

## タチウオ仔稚魚の生態と感覚器の発達

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## Development of the Sense Organs of Ribbonfish *Trichiurus lepturus* Larvae and Juveniles<sup>\*1</sup>

Gunzo Kawamura<sup>\*2</sup> and Masahiro Munekiyo<sup>\*3</sup>

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The morphology of the sense organs of the larvae and juveniles of the ribbonfish *Trichiurus lepturus* in Wakasa Bay was examined to obtain insights on changes in behavior and habitats with growth of the fish. Development of the sense organs proceeded in accord with the rest of the morphological development of the larvae and juveniles. Sense organs required for feeding were formed at the onset of exogenous feeding. The taste buds first appeared at the beginning of the postlarval period and increased in number in association with the pharyngeal teeth and gill arches. During the late phase postlarval period, the lateral line canal on the head and the olfactory rosette were formed. The retinae became duplex and developed horizontal cells in three layers; this is inferred to be advantageous for a piscivorous feeding habit. The presence of well developed sense organs synchronized with the active migration of postlarvae from offshore to coastal waters.

The ecology of the ribbonfish *Trichiurus lepturus*, a commercially important marine species in warm waters, has been investigated in Wakasa Bay by Munekiyo and his colleagues.<sup>1-7)</sup> However, due to restrictions in sampling gear and season, the early life history of this fish has been remained poorly understood.

It has been demonstrated that ontogenetic changes in behavior are closely related to sense organ morphogenesis in reared larval fishes.<sup>8-15)</sup> Studies on the degree of development of larval sense organs could supplement ecological researches in the field.

The objective of this study is to examine the degree of development of the sense organs in sea-caught ribbonfish larvae and juveniles, and to obtain insights on the changes in the behavior and habitats with growth of the fish. Since larval growth rates vary depending on food, temperature and other environmental factors,<sup>11,14)</sup> in the description and comparison of fish larval development, events are better evaluated in the same material used in ecological study.

### Materials and Methods

The fish used were collected from Wakasa Bay with larva nets and beach seine, and were the same material used by Munekiyo and Kuwahara.<sup>4,5)</sup>

The samples were collected in the years between 1980 and 1983, and preserved in 10% formalin. The specimens ranged from 5.4 mm to 94 mm in total length (TL), those larger than 20.5 mm TL collected only with beach seine.

For histological examination of the sense organs, the fish were embedded in paraffin, and 6  $\mu$ m thick sagittal and transverse sections were made and H.E.- or Azan- stained. In examining the retina, the kinds and numbers of visual cells present were ascertained by making counts of the cone ellipsoids in the visual cell layer, and of the cell nuclei in the outer nuclear layer. The ratio of cell nuclei to cone ellipsoids is greater than 1.0 where rods are present.<sup>9)</sup> Some specimens were used for the examination of the olfactory epithelium and free neuromasts with a scanning electronmicroscope. They were dehydrated in an ethanol series, critical point dried, and spattered with gold.

### Results

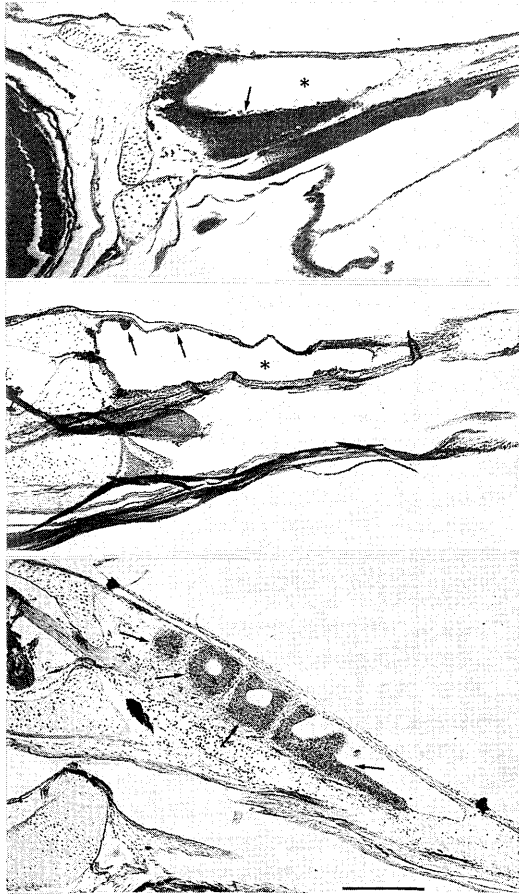
#### Eye

In the two smallest specimens (both 5.4 mm TL), the eyes were deeply pigmented. The lens was well developed and made of two layers. The retinal elements were arranged in layers, with the horizontal cells forming a single layer. The layers of visual cells, pigment epithelium, and outer

\*1 Contribution No. 59 from the Kyoto Institute of Oceanic and Fishery Science.

\*2 Faculty of Fisheries, Kagoshima University, Shimoarata, Kagoshima 890, Japan (川村軍蔵: 鹿児島大学水産学部)

\*3 Kyoto Institute of Oceanic and Fishery Science, Miyanomae, Miyazu, Kyoto 626, Japan (宗清正廣: 京都府立海洋センター).



**Fig. 1.** Sagittal sections showing the development of the olfactory organ of ribbonfish larvae. Top, 20.5 mm TL specimen with the dustpan-shaped, flat olfactory epithelium (arrow); middle, 37.6 mm TL with the slightly folded olfactory epithelium (arrows) lodged in the elongated olfactory sack (\*); bottom, 41.5 mm TL with the olfactory epithelium arranged in rosettes (arrows). Bar, 200  $\mu\text{m}$ .

nuclei were thickest at the temporal retinal part, implying a regional differentiation. The visual cells were all single cones; there were neither twin cones nor rods. The optic nerve fibers leaving the retina could be followed into the tectum in the serial sections.

The cell nuclei/single cone ellipsoids ratio was 1.0 for 5.8, 6.2, 8.5, 11.8, and 16.5 mm larvae. The ratio exceeded 1.0 in the temporal retinal part of a 20.5 mm larva, implying the first appearance of rods. The ratios were 1.5–1.8, 1.2, 2.6–2.8, 2.6–2.9 and 2.6–3.2 for 37.6, 41.5, 51.0, 89.0 and 94.0 mm specimens, respectively.

The horizontal cells formed two layers in

11.8 mm and three layers in 41.5 mm specimens.

#### *Lateral-line System*

The free neuromasts with cilia were found on the head of specimens at 5.4 and 11.8 mm, and on the trunk at 16.5 mm. Due to serious damage of the epidermis, free neuromasts were not observed in 5.8, 6.2 and 37.6 mm specimens and cupulae were all missing from the free neuromasts in other specimens.

In 20.5 mm specimens, the free neuromasts on the head began to sink into the dermis. Canal organs were first found on the head at 51.0 mm, and were completed on the head and trunk in 89 mm specimens.

#### *Olfactory Organ*

The nares were open and the olfactory epithelium was ciliated in the smallest specimens (5.4 mm). The olfactory epithelium progressively expanded to increase its surface area. It was dustpan-shaped open to the front at 8.5 mm, began to fold at 37.6 mm, and formed an immature olfactory rosette at 41.5 mm (Fig. 1).

#### *Taste Bud*

There were no taste buds in 5.4–5.8 mm larvae. The taste buds appeared first in the epithelium of the oral cavity of a 6.2 mm larva, and were numerous in the pharyngeal region of an 11.8 mm specimen that had well developed pharyngeal teeth, and on the gill arches of a 16.5 mm one that had gill rakers.

#### *Inner Ear*

The smallest specimens (5.4 mm) had well developed ossified inner ear with the basic elements: the utricle, saccule, and lagena all with ciliated neuromasts and the horizontal and vertical semi-circular canals.

### **Discussion**

The eyes, olfactory organs, free neuromasts, and inner ear were all well developed and innervated in the smallest specimens (5.4 mm TL), and may therefore be considered functional for light perception, chemoreception, mechanoreception and balance, respectively. All the sense organs, except the taste buds, are developed at the onset of feeding which takes place at 6.0 mm TL.<sup>4)</sup>

In the ribbonfish used here, age is unknown and descriptions of development are given on the basis of total length. Development of the sense organs

**Table 1.** Correlation between the typical behavioral changes and the ontogenetic development of the sense organs. The stages of development are adapted from Munekiyo (in preparation), and the behavioral changes, from Munekiyo and Kuwahara.<sup>4,5)</sup> TL, total length

Sense organ morphology (TL, mm)	Stage (TL, mm)	Behavior and habitat
Eyes, free neuromasts, olfactory epithelium, and inner ear are well developed (5.4)	Prelarval (~6)	Offshore habitat at depths of 80–120 m
Taste buds are formed (6.2)	Postlarval I, II (6~20)	Daytime feeding on zooplankton
Taste buds appear around pharyngeal teeth and gill rakers (11.8)		
Rod photoreceptors are formed (20.5)	Postlarval III (20~59)	Migrate shoreward
Free neuromasts at recess stage (20.5)		Benthic in coastal waters at depth of 30–40 m
Olfactory epithelium begin to fold (37.6)		Daytime feeding on zooplankton and fish
Retinal horizontal cells in three layers (41.5)		
Olfactory epithelium form rosettes (41.5)	Juvenile I (20~59)	Forming school Piscivorous
Canal organ is formed on the head (51.0)		
Canal organ is completed on the trunk (89.0)		

apparently proceeds in accord with the general morphological development of the larvae and juveniles. Based on body morphology, alimentary canal, teeth and other structures, Munekiyo<sup>\*1</sup> defined the stages of ribbonfish development as follows: prelarval, from hatching to around 6.0 mm; postlarval I, 6.0 to 6.3 mm; postlarval II, 6.3 to 20 mm; postlarval III, 20 to 59 mm; juvenile I, 59 to 117 mm; juvenile II, 117 to 163 mm. The remarkable changes in sense organ morphology are outlined in Table 1.

The postlarval III stage in the ribbonfish seems to be a part of the metamorphosis phase when many changes in body morphology as well as the sense organs, take place.

The visual cells are believed to be sensitive in the order of rod, twin cone, and single cone.<sup>16)</sup> Pure single-cone retinae have been demonstrated in many teleosts. The larvae of demersal fish are known to change their habitats from pelagic to benthic when rods appear, or when twin cones are formed.<sup>10,11)</sup> Adult ribbonfish have no twin cones,<sup>17)</sup> and the single cones of the larvae seem to be more sensitive compared to those of other fish species. Larva net tows showed that the eggs and prelarvae were most abundant in the middle and bottom layers (30–120 m with a peak at 75 m deep) of offshore waters,<sup>5)</sup> and the post-

larvae fed on zooplankton in daytime.<sup>4)</sup> The sensitive single cones would enable the postlarvae to feed where light intensity is low. No remarkable changes in behavior are found coincident with the appearance of the rod photoreceptors. However, rod vision probably enables ribbonfish larvae to feed in dim light and thus extend their feeding time for several hours, as suggested for the larvae of the northern anchovy *Engraulis mordax* by Bagarinao and Hunter.<sup>18)</sup>

Starting around 50 mm TL, ribbonfish larvae become piscivorous.<sup>4)</sup> Movement perception is important for piscivores in recognizing fast moving prey by sight. The horizontal cells, which are believed to be responsible for movement perception,<sup>19)</sup> are arranged in a single layer in early ribbonfish larvae, and in three layers at 41.5 mm, again in concert with the change in feeding habits of the larvae from plankton feeder to piscivore.

The appearance of the taste buds after the onset of exogenous feeding is common in marine fish larvae,<sup>11,12,18)</sup> and the gustatory sense seems to be of little importance for the early larvae. Since food selection may be expected to begin when the larvae have taste buds, as has been shown in the flounder *Paralichthys olivaceus*<sup>10)</sup> and largemouth bass *Micropterus salmoides*,<sup>15)</sup> the stomach contents of the ribbonfish should differ before and

\*1 M. Munekiyo (in preparation).

after the formation of taste buds. However, stomach content analysis at 10 mm length intervals did not show such selective feeding.<sup>4)</sup> Nevertheless, the taste buds develop in association with the pharyngeal teeth (at 11.8 mm) and with the gill rakers (at 16.5 mm), both food retention devices. Such timing is rational for secondary food selection by the gustatory sense.

There is no doubt that the lateral-line system and the inner ear are mechanoreceptors and that the olfactory epithelium is a chemoreceptor. However, since larval behavior by mechanoreception or olfaction at sea is unknown, correlation between the development of these sense organs and changes in behavior is not made in the present study.

Munekiyo and Kuwahara<sup>5)</sup> noted that the postlarvae migrate from offshore to coastal waters where more food is available, and suggested an active process involved in the migration. Active migration seems to be quite possible although the neural mechanisms involved are unknown. Since all sense organs are morphologically well developed when the larvae initiate the migration, the postlarvae might be able to perceive stimuli which attract them shoreward. Similar active migration has been suggested for the milkfish *Chanos chanos* postlarvae, which appear inshore in large numbers, and already have duplex retinae, taste buds, free neuromasts, and a ciliated olfactory epithelium.<sup>6)</sup>

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