



The costs of reproduction to males and females of a paternal mouthbrooding cardinalfish *Apogon notatus*

N. OKUDA

Department of Biology and Earth Sciences, Ehime University, 2–5 Bunkyo-cho, Matsuyama, P.O. Box 790-8577, Japan

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In the cardinalfish *Apogon notatus*, starving males mouthbrood the eggs, and females are more active than males in courtship and in attacks against conspecific intruders upon their breeding territory, but sexual ornaments are developed in males. Condition factor, hepatosomatic index and fat body-somatic index declined in both sexes during the breeding season. The deterioration of somatic condition was more severe in females, suggesting that the overall energetic costs were larger for females which produced more than twice as many clutches as males brooded in a season. Selective mortality of females could be due primarily to the depletion of their energy reserves. The increased mortality in females is a possible mechanism for the male-biased operational sex ratio which may provide the potential for sexual selection on males.

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Key words: Apogonidae; brood cannibalism; energetic cost; mortality; operational sex ratio; somatic condition.

INTRODUCTION

Mouthbrooding, which is a form of external bearing of offspring, has evolved independently among phylogenetically different fish groups (Blumer, 1982). It is effective in protecting offspring, especially under high predation pressure (Keenleyside, 1991). However, parents incur a large energetic cost of mouthbrooding because it forces them to fast throughout the parental phase (Oppenheimer, 1970; but see Yanagisawa *et al.*, 1996), in addition to energy expenditure for the mouthbrooding itself (Mrowka & Schierwater, 1988). Because of such energetic costs, the parents lower their somatic condition during the mouthbrooding period (Barberi *et al.*, 1992; Smith & Wootton, 1994; Balshine-Earn, 1995; Okuda & Yanagisawa, 1996a). Often the deterioration of parental somatic condition may cause an increase in mortality, suggesting a survival cost of mouthbrooding (Okuda & Yanagisawa, 1996a).

Mouthbrooding also imposes restrictions on the parent's reproductive success due to their limited buccal capacity (Welcomme, 1967; Hess, 1993; Okuda *et al.*, 1998). This reproductive constraint can have an important effect on sexual selection in mouthbrooding fishes. In species in which females mouthbrood eggs, such as some cichlids, males should compete intensely for the fertilization of eggs because females rear fewer eggs than males can fertilize. In such species, sexual selection actually acts more strongly on males, with sexual traits being more developed in males (McKaye, 1991). By contrast, where the male is the

Tel.: +81 (0)89 927 9622; fax: +81 (0)89 927 9630; email: nokuda@sci.ehime-u.ac.jp

mouthbrooder, the situation is reversed. For instance, in some cardinalfishes in which males provide mouthbrooding care alone, females are the predominant competitors for mates (Okuda & Yanagisawa, 1996b; Okuda, 1999a). This sex role reversal is rare among fishes, in spite of the fact that males perform parental roles exclusively in many species (Vincent *et al.*, 1992; Swenson, 1997).

Clutton-Brock & Vincent (1991) proposed that the direction of sexual selection could be predicted by the sexual difference in potential reproductive rate (i.e. the maximum number of offspring that each sex can produce per unit time). This index, together with the population sex ratio, comprise major components of the operational sex ratio, i.e. the ratio of sexually receptive males to females, which is an ultimate factor determining sexual selection (Emlen & Oring, 1977; Clutton-Brock & Parker, 1992; Kvarnemo & Ahnesjö, 1996). The theory predicts that sex role reversal should occur when the potential reproductive rate is higher in females under an equal population sex ratio, and thus when the operational sex ratio skews towards females. In sex-role reversed cardinalfishes, females have a higher potential reproductive rate since they can produce clutches at shorter intervals than males can mouthbrood them (Okuda & Yanagisawa, 1996b; Okuda, 1999a).

The subject species, *Apogon notatus* (Houttuyn) (Apogonidae), is also a paternal mouthbrooding cardinalfish, but it shows extraordinary sex roles. Like other apogonids, females have a higher potential reproductive rate than males and perform courtship and intraspecific aggression more actively (Kuwamura, 1983, 1985). From such reproductive features, Clutton-Brock & Vincent (1991) judged that *A. notatus* is sex-role reversed. However, in this fish, sexual ornaments are developed in males (N. Okuda, unpubl. data). Okuda (1999b) found that the operational sex ratio was male-biased in *A. notatus*. This is ascribed to male predominance in the adult population, which results from higher mortality for females (Okuda, 1999b). In other apogonids, the mortality is not different between the sexes (Okuda, 1999a) or may be higher in males because of the large costs of mouthbrooding (Okuda *et al.*, 1998).

In this study, the main purpose is to compare energy expenditure on reproduction between the sexes in terms of somatic weight loss in *A. notatus* and to discuss a possible mechanism for male-biased operational sex ratios associated with the differential mortality cost of reproduction between the sexes.

MATERIALS AND METHODS

STUDY SPECIES

Apogon notatus inhabits shallow waters of the west Pacific. In southern Japan, it is often a dominant species of the coastal reef fish community. It forms large shoals in mid-water from autumn to spring. Prior to the breeding season (June–September in this study site; Okuda, 1999b), females establish breeding territories on the boulder substratum to form pairs. Within the pairs, females are more active than males in courtship and in attacks against conspecific intruders into their territory. The breeding territory is maintained continually by females until several weeks after their last spawning. Both females and their mates stay away from their territory during the night, when they feed, mainly on small crustaceans, such as copepods, amphipods and decapods. In spite of this temporary absence, the fish return to the same sites every morning (Usuki, 1977).

Spawning takes place with the members of a pair in a parallel position. An egg mass spawned by a female is transferred quickly to her mate. Fertilization occurs just after gamete release and is ensured when the egg mass is in the male's mouth (Kuwamura, 1983). After post-spawning behaviour which continues for up to a few hours, males usually leave the female territory and join shoals of unpaired males, where they mouthbrood eggs until hatching in 8–14 days (Okuda, 1999b). Females, on the other hand, form a new pair with another male coming from such shoals within a day of spawning. Males never receive clutches from multiple females in a breeding cycle, and neither do females divide their clutch among multiple males. Both sexes have repeated reproductive cycles in a season and live up to 7 years (Okuda, 1997). When the breeding season ends, all fish become gregarious again.

SAMPLE COLLECTION

Adult fish were collected at Murote Beach, Shikoku Island, Japan, from January to November 1996, at intervals of one month in the breeding season and of two months in the non-breeding season (Table I). They were captured using a seine and hand net, with the aid of SCUBA. Prior to the first spawning, pair formation occurred in May, the pre-breeding month, and some fish remained paired until September, the last breeding month. However, in September, paired fish could not be caught because they fled quickly into a nearby shoal. In the non-breeding season, except for the pre-breeding month, the fish were sampled randomly from large shoals in mid-water. In other months, paired and unpaired fish were sampled individually; they could be sexed on the basis of a secondary sexual character (males have a longer lower lip) during these months. For each male, brooding status (i.e. mouthbrooding or not) was checked. The specimens were preserved in 70% ethanol after being fixed in 10% formalin for a few days.

In the laboratory, the standard length (L_S) of fish was measured to the nearest 0.1 mm and their body weight in wet condition to the nearest 1 mg. After the fish were dissected, their liver, fat body which is a visceral tissue forming a fat reserve, stomach and gonads were removed. The stomach contents were removed and weighed in wet condition. The carcass and each organ were dried at 60° C for 24 h and then weighed.

For each fish, somatic condition was estimated using the following indicators: the condition factor $K=100W \cdot L_S^{-3}$ where W is total dry body weight, hepatosomatic index $I_H=100W_H \cdot W^{-1}$ where W_H is dry liver weight, fat body-somatic index $I_F=100W_F \cdot W^{-1}$ where W_F is dry fat body weight. The stomach fullness index $I_S=100W_S \cdot W_w^{-1}$ where W_S is wet weight of stomach contents and W_w is wet body weight, was used as an indicator of food intake and the gonadosomatic index $I_G=100W_G \cdot W^{-1}$ where W_G is dry gonad weight as an indicator of gametic effort.

For each sex, these indices were compared among months using ANOVA if its requirements were fulfilled. A sexual difference in these indices was examined each month using Student's *t*-test. When a normal distribution after appropriate transformation did not fit the data, nonparametric Kruskal-Wallis tests for seasonal variations and Mann-Whitney *U* tests for sexual differences were performed. All statistical probabilities are two tailed. For descriptive purposes, means are given \pm S.E.

MEASUREMENT OF OFFSPRING SIZE AND NUMBER

To measure brood size (the number of eggs per brood) and egg size (egg diameter), a total of 28 pairs was captured just after direct observation of their spawning, from 11 June to 30 August 1995, the year preceding fish collection. The brood was removed quickly from the male's mouth under quinaldine anaesthetic. For each sex of a pair, the L_S was measured underwater to the nearest 0.5 mm and the fish was released at its capture site.

In the laboratory, 20 eggs were sampled from each brood and their diameter measured with an ocular micrometer under a dissecting microscope. Within-individual variation in egg size was so small ($s^2=0.003-0.010$ mm) that 20-egg samples could be regarded as representative of the brood. For each brood, the number of eggs was recorded and the total egg mass was weighed in dry condition. The relationship of brood size and egg size with parental body size was expressed by the allometric equation $y=ax^b$ after the data

TABLE I. The number of fish specimens and the sex ratio in months when they were sampled randomly

Month	Total		Paired		Unpaired		Sex ratio (Male : Females)	χ^2*	P
	Male	Female	Male	Female	Male	Female			
January	30	15	—	—	—	—	2.00	5.00	0.025
March	18	8	—	—	—	—	2.25	3.85	0.049
May	15	11	7	7	8	4	—	—	—
June	18	10	9	9	9	1	—	—	—
July	21	10	10	10	11	0	—	—	—
August	14	9	12	9	2	0	—	—	—
September	25	6	—	—	—	—	4.17	11.60	0.001
November	19	16	—	—	—	—	1.19	0.26	0.61
Total	160	85	38	35	30	5	—	—	—

*Deviation from an equal sex ratio was tested.

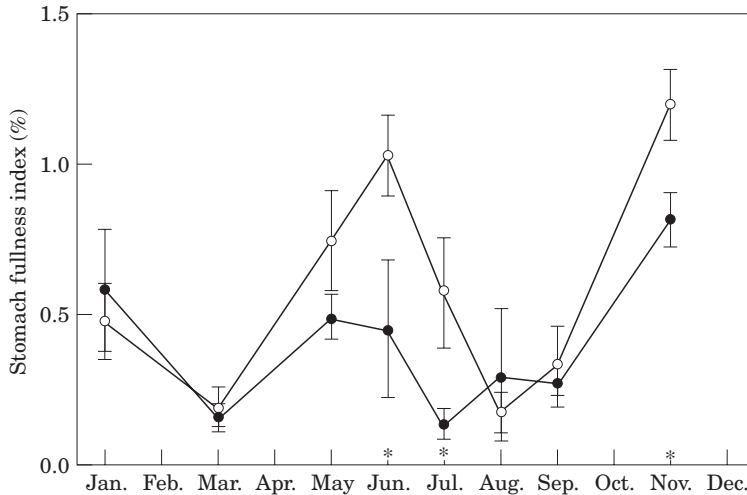


FIG. 1. Seasonal changes in mean stomach fullness index (I_S) for males (●) and females (○). Vertical lines are S.E. and sample sizes are in Table I. *, Significant sexual difference by Mann-Whitney U test ($P < 0.05$).

were log-transformed. As other possible factors affecting brood size and egg size, the spawning date and water temperature were incorporated into a stepwise multiple regression analysis on the assumption of linear relationships.

RESULTS

POPULATION STRUCTURE

Body size ranged from 56.0 to 93.2 mm L_S for males (78.8 ± 0.47 , $n=160$) and from 54.0 to 86.2 mm for females (75.0 ± 0.58 , $n=85$). Males were significantly larger than females ($t_{160,85} = -4.97$, $P < 0.0001$). In May, some specimens of unpaired fish were females, whereas all but one unpaired fish were males during the breeding season. In every month except November when fish were sampled randomly from shoals, the sex ratios were male-biased (Table I).

FEEDING AND REPRODUCTION

The stomach fullness index (I_S) varied greatly among months for males (Kruskal-Wallis test, $H=50.9$, d.f.=7, $P < 0.0001$) and for females ($H=38.6$, d.f.=7, $P < 0.0001$; Fig. 1). Sexual differences in this index were found in June, July and November, with male I_S being lower. In the breeding season, a large proportion of mouthbrooding males had empty stomachs (81.0%, $n=42$). This proportion was significantly higher than that for nonbrooding males sampled during the same period (9.1%, $n=11$; Fisher's exact probability test, $P < 0.0001$). Of eight mouthbrooding males whose stomachs were not empty, seven ate only eggs at the early developmental stage, and two of these males had stomachs full of eggs. The stomach of the remaining male who brooded eggs at the late stage included only unidentified food that was almost digested.

The gonadosomatic index (I_G) of females reached a peak in July and then declined towards the end of the season (Fig. 2). In the non-breeding season, most females degraded their ovaries, while some had large ovaries like mature

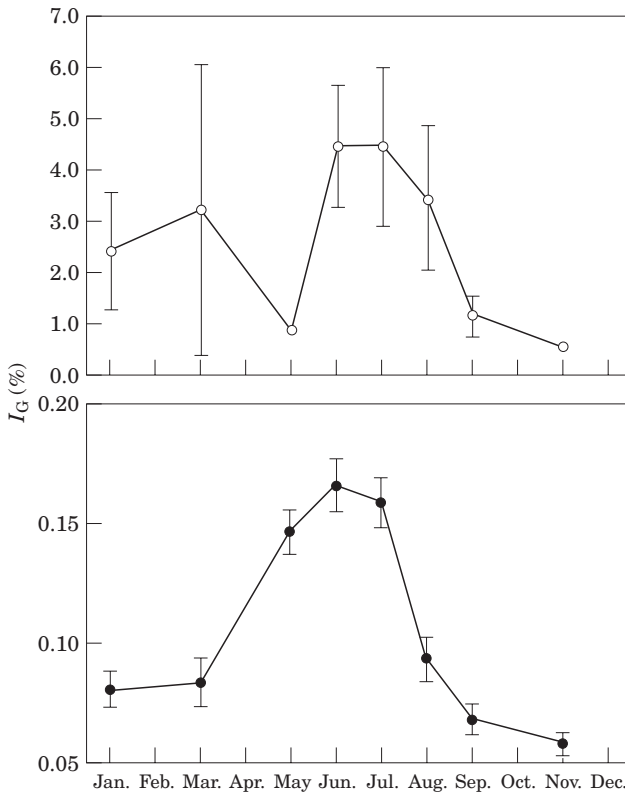


FIG. 2. Seasonal changes in mean gonadosomatic index (I_G) for females (○) and males (●). Vertical lines are S.E. and sample sizes are shown in Table I.

females, resulting in a great variance in I_G , with the highest individual values of 18.1% in January and 23.0% in March. Such ovaries were already necrotized. The cause of abnormal gonadal development is unknown. The I_G of males was lower than that of females by more than one order of magnitude, though it showed significant seasonal variations (ANOVA, $F_{7,152}=25.6$, $P<0.0001$).

Brood size was on average 3315 eggs (± 240) and mean egg size was 0.889 mm (± 0.008 , $n=28$). The mean dry brood weight was 0.439 g (± 0.029 , $n=28$), equivalent to 15.2% of maternal body weight estimated from the L_S of parental females using a regression line $y=4.38 \times 10^{-7} \times x^{3.66}$ (y , body weight; x , L_S) based on the sampling data from June to August.

Brood size was correlated positively with female body size ($r=0.71$, $P<0.0001$) and male body size ($r=0.79$, $P<0.0001$; Fig. 3). Such correlations, however, might be spurious because spawning pairs were highly 'size-assortative' ($r=0.83$, $P<0.0001$, $n=28$). The stepwise multiple regression analysis, further incorporating the spawning date and water temperature as independent variables, revealed that only male size had a significant positive effect on brood size (std. coef. = 0.73, $F=28.8$, $r^2=0.53$, $P<0.0001$). Egg size was correlated positively with both maternal size ($r=0.68$, $P<0.0001$) and paternal size ($r=0.53$, $P<0.005$; Fig. 3). It was found by stepwise multiple regression analysis that maternal size correlated

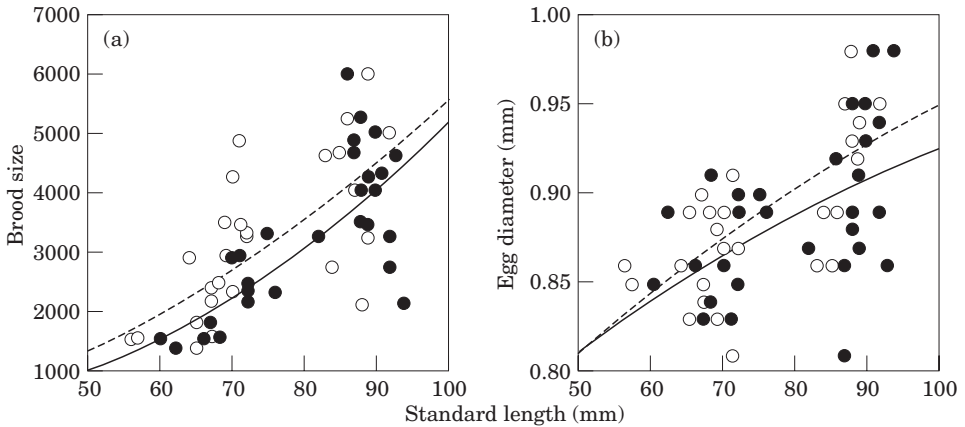


FIG. 3. The relationships between brood size and body size, and between egg size and body size for males (●) and females (○), respectively. Solid and dotted lines are regression curves for males and females, respectively. (a) Female: $y=0.548x^{2.003}$, male: $y=0.108x^{2.340}$, (b) female: $y=0.329x^{0.230}$, male: $y=0.391x^{0.187}$.

positively with egg size (std. coeff.=0.67, $F=27.3$) and the spawning date correlated negatively with egg size (std. coeff.= -0.31 , $F=5.94$; $r^2=0.59$, $P<0.0001$).

SOMATIC CONDITIONS

The mean condition factor (K), hepatosomatic index (I_H) and fat body-somatic index (I_F) all showed great seasonal variations for males (ANOVA, K : $F_{7,152}=12.6$, $P<0.0001$, I_H : $F_{7,152}=43.4$, $P<0.0001$, I_F : $F_{7,152}=9.1$, $P<0.0001$) and for females (K : $F_{7,77}=30.4$, $P<0.0001$, I_H : $F_{7,77}=52.3$, $P<0.0001$, I_F : $F_{7,77}=8.3$, $P<0.0001$; Fig. 4). For both sexes, these indices declined steadily early in the breeding season, with minimum values in August, and then recovered gradually toward winter.

All three indices were significantly lower for females than for males late in the breeding season (Fig. 4). These indices did not differ between mouthbrooding and non-brooding males in each breeding month (two-way ANOVA, K : $F_{1,47}=0.0$, $P=0.95$, I_H : $F_{1,47}=1.0$, $P=0.32$, I_F : $F_{1,47}=1.6$, $P=0.22$). In spring, although the I_H of females was significantly higher than that of males, it dropped suddenly from the pre-breeding month and fell below that of males in July. From May to August, the population mean of I_H declined by 70.8% for males and by 88.6% for females. Also in the I_F , such a reduction in the pre-breeding month was found for females. By August, females had nearly depleted their fat body. The average reduction in I_F from May to August was 61.7 and 97.2% for males and females, respectively.

DISCUSSION

REPRODUCTIVE COSTS

Somatic conditions, measured as K , I_H and I_F , deteriorated more in females than in males during the breeding season, suggesting a larger energy expenditure for females on reproductive activities. As indicated by the I_G , females expended

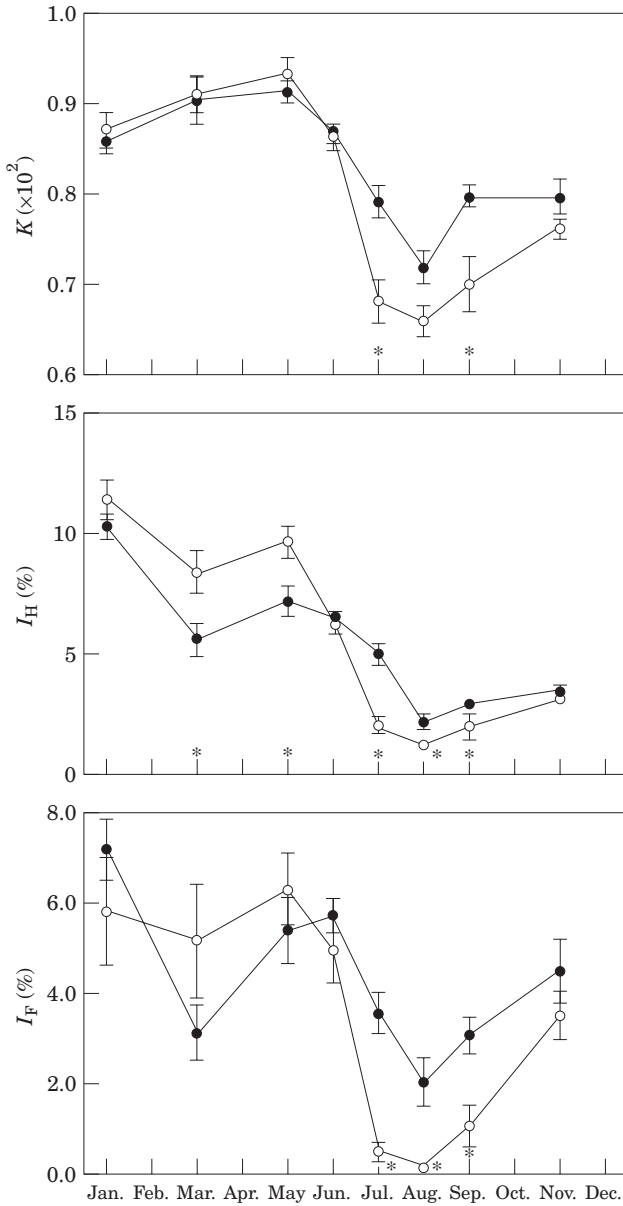


FIG. 4. Seasonal changes in mean condition factor (K), hepatosomatic index (I_H) and fat body-somatic index (I_F) for males (●) and females (○), respectively. Vertical lines are S.E. and sample sizes are shown in Table I. *, Significant sexual difference by Student's t -test ($P < 0.05$).

much energy on egg production, whereas males made little gametic investment. In all apogonids whose reproductive behaviour has been described, pair spawning is made in close proximity and no sneaking occurs, suggesting little or no possibility of sperm competition and thus a low demand for sperm. The small expenditure on sperm production has been reported also for tilapiine cichlids, especially for species with paternal mouthbrooding, which have the smallest

testis among fishes (Peters, 1971). The I_G of male *A. notatus* matches that of tilapiine cichlids. In *A. notatus*, since testis weight was consistently low for all breeding males at various maturing stages, their low I_G could not result from sperm depletion after its mass-release. Clearly, the energetic cost of gamete production is much larger for females in *A. notatus*.

For males, the reproductive cost is associated primarily with mouthbrooding. In the breeding season, males showed a lower I_S than did females. This was because often mouthbrooding males had empty stomachs. As is the case in some fishes, mouthbrooding prevents parents from feeding (Oppenheimer, 1970; Okuda & Yanagisawa, 1996a). Okuda (2000) reported that males of *A. notatus* spent 52.5% of the interspawning interval in mouthbrooding, implying that they would reduce their feeding opportunities by half compared with females. Hence, the decreased somatic condition of breeding males may be due mainly to fasting entailed by mouthbrooding, which is probably the major energetic cost of reproduction by males.

In contrast to *A. notatus*, the somatic condition of a congener, *Apogon doederleini* Jordan & Snyder, deteriorates more in males than in females (59.0% reduction in male I_H and 54.8% in female I_H ; Okuda & Yanagisawa, 1996a). In *A. doederleini*, since the number of broods raised by males is slightly fewer than that of broods produced by females (on average 5.6 for males and 6.3 for females; Okuda & Yanagisawa, 1996a), the energetic cost per brood is estimated to be higher for males. In *A. notatus*, by contrast, females produced more than twice as many broods as males raised (6.5 for females and 2.5 for males; Okuda, 1999b, 2000). Assuming that the average female produces 6.5 egg masses, each of which amounts to 15.2% of their body weight, female reproductive output is nearly equivalent to their own body mass. Although the energetic cost of egg production cannot be compared simply between these two species, high breeding frequencies by females of *A. notatus* might have imposed a larger energy expenditure on them, resulting in their more deteriorated somatic condition.

Female *A. notatus* may expend much further energy on the maintenance of their breeding territory. Within pairs of this fish, females play a primary role in territorial guarding (Okuda, 1999b). The females establish their breeding territory as early as 2 months before the breeding season and attack conspecific intruders perpetually throughout the daytime (Kuwamura, 1983). Chellappa & Huntingford (1989) demonstrated in the three-spined stickleback that territorial aggression is energetically costly. In *A. notatus*, females reduced their I_H and I_F during the pre-breeding period as well as during the breeding season, suggesting that territorial defence inflicts an energy loss on females. These results indicate that the overall energetic costs of reproduction are higher in females than in males.

In *A. doederleini*, liver weight is a good indicator of lipid reserve (Okuda & Yanagisawa, 1996a). In *A. notatus*, not only the liver but also the fat body was used as the lipid reservoir. This tissue is not found in *A. doederleini* and some other apogonids (N. Okuda, unpubl. data). Females of *A. notatus* decreased fat body weight more than did males early in the breeding season and almost depleted it in August. For fishes that live in seasonal environments, the lipid reserve affects mortality during an energetically stressful period, e.g. winter (Henderson *et al.*, 1988; Chellappa *et al.*, 1989; Griffiths & Kirkwood, 1995;

Hutchings *et al.*, 1999), and its sexual difference sometimes accounts for selective mortality between the sexes (Newsome & Leduc, 1975; Jonsson *et al.*, 1991). The much higher mortality for female *A. notatus* reported by Okuda (1999b) might be due to depletion of lipid reserves.

In this study, random sampling revealed that the adult sex ratio was male-biased. Okuda (1999b) reported that in the 1-year-old class of *A. notatus* the sex ratio did not deviate significantly from equality, suggesting that the primary sex ratio does not account for the male-biased adult population structure. Thus, the latter probably results from higher mortality in adult females. In non-territorial apogonids, in which females pay no cost of territoriality, the adult sex ratio is equal (e.g. *A. doederleini*, Okuda & Yanagisawa, 1996b; *A. niger*, Okuda, 1999a). Therefore, the male-biased population structure of *A. notatus* seems to be associated with female territoriality.

BROOD CANNIBALISM

The stomach contents analysis indicated that some mouthbrooding males ate their own eggs. Judging from the proportion of eggs eaten, most of such males are considered to have performed partial brood cannibalism. This type of filial cannibalism is the same as that reported for *A. doederleini* (Okuda & Yanagisawa, 1996a). Okuda & Yanagisawa (1996a) estimated that a small quantity of eggs cannibalized would not be enough to improve the deteriorated somatic condition of parental male *A. doederleini* (see also Smith, 1992). In *A. notatus*, brood size was correlated with paternal size but not with maternal size although egg size depended on maternal body size. In fishes, in general, batch fecundity is a function of female body size (Wootton, 1979). However, the brood size of apogonids is more strongly limited by the buccal cavity of males than by female body size (Okuda *et al.*, 1998). As in *A. doederleini* (Okuda *et al.*, 1998), a function of partial brood cannibalism by male *A. notatus* may be simply to adjust the brood size to their buccal capacity because overcrowding in the mouth will cause a deficiency of air supply to embryos and consequently increase offspring mortality.

The stomach contents analysis also showed that two mouthbrooding males ate a large number of eggs, suggesting that they were in the course of entire brood cannibalism. This cannibalism has been reported in another study in which marked males of *A. notatus* were observed in nature, but its incidence was relatively low (Okuda, 2000). Okuda (2000) suggested that males of *A. notatus* would be less likely to practice entire brood cannibalism than do males of *A. doederleini* because they were not in critical somatic condition and had little chance to remate after cannibalism due to low mate availability. In contrast with filial cannibalism, eating of the entire brood by unpaired males (i.e. hetero-cannibalism) occurred often in *A. notatus* (Okuda, 1999b, 2000). Brood cannibalism, whether it is filial or hetero-, can have the potential to skew the operational sex ratio towards males because males whose broods are cannibalized remain sexually receptive but their mates enter the refractory period to replenish eggs (Smith & Wootton, 1995). The overall brood loss was estimated to be 14.5% in *A. notatus* (Okuda, 2000). Therefore, brood cannibalism may also be a primary factor contributing to the male-biased operational sex ratio in this fish.

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References

- Balshine-Earn, S. (1995). The costs of parental care in Galilee St Peter's fish, *Sarotherodon galilaeus*. *Animal Behaviour* **50**, 1–7.
- Barbieri, L. R., dos Santos, R. P. & Andreatta, J. V. (1992). Reproductive biology of the marine catfish, *Genidens genidens* (Siluriformes, Ariidae), in the Jacarepaguá Lagoon system, Rio de Janeiro, Brazil. *Environmental Biology of Fishes* **35**, 23–35.
- Blumer, L. S. (1982). A bibliography and categorization of bony fishes exhibiting parental care. *Zoological Journal of the Linnean Society* **76**, 1–22.
- Chellappa, S. & Huntingford, F. A. (1989). Depletion of energy reserves during reproductive aggression in male three-spined stickleback, *Gasterosteus aculeatus* L. *Journal of Fish Biology* **35**, 315–316.
- Chellappa, S., Huntingford, F. A., Strang, R. H. C. & Thomson, R. Y. (1989). Annual variation in energy reserves in male three-spined stickleback, *Gasterosteus aculeatus* L. (Pisces, Gasterosteidae). *Journal of Fish Biology* **35**, 275–286.
- Clutton-Brock, T. H. & Parker, G. A. (1992). Potential reproductive rates and the operation of sexual selection. *The Quarterly Review of Biology* **67**, 437–456.
- Clutton-Brock, T. H. & Vincent, A. C. J. (1991). Sexual selection and the potential reproductive rates of males and females. *Nature* **351**, 58–60.
- Emlen, S. T. & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223.
- Griffiths, D. & Kirkwood, R. C. (1995). Seasonal variation in growth, mortality and fat stores of roach and perch in Lough Neagh, Northern Ireland. *Journal of Fish Biology* **47**, 537–554.
- Henderson, P. A., Holmes, R. H. A. & Bamber, R. N. (1988). Size-selective overwintering mortality in the sand smelt, *Atherina boyeri* Risso, and its role in population regulation. *Journal of Fish Biology* **33**, 221–233.
- Hess, H. C. (1993). Male mouthbrooding in jawfishes (Opistognathidae): constraints on polygyny. *Bulletin of Marine Science* **52**, 806–818.
- Hutchings, J. A., Pickle, A., McGregor-Shaw, C. R. & Poirier, L. (1999). Influence of sex, body size, and reproduction on overwinter lipid depletion in brook trout. *Journal of Fish Biology* **55**, 1020–1028.
- Jonsson, N., Jonsson, B. & Hansen, L. P. (1991). Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology* **39**, 739–744.
- Keenleyside, M. H. A. (1991). Parental care. In *Cichlid Fishes: Behaviour, Ecology and Evolution* (Keenleyside, M. H. A., ed.), pp. 191–208. London: Chapman & Hall.
- Kuwamura, T. (1983). Spawning behavior and timing of fertilization in the mouthbrooding cardinalfish *Apogon notatus*. *Japanese Journal of Ichthyology* **30**, 61–71.
- Kuwamura, T. (1985). Social and reproductive behavior of three mouthbrooding cardinalfishes, *Apogon doederleini*, *A. niger* and *A. notatus*. *Environmental Biology of Fishes* **13**, 17–24.
- Kvarnemo, C. & Ahnesjö, I. (1996). The dynamics of operational sex ratios and competition for mates. *Trends in Ecology & Evolution* **11**, 404–408.
- McKaye, K. R. (1991). Sexual selection and the evolution of the cichlid fishes of Lake Malawi, Africa. In *Cichlid Fishes: Behaviour, Ecology and Evolution* (Keenleyside, M. H. A., ed.), pp. 241–257. London: Chapman & Hall.
- Mrowka, W. & Schierwater, B. (1988). Energy expenditure for mouthbrooding in a cichlid fish. *Behavioral Ecology and Sociobiology* **22**, 161–164.
- Newsome, G. E. & Leduc, G. (1975). Seasonal changes of fat content in the yellow perch (*Perca flavescens*) of two Laurentian Lakes. *Journal of the Fisheries Research Board of Canada* **32**, 2214–2221.

- Okuda, N. (1997). Life history and sexual strategies of the cardinal fish (Pisces: Apogonidae) in the temperate sea. Doctoral thesis, Kyoto University.
- Okuda, N. (1999a). Female mating strategy and male brood cannibalism in a sand-dwelling cardinalfish. *Animal Behaviour* **58**, 273–279.
- Okuda, N. (1999b). Sex roles are not always reversed when the potential reproductive rate is higher in females. *The American Naturalist* **153**, 540–548.
- Okuda, N. (2000). Interspecific differences in male cannibalistic behavior between two sympatric cardinalfishes (Pisces: Apogonidae). *Journal of Ethology* **18**, 5–10.
- Okuda, N. & Yanagisawa, Y. (1996a). Filial cannibalism by mouthbrooding males of the cardinal fish, *Apogon doederleini*, in relation to their physical condition. *Environmental Biology of Fishes* **45**, 397–404.
- Okuda, N. & Yanagisawa, Y. (1996b). Filial cannibalism in a paternal mouthbrooding fish in relation to mate availability. *Animal Behaviour* **52**, 307–314.
- Okuda, N., Tayasu, I. & Yanagisawa, Y. (1998). Determinate growth in a paternal mouthbrooding fish whose reproductive success is limited by buccal capacity. *Evolutionary Ecology* **12**, 681–699.
- Oppenheimer, J. R. (1970). Mouthbrooding in fishes. *Animal Behaviour* **18**, 493–503.
- Peters, H. M. (1971). Testis weights in Tilapia (Pisces: Cichlidae). *Copeia* **1971**, 13–17.
- Smith, C. (1992). Filial cannibalism as a reproductive strategy in care-giving teleosts? *Netherlands Journal of Zoology* **42**, 607–613.
- Smith, C. & Wootton, R. J. (1994). The cost of parental care in *Haplochromis 'argens'* (Cichlidae). *Environmental Biology of Fishes* **40**, 99–104.
- Smith, C. & Wootton, R. J. (1995). The effect of brood cannibalism on the operational sex ratio in parental teleost fishes. *Reviews in Fish Biology and Fisheries* **5**, 372–376.
- Swenson, R. O. (1997). Sex-role reversal in the tidewater goby, *Eucyclogobius newberryi*. *Environmental Biology of Fishes* **50**, 27–40.
- Usuki, H. (1977). Underwater observations and experiments on pair formation and related behaviours of the apogonid fish, *Apogon notatus* (Houttuyn). *Publication of Seto Marine Biology Laboratory* **24**, 223–243.
- Vincent, A., Ahnesjö, I., Berglund, A. & Rosenqvist, G. (1992). Pipefishes and seahorses: are they all sex role reversed? *Trends in Ecology and Evolution* **7**, 237–241.
- Welcomme, R. L. (1967). The relationship between fecundity and fertility in the mouthbrooding cichlid fish *Tilapia leucosticta*. *Journal of Zoology (London)* **151**, 453–468.
- Wootton, R. J. (1979). Energy costs of egg production and environmental determinants of fecundity in teleost fishes. *Symposia of the Zoological Society of London* **44**, 133–159.
- Yanagisawa, Y., Ochi, H. & Rossiter, A. (1996). Intra-buccal feeding of young in an undescribed Tanganyikan cichlid *Microdontochromis* sp. *Environmental Biology of Fishes* **47**, 191–201.