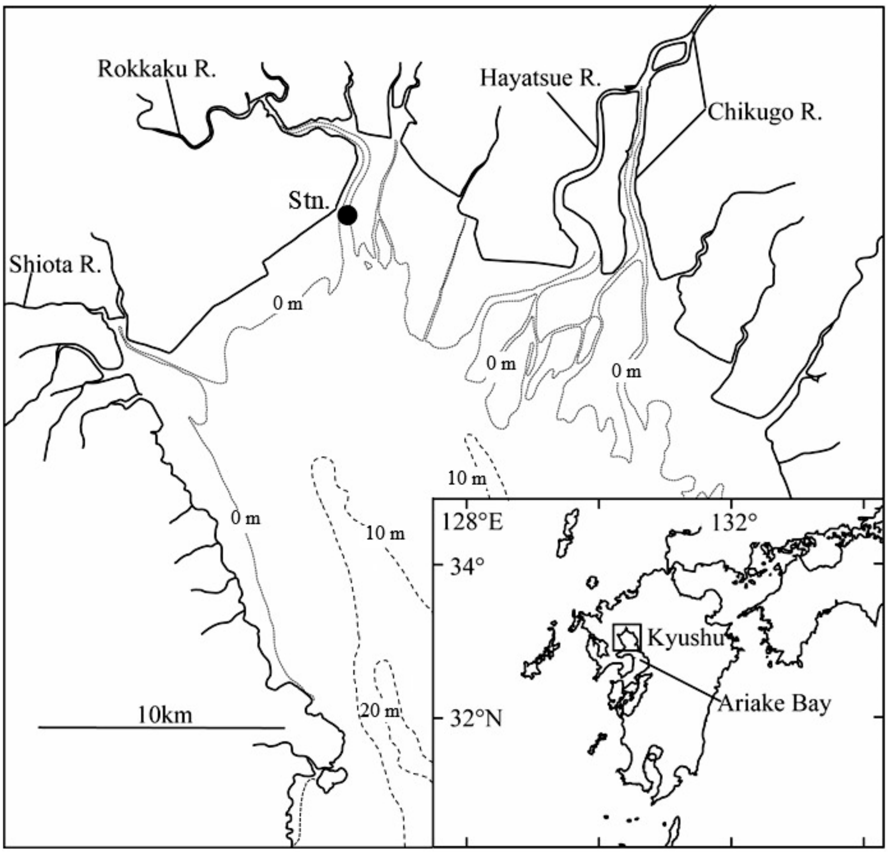


**Fig. 1** Chart of Ariake Bay showing stations where fish larvae and juveniles were collected on 20 July 2016. Solid circle (Stn.) indicates the station for discrete-depth horizontal tows with a larva net, near-bottom net, and beam trawl.

The unlabeled lengths in the present study indicate body length (BL). To better understand the metamorphic phenomenon of the species, a maximum of 100 specimens collected using discrete-depth horizontal tows were randomly selected and their eye diameter and head length were measured.

Water temperature (℃), salinity, and turbidity (NTU) were measured every hour at 0.5 m depth-intervals from the surface to the bottom using a Compact-CTD (ASTD102, JFE Advantech). The current was measured with an ADCP (WHSZ12000-I-UG12, RD Instruments) at 0.5 m depth-intervals from a depth of 1 m to the bottom.

*O. lacepedii* larvae and juveniles (Fig. 2) were identified as species based on adult meristic characteristics (counts of dorsal and anal fin rays and vertebrae) and distribution of melanophores (Dotsu, 1957). The representative series of specimens used in this study were deposited at the Usa Institute of Marine Biology, Kochi University.

## Results

### Descriptions of larvae and juveniles (Fig. 2)

**Morphology.** The metamorphosis of the species started and completed at ca. 10.0 mm and

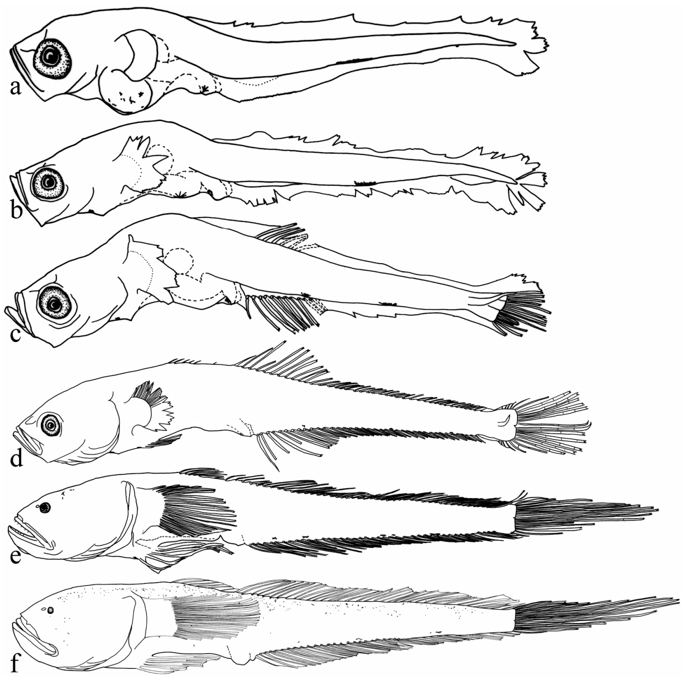


**Fig. 2** Developmental stages of *Odontamblyopus lacepedii* larvae and juveniles. a, 2.9 mm BL yolk-sac larva (UKU-433000); b, 3.7 mm BL preflexion larva (UKU-433001); c, 4.3 mm BL flexion larva (UKU-433002); d, 9.8 mm BL postflexion larva (UKU-433003); e, 12.1 mm BL juvenile (UKU-433004); f, 15.3 mm BL juvenile (UKU433005).

12.0 mm, i. e., the eyes were enlarged with growth during the pelagic period (ca. 3.0–10.0 mm) and started to degenerate and become vestigial just before settlement with only 2 mm increase in body length (Fig. 3). During this period, the larvae were vertically distributed from the surface to the bottom (Fig. 3).

The caudal anlagen began to develop at approximately 4 mm with notochord flexion, and it was fully developed at approximately 10 mm. The caudal fin had longer principal rays in the lower lobe than in the upper lobe (Fig. 2f). Dorsal and anal anlagen appeared at approximately 4 mm, their incipient soft rays began to differentiate at approximately 4 mm in pre-metamorphic larvae, and all soft rays were present at approximately 10 mm in juveniles. Incipient rays in the pectoral fin and pelvic bud were present at ca. 10 mm in the pre-metamorphic stage (Fig. 2d), and they were fully completed at ca. 12 mm in the metamorphosing stage (Fig. 2e).

**Pigmentation.** The distribution of melanophores was sparse in the larvae during metamorphosis (Fig. 2a-e). Distinct melanophores were visible at the ventral margin of the tail in the smallest pre-metamorphic larvae (Fig. 2a), which were irregularly distributed in the later-stage larvae and juveniles (Fig. 2b-e). Ventral abdominal melanophores were found in the early pre-metamorphic larvae (Fig. 2a, b) but disappeared in metamorphosing larvae and juveniles (Fig. 2e, f). In juveniles approximately 15 mm in

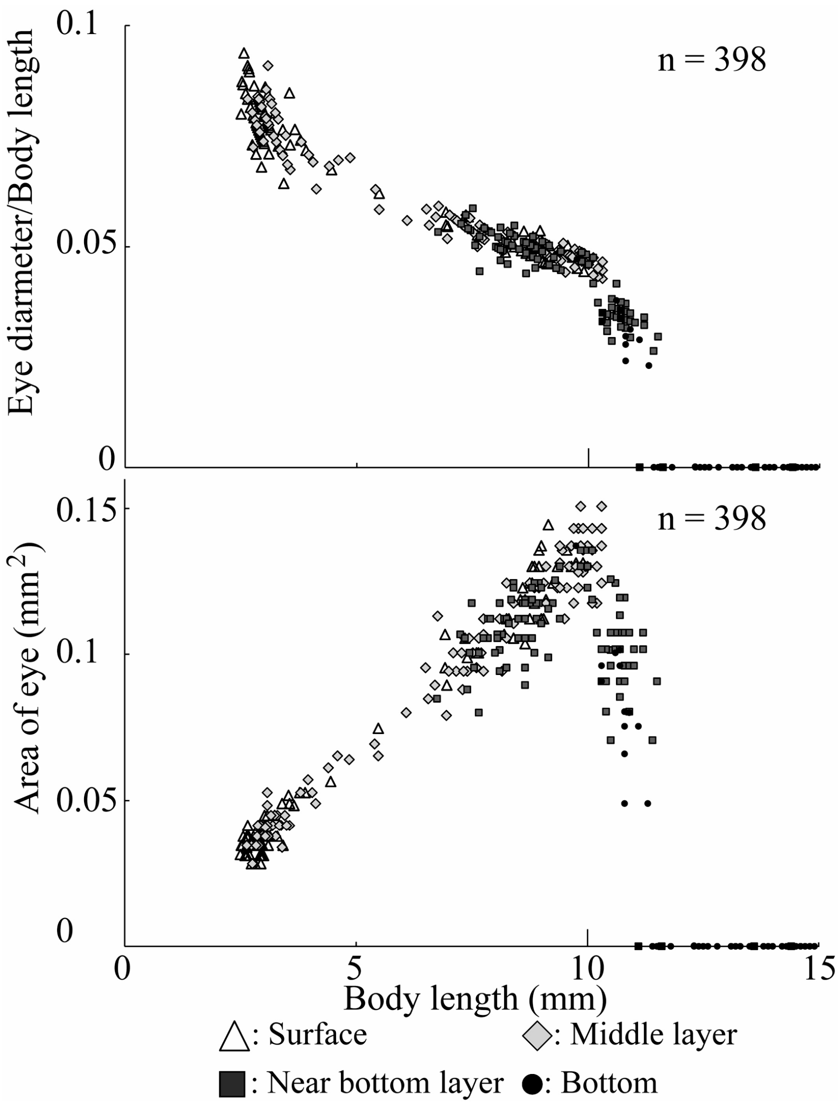


**Fig. 3** The relationships among vertical distribution, eye diameter/body length (top), and area of eye in the standard length of *Odontamblyopus lacepedii* larvae and juveniles. Open triangle, gray diamond and square, and solid circle indicate specimens collected at the surface, middle and near-bottom layers, and bottom, respectively.

diameter, small melanophores were scattered dorsolaterally on the head and trunk (Fig. 2f).

**Tidal changes in the distribution of larvae**

**Physical conditions (Fig. 4).** Strong tidal currents, which reached a maximum velocity of ca. 1.5 kt, within the estuary drastically altered the vertical structure of the water column, and the current velocity was slightly higher in the surface layers than in the bottom layers during

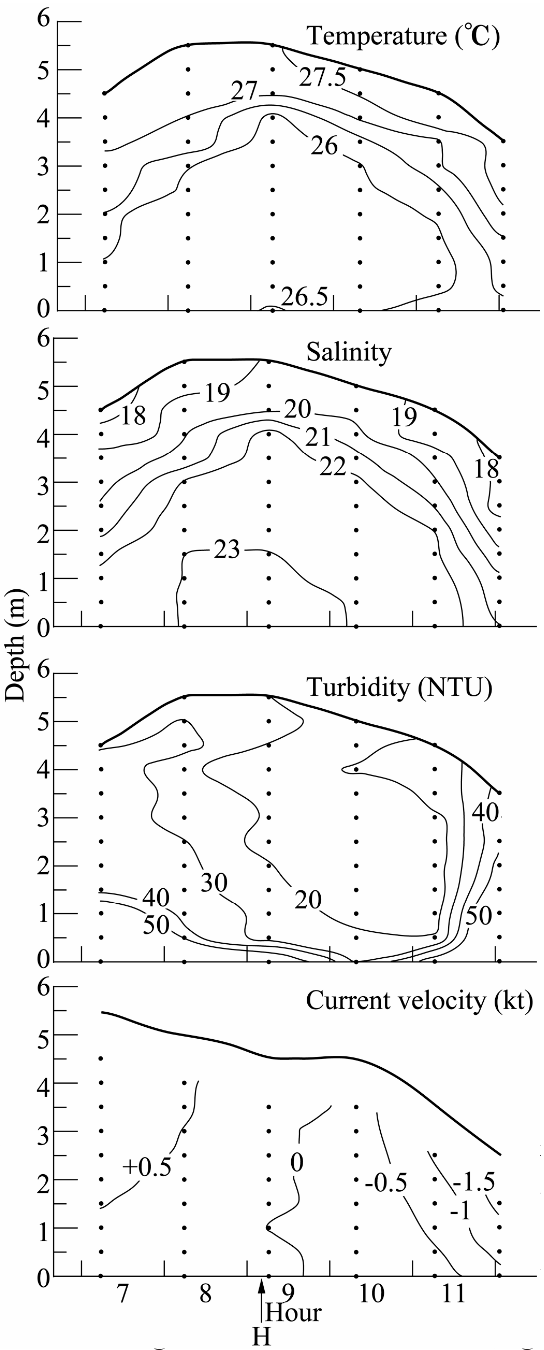


**Fig. 4** Changes in the vertical profiles of water parameters at Stn. with tidal cycle. Flood and ebb velocities are denoted as + and -, respectively. *H* indicates the hour of high tide.

5). During the survey, the yolk sac, preflexion, and flexion larvae of *O. lacepedii* were distributed in the surface and middle layers, with a maximum density of 4136 /1000m$^3$ at low tide (12:00), but did not appear in near-bottom layers or on the bottom, except in near-bottom layer at 8AM. Juveniles (< 10 mm) were mainly distributed from the surface to near-bottom layers except in the surface layer at 10AM, after high tide. Juveniles (> 10 mm) were mainly distributed in the near-bottom and bottom layers during the survey.

## Discussion

The morphological results for the larvae and juveniles obtained in the present study are consistent with those of Dotsu (1957), who used natural larvae. The yolk-sac larvae observed in this study were ca. 3.0 mm. In a study by Dotsu and Takita (1967), the larvae were 3.3 to 3.5 mm TL immediately after hatching; therefore, the larvae in the present study were determined immediately after hatching. No eggs of *O. lacepedii* have been found in the wild, but based on the distribution of yolk-sac larvae and juveniles, it is speculated that they hatch near the mouth of the river and then settle on the river bottom in the tidal areas (Aoyama *et al.*, 2007). This suggestion is supported by the results of the present study, conducted near the river mouth, which *O. lacepedii* was observed from the yolk-sac larvae immediately after hatching to juveniles and settling on the bottom.

Their eyes were still enlarged with growth during the pelagic period but suddenly began degenerate and became vestigial just before settlement at a 2-mm increment in body length (Fig. 3). During this period, the larvae were vertically distributed from the surface and middle layers to the near-bottom and bottom layers, and their pelvic fins rapidly developed. These results

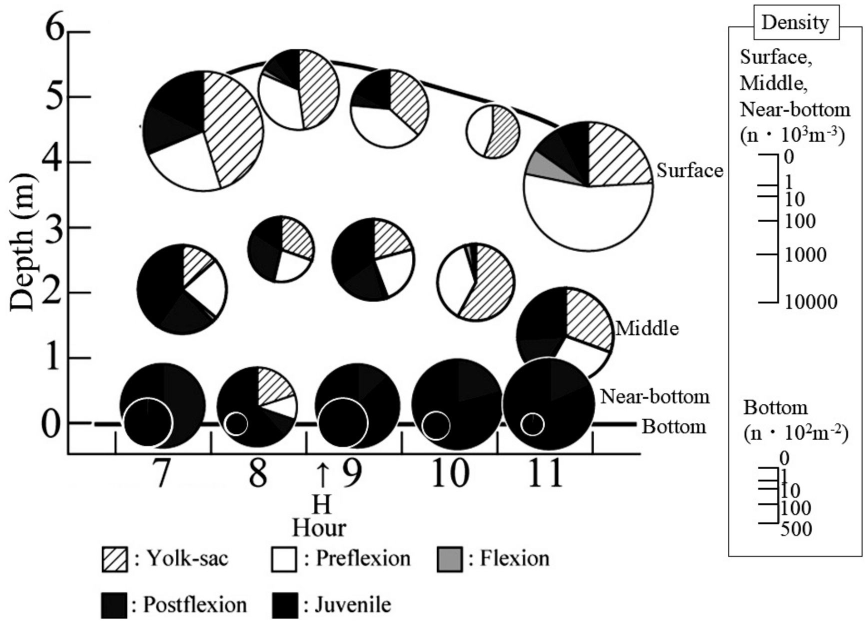


**Fig. 5** Vertical profiles of *Odontamblyopus lacepedii* larvae and juveniles collected with a larva net, near the bottom net and beam trawl at Stn. with tidal cycle on 20 July 2016. The circles indicate Time and depth of collections. The diameter of each circle is drawn in proportion to the cube root of density (n・$10^3$ $m^{-3}$) for the surface, middle, and near-bottom layer samples and the square root of density (n・$10^2$ $m^{-2}$) for the bottom samples. *H* indicates the hour of high tide.

indicate that eye degeneration is synchronized with species settlement. The habitat has higher turbidity near the bottom than in the surface and middle layers, and it is suggested that the species changed its lifestyle to become more similar to adults.

However, the blind cave fish *Anoptichthys jordani* has a small eye during the first three days after hatching (ZILLES *et al*., 1983). After approximately ten days, the eyeball was below the level of the surrounding epidermis. The orbital diameter diminished and did not allow a general view of the entire surface of the eyeball. Over the following weeks, the eyeball is gradually covered by epidermal tissue (ZILLES *et al*., 1983). This difference is caused by the difference between the caves, where the environment changes little generally or temporally, and the estuary in Ariake Bay, where the environment changes significantly temporally.

The changes in vertical distribution of *O. lacepedii* with its development will be compared with those of other fish species distributed in the Ariake Bay. The vertical distribution of two clupeoid fishes, *Ilisha elongata* and *Sardinella zunasi*, did not appear to change significantly with development (WANG *et al*., 2021). The change in the vertical distribution associated with metamorphosis in *Cynoglossus lighti*, which undergoes remarkable morphological changes during its early life history (YAGI *et al*., 2009), is not as synchronized as that in *O. lacepedii*. Unlike the three species mentioned above, the vertical distribution of *O. lacepedii* significantly changed during metamorphosis. This difference may be because *O. lacepedii* has adapted to the unique environment of the Ariake Bay, with adults having a unique lifestyle of burrowing in the silty mud bottom.

On the other hand, when comparing the structural or functional changes with settlement of *Acanthogobius flavimanus*, belonging to Oxudercidae, with those of *O. lacepedii*, it was found that although the eyes of *A. flavimanus* did not degenerate, rapid changes in various characteristics, such as gaining broader upper-field view capability, occurred as the fish transitioned to a benthic lifestyle (Kanou *et al.*, 2004). These phenomena suggest that Oxudercidae is a group capable of rapid structural and functional changes in synchronization.

To date, little is known about the metamorphosis of *O. lacepedii* in the wild, in this study, based on a detailed spatiotemporal survey of the estuary area in the innermost part of Ariake Bay, morphological and ecological changes in *O. lacepedii* were synchronized. It is speculated that the rapid morphological change that occurred when *O. lacepedii* settled on the bottom is an example of potential of this species being realized in order to adapt to the large tidal ranges and high turbidity found in the Ariake Sea and part of the eastern coast of Eurasia. There is no knowledge regarding the morphology associated with ecological changes in the larvae and juveniles of this species in Asian continent, and so a comparison cannot be made, however, as this species is considered to be a continental relict species, the characteristics of this species in the Ariake Bay are thought to be common to the same species distributed on the Asian continent.

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