

Morphological characteristics of the Ryukyuan paradise fish *Macropodus opercularis* (Perciformes: Belontiidae)

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Abstract

The paradise fish, *Macropodus opercularis*, was once thought to have been introduced to the Ryukyu archipelago from China. However, recent analyses have indicated regional differences in their reproductive characteristics. Therefore, the present study compared the morphological characteristics of the Ryukyuan population with those of continental populations from China and Vietnam by analyzing 27 external characteristics and vertebral morphologies in 10 specimens collected from Okinawa Island. The Ryukyuan population showed significantly deeper and wider heads and shorter caudal fins than those of the continental populations, and local variations were observed in some countable characteristics (lateral line scales, caudal vertebrae, and soft rays on the unpaired fins) among the three populations. These results imply the presence of a cryptic local population of paradise fish.

Keywords: East Asia, Intraspecific diversity, Discontinuous distribution; Biogeography, Nativeness.

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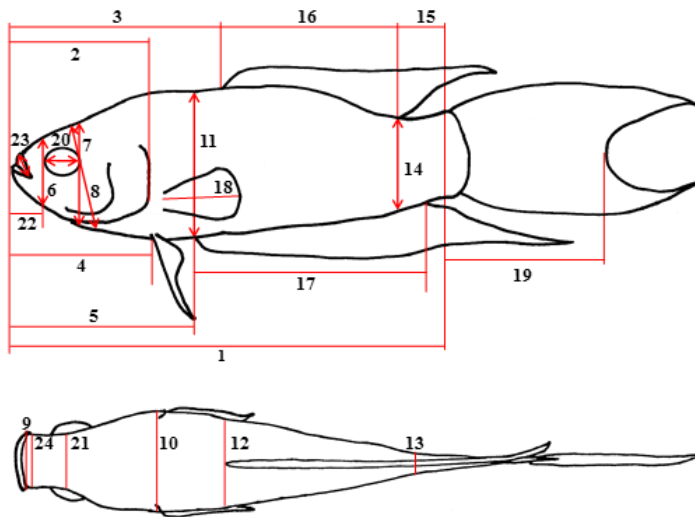
Introduction

The paradise fish, *Macropodus opercularis*, is distributed in southern China (south of Fujian and Hainan Island), Taiwan, Orchid Island, north-eastern Lao People's Democratic Republic, northern Vietnam, and the Ryukyu archipelago of Japan (Kitagawa and Hosoya 2016). This species, known as “fighting fish,” is a popular aquarium fish used for fish fights in East–Southeast Asia (Oka and Ohashi 1997). However, its wild populations have decreased throughout its range because of overexploitation; therefore, this species has been categorized as “Critically Endangered” in the 2019 Red List of Threatened Species, Japan, and as a protected species in Taiwan (Cheng et al. 2017; Ministry of the Environment Japan 2019). The Ryukyuan population of paradise fish was once considered non-native, given that the Ryukyu Kingdom had a long history of trading with Chinese dynasties (Kuroiwa 1927; Aoyagi 1948; Kouchi 1991). However, Kitagawa et al. (2013) have recently confirmed that the Ryukyuan and Chinese populations of paradise fish have slight regional differences in their reproductive characteristics. Since then, several studies have investigated the origin of the Ryukyuan paradise fish. However, Kitagawa and Hosoya (2016) were unable to determine whether the Ryukyuan population was naturalized or native through a literature survey. Although Kano et al. (2017) have reported that the Ryukyuan population is closely related to the Taiwanese population through mitochondrial DNA analysis, they did not evaluate its nativeness.

As stated above, several reports have elucidated the origin of the Ryukyuan paradise fish, but its morphological information has not yet been reported. Local variations in the paradise fish have been investigated by Freyhof and Herder (2002), who conducted a taxonomic review of the genus *Macropodus* inhabiting Vietnam, and Winstanley and Clements (2008), who reported some differentiation in the external shape between the Chinese and Vietnamese populations. However, to the best of our knowledge, no morphological data have been collected for the Ryukyuan population despite the importance of such data in estimating the origin of this population and contributing to the taxonomic review of the genus *Macropodus*. Therefore, the present study aimed to compare the external shape and vertebral morphology of the Ryukyuan paradise fish with those of the

Table 1. Samples of the Ryukyuan paradise fish, *Macropodus opercularis*, used in the analysis.

Registry No.	Preservative	Locality
KUN-P 44906	20% formalin	Kadena, Nakagami, Okinawa
KUN-P 44907	20% formalin	Kadena, Nakagami, Okinawa
KUN-P 44908	20% formalin	First-generation descendants of fish from Kadena, Nakagami, Okinawa
KUN-P 44909	20% formalin	First-generation descendants of fish from Kadena, Nakagami, Okinawa
KUN-P 44910	70% ethanol	Takiyamabaru, Naha, Okinawa
KUN-P 44911	70% ethanol	Takiyamabaru, Naha, Okinawa
KUN-P 44912	70% ethanol	Takiyamabaru, Naha, Okinawa
KUN-P 44913	70% ethanol	Takiyamabaru, Naha, Okinawa
KUN-P 44914	70% ethanol	Takiyamabaru, Naha, Okinawa
KUN-P 44915	70% ethanol	Takiyamabaru, Naha, Okinawa

**Figure 1.** Morphological measurements of the paradise fish *Macropodus opercularis*. 1: Standard length, 2: head length, 3: predorsal length, 4: prepelvic length, 5: preanal length, 6: head depth in front of the eyes, 7: head depth behind the eyes, 8: head depth at nape, 9: head width at lachrymal, 10: head width at operculum, 11: body depth at anal fin origin, 12: body width at dorsal fin origin, 13: body width at the end of the dorsal fin base, 14: body depth at the end of the dorsal fin base, 15: postdorsal length, 16: length of the dorsal fin base, 17: length of the anal fin base, 18: length of the pectoral fin, 19: length of the middle caudal fin ray, 20: eye diameter, 21: interorbital width, 22: snout length, 23: upper lip length, and 24: mouth width.

continental populations.

Material and Methods

From the Ryukyuan population, two individuals from the Kadena town in Okinawa (KUN-P 44906 and 44907), two first-generation descendants of fish derived from the Kadena town (KUN-P 44908 and 44909), and six individuals from the Naha city, Okinawa (KUN-P 44910–44915) were used as samples (Table 1). These specimens were euthanized using 2-phenoxyethanol (0.3 mL/L) and were preserved in 20% formalin (for KUN-P 44906–44909) or 70% ethanol (for KUN-P 44910–44915). Further, the external shape of each individual was examined to determine 27 characteristics (Fig. 1), as described by Freyhof and Herder (2002) and Winstanley and Clements (2008). The descriptions, counts, and measurements of the characteristics were obtained based on Hubbs and Laglar (2004). In addition, the vertebrae and fin rays were counted using soft X-rays. These data were then compared with published values for the Chinese and Vietnamese populations (Freyhof and Herder 2002; Winstanley and Clements 2008; Hosoya 2013). Statistical analysis was performed by the software R.3. 4. 1 (R Core Group 2017).

Results and Discussion

The morphometric data are presented in Tables 2 and 3. The Ryukyuan paradise fish had significantly deeper and wider heads and shorter caudal fins than the Vietnamese specimens (Welch's t-test, $P < 0.05$; Table 2; Freyhof and Herder 2002). Furthermore, the countable characteristics of the Ryukyuan paradise fish were

Table 2. External shape measurements for the Ryukyuan and continental populations of paradise fish, *Macropodus opercularis*.

	Ryukyuan (KUN-P 44906-44915, n = 10)				Vietnamese (n = 21) [†]			
	mean	SD	min	max	mean	SD	min	max
SL (mm)	44.9	6.3	33.5	53.0	41.2	-	21.5	53.1
In percents of SL [‡]								
Head length	32.8	1.5	30.1	35.7	33.2	1.4	30.6	36.2
Predorsal length	50.8	3.4	46.1	54.6	49.3	1.6	46.4	52.2
Prepelvic length	38.4	2.2	33.7	40.4	38.9	1.7	35.7	42.3
Preanal length	49.1	2.0	44.6	51.5	48.9	1.7	44.7	51.5
Head depth in front of eye [*]	16.3	1.3	14.7	19.1	15.1	0.9	13.2	16.6
Head depth behind eye ^{**}	24.0	0.9	23.0	26.3	22.4	1.4	19.7	24.0
Head depth at nape ^{**}	25.4	0.8	24.6	26.8	23.1	0.8	21.9	24.8
Head width at lachrymal	12.0	0.8	10.6	13.3	11.8	1.0	9.8	14.1
Head width at operculum ^{**}	18.8	1.5	15.8	21.5	16.7	1.1	14.7	18.6
Body depth at anal-fin origin	36.2	1.9	32.2	39.2	36.1	2.3	33.2	40.1
Body width at dorsal-fin origin	14.9	2.2	12.1	18.1	16.0	1.4	13.1	18.3
Body width at end of dorsal-fin base	6.5	1.7	4.3	9.2	6.2	1.0	4.0	7.2
Body depth at dorsal-fin base end	24.3	2.8	20.8	29.9	23.5	2.0	20.2	26.8
Postdorsal length	14.7	1.1	11.9	15.4	14.3	2.6	9.5	19.1
Length of dorsal-fin base	40.6	3.6	35.2	46.1	39.1	2.4	33.2	44.3
Length of anal fin base	53.7	3.0	50.1	60.2	55.0	2.5	48.5	58.8
Length of pectoral fin	25.2	1.7	21.7	27.8	24.9	2.0	19.9	27.6
Length of middle caudal-fin ray ^{**}	30.0	1.7	27.8	32.9	34.9	3.7	28.5	41.9
In percents of head length								
Eye diameter	27.7	1.4	26.0	30.0	26.7	1.9	24.0	29.5
Interorbital width ^{**}	34.0	2.7	28.9	37.9	31.0	2.2	26.7	35.0
Snout length	25.8	3.4	18.1	29.6	25.9	1.5	22.8	28.6
Upper lip width	6.3	1.1	4.8	8.1	7.1	1.3	5.2	10.3
Mouth width	27.8	5.3	20.1	34.2	25.0	4.5	18.3	32.4

[†]Values obtained from Freyhof and Herder (2002).

[‡]Significant differences between the Ryukyuan and continental individuals are indicated by asterisks (Welch's t-test [R 3.4.1, windows]: * $P < 0.05$ and ** $P < 0.01$).

identical to those of the typical paradise fish (Freyhof and Herder 2002; Hosoya 2013); however, some local variations were observed in the lateral line scales, caudal vertebrae, and dorsal and anal fin rays (Table 3).

These results suggest that the Ryukyuan paradise fish has unique characteristics that differ from those of the continental populations. This is thought to have resulted from either a bottleneck effect occurring during the initial diffusion of the species to the Ryukyu archipelago or a founder effect resulting from transplantation. However, even if the Ryukyuan population was introduced, adaptation to the island ecosystem is unlikely to have occurred because this introduction most likely took place only 4-6 centuries ago (Kitagawa and Hosoya 2016). Therefore, although the original distribution area of the Ryukyuan paradise fish has not yet been identified, it appears to be a cryptic local population of a “short fat type” fish distributed within the islands of East Asia. Examination of the morphological characteristics of the Taiwanese paradise fish is considered crucial for estimating the nativeness of the Ryukyuan population, and additional taxonomic research in the future will elucidate its placement within the genus *Macropodus*.

Table 3. Number of fin rays and vertebrae in the three populations of paradise fish, *Macropodus opercularis*.

Dorsal Spines	13	14	15						Mean [†]
Chinese [‡]	5	12	1						13.78
Vietnamese [‡]	14	6							13.30
Ryukyuan [§]	5	3	2						13.70
Dorsal soft rays	5	6	7	8					
Chinese [‡]	2	11	5						6.17 ^a
Vietnamese [‡]		6	13	1					6.75 ^b
Ryukyuan [§]			3	7					7.70 ^{a,b}
Anal spines	15	16	17	18	19	20	21		
Chinese [‡]	1	1	1	6	9				18.17 ^a
Vietnamese [‡]			1	2	10	7			19.15 ^b
Ryukyuan [§]				4	3	2	1		19.00
Anal soft rays	9	9	10	11	12	13	14	15	
Chinese [‡]	1	1	1	3	9	2	1		11.56
Vietnamese [‡]				3	7	10			12.35 ^b
Ryukyuan [§]						4	5	1	13.70 ^{a,b}
Scales on lateral line	29	30	31	32					
Chinese [‡]	2	12	5	2					30.33
Vietnamese [‡]	2	2	12	4					30.90 ^a
Ryukyuan [§]	1	8	1						30.00 ^a
Abdominal vertebrae	8	9	10						
Chinese [‡]		7	1						9.13
Vietnamese [‡]	1	6	1						9.00
Ryukyuan [§]		10							9.00
Caudal vertebrae	16	17	18	19	20				
Chinese [‡]	1	1	6						17.63 ^{a,b}
Vietnamese [‡]			1	6	1				19.00 ^a
Ryukyuan [§]			1	9					18.90 ^b
Total vertebrae	25	26	27	28	29				
Chinese [‡]	1	1	5	1					26.75 ^a
Vietnamese [‡]			2	4	2				28.00
Ryukyuan [§]			1	9					27.90 ^a

[†]Significant differences among groups are indicated by same alphabetical letters (Steel-Dwass test [R 3.4.1, windows], $P < 0.01$); [‡] Values obtained from Winstanley and Clements (2008); [§] Samples KUN-P 44906–44915.

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