Sexual Difference in Buccal Morphology of the Paternal Mouthbrooding Cardinalfish Apogon doederleini

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Sexual Difference in Buccal Morphology of the Paternal Mouthbrooding Cardinalfish *Apogon doederleini*

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ABSTRACT—The buccal morphology was compared between the sexes of the cardinalfish *Apogon doederleini*, in which males provide mouthbrooding. The brood size increased proportionally with male buccal space, which increased with the fourth power of the standard length. In the breeding season, males had a larger buccal space than females, whereas there was no sexual difference in the non-breeding season, suggesting sexually different flexibility in the buccal morphology. In spite of a selective advantage to males with a larger mouth, they did not show a higher allometric growth of buccal characters or higher body growth than females. In males, the urohyal was shorter and its height to length ratio was greater than in females. This osteological modification, accompanied by depression of the lower jaw and abduction of the suspensorium, would allow males to expand their buccal cavity more effectively.

Key words: Apogonidae, functional morphology, mouthbrooding, osteology, sexual dimorphism

INTRODUCTION

Mouthbrooding has evolved independently among phylogenetically different fish groups (Blumer, 1982). It has been considered that mouthbrooders evolved from substrate brooders with the habit of mouthing eggs or orally transferring them from one nest to another (Oppenheimer, 1970). Mouthbrooding is effective in protecting offspring, especially under high predation pressure (Keenleyside, 1991). In some mouthbrooding fishes, the rate of brood loss due to egg predation is very low (Okuda and Yanagisawa, 1996a; Okuda, 1999).

Mouthbrooding involves behavioural and physiological adaptations (Oppenheimer, 1970). It may also lead to morphological modification and specialization that increase the mouthbrooding parent's buccal capacity to carry more offspring, e.g., catfishes (Lee, 1937; Taylor, 1983), cardinalfishes (Lachner, 1953; Omori and Takahashi, 1980) and jawfishes (Smith-Vaniz, 1972; Anderson and Smith-Vaniz, 1976; Hess, 1993).

Among marine fishes, the largest group with mouthbrooding habit is the cardinalfish (Apogonidae), which consists of 300 species or more. In all the species for which this reproductive behaviour has been reported, males alone provide mouthbrooding (Kuiter and Kozawa, 1999). In some small species of this family, sexual dimorphism is remarkable, with males having the larger and deeper head (Lachner, 1953). However, in the subject species, *Apogon doederleini*, there is no clear sexual dimorphism (Okuda and Yanagisawa, 1996b) or size difference (Okuda et al., 1998), excepting the breeding season when males are distinguishable from females, by their mouth expansion for mouthbrooding. The main purpose of this study is to compare the buccal morphology quantitatively between the sexes of *A. doederleini* and to elucidate the mechanism for its seasonal changes. We also discuss the possible functional significance of sexual difference in buccal morphology.

MATERIALS AND METHODS

Sample collection

We collected *A. doederleini* at three sites (Murote Beach, Funakoshi Beach and Arakashi Beach) of Uchiumi Bay, Shikoku Island, Japan, from May to December 1995, with the aid of SCUBA. We used 101 fish specimens for morphological measurements (Table 1). We sexed the fish based on direct observations of gonads under dissection. In the breeding season (May-August), 26 of 32 males collected were mouthbrooding. The egg mass in their buccal cavity was removed underwater immediately after catching. All egg masses, except two that we failed to collect, were frozen for measurements in the laboratory. For all specimens in the breeding season and some in the non-breeding season, we moulded the buccal cavity by injecting silicon rubber fully into their mouth to estimate the maximum buccal volume (i.e., silicon treatment; Table 1). All specimens were preserved in 95% ethanol after being fixed in 10% formalin.

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Table 1. The number of fish specimens and their treatment.

Season	Sex	N	Treatment	
			Silicon	No
Breeding	Male	32	32	0
	Female	8	8	0
Non-breeding	Male	28	6	22
	Female	33	10	23
	Total	101	56	45

Morphological measurements

For each specimen, we measured 15 morphometric characters (Fig. 1, Table 2): SL is a body size parameter and the others associated with the head or mouth regions (see Barel *et al.*, 1977 for the terminology). These characters were measured with a pair of sliding calipers to the nearest 0.05 mm. We also measured some osteological characters for 38 specimens (28 males and 10 females) including those in the breeding and non-breeding seasons. Prior to measurements, we stained specimens with Alizarin Red-S after immersing them in 4–10% KOH for 1–2 weeks. We measured the length of hyoid (HYL), and the length of urohyal (UHL) and its height (UHH) (Fig. 2), using an ocular micrometer under a dissecting microscope.

For 56 specimens with silicon treatment, we removed moulding silicon from their mouth and then dried and weighed it. The maximum buccal volume (mm^3) was calculated from the dry silicon weight (mg) divided by its density (1.0525 mg/mm^3). For each of 24 egg masses, we counted the number of eggs and measured the diameter (D) of 20 spherical eggs. The volume (mm^3) of each brood was estimated by multiplying the mean egg volume $(\frac{4}{3}\pi\left(\frac{D}{2}\right)^3)$ by the total number of eggs.

Statistical analysis

To examine sexual dimorphisms, we used data from 40 specimens with silicon treatment in the breeding season and from 45 specimens with no treatment in the non-breeding season (Table 1). The buccal cavity of the former is expanded maximally and that of the latter is in a normal condition. Based on the allometric relation-
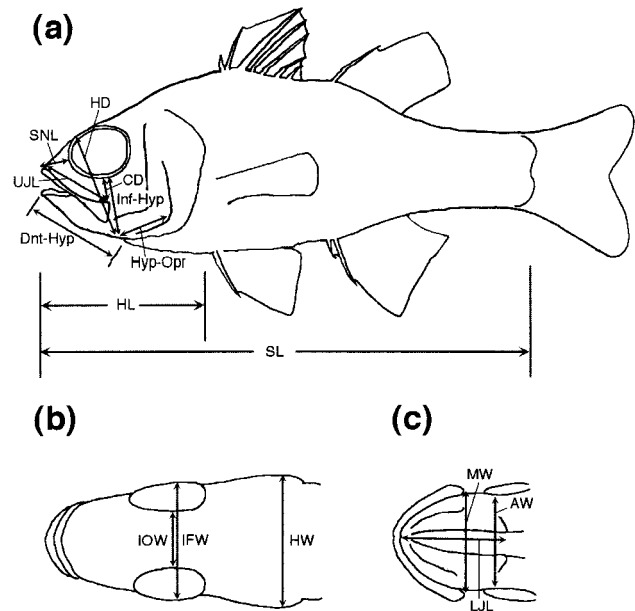

Fig. 1. A diagram of morphological measurements. A lateral view (a) of *A. doederleini* and dorsal (b) and ventral (c) views of its head. Morphological characters are given abbreviation (see Table 2 for their definition).

ships, all morphometric variables were log-transformed and linear-regressed against body size ($y=ax^b$; y:trait value, x: body size, a,b: constant). For standardization of the body size, we used head length subtracted from standard length (SL–HL) because the head regions varied sexually and seasonally. We performed ANCOVA to compare these regression equations between sexes or between seasons, provided that their slopes are parallel to each other. With the ANCOVA, trait values are expressed by the antilogarithmic mean after correcting for the log (SL–HL). We also performed two-factor ANCOVA with Scheffé's Multiple Contrasts to view how the maximum buccal volume is affected by two factors, sex and sea-

Table 2. Characters used for morphometric measurements

| Character	Abbreviation	Definition
Standard length	SL	From the rostral tip of the upper jaw to the base of the caudal fin
Head length	HL	From the anterior tip of the upper jaw to the posterior end of the gill-cover
Snout length	SNL	From the rostral tip of the upper jaw to the rostral edge of the eye
Upper jaw length	UJL	From the anterior end of the premaxilla to the distal tip of the maxilla
Lower jaw length	LJL	From the anterior end of the dentary to the rear edge of the retro-articular
Dentary-Hypohyal length	Dnt-Hyp	From the rostral tip of the dentary to the caudal tip of the hypohyal
Infraorbital-Hypohyal length	Inf-Hyp	From the dorsal edge of the second infraorbital to the rostral tip of the hypohyal
Hypohyal-Opercular length	Hyp-Opr	From the rostral tip of the hypohyal to the anteroventral edge of the opercle
Cheek depth	CD	From the ventral margin of the orbit to the caudal tip of the maxilla
Interorbital width	IOW	Between points on the dorsal bony margin of the left and right orbits
Head depth	HD	From the caudal tip of the premaxillary pedicel to the rostral tip of the hypohyal
Mouth width	MW	Between the posterior tips of the left and right maxillae
Head width	HW	Maximum width of the head region
Angular width	AW	Between the outer edges of the left and right angulars
Infraorbital width	IFW	Between the outer points of the left and right infraorbitals
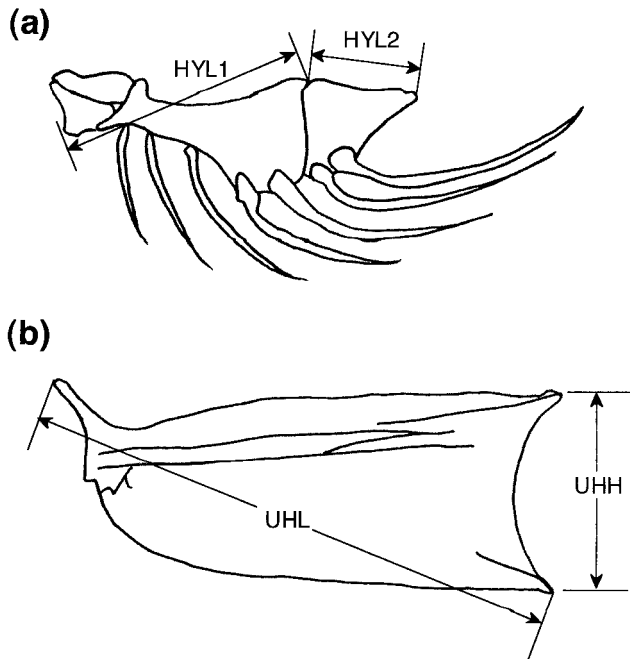
Fig. 2. A diagram of osteological measurements. A lateral view of hyoid (a) and urohyal (b). The length of hyoid (HYL) is the sum of HYL1 and HYL2
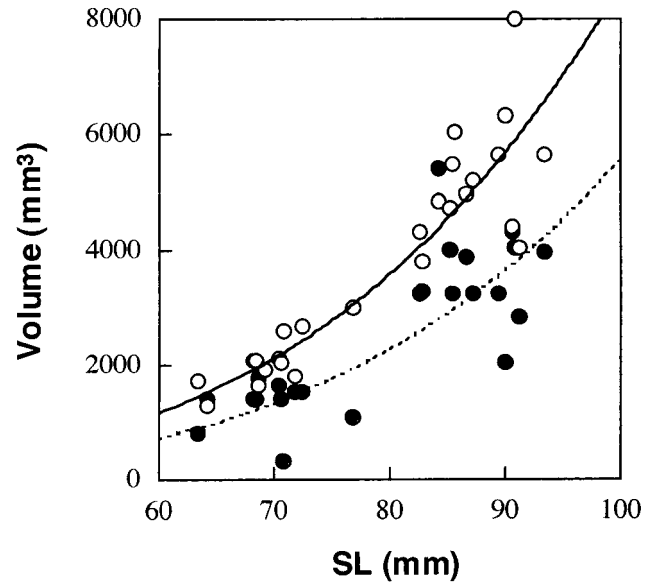

Fig. 3. The relationships between the maximum buccal volume and standard length (open circles), and between the brood volume and standard length (closed circles). A solid line is the regression curve for the buccal volume ($y=10^{-3.87}x^{3.90}$) and a dotted line for the brood volume ($y=10^{-4.20}x^{3.97}$).

son, or by their combined effect.

In order to determine which morphometric characters account for variation in the maximum buccal volume, we took two approaches, using log-transformed data of morphometric measurements for all 56 specimens with silicon treatment. First we performed a Principal Component Analysis (PCA) to extract overall patterns of covariation among morphometric variables because these variables are highly correlated with each other. Then we incorporated the extracted components as explanatory variables into a model of multiple regression analysis, which determines to what degree each component can explain variation in the maximum buccal volume. The buccal volume, a criterion variable, was transformed into a linear dimension by taking the cube root.

As another approach, we incorporated 15 morphometrics all together into the multiple regression analysis after substituting their residuals of log-log regressions against the body size (SL–HL). This procedure succeeded in making covariance between the variables negligible, thus reducing the effect of colinearity on the multiple regression analysis (Reist, 1985). We adopted full and reduced models, the latter being calculated by a stepwise method.

All statistical probabilities are two tailed. For descriptive purposes, means are given±SD

RESULTS

Buccal volume and brood size

The maximum buccal volume of mouthbrooding males ranged from 1311.2 mm³ to 7999.9 mm³ (3802.6 ± 1817.3, $n=26$). It increased proportionally with about the fourth power of SL ($r=0.95$, $p<0.001$; Fig. 3). An average brood consisted of 7835 eggs (±3638, $n=24$) whose diameter was 0.845 mm (±0.047). Large males mouthbrooded larger ($y=10^{-0.66}x^{3.07}$ where y is D and x SL; $r=0.70$, $p<0.001$) and more eggs ($y=10^{-2.00}x^{3.08}$ where y is the number of eggs

and x SL; $r=0.68$, $p<0.001$). The volume of a brood also increased proportionally with the SL, showing the similar curve to that of the maximum buccal volume ($r=0.77$, $p<0.001$; Fig. 3). The proportion of the brood volume to the maximum buccal volume was on average 69.8% (±24.1, $n=24$). The maximum buccal volume of mouthbrooding males (adjusted mean=3147.7 mm³, $n=26$) was larger than that of non-brooding males in the breeding season (2558.6 mm³, $n=6$, ANCOVA, $F=4.81$, df=1, $p<0.04$).
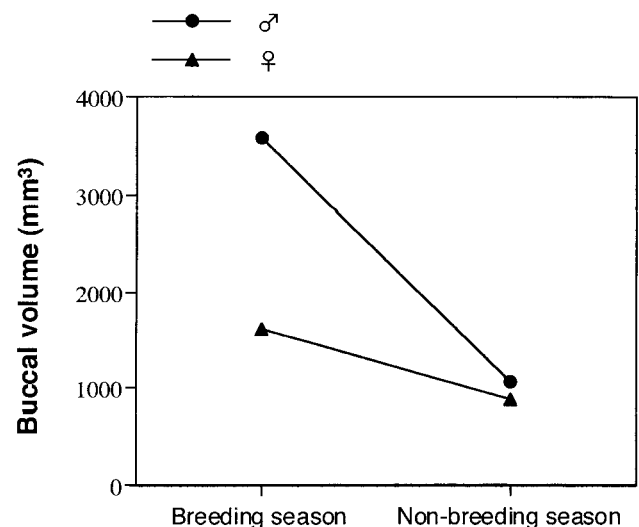
There was a significant interactive effect of sex and

Fig. 4. Effects of sex (males: circles and females: triangles) and season (breeding and non-breeding seasons) on the maximum buccal volume.

Table 3. Sexual differences in buccal morphometrics (mm*) in the breeding and non-breeding seasons.

Character	Breeding season				Non-breeding season			
	Male	Female	F	p	Male	Female	F	p
HL	31.12	29.04	13.17	0.001	29.92	29.92	0.01	0.94
SNL	9.40	8.55	20.96	0.001	7.62	7.50	0.43	0.52
UJL	14.86	14.59	0.90	0.35	15.45	15.49	0.04	0.84
LJL	18.45	16.79	17.28	0.001	18.37	18.37	0.00	0.97
Dnt-Hyp	18.24	12.68	63.52	0.001	7.60	7.78	0.40	0.53
Inf-Hyp	18.32	14.13	34.10	0.001	8.36	8.15	0.97	0.33
Hyp-Opr	18.41	18.11	0.44	0.51	20.23	19.95	0.38	0.54
CD	5.16	4.67	4.99	0.03	3.28	3.19	0.33	0.57
IOW	6.30	6.18	0.48	0.50	6.47	6.65	2.32	0.14
HD	25.06	20.37	38.51	0.001	14.39	14.39	0.00	0.97
MW	20.51	19.10	5.46	0.03	10.84	10.38	1.20	0.28
HW	22.65	21.28	3.97	0.05	17.86	17.34	1.53	0.22
AW	18.49	14.83	28.23	0.001	5.02	5.00	0.00	0.96
IFW	19.54	19.23	0.47	0.50	16.41	16.11	0.58	0.45

* Adjusted for body size (SL–HL) with ANCOVA

season on the buccal volume (ANCOVA, F=10.01, df=1, p<0.003; Fig. 4). The buccal volume in the breeding season was significantly larger than that in the non-breeding season for both males (Scheffé's Multiple Contrasts, F=82.28, df=1, p<0.001) and females (F=17.63, df=1, p<0.001). In the breeding season, the sexual difference in the buccal volume was significant (Scheffé's Multiple Contrasts, F=38.79, df=1, p<0.001), whereas there was no difference in the non-breeding season (F=1.27, df=1, p=0.26).

Morphometric data

Buccal morphometrics were compared between the sexes (Table 3). In 10 of 14 characters, males showed significantly larger values than did females in the breeding season, but there was no sexual difference in any characters in the non-breeding season.

A PCA showed that two principal components were extracted from 15 morphometric variables and that these two components explained 93.1% of variance in original data (Table 4). Within the first principal component, all variables had a positive and great value of factor loading, which means this component represents size factor. With a cut-off absolute value of 0.5, the second principal component consisted of AW, Dnt-Hyp and Inf-Hyp those of which show positively high factor loadings and Hyp-Opr, IOW, SL and UJL showing negatively high factor loadings. To view overall patterns of variance in morphometric variables, factor scores were calculated for each individual and they were plotted in Fig. 5 to compare between sexes and seasons. The first component explained variance in the morphometrics between seasons (two-factor ANOVA, F=6.76, df=1, p<0.02,) but not between sexes (F=2.87, df=1, p=0.10). The second component succeeded in discriminating between the sexes (two-factor ANOVA, F=8.91, df=1, p<0.004) as well as

Table 4. Eigenvalues of principal components and factor loadings for each morphometric variable with a PCA.

Variables	First principal component	Second principal component
SL	0.83	−0.53
HL	0.90	−0.41
SNL	0.95	−0.10
UJL	0.83	−0.53
LJL	0.87	−0.37
Dnt-Hyp	0.76	0.58
Inf-Hyp	0.82	0.53
Hyp-Opr	0.73	−0.65
CD	0.79	0.45
IOW	0.78	−0.58
HD	0.89	0.37
MW	0.84	0.48
HW	0.94	0.20
AW	0.68	0.70
IFW	0.97	−0.04
Eigenvalue	10.61	3.36
% of variance	70.7	22.4
Cumulative %	70.7	93.1

between seasons (F=91,34, df=1, p<0.001), reflecting male lower jaw structure expanded more laterally (i.e., increasing AW) and more posteroventrally (i.e., increasing Dnt-Hyp and Inf-Hyp) only in the breeding season. Both components had positive effects on the maximum buccal volume (Multiple regression analysis, R^2=0.92, n=56 p<0.001, 1st component: F=412.60, β=0.81, 2nd component: F=170.03, β=0.52).

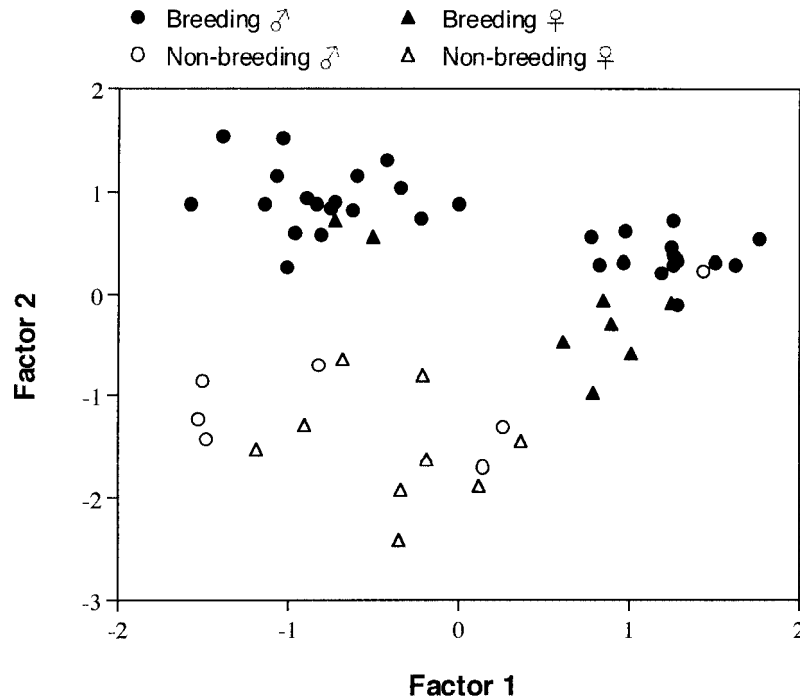Effects of individual characters on the maximum buccal

Fig. 5. Factor scores of PCA for each individual of males (circles) and female (triangles) in the breeding (closed) and non-breeding (open) season.

Table 5. The effects of morphometric variables on the maximum buccal volume.

Character	Full model		Reduced model	
	β	t	β	t
SL	2.56	6.04*		
HL	−2.58	−6.06*		
SNL	0.06	0.66		
UJL	−0.11	−1.51		
LJL	0.05	0.80		
Dnt-Hyp	0.34	1.25	0.53	4.61
Inf-Hyp	−0.03	−0.14		
Hyp-Opr	0.07	0.92		
CD	−0.02	−0.19		
IOW	0.01	0.16		
HD	0.30	0.99		
MW	−0.15	−0.92		
HW	0.18	0.94		
AW	0.45	2.27*	0.43	3.70
IFW	−0.16	−0.90		
Adjusted R^2	0.92		0.86	
F	43.38		172.80	
p	0.001		0.001	

β: Standardized partial regression coefficient
* $P<0.05$

Table 6. Sexual differences in osteological characters (mm*)

Characters	Male	Female	F	p
HYL	14.96	15.38	2.29	0.14
UHL	10.81	10.19	8.96	0.005
UHH	3.95	4.06	1.28	0.27

* Adjusted for body size (SL–HL) with ANCOVA

volume were also examined using multiple regression analysis (Table 5). A full model showed that SL and AW had a significant positive effect on the buccal volume and HL a negative effect, whereas a reduced model showed that Dnt-Hyp and AW could enter a regression equation as significantly positive factors.

Osteological characters were compared between the sexes (Table 6). The HYL and UHH did not differ between the sexes, but the UHL was significantly shorter in males than in females. The height to length ratio of the urohyal (UHH/UHL) was 0.40 for males (±0.03, $n=28$) and 0.37 for females (±0.03, $n=10$), significantly higher in males (t-test, $t=-3.03$, df=36, $p<0.005$).

DISCUSSION

In *A. doederleini*, males mouthbrooded a larger number of eggs as their body size and thus allometric buccal cavity increased. This is attributable partly to highly size-assortative matings found in this fish, in which large males mate with large females producing many eggs (Okuda *et al.*,

1998). However, the brood/buccal volume ratio in Fig. 3 indicated that many males mouthbrooded fewer eggs than expected from their size-assortative matings (r=0.84; Okuda *et al.*, 1998), suggesting that a little space was left in their buccal cavity. Okuda and Yanagisawa (1996a) reported in this species that males frequently ate a small portion of the egg mass soon after the onset of mouthbrooding, in spite of their less energetic benefits. This type of cannibalism would function as adjustment of the brood size to their buccal cavity because overcrowding in the mouth might cause a deficiency of oxygen supply to embryos and consequently increase the overall mortality for offspring (Okuda *et al.*, 1998). Similar brood reduction during the early embryonic development, though its causal factor is unclear, has been reported for a mouthbrooding cichlid *Tilapia leucosticta* (Welcomme, 1967). In mouthbrooding jawfishes, Hess (1993) believes that a lower brood/buccal volume ratio could lead to more efficient ventilation and hence more accelerated embryonic development. It is probable that mouthbrooding parents often adjust the brood size to their buccal capacity so as to increase the mouthbrooding efficiency.

In *A. doederleini*, males had larger buccal capacity than females in the breeding season, showing larger values in many buccal morphometrics. In the non-breeding season, however, the buccal volume and buccal morphometrics did not differ between the sexes. These results indicate that the buccal morphology itself does not differ between the sexes but its plasticity does, with male buccal cavity being more expansible.

In many paternal mouthbrooders, males have enlarged or modified buccal characters (Lee, 1937; Lachner, 1953; Smith-Vaniz, 1972; Anderson and Smith-Vaniz, 1976; Omori and Takahashi, 1980; Taylor, 1983; Hess, 1993). These studies were usually conducted in the breeding season of the subject species. As in *A. doederleini*, such a sexual dimorphism may be due to temporal morphological changes accompanied by mouthbrooding (Lee, 1937), though some species show sexually different allometric growth of buccal characters or morphological specialization (Lachner, 1953; Smith-Vaniz, 1972; Anderson and Smith-Vaniz, 1976; Taylor, 1983).

Interestingly, female buccal cavity was also expansible in the breeding season although its expansibility was small relative to that of males. In this fish, breeding females rarely show physically competitive behaviours, such as mouth wrestling, and they do not feed on specific food items with which only individuals with large mouths can handle (personal observation). Hence the expansibility of female buccal morphology cannot be explained by their competition and feeding habit. Considering that currently existing cardinalfishes are all paternal mouthbrooders (Kuiter and Kozawa, 1999), this phenomenon is very intriguing, but it is premature that we say anything about the reason why female mouth was expansible in the breeding season.

In some cichlids in which females provide mouthbrooding, the buccal size is enlarged in males but not in females

(Oliveira and Almada, 1995). In these species, a larger mouth is more advantageous to males in male-male aggressive competition such as gaping and biting, suggesting that the sexual dimorphism of buccal characters could evolve through sexual selection. Such a selective advantage to males with a larger mouth has been reported for many fishes in which males provide substrate brooding or no care (reviewed by Shine, 1989). Even in paternal mouthbrooding fishes, it cannot be denied that modification of male buccal characters would be a by-product of the sexual selection. However, this does not seem to be the case for *A. doederleini*, in which mating competition is less intense among males (Okuda and Yanagisawa, 1996b).

Natural selection should favour parents with the larger buccal capacity if an increased buccal cavity is not disadvantageous for feeding. Since cardinalfishes are usually opportunistic nocturnal feeders on macro zooplankton (Collette and Talbot, 1972), the ecological constraints on mouth size will not be severe. In *A. doederleini*, nevertheless, there was no apparent sex-specific selection on the allometric growth of buccal characters. Selection for increased body size, which was one of factors effective in increasing the buccal space, does not also seem strong in this species because males show the determinate growth same as that of females (Okuda *et al.*, 1998).

For males of *A. doederleini*, the increase in their buccal capacity was achieved only through the flexible alteration of buccal morphology. A PCA indicated that male lower jaw but not other head parts such as upper jaw was more expansible in the breeding season. In addition, a multiple regression analysis showed that an increase in Dnt-Hyp (i.e., depressing the lower jaw) and AW (i.e., abducting the suspensorium) involved in increasing the buccal capacity. Males also had the shorter urohyal with the higher UHH/UHL ratio than did females. The urohyal mediates between the shoulder girdle and the hyoid through musculus sternohyoideus. As the m. sternohyoideus contracts, the urohyal is braced together with the hyoid posteroventrally, followed by depression of the lower jaw and abduction of the suspensorium (Liem, 1980). By this mechanism, the buccal cavity can be expanded. The urohyal with a high UHH/UHL ratio can be held by the thicker m. sternohyoideus, as actually observed for male *A. doederleini* (personal observation). Since the contractile force depends on the number of muscle fibre (Basmajian, 1974), the urohyal supported by a thicker m. sternohyoideus will depress the floor of the buccal cavity more strongly and more posteroventrally. Moreover, the urohyal can slide in broader trajectory, as it is shorter. This osteological modification may be a consequence of morphological adaptation for mouthbrooding.

ACKNOWLEDGEMENTS

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